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DIVERSITY AND SYSTEMATICS OF AMBROSIA BEETLES (CURCULIONIDAE: SCOLYTINAE, PLATYPODINAE) WITH EMPHASIS ON XYLEBORINA

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By

Jiri Hulcr

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Abstract

DIVERSITY AND SYSTEMATICS OF AMBROSIA BEETLES (CURCULIONIDAE: SCOLYTINAE, PLATYPODINAE) WITH EMPHASIS ON XYLEBORINA

By

Jiri Hulcr

Ambrosia beetles (Curculionidae: Scolytinae, Platypodinae), woodboring beetles living in a nutritional symbiosis with wood-decomposing fungi, dominate beetle faunas of the tropics and belong to the most pestiferous insects. This study consists of four chapters related to ecology, evolution, and systematics of ambrosia beetles:

A study of the spatial turnover of ambrosia beetle community in Papua New Guinea showed, that the composition of local communities of ambrosia beetles does not display statistically significant turnover over 1000 km.

A discovery of a previously unknown foraging strategy in ambrosia beetles – mycocleptism (fungus stealing) – is presented. Analysis of fungal communities associated with mycocleptae and morphological adaptations of the beetles show ecological and evolutionary stability of the strategy.

A phylogenetic analysis of morphological characters of Xyleborina (Scolytinae) distinguished phylogenetically informative characters from uninformative, and provided preliminary revision of the generic concept.

A monograph of Xyleborina of New Guinea presents a comprehensive revision of genus- and species-level classification of the group. Introduced are eleven new genera, 69 new combinations, and 87 synonymies.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Introduction

“Ambrosia beetle” is an ecological rather than a taxonomic term. It refers to beetles living in a symbiotic relationship with “ambrosia fungi”. Typically, the beetle excavates tunnels (called galleries) into the sapwood of its woody host where it releases spores of the symbiotic fungus, stored in special cuticular pouches called mycangia. The fungus germinates, enters the woody tissues and extracts nutrients from them. The beetle and its progeny feed solely on fruiting bodies and exposed mycelium of the symbiont. Exploitation of the fungi as a food source allows almost all ambrosia beetles the use of a wide diversity of host trees (Beaver, 1979), Hulcr et al, in prep.). The beetles are completely dependent on their fungal symbionts in terms of nutrition, developmental hormones, control of detrimental fungi, and other biological factors (Kok, 1977; Norris, 1977). The ambrosia habit evolved several times independently in two groups of weevils whose ancestral habit is phloem feeding: Scolytinae (“bark and ambrosia beetles”, mostly phloem feeders; several independent acquisitions of the ambrosial habit) and Platypodinae (“ambrosia beetles” or “pinhole borers”, almost all but the most primitive species are ambrosia beetles; (Kuschel, 2006; Marvaldi, 1997)). In some cases, the resistance of the symbiotic consortium against general wood decomposers and other opportunistic fungi is supported by the presence of symbiotic bacteria (Actinomycetes; Cardoza et al., 2006; Scott et al., 2008). The significance of bacteria has not been studied for most ambrosia beetle species.

The most species rich and widely distributed group of ambrosia beetles within the Scolytinae is the subtribe Xyleborina with almost 1300 described species. The group can be distinguished from other scolytines (especially from the ancestral Dryocoetina (Jordal, 2002a)) by the circular, dorsoventrally flattened antennal club with the first segment often conspicuously sclerotized, by the slightly impressed submentum, by arcuate and flattened meso- and metatibiae armed with 6 or more denticles (unless secondarily reduced), and by a pronotum strongly convex anterodorsally, armed with asperities on the anterior slope. Biologically, this group is clearly defined by the combination of a haplodiploid genetic system in which haploid males are flightless and often dwarfed, extreme inbreeding, and the ambrosial symbiosis with fungi. These individual biological features are found elsewhere in Scolytinae, however their combined occurrence in Xyleborina is unique. These are also hypothesized to be the cause of a rapid radiation of the subtribe that has produced nearly 1300 species since the early Oligocene (Jordal *et al.*, 2000). Unfortunately, both the rapid diversification and inbreeding are likely causes of the unclear species limits and a relative lack of clearly definable morphological characters (Hulcr et al., 2007a).

The broad objective of the presented study is to describe the geographical, ecological and morphological diversity of ambrosia beetles with emphasis on South-East Asia and Papua New Guinea (PNG), the region that harbors the greatest diversity of the focal group, the Xyleborina. Four topics are addressed:

1) a study of the spatial turnover of Xyleborina community composition (complementing previous studies addressing other potential correlates of xyleborine diversity),
2) a study of the evolution of a newly discovered foraging strategy – mycocleptism (fungus stealing),

3) a phylogenetic analysis of morphological characters of Xyleborina and initial revision of several genera,

4) and a comprehensive monograph of Xyleborina of New Guinea with major revision of their genus- and species-level classification

1 - Patterns in diversity of tropical ambrosia beetles

One of the major questions of contemporary community ecology is whether patterns in organismal diversity are emergent properties of complex stochastic systems or a product of variation of environmental factors (Hubbell, 2001; O'Neill, 2001). To test which offers a better explanation for the observed diversity patterns, reliable quantification of these patterns from nature has to be obtained and their fit to models based on selected predictors must be assessed. I have evaluated the importance of two environmental predictors for insect community structure: differential food resources (host specificity), and geographical distance (beta diversity). Host specificity of ambrosia beetles proved to be low, thus feeding niche partitioning does not seem to have driven the generation of high diversity in ambrosia beetles (Hulcr et al., 2007b). The study of host specificity is not considered a part of the dissertation.

In the first chapter of the dissertation, I have addressed another factor potentially structuring organismal diversity – geographic distance. I assessed the effect of geographical distance on insect species turnover in a setting where all other environmental factors were constant. I sampled ambrosia beetles (Coleoptera, Curculionidae: Scolytinae and Platypodinae) from three sites on a 1000 km transect in lowland rainforests in northern Papua New Guinea. With the help of local parataxonomists, I sampled 12,751 ambrosia beetle individuals following a standardized sampling scheme. I discovered there is no correlation between community similarity and geographical distance; the number of species collected at individual sites approached a statistically predicted total number of species. Several analyses supported the hypothesis that ambrosia beetles in lowland rainforests across northern New Guinea beetles represent a single community. Most beta diversity studies of animals have been performed between sites with varying environment or altitude (Beck & Chey, 2006; Novotny & Weiblen, 2005) or based on insufficient sampling (Erwin, 1982). Here I was able to eliminate both confounding factors and show that the distance alone has a negligible effect. The study has been published (Hulcr et al., 2007c; Novotny et al., 2007).

2 – Mycocleptism – a novel foraging strategy in ambrosia beetles

During my fieldwork in several tropical localities I discovered an unknown foraging strategy in some ambrosia beetles, putatively termed mycocleptism, or "fungus stealing". Three lines of evidence show that mycocleptism is an evolutionarily and ecologically stable phenomenon: 1) patterns of co-occurrence between the mycocleptic parasites and their provider species, 2) transmission of fungal strains from the galleries of the provider species into those of the mycocleptic species, and 3) the reduction of mycangia (symbiont-transporting organs) in mycocleptic beetles.

3 – Revision of genus-level classification of Xyleborina.

While the alpha taxonomy of scolytines and platypodines has seen a rather steady influx of papers during the last few decades (mostly by R. A. Beaver, D. E. Bright, F. Browne, S. L. Wood), the above-genus taxonomy of both subfamilies has been attended largely only by S. L. Wood (Wood, 1978, 1993). The Catalog of Scolytidae and Platypodidae

(Wood & Bright, 1992) based on his classification has become a standard and broadly accepted framework of scolytine and platypodine classification. Only recently have other systematists started reassessing the traditional system using phylogenetic methods and molecular characters (Cognato & Sperling, 2000; Jordal et al., 2000; Jordal, 2002a).

One of the scolytine groups with least-well understood relationships and an ambiguous classification is the subtribe Xyleborina (Hulcr et al., 2007a). S. L. Wood in his revision of the scolytid genera even stated that the generic classification of the group was "tentative and flawed" (Wood, 1978). Until now there were 25 genera recognized, however, these were inferred without the use of phylogenetic methods. As a result, generic boundaries often overlap, genera are defined by non-diagnostic characters and the largest genus *Xyleborus* is clearly a "dump basket" containing 534 species (over 40% of the whole group). Cladistic analysis of morphological characters of the subtribe Xyleborina (Curculionidae, Scolytinae) was carried out using a matrix of 42 characters in 196 species of Xyleborina. The analysis evaluated 1) the reliability of the morphological characters currently used in the xyleborine classification, 2) tested validity of genera currently delimited with these characters and 3) proposed and tested novel characters. Examination of individual characters revealed little phylogenetic information content in many characters currently used for delimiting genera. Phylogenetically stable characters were defined and illustrated. Monophyletic and polyphyletic genera were distinguished, four old genera were resurrected, 29 new combinations at the species level are given.

Based on the character matrix assembled for the revision of Xyleborina, an illustrated multiple-entry electronic key for the updated xyleborine classification has been created. The key can be accessed through www.scolytid.msu.edu. (Many additional genera and an updated key have been produced in chapter 4, the Monograph of Xyleborina of New Guinea).

4 – Monograph of Xyleborina of Papua New Guinea

There are very few monographs on xyleborines, or of scolytines including xyleborines, for any particular area (Bright, 1968; Maiti & Saha, 2004; Rabaglia et al., 2006; Schedl, 1962; Wood, 1982). Of these, only two refer to tropical areas (India: Maiti and Saha 2004, and Africa: Schedl 1962), and none exists for the area where the xyleborine fauna is the most diverse - SE Asia and Oceania. The combination of xyleborine material accumulated during our collecting in Papua New Guinea and obtained via our collaboration with other collections and museums allowed us to obtain specimens of almost all species ever collected in Papua New Guinea. For many species, we can compare multiple specimens (up to thousands), which allows us to study within-species morphological variation. Further, more than 44,000 PNG xyleborine specimens of 128 species or morphospecies have been stored in anticipation of their utility in molecular study, facilitating the use of DNA sequences for corroboration of species boundaries.

CHAPTER 1

Low beta diversity of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae and Platypodinae) in lowland rainforests of Papua New Guinea

Abstract

We assessed the effect of geographical distance on insect species turnover in a situation where other major environmental factors, including host plant species, altitude, and climate, were constant. We sampled ambrosia beetles (Coleoptera, Curculionidae: Scolytinae and Platypodinae) from four tree species (*Artocarpus altilis*, *Ficus nodosa*, *Leea indica*, and *Nauclea orientalis*) at three sites forming a 1000 km transect in lowland rainforests of northern Papua New Guinea. A standardized volume of wood from trunk, branches, and twigs was sampled for ambrosia beetles from three individuals of the four tree species at each site. Each tree was killed standing and left exposed to beetle colonization for 20 days prior to sampling. We obtained 12,751 individuals from 84 morphospecies of ambrosia beetles. We surveyed most of the local species richness at each site, predicted by Chao2 species richness estimates. The similarity of ambrosia beetle communities, estimated by Chao-Sorensen index, was not correlated with their geographical distance. Likelihood analysis and Q-mode analysis using Monte Carlo-generated null distribution of beetles among sites supported the hypothesis that the assemblages of ambrosia beetles at different sites are drawn from the same species pool, regardless of their geographical distance. Tree part (trunk, branch, or twig) was more important predictor of the composition of ambrosia beetle communities than was the host species or geographical location. All three variables, however, explained only a small portion of variability in ambrosia assemblages. The distribution of ambrosia beetles among tree parts, tree species and study sites was mostly random, suggesting limited importance of host specificity or dispersal limitation.

Introduction

One of the major questions of contemporary community ecology is whether patterns in species diversity are determined by environmental factors, inter-specific interactions or emergent properties of complex stochastic systems (Hubbell 2001, O'Neill 2001). A crucial concept describing the patterns of species spatial distribution is beta diversity, the turnover of species composition of communities in space (Bell 2001). However, the actual rate of species turnover in space is disputed, as well as the roles of mechanisms that cause it.

The classical target of studies of spatial patterns in organismal distribution is the correspondence of species distribution with environmental discontinuities and gradients (Begon et al., 1996). An alterantive approach is to deem species ecologically equivalent and study non-deterministic processes driving their distribution (Novotny and Weiblen, 2005). Some of the most important dynamic factors in species distribution are dispersal, speciation and extinction, and the changes of distribution in time caused by geological processes. Dispersal is expected to lower the differences between communities, although the link between dispersal mode or capacity and the species distribution is missing (Soinien, 2007). Speciation and extinction are expected to increase variability among distant communities, but the resulting rate of community diversification is unknown and likely variable between different kinds of organisms. Geographical barriers, or their historical legacies, are known to drive speciation, extinction, and community differentiation (Brooks and McLennan 2002).

These biological processes influencing species distribution often depend on environmental determinants, but also introduce a large stochastic component (Hubbell

2001). For example, in a large homogeneous habitat such as tropical lowland rainforests, even groups with different life histories such as tropical trees and insects, exhibit similar patterns of species turnover associated with distance. Both groups show aggregate distribution on smaller scales, but low species turnover on large scales (Beck and Chey 2006, Condit et al. 2002, Novotny et al. 2007).

Measures of beta diversity also crucially depend on methodological assumptions. Spatial beta diversity can be understood either as a turnover of species along a geographical vector, or as a dimension-less difference between local and regional diversity. The relationship between the two concepts is debated (Legendre et al., 2005, Tuomisto and Ruokolainen, 2006); this study is concerned only with the first, spatially explicit concept. Observations of species spatial distribution are highly influenced by the chosen geographical scale (Levin, 1992). Organismal communities typically show patchiness of populations on small geographical scales (less than tens of kilometers) but more even distribution on larger scales (Koleff and Gaston 2002, Lucky et al. 1998). Comparison of communities also depends on the completeness and eveness of sampling, especially in species-rich communities with highly uneven abundance distribution. For example, insect samples from the canopy of Amazonian rainforest suggest large differences between localities no more than 30 km apart (Erwin et al. 2005). However, the samples were dominated by species encountered as single individuals, thus it is unclear whether the apparent high beta-diversity reflects high species turnover, or is an artifact of omission of many rare species. On the other hand, rare species often have limited distribution and may be a source of genuine dissimilarity (Brown 1984). To distinguish between rare species unsampled by error and species genuinely absent, thorough sampling is necessary.

To study the effects of non-deterministic factors on beta diversity, we used a model system where all determinants of species distribution except distance, geological history, and stochastic biological processes, could be factored out, and where near-exhaustive species sampling is possible. The model system used was a community of tropical wood-boring ambrosia beetles (Col., Curculionidae, Scolytinae and Platypodinae) in lowland rainforests of Papua New Guinea. Ambrosia beetles colonize dying trees and feed on symbiotic xylosaprophagous ambrosia fungi that they introduce into the trees (Beaver 1989, Farrell et al. 2001). Exploitation of the fungi as a food source have allowed ambrosia beetles to utilize a wide variety of host trees (Beaver 1979, Hulcr et al. 2007), thus eliminating the local tree community composition as a factor influencing geographical distribution of species. Many ambrosia beetle species are capable of quick dispersal and establishment in new habitats, and belong among the most widespread invasive species (Allen and Humble 2002, Haack 2006). Some species of Scolytinae can fly distances up to 50 km per generation (Forsse and Solbreck 1985), and effectively track their hosts over large geographical areas following major changes in geography and climate (Sallé et al. 2007).

Studies focused on spatial distribution of scolytine beetles are mostly concerned with individual temperate phloem-feeding (non-ambrosial) pest species (Byers 1992, Cognato et al. 2005, Logan et al. 1998, Sallé et al. 2007). Studies on spatial structure of entire scolytine communities are rare, and have been also limited to temperate phloem feeders (Jordal and Hewitt 2004, Peltonen et al. 1998). Thunes (1998) studied ambrosia beetles in a neotropical rainforest in Costa Rica and found an uneven spatial distribution on a scale of less than 4 km^2, but was unable to distinguish between its causes, such as patchiness of resources or aggregation based on chemical communication. Deyrup and Atkinson (1987) showed substantial dissimilarity between distant communities of neotropical ambrosia beetles; however, variation in environmental conditions between the localities confounded the effect of environmental variation and that of distance.

Papua New Guinea (PNG) is one of the few remaining regions with extensive continuous lowland rainforests. PNG has a complex and recent history of geological changes. These processes may cause faunal dissimilarity or promote endemism in different parts of apparently homogeneous lowland rainforests (Polhemus and Polhemus 1998, Turner et al. 2001).

Our study quantified beta diversity of communities of tropical ambrosia beetles and examined the processes that have influenced it. We compared thouroughly sampled ambrosia beetles assemblages between sites up to 1,000 km apart while keeping constant major environmental variables including host plant, forest type, elevation and climate. Given the spatial scale of our sampling, we predict that low species turnover among sites would indicate unlimited dispersal as the most important factor in species distribution, while high species turnover would point to recent geological separation of sites or local speciation or extinction.

Methods

Beetles were collected from three study sites that formed a 1000 km transect through a continuous lowland rainforest on the northern side of Papua New Guinea (Figure 1, Table

1). All three sites were at a similar altitude (between 100 – 200 m above the sea level), with minimal seasonal variation, and similar amounts of annual rainfall (3000 – 4000 mm) (Parsons 1999). The mosaic of primary and secondary lowland humid rainforest at each site is classified as mixed evergreen hill forest (Paijmans 1976) with very diverse vegetation (152 woody species of diameter at breast height (DBH) >5 cm per ha in Ohu village; Novotny et al. 2004). The sampling was conducted between February and June of 2006. Two independent periods of sampling were completed in the Madang site (Madang 1 and Madang 2; Table 1) to examine the effect of increased sample size on diversity estimates.

Table 1: Study sites in northern lowlands of Papua New Guinea.

site	province	latitude	longitude	altitude (m)	date (2006)
Utai village	Sandaun	S 3° 23'	E 141° 35'	210	April
Madang (Ohu village)	Madang	S 5° 15	E 146° 40'	120-200	February (Madang 1), May (Madang 2)
Popondetta (Ohiki village)	Oro	S 8° 48	E 148° 13'	200	May

Ambrosia beetles were sampled from four tree species at each site: *Artocarpus altilis* (Parkinson) Fosberg (Moraceae), *Ficus nodosa* Teijsm. & Binn (Moraceae), *Leea indica* Merr. (Leeaceae), and *Nauclea orientalis* L. (Rubiaceae). These tree species were selected because they were abundant at all sites and represented both closely and distantly related species. The low number of sampled tree species was due to logistic reasons, and is considered sufficient for obtaining representative proportion of local species. Ambrosia beetles display little or no host specificity, and neither abundance nor phylogenetic position of a host tree has a significant effect on the composition of the colonizing ambrosia beetle assemblage (Hulcr et al., 2007). At each site, three individuals of each tree species of a breast height diameter (DBH) 20-25 cm (15-20 cm for *Leea indica*) were selected as *in situ* bait trees. Trees from both primary and secondary forest were used.

Bait trees were killed standing by girdling and burning at the trunk base, which triggered colonization by the beetles. Trees were girdled by first removing an approximately 30 cm wide circumferential strip of bark and creating a 30 cm wide wounded with multiple cuts. After 20 days, the bait tree was felled and the following samples were taken: 1) A 1 m long portion of trunk base including burned, girdled, and untreated surface, 2) A combined 2 m length of branch pieces (diameter 2-10 cm), and 3) a total of 2 m of pieces of twigs (diameter less than 2 cm) with apparent beetle infestation. The trunk base was cut into 5 cm thick slices to facilitate dissection of beetles. All timber samples were dissected by hand; all adult ambrosia beetles of the parental generation were removed and stored in ethanol. The tree preparation, dissection, and beetle sampling were performed with the help from parataxonomists and local villagers (Basset et al. 2000). Voucher specimens were deposited in the A. J. Cook Arthropod Research Collection, Michigan State University, the Forest Research Institute Insect collection in Lae, Papua New Guinea, the Natural History Museum, London, the Smithsonian Institution, Washington, D. C., and the Natürhistorisches Museum, Vienna.

To estimate the completeness of sampling at a single site, we compared the sample Madang 1 with both samples Madang 1 and Madang 2 combined, i.e., with doubled sampling effort at the same site. That allowed us to assess the precision of analytical estimates of the total species richness derived from our typical sample size.

There are a number of estimators of total local species diversity, mostly utilizing the asymptotic relationship between the increase in sample size and the cumulative number of species. Of the seven indices used to estimate the total number of species from the combined sample of Madang 1 and Madang 2 (Chao 1, Chao 2, Bootstrap, 1st order Jackknife, 2nd order Jackknife, ACE, and ICE; Colwell 2005), most converged on similar total number of estimated species. Chao 2 was selected for the subsequent estimates of species richness, as it was least dependent on the sample size compared to other indices (Figure 2) and was reported to give robust estimates even when a large portion of species is missing from samples (Colwell and Coddington 1994). EstimateS software was used to calculate diversity statistics (Colwell 2005).

Between-site pair-wise similarity was measured by the Sørensen index modified by Chao for raw data (Chao et al. 2005). The probability that two individuals randomly sampled from sites A and B belong to the same species was calculated as $p_c = (n_{iA}/N_A)(n_{iB}/N_B)$, where n_{iA} is the number of individuals of species i collected at site A, and N is the abundance of all ambrosia beetles collected at that site (Novotny et al. 2007). To test whether ambrosia beetle community similarity decreases with distance, we performed linear regression of pair-wise Chao-Sørensen community similarities between sites versus pair-wise geographical distances, and regression of the probability that two beetles randomly drawn from two sites are conspecific (p_c) versus pair-wise log-distance. The latter model was tested since it was shown to approximately fit the similarity decay in Neotropical tree communities (Condit et al. 2002). Each regression analysis was applied to two types of similarity data – pairwise similarities between whole communities at different sites, and pair-wise similarities between communities on individual conspecific trees. Significance of each correlation was assessed with a Mantel test. The two samples from Madang were used independently with mutual geographical distance of zero. Where multiple tests of the same hypothesis were conducted, the level of statistical significance was adjusted by Bonferroni correction.

We tested the hypothesis that the samples from the three study sites were randomly drawn from a single regional pool of species. We used a likelihood approach to test the uniformity of abundance distribution and a Q-mode analysis of community similarity. We compared the likelihood of three models of abundance distribution: 1) each locality is characterised by different abundance distributions, 2) Madang 1 and Madang 2 have the same abundance distribution (individuals per each species summed up), while Popondetta and Utai each has a unique abundance distribution, and 3) all samples are drawn from a single community and thus have a similar abundance distribution (beetle individuals were summed within species across all sites). Assuming that the sampling distribution of species is a multinomial distribution, the likelihood function for s species distributed among J individuals is:

$$L(\mathrm{x}, \rho, J) = -\Sigma \mathrm{i}\, x(i) \log(\mathrm{e})\, \rho(i) ,$$

where $x(i)$ = the number of individuals of species i and $\rho(i) = x(i)/J$. The right side is equal to H' (Shannon diversity index). The likelihood of each of the three models described above was determined by estimating unique parameters for each species abundance distribution implied by the model. The likelihoods were adjusted for overfitting with the Akaike Information Criterion (AIC)

$$\mathrm{AIC}_{\mathrm{A}} = 2\,L_{\mathrm{A}} + 2\,(K_{\mathrm{A}} - 1),$$

where L_{A} is the likelihood and K_{A} is the number of parameters of model A (Burnham and Anderson 2002). The model with the lowest AIC was chosen as the preferred model of abundance distribution across the sites.

To test the hypothesis that samples from different localities represented a single community, we compared the average observed pairwise similarity between sites to a null model of distribution of similarity (Gotelli and Graves 1995). To obtain the null model, abundance values of beetle species at individual trees were redistributed randomly among all sites. We explicitly assumed a uniform abundance distribution across sites, and tested the assumption by the likelihood test above. The redistribution of species records was constrained to within tree species since different tree species accumulated different numbers of beetle individuals and species. The randomization was repeated 1000 times, and the resulting model distribution of average pairwise similarities was used for a one-tailed test of non-randomness of the observed average pairwise similarity between sites. Chao-Sørensen index for raw data was used as the similarity measure. Sample Madang 2 was not used in this analysis, since the randomization procedure assumes equal sample size for each site.

To compare and visualize the effects of site, tree species, and tree parts on the composition of beetle communities, we performed multivariate ordination analysis using Canoco 4.5 (ter Braak and Smilauer 2003). The highly uneven abundances of scolytid species were $\log_{10}(x+1)$ transformed. States of each variable were used as independent complementary variables, i.e., sites represented three variables, tree parts represented three variables, and tree species represented four variables. Correspondence Analysis was used to determine the amount of correlation in distribution of individual species within the beetle community. Canonical Correspondence Analysis was used to explore the effect of tree species, tree part and locality on the distribution patterns in the beetle species distribution. The differential contributions of individual variables to the overall explained variance was calculated by variation partitioning:

1) We measured the proportion of variation explained by all canonical axes (constrained by the variables) when all variables are used in the analysis (v_{total}).

2) We measured the proportion of the total variance explained by each of the three subsets of variables individually (tree parts = v_{parts}, tree species = v_{trees}, sites = v_{sites}).

For each variable, we calculated the ratio of all eigenvalues from unconstrained CA to the sum of all canonical eigenvalues when the two remaining variables were held as covariates.

3) The effect of interactions between variables v_{inter} was calculated as:

$$v_{inter} = v_{total} - (v_{parts} + v_{trees} + v_{sites})$$

Rarity or absence of a species in a sample may be a result of true rarity/absence at a site, or of undersampling. The probability that a species is present at a particular site when N individuals are randomly distributed among n sites is $p = 1-(1-1/n)^N$. For our three sites, $p > 0.95$ when $N \geq 8$. Thus, to examine the influence of rare species on our analyses of community similarity, we calculated selected analyses twice: once with all species included and once with dataset containing only species of which more than seven individuals were encountered. This process excluded 36 species from the total of 86, which represented less than 1% of individuals.

We excluded one ambrosia beetle species, *Xylosandrus crassiusclus* Motsch., from analyses of site similarity. *X. crassiusculus* is most likely a non-indigenous species recently introduced to New Guinea (R. A. Beaver, pers comm.; Hulcr, unpubl). It is very abundant near the town of Madang, but has apparently not yet spread to other sites.

Results

In total, 12,751 ambrosia beetle individuals representing 84 morphospecies were collected from all three sites. All species belonged to one of two distinct taxa, Platypodinae (5467 individuals) or Xyleborina (7284 individuals). Sixty eight (81%) of these morphospecies have been already taxonomically described (see Supplementary data).

Although the number of species we collected in a single sample did not reach the estimated total number of local species, it was sufficient for calculating robust diversity estimates (Figure 2). For example, the total number of species in the Madang area was estimated to 68, based on the sample Madang 1 with 58 actually collected species. With the inclusion of Madang 2, the number of collected species reached 65, and the estimate increased to 70. The total local diversity estimate derived from the single Madang 1 dataset falls within the 95% confidence interval of the estimate derived from both samples (67-83, Figure 2), and is independent of sample size for samples of more than 60% of our actual sample size.

The total number of ambrosia beetle species occupying the lowland rainforests of northern PNG was estimated to be 98 by Chao 2 (*SD* = 7.03, Figure 3). The estimate was calculated with all tree samples combined, regardless of the site. The estimate was only slightly dependent on the sample size for datasets larger than 1/3 of our actual sample size.

Forty-four of the 48 species that were sufficiently abundant for the analysis were present in more than one site, while only four species were restricted to a single site (Figure 4). The average proportion of species shared between sites was 72.6%, and the average community similarity measured by Chao-Sørensen index was 0.948 (SD=0.028). When undersampled species were included in the analysis, the average proportion of shared species dropped to 63%, but the average Chao-Sørensen similarity remained nearly identical (0.940, SD= 0.024). Similarity of the two samples Madang 1 and Madang 2 approached unity (Chao-Sørensen = 0.998, SD=0.002). The number of sites occupied by a species was correlated with the logarithm of its total abundance (for species of $N > 7$, $n = 48$; $r = 0.523$, $P < 0.001$).

Table 2: Pairwise comparisons of ambrosia beetle community similarity between sites (Chao-Sørensen index). Madang 1 and Madang 2 are two independent samples from the same site.

	Utai	Madang 1	Madang 2
Madang 1	0.978		
Madang 2	0.977	0.998	
Popondetta	0.983	0.918	0.924

Pairwise similarity of samples from different sites was similar to pairwise similarity of two independent samples from the same site (Madang 1 and Madang 2; Table 2). There was no significant correlation between pairwise similarities of beetle assemblages and pairwise distances between localities (mean Chao-Sørensen index of similarity = 0.955; $n = 6$; $r = -0.109$, Mantel test $P = 0.40$; Figure 5). Also, there was no significant correlation between similarities of samples from individual conspecific trees and the distances between the trees (*A. altilis* $r = 0.002$, $P = 0.495$; *F. nodosa* $r = -0.266$, $P = 0.100$, *L. indica* $r = 0.244$, $P = 0.894$, *N. orientalis* $r = 0.287$, $P = 0.055$; in *L. indica* $n = 55$, in other cases $n = 66$). The probability that two beetles randomly sampled from two different sites would be conspecifics did not decrease significantly with log-distance ($n = 6$, $r = -0.762$; Mantel test $P = 0.08$; Figure 5). Also the probability that two beetles randomly sampled from two conspecific trees would be conspecifics did not decrease with log-distance (*A. altilis* $r = 0.061$, $P = 0.329$; *F. nodosa* $r = -0.270$, $P = 0.052$, *L. indica* $r = 0.019$, $P = 0.433$, *N. orientalis* $r = 0.217$, $P = 0.085$; in *L. indica* $n = 55$, in other cases $n = 66$). When undersampled species were included in the analysis, all the above correlations of community similarity with distance remained insignificant at the level of $\alpha = 0.05$, except the distance decay of community similarity on *F. nodosa* ($r = -0.289$, $P = 0.045$) which was however insignificant under Bonferroni correction ($\alpha = 0.0125$).

Of the four models of abundance distribution tested by the likelihood test, the model assuming that all samples come from a single distribution had the best (lowest) AIC-corrected likelihood score, and was thus selected as the model that best fit the data. The AIC-corrected likelihood scores were 343.6 for the model of all samples pooled together, 898.3 for the model pooling two Madang samples and keeping Utai and Popondetta separately, and 1134.4 for the model treating all four samples separately.

The hypothesis that samples from all three sites are no more different than three random samples from a single population was upheld (mean Chao-Sørensen index of pairwise similarity = 0.948, median of the modeled distribution of mean pairwise similarities = 0.973, Monte Carlo test $P = 0.069$). When undersampled species were included in the analysis, the similarity among communities was marginally lower than random (mean Chao-Sørensen pairwise similarity = 0.935, median of the modeled distribution of mean pairwise similarities = 0.959, $P = 0.02$)

The Correspondence Analysis revealed weak correlations among the distribution patterns of individual species. The first ordination axis explained 10.4% of the total variation; the first four axes together 34.5% of the variation. The Canonical Correspondence Analysis showed significant, differential, and uncorrelated influence of the tested variables on ambrosia beetle distribution (Figure 6). The variables most strongly correlated with the first, second, and third ordination axes were, respectively: (1) all three hosts parts, (2) the host species *L. indica* and *A. communis*, and (3) all three sites. The correlation between environmental variables and the beetle species distribution was highly significant (Monte Carlo test, 999 permutations, $P = 0.001$). However, the canonical axes (constrained by the environmental variables) explained only 18% of the total variation (sum of all eigenvalues from Correspondence Analysis = 6.993, sum of all canonical eigenvalues = 1.248).

Variation partitioning revealed low and mutually uncorrelated contribution to the explained variability by all three sets of variables. The most important variables for the species distribution in our sample were the tree parts (9.0% of the variation), slightly less important were tree species (7.2%), and the least important was the site (4.2%). Interactions between the variables were negligible (0.2% of the variation), showing a lack of interdependence among the variables.

The average number of beetle species colonizing an individual tree was approximately equal for all tree species (17.5, *A. altilis*; 19.8, *F. nodosa*;15.7, *N. orientalis*) except *Leea indica*, where the numbers of colonizers were substantially lower (7.8 beetle species per tree individual). However, the beetle community on *L. indica* was no less species rich than communities on other hosts when these are computationally rarefied. In *L. indica*, 484 beetle individuals yielded 31 spp., compared to >1800 individuals necessary to yield 31 spp. in *A. altilis*, >1200 in *N. orientalis*, and >1000 in *F. nodosa* (rarefied using MaoTau function in EstimateS).

Discussion

Most of the 84 morphospecies were species known to science (*n* = 67; 78%), while the remaining had uncertain or undescribed status. The high proportion of known species reflects extensive collecting and descriptive work on New Guinea ambrosia beetles (e.g., Schedl 1969a, 1969b, 1972a, 1972b, 1975; Gray and Wylie 1974; Roberts 1986, 1989) combined with broad distribution of many species documented in this study.. This is in agreement with several other studies showing that many non-cryptic or economically important insect groups from Papua New Guinea may be known to larger extent than often assumed (Miller et al. 2003, Novotny and Missa 2000). On the other hand, identification of most of the species required a several-year-long effort, which illustrates the contemporary 'taxonomic impediment' (Wheeler et al. 2004). Despite the fact that most species have been described, their identification is extremely difficult since the type material is scattered in museums worldwide, the published information is inadequate for species diagnosis, and within-species variability has never been sufficiently studied.

The tree species *Leea indica* proved to host a comparatively depauperate ambrosia beetle community. It is unclear whether this is due to chemical components of the tree's tissues, the small size of the tree, or other factors. Although nearly all ambrosia beetles in Papua New Guinea are host generalists (Hulcr et al. 2007), some tree species are more attractive than others to the whole beetlee assemblage. Subsequently, the more frequent colonization of these trees by all species result in higher species richness.

Even though our sampling at each study site was not exhaustive, it permitted a robust estimate of the total species richness and similarity between sites. The total number of species recorded in two combined samples from Madang approached the estimated total richness, suggesting that there were probably few unsampled species.

The rate of species turnover of ambrosia beetles in lowland New Guinea proved to be extremely low, as the decrease of community similarity with distance was insignificant. Both xyleborines and platypodines displayed the same lack of site fidelity. Low species turnover at distances up to 500 km was shown also for the communities of moths from the same area region (Novotny et al. 2007). Our study shows that even doubling the geographical scale does not decrease similarity of the studied insect communities.

The number of sites occupied by a species is correlated with its total abundance. This suggests that failure to collect a species at all sites might have been due to undersampling. However, rare species often have restricted ranges (Rosenzweig 1995). Although we are unable to distinguish between incomplete sampling and actual range restriction, we believe that the observed high similarity among sites was not a result of omission of rare endemic species. Inclusion or exclusion of undersampled species had only marginal effect on the results. Although their inclusion made the between-site similarity appear slightly lower than random, it was caused by the increase in similarity of the resulting null model, not by the decrease in the observed similarity, and the effect was not correlated with distance. Further, our sampling strategy allowed for collecting most of the species present at a locality, as can be seen in the case of two samples from a single site, which were nearly identical.

The neutral model of beta diversity by Hubbell (2001) predicts a linear decrease in faunal similarity with the logarithm of distance. This model has been supported by data from Neotropical tree communities on scales of tens of kilometers, but the decay of community similarity on larger geographic scales was slower than the model predicted (Condit et al. 2002). Other models of rainforest tree communities are based on dispersal, rather than on niche-based processes, and predict slower species turnover rate than is observed in the field (Duivenvoorden et al. 2002). In our samples spanning a 1000 km distance, the similarity between communities does not decrease linearly with log-distance.

This study showed the importance of controlling environmental variables for beta diversity estimates. Separating the effects of host and habitat availability from that of geographical distance has been an important issue in studies of beta diversity of insects, and has required *a posteriori* statistical tools to estimate the effect of each variable (Beck and Chey 2006, Novotny et al. 2007). Ambrosia beetles are host generalists, therefore in most cases the presence or absence of an ambrosia beetle species at a particular site is independent of the composition of the local tree community.

Insect dispersal propensity ranges from slow migrants that, despite their capacity for flight, can remain on a single patch of suitable habitat for many generations (Spitzer and Danks, 2006) to efficient migrants that are often the first organisms to colonize new habitats (Thornton et al., 2001). Ambrosia beetles are moderate to good dispersers, as each new generation seeks new breeding trees, and the distances between suitable dead trees can be substantial. Our study showed that unlimited dispersal results in community homogenization over large distances, provided the studied habitat and niche availability are uniform.

Although each of the three sites sampled in this study is characterized by a similar forest type, each of the sites lies on a geologically independent Pacific terrane. Polhemus and Polhemus (1998) suggested that this has affected the present day distribution of New

Guinea aquatic Heteroptera, a group with limited dispersal propensity and strict habitat requirements. However, accretion of these terranes to the New Guinea island and the collision-related uplifting took place at least 5 million years ago (Hall 2002), making its effect on contemporary ambrosia beetle population separation extremely unlikely. More recent events led to the separation of the northern (Utai) and the two southern sites (Madang and Popondetta) by a sea incursion in the Sepik and Ramu floodplains around 6,000 years ago, and, perhaps more importantly, the climate and vegetation cover of parts of the lowlands was different during the colder and drier periods of the Pleistocene (Nix and Kalma 1972). However, even if these dispersal barriers and habitat changes had previously influenced the geographical structure of the lowland ambrosia beetle community, our data suggest that the effect apparently disappeared within the last several thousand years. The results of this and previous analyses (Hulcr et al. 2007), aimed at discerning the factors correlated with ambrosia beetle diversity, suggest that, host specificity, microhabitat specificity and separation by distance do not isolate ambrosia beetle populations and thus do not promote speciation. This adds credibility to alternative hypotheses, suggesting that it is a separation by major habitat differences, such as those associated with altitude, or major barriers to dispersal, such as sea, that generate the diversity of tropical ambrosia beetles.

Figures

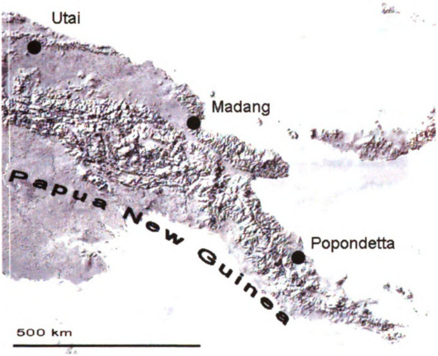

Figure 1: Sampling sites in northern Papua New Guinea, South Pacific.

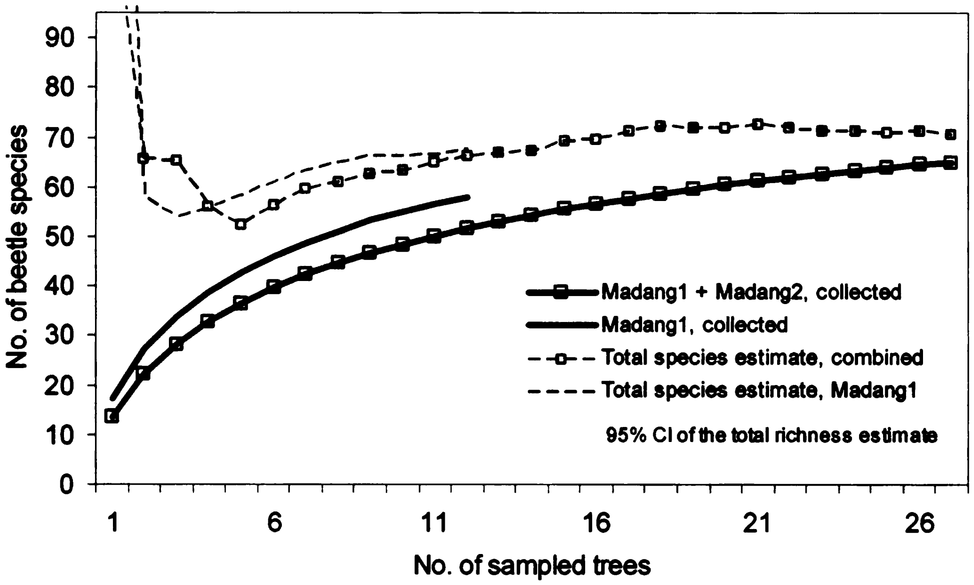

Figure 2: Species accumulation curves and total species richness estimates for Madang 1 sample and for the combined samples Madang 1 and Madang 2. A single sample (Madang 1) does not reach the estimated total number of species, but is sufficient for a robust estimate. Doubling the sampling effort yields species richness falling within the 95% CI of the total estimate (shaded area). Accumulation curves were derived with Mao Tau algorithm in EstimateS (Colwell 2005). Independent analysis of Madang 2 gave nearly identical result as Madang 1 (not shown).

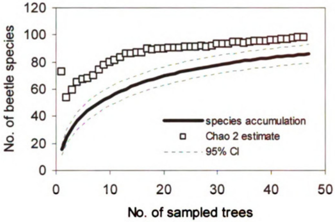

Figure 3: Species accumulation curve for all samples combined and the estimate of total species richness of ambrosia beetles in northern lowlands of Papua New Guinea. The solid line represents the species accumulation curve derived analytically with the Mao Tau function in EstimateS. Dashed lines indicate 95% confidence intervals. Squares – Chao 2 estimate of the total number of species as it varies with the number of tree samples included. Complete data for all 48 tree individuals regardless of site were included.

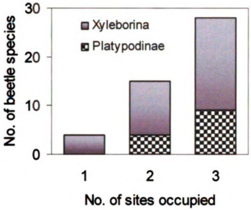

Figure 4: Distribution of ambrosia beetles species among the three study sites in northern Papua New Guinea. Sample Madang 2 was not included. Only sufficiently abundant species were included to prevent inflation of the first category.

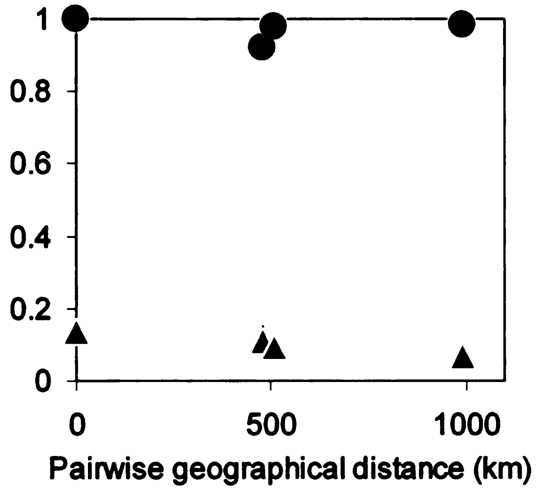

Figure 5: Similarity decay of ambrosia beetle communities over geographical distance (Chao-Sørensen index and the probability that two individuals randomly sampled from two different sites in northern lowlands of PNG would be conspecifics. Both relationships are statistically not significant (similarity decay: *r* = -0.109, Mantel test *P* = 0.40; probability of random individuals being conspecific: *r* = - 0.762, Mantel test *P* = 0.08). The two independent samples from Madang (Madang 1 and Madang 2), treated as independent data sets with a geographic distance of zero.

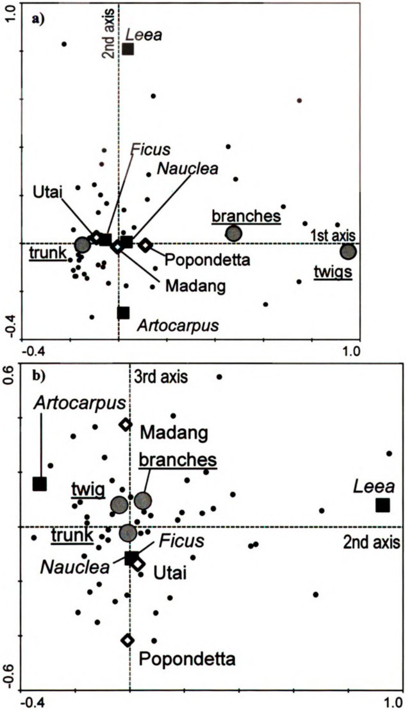
a)
1.0
-0.4
-0.4
1.0
2nd axis
1st axis
Leea
Ficus
Nauclea
Utai
branches
trunk
twigs
Popondetta
Madang
Artocarpus
b)
0.6
-0.6
-0.4
1.0
3rd axis
2nd axis
Artocarpus
Madang
branches
twig
Leea
trunk
Ficus
Nauclea
Utai
Popondetta

Figure 6: CCA ordination diagrams of explanatory variables with the a) 1st and 2nd canonical ordination axes and b) 2nd and 3rd canonical ordination axes. From the explanatory variables, tree parts (circles) are most correlated with the first canonical axis, hosts (*L. indica* and *A. communis*, squares) with the second axis and sites (diamonds) with the third axis, rather weakly. Dots represent ambrosia beetle species.

CHAPTER 2

Repeated evolution of theft in fungus-farming ambrosia beetles (Coleoptera: Curculionidae: Scolytinae)

Abstract

Ambrosia beetles exploit the cellulolytic capacity of their symbiotic ambrosia fungi, which allowed them to colonize nearly every habitat with woody vegetation and dominate beetle faunas of tropical rainforests. We discovered a previously unknown parasitic level of this foraging strategy in some ambrosia beetles for which we propose the term mycocleptism. Mycocleptic species bore brood galleries next to existing brood galleries containing fungal gardens, which were created by other ambrosia beetle species. Mycelia originating from the established fungal gardens enter the mycocleptes' galleries and generate new fungal gardens. The benefits of parasitism on a successfully established gallery include an abundance of fungal food, while avoiding the risk of fungal transport failure, the risk of fungal germination failure, and the risk of symbiotic fungus death. Mycocleptism appears to be a species-specific association. Three independent origins of mycocleptism are confirmed (Xyleborina: *Biuncus* spp. and *Ambrosiophilus* spp., Scolytini: *Camptocerus suturalis*), and several putative mycocleptae are reported. Phylogenetic and morphological analysis of a clade containing *Biuncus*, the largest mycocleptic group, reveals secondary loss of fungus-transporting organs (mycangia) concurrent with the origin of mycocleptism. Extraction, cloning and comparison of DNA from fungi from many galleries of the beetle associates show that mycocleptous species always adopt fungal assemblages of the donor species.

Introduction

The majority of important adaptive shifts during biological evolution were achieved by *de novo* co-operative associations between two organisms (Maynard Smith & Szathmáry, 1995). Mutualistic symbioses, such as the endosymbiotic organelles in the eukaryotic cell, arbuscular mycorrhiza, or the microbial microcosm in vertebrate gut, led to dramatic increase in macroevolutionary performance of the associated lineages. The combination of stable environment often provided by one of the partners, and the catabolic or synthetic capacity of the other, often microbial partner, allowed associated lineages to traverse adaptive valleys and access niches not available to unassociated competitors. Consequently, mutualistic consortia such as fermentative herbivores or mycorrhizal plants dominate the mass and energy flow in terrestrial ecosystems.

The most abundant component of Earth's biomass is lignocellulose in the plant cell wall, especially in wood, representing potentially unparalleled resource for secondary consumers. For most animals, however, wood as a source of energy is inaccessible due to their lack of cellulolytic apparati. Thus nearly all instances of animal consumption of wood employ obligate microbial or fungal symbionts (Douglas, 2009). The overwhelming majority of these instances occur among insects, with one of the most remarkable and successful examples being external symbiont farming. Insect farming arose independently in termites (Isoptera: Macrotermitidae), ants (Hymenoptera: Formicidae: Attinae) and multiple times in ambrosia beetles (Coleoptera: Curculionidae: Scolytinae and Platypodinae)(Mueller & Gerardo, 2002). Many studied cases of these three symbiotic systems include symbionts from three phyla (Currie et al., 2003; Hongoh et al., 2006): the insect providing habitat and raw materials, fungus digesting the supplied material and providing most or all of the insect nutrition, and antibiotic-producing bacteria, role of which is not yet fully understood (Mueller et al., 2008). Other convergent features include active vertical transmission of microsymbionts by the insect and ecological dominance in respective ecological niches.

A very promising group for studying the evolution of symbiont farming are the scolytine beetles, given the multiple evolution of fungal dependence from unrelated herbivorous ancestors (Farrell et al., 2001), including ancient as well as recent origins (Hulcr et al., 2007). Scolytine beetles have been traditionally classified into phloeophagous bark beetles (consuming host tree tissues, mostly phloem) and ambrosia beetles (creating galleries in nutrient-poor xylem and consuming symbiotic wood-digesting fungi). However, while phloeophagy and mycetophagy are indeed two most common feeding strategies, they represent only two extremes on the gradient of mutual dependence between beetles and fungi. Between them lie strategies such as phloem-dwellers feeding primarily on fungi (Harrington, 2005; Six, 2003), feeders on twigs with a prior fungal infection (Deyrup, 1987), or xylem-borers whose larvae feed on a mixture of mycelium and xylem (Roeper, 1995). While details of the relationship between beetles an fungi vary substantially between lineages, one feature is shared among all fungus-feeding scolytines: the presence of mycangia, cuticular structures adapted to transport of symbiont innoculum (Beaver, 1989; Cardoza et al., 2006; Six, 2003). Unfortunately, a comprehensive analysis of the evolution of fungus-feeding in scolytine beetles has not yet been possible, since only a preliminary phylogeny for the whole group exists (Farrell et al., 2001).

Here we report the discovery of a foraging strategy of several unrelated clades of ambrosia beetles, which represents a yet-unknown level of complexity in this system. Some ambrosia beetles have evolved a strategy not known in any other organisms besides humans – crop stealing. Hence, we have termed the strategy mycocleptism, "fungus-stealing". Mycocleptic species bore brood galleries next to existing brood galleries containing fungal gardens, which were created by other ambrosia beetle species (provider species). Mycelia originating from the established fungal gardens enter the mycocleptes' galleries and generate new fungal gardens (Figure 7). We hypothesize that the result of this behavior is exploitation of the growth of the ambrosia mycelium in the xylem tissue surrounding the provider species' gallery. This hypothetical scenario has several assumptions, some which we test in this study: 1) the mycocleptae species occur predominantly or always in the immediate vicinity of the providers' galleries, 2) the mycocleptae share the fungi with their providers, and 3) the mycocleptae do not have the means to transport their own symbionts..

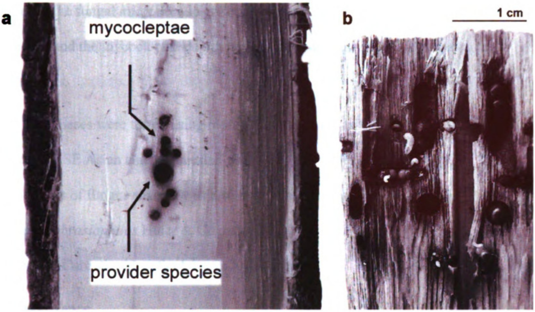

Figure 7: Examples of mycocleptism. A – Entrances of multiple small galleries of *Biuncus papatrae* concentrated in an area stained by symbiotic fungi of *Anisandrus ursa* (single large entrance). B – Galleries of *Biuncus duodecimspinatus* (small orange species) intertwined in the wood with those of *Hadrodemius globus* (large dark species). Branches of *Ficus* sp., Papua New Guinea, photo: J. H.

Methods

Mycocleptae beetles, their host beetles, and the symbiotic fungi were collected in five localities: two lowland sites in Papua New Guinea (Madang, 200m, 145°40' E, 5°14' S; Popondetta, 220 m, 148°12' E, 8°48' S), two higher elevation sites in Papua New Guinea (Kanga, 500 m, E 147°38', S 8°46', and Mu, 1800 m, 145°02' E, 6°05' S), and one locality in Sabah, Malaysia 117°50' E, 4°58 N).

To test the hypothetical mycocleptic associations, three lines of evidence were examined, corresponding to the following assumptions: the mycocleptae actively seek the provider species, the fungal microflora in galleries of the mycocleptae reflect that of the provider species, and the mycocleptae do not possess their own means of transporting the symbionts.

All hypotheses were tested using representatives of the largest known mycocleptous clade, the SE Asian and Melanesian genus *Biuncus* Hulcr & Cognato (2009). The hypothesis of fungus sharing was also tested with representatives of a second mycocleptic genus *Ambrosiophilus* Hulcr & Cognato (2009) from the same region. Both genera belong to Curculionidae: Scolytinae: Xyleborina.

Co-occurence

The hypothesis of mycocleptae actively seeking the provider species was tested using the patterns of co-occurrence of the two participants. During our field collecting in New Guinea and Borneo, we selected ten dead trees or branches colonized by provider species, and sampled them completely (Table 1). We recorded whenever a putative mycocleptic species was found 1) in the direct vicinity of a provider species' gallery (within 0-10 mm), 2) in an independent gallery and alive (evidence of active gallery extension, occurrence of brood), and 3) in an independent gallery and dead. The significance of differences between categories was assessed with Repeated Measures ANOVA.

Fungus sharing

To test whether galleries of mycocleptae contain the same fungi as those of their putative hosts, we sampled and sequenced fungal DNA directly from the galleries of both the mycoclepae and their hosts, as well as from unassociated ambrosia beetle species occupying the same trees.

Beetle galleries collected in the field were preserved either in 100% EtOH and frozen, or stored in mineral oil at 4°C to preserve viable fungi. Fungal tissue was scraped from walls of the beetle galleries, the mixture of wood and fungal tissue was ground in Qiagen ATL buffer, and the genomic DNA extracted using Qiagen DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA). Fungal rDNA of the ITS I region (between SSU RNA and 5.8S RNA) was amplified using primers ITS1F (forward, optimized for fungi (Gardes & Bruns, 1993)) and ITS2 (reverse, general (White et al., 1990)). For greater PCR amplification yield of the potentially degraded or rare fungal DNA, we used Qiagen HotStar HiFidelity Polymerase Kit. The PCR started with 15 minutes of 95°C. The subsequent PCR profile used was 40 cycles of 93°C (30 s), 53°C (45s), 72°C (60 s), followed by 7 minutes of 72°C for final elongation.

The PCR product was cloned into chemically competent *E. coli* cells in Invitrogen TOPO-TA cloning kit. Successful transformants were visualized by addition of X-gal, and 24 colonies from each beetle gallery were used as template for PCR with M13 forward and reverse primers, and a Promega GoTaq polymerase. The PCR product was purified using ExoSAP-IT PCR Clean-up Kit (USB Corp.) and sequenced in the RTSF center at Michigan State University. Sequence chromatograms were analyzed and clone libraries for individual galleries were prepared in Sequencher (Gene Codes Corp.). Unique sequences have been deposited in GenBank (FJ807989- FJ808073). Fungal ITS sequences were identified by NCBI BLAST (blastn), chimeras and non-fungal sequences were excluded. Fungal species accumulation curve was derived using the Mao Tau function (analytical analog of randomized resampling) in EstimateS (Colwell, 2005).

We tested whether the composition of fungal communities in galleries of mycocleptae are governed by species identity of the mycocleptae or by species identity of their hosts. We created a matrix of all pairwise similarities between fungal communities in all sampled galleries measured by Sørensen index for presence/absence data. From this dataset, we first measured 1) the average similarity between fungal communities of unassociated heterospecific beetles, and 2) the average similarity of fungal communities of conspecific beetles. These two measures provide the range of theoretical similarity from lowest to highest, respectively, expectable in the ambrosia ecosystem. They assume, respectively, that 1) diverse ambrosia beetles with no major ecological or evolutionary link have dissimilar fungal associates, while 2) conspecific ambrosia beetles tend to harbor similar fungal communities. The lower and upper 95% confidence interval estimates around the mean of the pairwise similarity among heterospecific (1) and among conspecific (2) galleries were obtained by bootstrapping (1000 random samples with replacement). These intervals were used to determine whether or not they contain the following means: 3) the empirical mean of pairwise similarities between fungal communities of conspecific mycocleptae associated with different hosts and 4) the empirical mean of pairwise similarities between fungal communities of mycocleptae and their hosts. These comparisons test the hypotheses that (3) the average similarity of fungal communities in galleries of conspecific mycocleptae which do not share the same beetle host will be equal to the similarity among general heterospecific beetles, and (4) the average similarity of fungal communities of mycocleptae and their beetle hosts will be equal to or higher than that among conspecific beetles. The bootstrap sub-samples were of the same size as the empirical samples with which they were compared ($n = 11$ for similarity between mycocleptae and hosts, $n = 12$ for similarity between conspecific mycocleptae with different hosts).

We also tested the effect of sharing a tree on the similarity of fungal communities between beetle galleries. First we tested whether sharing a tree increases the similarity between fungal communities of random heterospecific beetles. Then we tested whether the increase of similarity caused by sharing a tree can explain the similarity between fungal communities of mycocleptae and their hosts. In both tests, the difference between empirical mean similarities (heterospecifics in the same tree – heterospecifics in different trees; mycocleptae and hosts – heterospecifics in the same tree) was compared to a distribution of differences between means of datasets of the same proportions, where the similarities were randomly reshuffled among the two categories (resampling without replacement, 1000 replicates). The 95% quantile of the resampled distribution served as a statistic for the significance of the empirical mean difference.

To corroborate the culture-independent data, fungal inhabitants of several gallery samples from the same trees and beetle species were cultured. To enrich for scolytine-associated fungi, we used yeast-malt extract agar with or without cycloheximide (Hulcr et al., 2007; Kolarik & Hulcr, 2008). The culturing procedures and detailed results will be described elsewhere (M. Kolarik, unpubl.).

Mycangia

The hypothesis that mycocleptae do not possess their own means of transporting fungal inoculum was tested by examination of the presence or absence of mycangia in related mycocleptae and non-mycocleptic species. Three kinds of mycangia are present in Xyleborina – elytral, mandibular, and mesosternal (Francke-Grosmann, 1967; Goto, 1998). Elytral mycangia are easily detectable on the bases of beetle elytra by mycangial openings and associated vestiture. The presence of mesonotal mycangia is usually apparent due to mycangial tuft of setae on the basis of pronotum. Only beetle dissection can confirm the absence of mesonotal mycangia and the presence of the internal mandibular mycangia. Representatives of mycocleptae (*Biuncus duodecimspinatus*) and non-mycocleptic species with known mesothoracal mycangia (*Xylosandrus germanus* and *Eccoptopterus spinosus*), and with unknown mycangial status (*Xyleborus affinis*) were dissected. Beetles were fixed in 96% ethanol, immersed in 30% hydrogen peroxide for 24 hours to soften the exoskeleton, and embedded in paraffin. The preparates in paraffin were soaked in 30% hydrogen peroxide overnight, after which they were sectioned on a rotary microtome at 5 µm's and stained with hematoxylin and eosin.

To infer the pattern of mycangial evolution , we mapped the presence and absence of mycangia on a five-gene phylogeny of Xyleborina. We obtained partial sequences of the mitochondrial COI, 28S ribosomal, ArgK, EF1-alpha, and CAD genes for 188 species of Xyleborina; detailed description of methods and a large-scale phylogeny of Xyleborina will be published elsewhere (Cognato et al., 2009). A subset of these species suitable to illustrate the evolution of mycangia was selected here to reconstruct a partial phylogeny of Xyleborina. Sequences were concatenated (3263 bp sites total, 1047 parsimony informative). Cladistic phylogeny reconstruction was done by first finding the shortest tree in TNT (driven search with initial search level 60, search continued until shortest tree was found 10 times), the Majority Rule consensus of 10 MP trees was then submitted to PRAP (Müller, 2004) for calculation of Bremer support (200 parsimony ratchet iterations, each with TBR swapping).

Results

We confirmed three cases of independent origin of mycocleptism – most species in the genera *Biuncus* and *Ambrosiophilus* (both Xyleborina) in the Paleotropics, and *Camptocerus suturalis* (Scolytina) in South America (S. Smith, unpubl), based on the regularity of associations with their host species (data not shown). Several other putative records remain to be confirmed (*Euwallacea* sp. in Africa, B. H. Jordal, unpubl.; *Xylosandrus hulcri* and *Crossotarsus imitatrix* in New Guinea, J. Hulcr, unpubl.).

Co-occurrence

Complete sampling of all beetles from ten selected trees showed, that almost all mycocleptae establish their galleries exclusively in close proximity of galleries of their host beetles (Table 1; $N = 92$, $k_{\mathrm{samples}} = 13$, $\mathrm{df}_t = 2$ ($\mathrm{df}_e=24$), $F = 35.51$, $p < 0.0001$). Mycocleptae from the genus *Biuncus* also occasionally created galleries on their own, however the beetles died in approximately half of these.

Mycocleptic associations displayed a notable degree of specificity. For example, wherever the free-living *Anisadrus ursa* was found in New Guinea, it was often accompanied exclusively by the mycoceleptic *Biuncus papatrae*. Similarly, *Hadrodemius globus* was regularly accompanied by *Biuncus duodecimspinatus*. Some associations seem to span large geographic areas. For example, host beetles of the genus *Amasa* were found followed by the same morphotype of *Biuncus justus* in both New Guinea and Sabah, Malaysia.

Table 3: Ten selected trees or branches completely sampled for mycocleptae and their provider species. Most mycocleptae establish their galleries in close vicinity of their

provider species' galleries. Several *Biuncus* spp. occasionally establish independent galleries, but their survival seems to be low.

sample	**locality**	**host beetle**	**mycocleptes**	**No. of mycocleptes next to host's entrance**	**No. of mycocleptae alone, alive & dead**
crown of Nauclea orientalis	New Guinea	*Eccoptopterus spinosus*	*Biuncus haberkorni*	8	2 & 1
			Biuncus justus	14	2 & 2
			Biuncus 12-spinatus	8	0 & 1
branch of Leea indica	New Guinea	*Xylosandrus crassiusculus*	*Biuncus 12-spinatus*	3	0
			Biuncus papatrae	2	0
palm trunk	New Guinea	*Anisandrus ursa*	*Biuncus papatrae*	6	0
small tree trunk	New Guinea	*Crossotarsus longicornis*	*Crossotarsus imitatrix*	9	0
branch of Ficus sp.	New Guinea	*Hadrodemius globus*	*Biuncus 12-spinatus*	5	1 & 0
Dipterocarp branch	Borneo	*Xyleborus latus*	*Ambrosiophilus restrictus*	11	0
branch	New Guinea	*Amasa resectus*	*Biuncus justus (large)*	2	0
branch	Borneo	*Amasa resectus*	*Biuncus justus (large)*	1	0
branch	New Guinea	*Beaverium insulindicus*	*Ambrosiophilus semicarinatus*	5	0
branch	New Guinea	*Xylosandrus ursa*	*Biuncus papatrae*	10	0

Fungus sharing

The survey of fungal rDNA ITS sequences in galleries of 15 species of ambrosia beetles (29 individual galleries) revealed 52 fungal strains spanning most of the fungal phylogenetic diversity (Tab 4.). There were 95 beetle-fungus associations. The richness of fungal community ranged from 1 to 8 species per gallery, with 4.4 species on average.

The species accumulation curve did not begin a plateau, indicating that the local richness of ambrosia fungi is apparently greater than in our small sample (Figure 8).

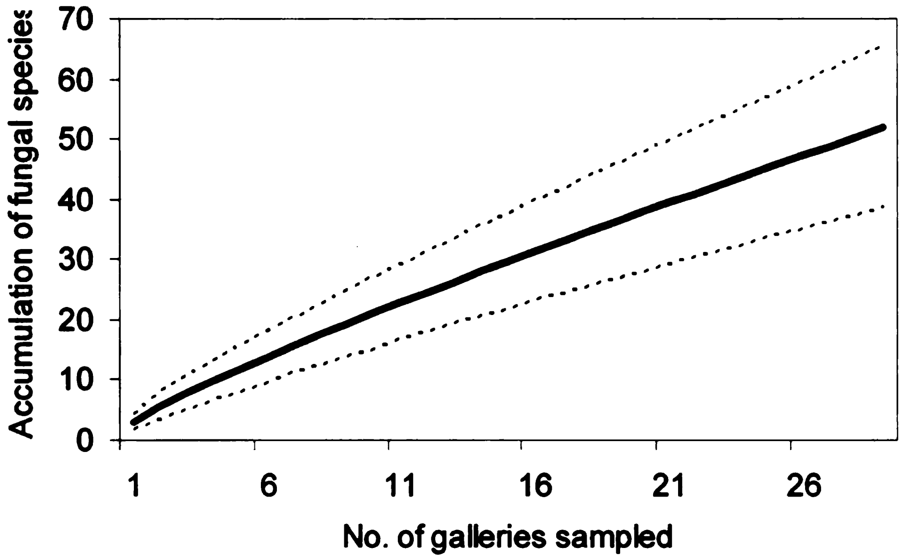

Figure 8: The steeply rising accumulation of fungal species across sampled ambrosia beetle galleries. The diversity of fungi in the ambrosia microhabitat in New Guinea is significantly greater than what could have been contained in our study. Main line – Mao Tau analytical estimate of species accumulation, dashed lines – 95% upper and lower bounds of the estimate.

Every gallery was inhabited by at least 1 sp. of *Ceratocystis* (6 spp. total), followed by *Fusarium* or its close relatives (70% galleries , 13 spp.), diverse yeasts (56% galleries, 18 spp.), and 16 other species of fungi, both Ascomycota and Basidiomycota (Supplementary information). No major group of subcortical fungi seems to have been omitted, since the analysis yielded a diverse set of expected subcortical fungi, with two exceptions. The two missing exceptions are the genera *Raffaelea* and *Ambrosiella*, which are the most commonly reported ambrosia fungi worldwide (Beaver, 1989). The absence of the two genera was confirmed by BLAST search with our sequences, as well as by direct comparison of our sequences to ITS sequences identified as *Ambrosiella* and *Raffaelea* in the NCBI database. The subsequent *in vitro* culturing on media designated for ambrosia fungi revealed similar fungal community, i.e., dominated by *Ceratosystis* spp. and *Fusarium* aff. spp., while no *Ambrosiella* or *Raffaelea* was detected.

The average pairwise Sørensen similarity of fungal communities (Figure 9) was very low among unassociated heterospecific non-mycocleptic beetles (S(mean) = 0.184, n = 346), and much higher between galleries of conspecific non-mycocleptic beetles (S(mean)= 0.489, n = 9). However, the latter was lower than expected if fungus-beetle relationships were species-specific. The average similarity between galleries of conspecific mycocleptae associated with different hosts (S(mean) = 0.365, n = 12) was greater that the similarity between galleries of free-living heterospecific beetles (bootstrap 97% quantile, S = 0.357, P = 0.022), but much smaller than the average similarity between galleries of free-living conspecifics (bootstrap 97% quantile, S = 0.389, $P < 0.001$). Thus, fungal assemblages in the galleries of mycocleptae may be to some extent governed by the mycocleptes species identity, but they are significantly less similar than within other ambrosia beetle species. On the other hand, the average similarity of fungi between galleries of mycocleptae and their hosts is the highest average pairwise similarity in our sample (S(mean) = 0.588, n = 11). It is significantly higher that the average similarity between regular heterospecifics (bootstrap 97% quantile, S = 0.352, $P < 0.001$), and lies on the upper end of the distribution of similarities among conspecifics (bootstrap 97% quantile, S = 0.603, P = 0.056). This suggests that, the composition of fungal community in a gallery of a mycocleptes mostly reflects the fungal community present in the gallery of the host species.

The variation in similarities between fungal communities was high. For example, although the overlap between fungi associated with heterospecific free-living beetles was low on average, several unrelated beetle pairs shared a single fungus strain (S(mean) = 1.0). Also the similarity between mycocleptae and their hosts ranged between 0 and 1, although the extremes were rare.

Fungal communities of random beetles occupying the same tree are significantly more similar than those of beetles from different trees (from the same tree, S(mean) = 0.292, n = 21; from different tree, S(mean) = 0.177, n = 325, P = 0.008). However, the similarity of fungal communities between mycocleptae and their hosts is still significantly higher than that between random heterospecifics sharing a tree (mycocleptae and hosts, S(mean) = 0.588, n = 11; $P < 0.001$).

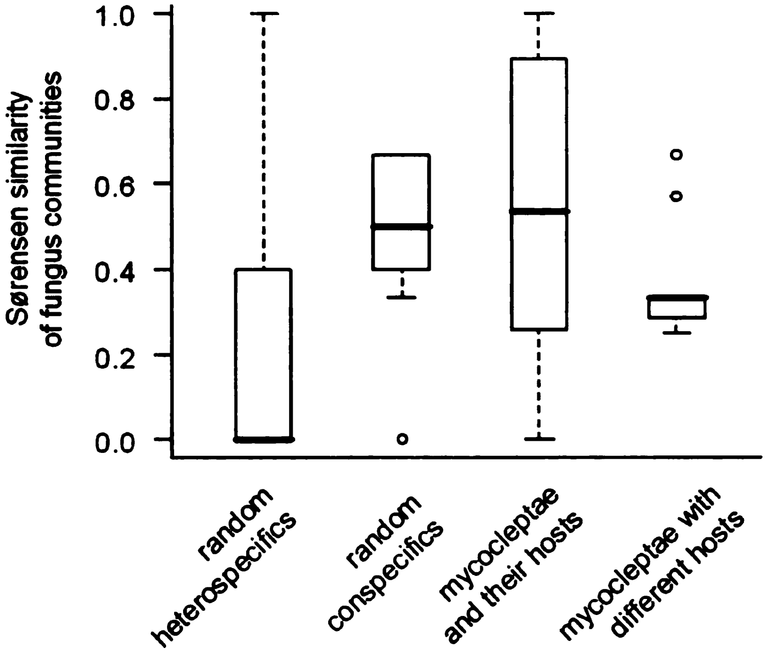

Figure 9: Pairwise similarity between fungal assemblages in ambrosia beetle galleries. Thick line: median, box: quartiles, whiskers or dots: minimum and maximum, or outliers.

Mycangia

Dissections of mycocleptic *Biuncus duodecimspinatus* and their comparison with dissections of non-mycocleptic beetles revealed that *B. duodecimspinatus* does not have any known type of mycangia (Figure 4). *Xyleborus affinis* was shown to have mandibular mycangia, *Xylosandrus germanus* and *Eccoptopterus spinosus* were confirmed to have mesothoracal mycangia (Figure 5).

The cladistic reconstruction of reduced Xyleborina phylogeny resulted in 10 MP trees 8747 steps long. Mapping mycangial types on the phylogeny revealed, that each mycangium type evolved once, and mandibular mycangia was the plesiomorphic trait. The mycocleptic genus *Biuncus*, which lacks mycangia, is deeply nested within a clade of species with mesothoracic mycangia, thus the absence of mycangium in *Biuncus* is a derived loss (Figure 5).

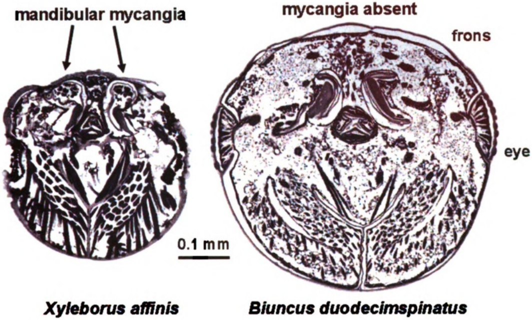

Figure 10: Horizontal cross-section of heads of ambrosia beetle *Xyleborus affinis* and the mycocleptic species *Biuncus duodecimspinatus*. Mandibular mycangia containing fungal matter are present in *X. affinis* and absent in *B. duodecimspinatus*.

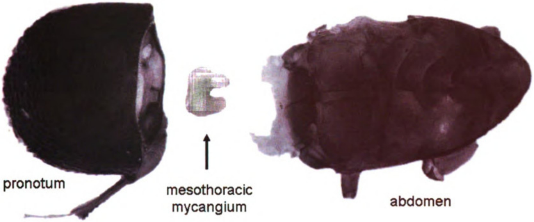

Figure 11: Mesothoracic mycangium in dissected *Xylosandrus germanus*. This structure is absent in all examined mycocleptic *Biuncus*.

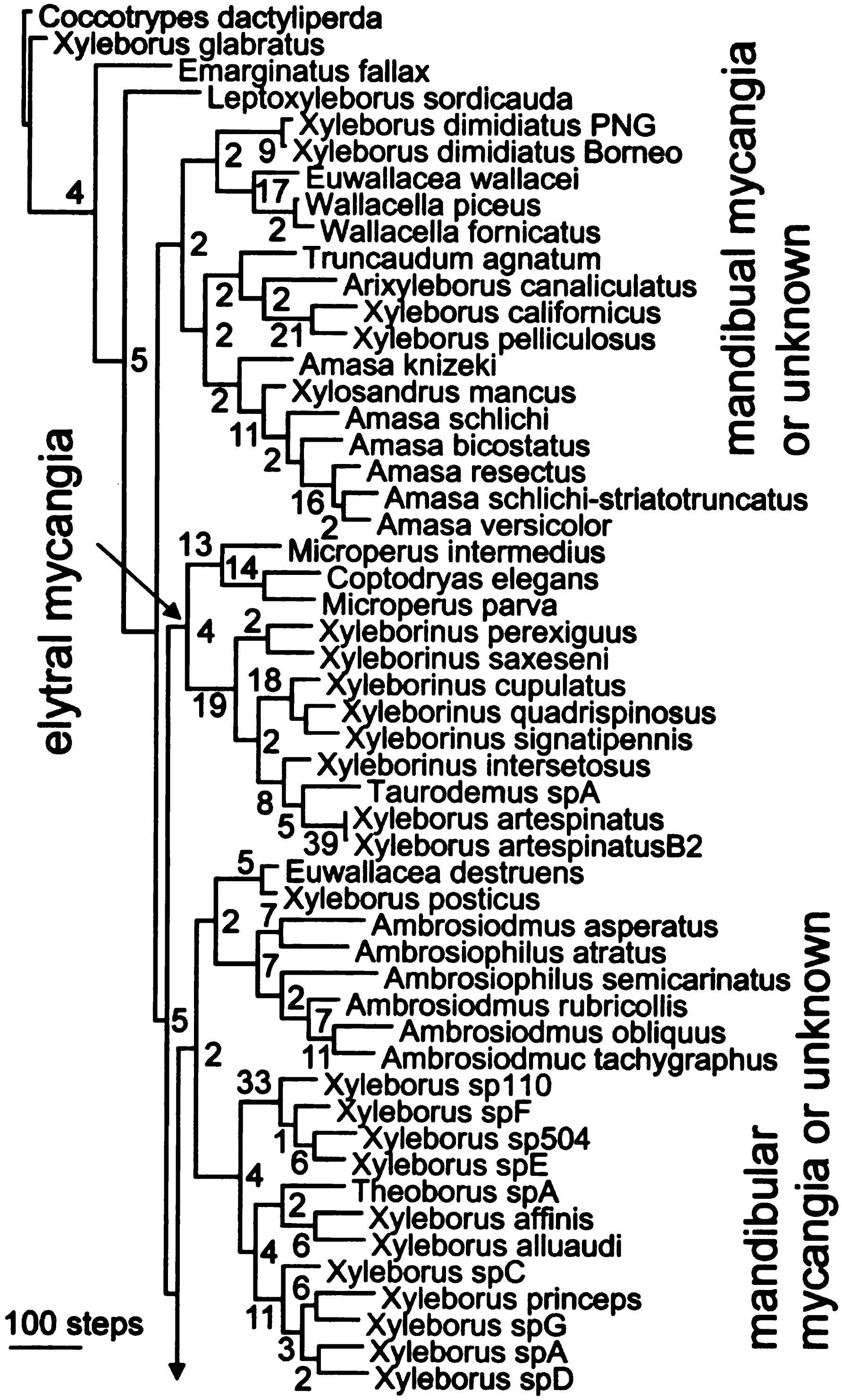

Figure 12: Cladistic analysis of a subset of Xyleborina, Majoroity Rule consensus phylogram of 10 MP trees. Each mycangium type had a single origin. The lack of

mycangia in the mycocleptic genus *Biuncus* (green) is inferred to be a derived loss of the mesothoracal mycangium. Numbers indicate Bremer support, showing high support for the derived position of *Biuncus*. "m" denotes confirmed cases of mycocleptism.

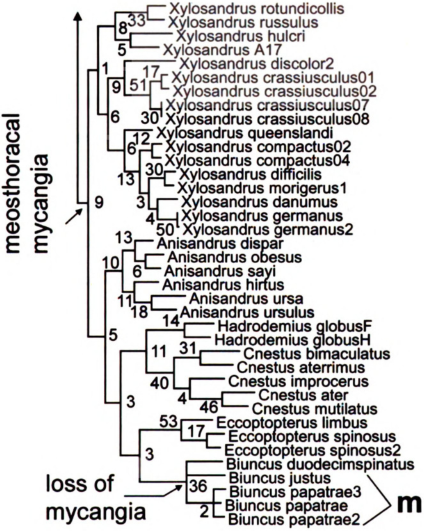

Figure 12 (cont'd).

Discussion

Although anecdotal observations of putative "commensalism" in ambrosia beetles have been previously published (Beaver, 1976; Kalshoven, 1960a), this is the first study to assemble evidence for the existence of mycocleptism as an adaptive strategy to obtain incoculum of ambrosia fungi. The benefits of this relationship to the mycocleptae include an abundance of fungal food while preempting the risk 1) of the failure to transport symbionts, 2) of the failure of the fungi or bacteria to germinate and 3) the risk of fungal garden collapse due to the competition by inedible saprophages. Mycocleptic beetles incur loss to the host beetle in two ways. First, in many cases they bore their galleries through the host's galleries, which often involves destroying a significant proportion of the host's brood (J. Hulcr & S. Smith, unpubl.). Further, by exploiting a significant volume of fungus in the surrounding wood, they decrease the amount of fungal matter which would otherwise be utilized by the host's brood. The amount of symbiotic fungus available to scolytine larvae is a limiting resource, which directly affects their development (Ayres et al., 2000, Bleiker & Six, 2007).

Mycocleptism evolved multiple times independently, and in every major tropical region of the world. Some of the mycocleptic associations may be geographically widespread and evolutionarily very stable, as evidenced by species specificity of most mycocleptic associations throughout most of New Guinea, and, in one putative case, throughout the Australasian region.

It is not known whether all species of the mycocleptic clades employ the mycocleptic habit, and it is unclear whether mycocleptism is an obligate strategy. Several *Biuncus* spp. have been recorded successfully breeding on their own (Beaver, 1976; Kalshoven, 1960a). These may represent either evolutionary reversals to a typical ambrosia habit, or may be evidence that mycocleptism is facultative for some species.

Mycocleptism is only one of several ways by which ambrosia beetles exploit pre-established ambrosia gardens. Species of the Neotropical genera *Sampsonius* (Xyleborina) and *Tricolus* (Corthylina) and several genera of Crypturgini (Jordal, 2006; Schwarz, 1894; Wood, 1982) are inquiline parasites specialized on colonizing galleries built by other ambrosia beetles. At least in case of females of *Sampsonius* spp., which target active galeries of *Dryocoetoides* spp. (Jordal et al., 2000), the colonization involves killing and consuming the inhabitants (J. H., unpublished observations). It is not known whether inquiline parasites inoculate their own fungal associates into the invaded gallery, or if they accept the host's fungus garden, which would be a special case of mycocleptism. The inquiline parasites are not related to any of the confirmed mycocleptae *s. str.*, and each case seems to have evolved from unrelated free-living ancestors (Cognato et al., 2009).

It remains unclear what cues the mycocleptae follow to locate their host beetles. Volatiles emitted by the fungi are an unlikely cue, since a single mycocleptic species associate with galleries dominated by different fungi. The relationship between mycocleptae and their host is relatively species-specific and thus may be mediated by pheromones. There is some evidence that even haplo-diploid xyleborines may engage in semiochemical intraspecific communication (Karunaratne et al., 2008), but no pheromones have been reported (Klimetzek et al., 1986).

An intriguing result of this work is the evidence that fungal gardens of tropical ambrosia beetles harbor large diversity of fungi. From occurrence data, it is difficult to ascertain which fungal species are nutritionally beneficial symbionts transmitted by the beetles, and which are opportunists. The abundance of Hypocreales, especially *Fusarium* spp., in the galleries of many unrelated ambrosia beetles is surprising. *Fusarium* spp. are common saprophages in soil and forest ecosystems, and have only rarely been reported as symbionts of scolytine beetles (Morales-Ramos et al., 2000; Norris, 1979). We cannot conclude whether or not *Fusarium* interacts with the beetles studied here.

Even more surprising is the total absence of *Ambrosiella* and *Raffaelea* spp. The two genera are the most commonly reported fungal symbionts of ambrosia beetles worldwide (Beaver, 1989; Blackwell & Jones, 1997; Rollins et al., 2001). The replacement of *Ambrosiella* and *Raffalelea* as primary symbionts of ambrosia beetles in a whole region by fungi which have not been reported as nutritional symbionts, contradicts the assumption of ambrosia fungi being the "tamed crop" (Mueller et al., 2005). Traditionally it was assumed that the ambrosia fungus strain was selected and the purity of garden maintained by the beetle (Mueller et al., 2005). This would likely lead to a narrow garden diversity, perhaps to a single strand of utilized fungus as in the case of the actively weeding leafcutter ants (Bot et al., 2001; Currie et al., 2003). However, such behavior has never been observed in the beetles.

In fact, the fungus community composition is only weakly determined by the beetle host identity. The increased similarity of communities of fungi between galleries on the same tree suggest frequent horizontal exchange of symbionts, or frequent incursion of fungi from ambient wood into beetle galleries. Examples of unrelated ambrosia beetles sharing fungi through the colonized tree have been published (Gebhardt et al., 2004). If future studies confirm the extensive infidelity between ambrosia beetles and fungi observed here, the current paradigm of a moderately tight coevolution between "farmers and crop" with only occasional horizontal switches (Beaver, 1989; Farrell et al., 2001; Francke-Grosmann, 1967; Mueller & Gerardo, 2002; Mueller et al., 2005) may need to be re-evaluated. It is more likely that the ambrosia fungus community composition is determined by other mechanisms, either by interspecific competition, or by bacteria-derived antifungal chemicals, or by neutral community assembly processes.

Table 4: Fungal strains of rDNA ITS from galleries of mycocleptic and free-living beetles and identified using NCBI BLAST. myco = mycocleptes, free = provider species, unass = unassociated.

association	GenBank_ID	strain id	beetle	habit	determination
1	FJ808015	>F266jus_366B	Biuncus justus	mycocl.	Ceratocystis sp. 87
1	FJ808014	>F266jus_366A	Biuncus justus	mycocl.	Hypocreales sp. LM583 18
1	FJ808012	>F063mor_367A	Xylosandrus morigerus	free	Hypocreales sp. LM583 18
2	FJ808030	>F354nig_368A	Biuncus papatrae (montane)	mycocl.	Ceratocystis sp. 87
2	FJ808020	>F325rot_369A	Xylosandrus russulus	free	Candida sp. BCMU BX02
2	FJ808021	>F325rot_369B	Xylosandrus russulus	free	Ceratocystis sp. 87
3	FJ808024	>F342bic_370A	Xylosandrus hulcri	mycocl.	Ceratocystis sp. 87
3	FJ807993	>F325rot_371A	Xylosandrus russulus	free	Ceratocystis sp. 87
4	FJ808025	>F352min_372I	Biuncus niger	mycocl.	ascomycete 1
4	FJ808026	>F352min_372F	Biuncus niger	mycocl.	Ascomycete sp. Artz 103
4	FJ807995	>F352min_372G	Biuncus niger	mycocl.	Basidiomycete
4	FJ807997	>F352min_372D	Biuncus niger	mycocl.	Candida sp. BCMU BX02
4	FJ807996	>F352min_372B	Biuncus niger	mycocl.	Ceratocystis sp. 87
4	FJ808028	>F352min_372A	Biuncus niger	mycocl.	Fusarium proliferatum is
4	FJ808027	>F352min_372H	Biuncus niger	mycocl.	Neonectria liriodendri s
4	FJ808029	>F352min_372E	Biuncus niger	mycocl.	Saccharomycetales sp.
4	FJ807994	>F325rot_373B	Xylosandrus russulus	free	Basidiomycete
4	FJ808022	>F325rot_373A	Xylosandrus russulus	free	Candida sp. BCMU BX02
4	FJ808023	>F325rot_373C	Xylosandrus russulus	free	Ceratocystis sp. 87
5	FJ808032	>F384con_375A	Biuncus sp. 384	mycocl.	Ceratocystis sp. 87
5	FJ808031	>F379ate_374A	Cnestus ater	free	Ceratocystis sp. 87
6	FJ808034	>F384con_377C	Biuncus sp. 384	mycocl.	ascomycete 1
6	FJ807998	>F384con_377E	Biuncus sp. 384	mycocl.	Candida sp. BCMU BX02
6	FJ808000	>F384con_377A	Biuncus sp. 384	mycocl.	Ceratocystis sp. 87

Table 4 (cont'd).

6	FJ807999	>F384con_377F	Biuncus sp. 384	mycocl.	Hypocreales sp. LM583 18
6	FJ808033	>F384con_377G	Biuncus sp. 384	mycocl.	Lentinus tigrinus
6	FJ808035	>F384con_377D	Biuncus sp. 384	mycocl.	Uncultured soil fungus c
6	FJ808003	>F399scpl_376G	Scolytoplatypus javanus	free	ascomycete 1
6	FJ808039	>F399scpl_376C	Scolytoplatypus javanus	free	Ascomycete sp. Ano18 int
6	FJ808001	>F399scpl_376D	Scolytoplatypus javanus	free	Candida sp. BCMU BX02
6	FJ808004	>F399scpl_376A	Scolytoplatypus javanus	free	Ceratocystis sp. 87
6	FJ808005	>F399scpl_376B	Scolytoplatypus javanus	free	Ceratocystis sp. 87
6	FJ808002	>F399scpl_376F	Scolytoplatypus javanus	free	Sterigmatomyces halophil
6	FJ808036	>F399scpl_376E	Scolytoplatypus javanus	free	Uncultured soil fungus c
7	FJ808042	>F019biu_392C	Biuncus papatrae	mycocl.	basidiomycet
7	FJ808040	>F019biu_392A	Biuncus papatrae	mycocl.	Candida sp. YI-2007b ge
7	FJ808041	>F019biu_392B	Biuncus papatrae	mycocl.	Ceratocystis sp. 87
7	FJ808057	>F032cra_391C	Xylosandrus crassiusculus	free	Basiomycete sp. UASWS033
7	FJ808059	>F032cra_391E	Xylosandrus crassiusculus	free	Candida sp. YI-2007b ge
7	FJ808058	>F032cra_391D	Xylosandrus crassiusculus	free	Ceratocystis sp. 87
7	FJ808056	>F032cra_391A	Xylosandrus crassiusculus	free	Fusarium sp. XL-B32 18S
8	FJ808043	>F019biu_394A	Biuncus papatrae	mycocl.	Ceratocystis paradoxa st
8	FJ808044	>F019biu_394B	Biuncus papatrae	mycocl.	Saccharomycetales sp.
8	FJ808045	>F019biu_394C	Biuncus papatrae	mycocl.	Saccharomycodaceae sp.
8	FJ808063	>F032cra_393D	Xylosandrus crassiusculus	free	Ceratocystis paradoxa st
8	FJ808060	>F032cra_393B	Xylosandrus crassiusculus	free	Ceratocystis savannae is
8	FJ808061	>F032cra_393A	Xylosandrus crassiusculus	free	Saccharomycetales sp.
8	FJ808062	>F032cra_393C	Xylosandrus crassiusculus	free	Saccharomycetales sp.
9	FJ808064	>F149urs_395A	Anisandrus ursa	free	Saccharomycetales sp.
9	FJ808065	>F149urs_395B	Anisandrus ursa	free	Saccharomycetales sp.
9	FJ808066	>F149urs_395C	Anisandrus ursa	free	Saccharomycetales sp.

Table 4 (cont'd).

9	FJ808047	>F019biu_396D	Biuncus papatrae	mycocl.	Ceratocystis sp. 87
9	FJ808048	>F019biu_396A	Biuncus papatrae	mycocl.	Saccharomycetales sp.
9	FJ808046	>F019biu_396B	Biuncus papatrae	mycocl.	Saccharomycetales sp.
9	FJ808049	>F019biu_396C	Biuncus papatrae	mycocl.	Saccharomycetales sp.
10	FJ808067	>F149urs_397C	Anisandrus ursa	free	Candida orthopsilosis st
10	FJ808068	>F149urs_397A	Anisandrus ursa	free	Ceratocystis sp. 87
10	FJ808069	>F149urs_397B	Anisandrus ursa	free	Saccharomycetales sp.
10	FJ808050	>F019biu_398A	Biuncus papatrae	mycocl.	Ceratocystis sp. 87
10	FJ808052	>F019biu_398C	Biuncus papatrae	mycocl.	Hypocreales sp. LM583
10	FJ808051	>F019biu_398B	Biuncus papatrae	mycocl.	Saccharomycetales sp.
11	FJ808071	>F149urs_399B	Anisandrus ursa	free	Ceratocystis sp. 87
11	FJ808070	>F149urs_399A	Anisandrus ursa	free	Saccharomycetales sp.
11	FJ808072	>F149urs_399C	Anisandrus ursa	free	Saccharomycetales sp.
11	FJ808055	>F019biu_400C	Biuncus papatrae	mycocl.	Ceratocystis sp. 87
11	FJ808053	>F019biu_400A	Biuncus papatrae	mycocl.	Saccharomycetales sp.
11	FJ808054	>F019biu_400B	Biuncus papatrae	mycocl.	Saccharomycetales sp.
unass	FJ808018	>F266jus_379A	Biuncus justus	mycocl.	Ceratocystis sp. 87
unass	FJ808019	>F266jus_379C	Biuncus justus	mycocl.	Hypocreales sp. LM581 18
unass	FJ808017	>F266jus_379B1	Biuncus justus	mycocl.	Phomopsis sp. ZH34 18S r
unass	FJ808016	>F266jus_379B2	Biuncus justus	mycocl.	Phomopsis sp. ZH34 18S r
unass	FJ808037	>F426cros_384A	Crossotarsus sp. cincinnatus	free	Ceratocystis sp. 87
unass	FJ808038	>F426cros_384B	Crossotarsus sp. cincinnatus	free	Nectriaceae sp. LM388 18
unass	FJ808011	>F036for_381B	Wallacella fornicatus	free	Ceratocystis sp. 87
unass	FJ808009	>F036for_380A	Wallacella fornicatus	free	Hypocreales sp. LM210 18
unass	FJ808010	>F036for_381A	Wallacella fornicatus	free	Hypocreales sp. LM210 18
unass	FJ807991	>F023per_383C	Xyleborus perforans	free	Ceratocystis sp. 87

Table 4 (cont'd).

unass	FJ807990	>F023per_383G	Xyleborus perforans	free	Ceratocystis sp. 87
unass	FJ808007	>F023per_383E	Xyleborus perforans	free	Hypocreales sp. LM583 18
unass	FJ808006	>F023per_383A	Xyleborus perforans	free	Saccharomycetales sp.
unass	FJ807992	>F023per_383F	Xyleborus perforans	free	Saccharomycetales sp.
unass	FJ807989	>F023per_383D	Xyleborus perforans	free	Uncultured soil fungus c
unass	FJ808073	>F063mor_382A	Xylosandrus morigerus	free	Ceratocystis sp. 87
unass	FJ808008	>F063mor_382B	Xylosandrus morigerus	free	Ceratocystis sp. 87
unass	FJ808013	>F063mor_382B	Xylosandrus morigerus	free	Hypocreales sp. LM583 18

CHAPTER 3

Cladistic review of generic taxonomic characters in Xyleborina (Coleoptera: Curculionidae: Scolytinae)

Abstract

A cladistic analysis of morphological characters of the subtribe Xyleborina (Curculionidae, Scolytinae) is presented. Examination of individual characters revealed little phylogenetic information in many characters currently used for delimiting genera. Phylogenetically stable characters were used for evaluation of the contemporary generic concept. The following genera have been recovered as monophyletic: *Cnestus*, *Dryocoetoides*, *Eccoptopterus*, *Xylosandrus*, *Schedlia*, *Sampsonius* and *Taurodemus*. The following genera have been found to be polyphyletic: *Amasa*, *Ambrosiodmus*, *Arixyleborus*, *Coptoborus*, *Coptodryas*, *Cryptoxyleborus*, *Cyclorhipidion*, *Euwallacea*, *Leptoxyleborus*, *Taphrodasus*, *Theoborus*, *Webbia*, *Xyleborinus* and *Xyleborus*. The analysis permitted the resurrection of four genera: *Anisandrus*, *Microperus*, *Pseudowebbia* and *Streptocranus*. A number of new combinations at specific level are given: *Anisandrus cornutus* (Schaufuss, 1891), *A. dispar* (Fabricius, 1792), *A. eggersi* (Beeson, 1930), *A. improbus* (Sampson, 1913), *A. longidens* (Eggers, 1930), *A. maiche* Stark, 1936, *A. obesus* (LeConte, 1868), *A. sayi* Hopkins, 1915, *A. apicalis* (Blandford, 1894), *A. hirtus* (Hagedorn, 1904), *Microperus myristicae* (Schedl, 1939), *M. eucalypticus* (Schedl, 1938), *M. huangi* (Browne, 1983), *M. intermedius* (Eggers, 1923), *M. kadoyamaensis* (Murayama, 1934), *Pseudowebbia armifer* (Schedl, 1942), *P. seriata* Browne, 1963, *P. squamatilis* (Schedl, 1955), *P. trepanicauda* (Eggers, 1923), *P. curvatus* (Browne, 1986), *Streptocranus bicolor* Browne, 1949, *S. bicuspis* (Eggers, 1940), *S. capucinulus* Schedl, 1942), *S. forficatus* (Schedl, 1957), *S. fragilis* Browne, 1949, *S. longicauda* Browne, 1960, *S. longispinis* Browne, 1986, *S. mirabilis* Schedl, 1939, *S. usagaricus* (Eggers, 1922), *S. sexdentatus* (Eggers, 1940). Characters most

useful for generic-level taxonomy of Xyleborina were identified and their states refined and illustrated. An accompanying illustrated multiple-entry electronic key for the updated xyleborine classification has been published on-line at www.scolytid.msu.edu.

Introduction

Stephen L. Wood's Reclassification of the Genera of Scolytidae (Wood, 1986) was the first publication to place the chaotic classification of bark and ambrosia beetles (Coleoptera, Curculionidae, Scolytinae) within an evolutionary framework. This publication synthesized scattered generic descriptions, redefined generic boundaries, and attempted to infer taxonomic relationships. Unfortunately, a reclassification of subtribe Xyleborina, one of the most diverse and economically important groups of scolytids, was exceptionally problematic. Wood's (1986) introduction to the tribe was foreboding and stated, in part, that the generic classification of the subtribe was tentative and flawed.

Females of Xyleborina can be distinguished from other scolytines by the circular, dorsoventrally flattened antennal club with the first segment often conspicuously sclerotized, by the depressed submentum, by arcuate and flattened meso- and metatibiae armed with six or more denticles (unless secondarily reduced), and by a pronotum strongly convex anterodorsally, armed with asperities on the anterior slope. Biologically, this group is defined clearly by the combination of a haplodiploid genetic system in which haploid males are flightless and often dwarfed, and show extreme inbreeding, and obligate nutritional symbiosis with xylophagous fungi (the ambrosial habit, or "fungus gardening"; Francke-Grosmann,1967; Beaver, 1989; Jordal *et al.,* 2000; Farrell *et al.*, 2001). Although these biological features are found elsewhere in Scolytinae, their combined occurrence in Xyleborina is unique. These biological features are also hypothesized to be the cause of a rapid radiation that has produced nearly 1400 species since the early Oligocene (Jordal *et al.*, 2000). Both the rapid diversification and inbreeding are likely causes of unclear species limits and a relative lack of clearly definable morphological characters.

Contemporary systematics recognizes monophyletic groups of organisms as evolutionary entities, which form the basis of taxonomy and nomenclature (Hennig, 1966). Monophyletic groups are defined by synapomorphic characters, which are shared by an ancestor and all its descendents. However, taxonomic groups often are not defined by synapomorphies, and only unique combinations of homoplasies define clades. Numerous morphological attributes have been proposed to define the genera of Xyleborina (Hopkins, 1915; Wood, 1980, 1983, 1986; Maiti & Saha, 2004) but it is untested if these characters represent synapomorphies. This study examines the utility of morphological characters to define monophyletic groups of Xyleborina species and the association of these groups with current generic nonmenclature (Wood & Bright, 1992; Bright & Skidmore, 1997, 2002). Trees resulting from a cladistic analysis of 193 species using 40 characters allow evaluation of the monophyly of genera and the relative phylogenetic information of the characters. Identification of several monophyletic groups allows a partial revision of the current classification.

Since the inclusion of the family Scolytidae into the family Curculionidae as a subfamily (Marvaldi, 1997; Kuschel *et al.*, 2000), previous scolytine tribes (e.g., Xyleborini sensu Wood & Bright, 1992) are currently treated as subtribes (Xyleborina; Arnett *et al.*, 2002; Rabaglia *et al.*, 2006). This classification is followed in this paper.

Methods

Cladistic analysis was based on 39 morphological characters in 193 species of Xyleborina. Species of Xyleborina were sampled evenly from currently valid genera. For most genera, we scored 25% of species. Only the most speciose genus, *Xyleborus* Eichhoff (534 sp.) was represented by less than 10% of species. In *Hadrodemius* Wood only one species was available. Two species of *Premnobius* Eichhoff were selected as outgroups, since *Premnobius* was previously considered a genus of Xyleborina (Wood, 1986), and because *Premnobius* belongs among the groups most closely related to Xyleborina (e.g. Farrell *et al.,* 2001; Cognato, unpubl.).

The analysis presented is based on female morphology. Males, which are cryptic and rare, most often occurring within maternal galleries in very low numbers, and are unknown for most species. Type species of all xyleborine genera were examined, except for *Amasa*, *Sampsonius* and *Taurodemus*, for which only non-type species were available at the time of the study.

The set of characters for this study has been compiled from the literature (Hagedorn, 1912; Hopkins, 1915; Wood, 1986; Maiti & Saha, 2004) and from our own studies. All the characters extracted from the literature fall into one of three groups (Table 5):

1) characters included in the analysis (Table 5)

2) characters excluded from the analysis due to ambiguous definition of their states (Table 6)

3) characters that are impossible to use because they are damaged or inaccessible in many examined specimens (Table 6). For example, the majority of scolytid type specimens in Schedl's collection in Natural History Museum, Vienna, are glued to mounting boards

which precludes the use of many ventral characters. The character matrix is provided as on-line supplementary material.

The independence of several characters in the analysis is suspect. For example, pronotum types (characters 9, 14) include the pronotal length to width ratio (character 2), and antenna type (character 8) is composed of characters 21 (central portion of the apical margin of 1st club segment), 19 (extent of the 1st club segment) and 18 (posterior face of antennal club). Developmentally or otherwise correlated characters should not be used in cladistic analyses, as they function as non-independent pseudoreplications (Kluge, 1985) and could potentially skew the resulting tree. However, in this study, analysis of the phylogenetic correlation of all available characters was a higher priority than the finalization of the relationships among taxa.

Phylogenetic analysis was performed using TNT software (Goloboff *et al.,* 2003). Driven search employed all four search modules (Sectorial search (RSS & CSS), Ratchet, Drifting and Tree fusing). Default settings were used except that trees were fused globally after every hit and search continued until the minimal length tree was found 10 times. Random seed was set to 1. Tree-bisection-&-reconnection (TBR) swapping was performed on the resulting trees to search for more non-duplicate maximum parsimony (MP) trees holding a maximum of 10,000 trees. Trees were filtered for duplicates. Islandic structure of the distribution of MP trees in tree space was not examined. Distribution of characters among taxa was examined using randomly selected MP trees, relationships between taxa were inferred from the strict consensus tree (see Figure 1 in Hulcr et al. 2007a). Bootstrap analysis of branch support was performed with Winclada (Nixon, 1999).

The cladistic analysis provided us with a measure of phylogenetic information content for each character. Homoplasy for each character was measured with the retention index (ri) (Farris, 1989). Two continuous characters were used (length/width ratio of pronotum and elytra). Both have a gradual distribution, which hampers the division into discrete states. Thus the optimal number of states used for these continuous characters was determined by maximizing consistency of the assigned states with a phylogenetic hypothesis based on all characters. The scales of both characters were divided into thirds, fourths, fifths and sixths and each of these segments was assigned a discrete state. The rescaled characters were treated as additive. Separate analyses were performed with the datasets each containing one of the rescaled continuous characters and the discrete characters, and retention index (ri) was calculated for the character in question. Differences among the ri's of the differently rescaled continuous characters were minor; however, the highest indices were found in the character "pronotum l/w ratio" when divided into thirds, and in the character "elytra l/w ratio" when divided into fifths. These two character codings were used for the final analysis.

For the purpose of consistent coding and feasibility of communication between taxonomists, states of the most useful characters have been formalized. Dorsal and lateral types of pronotum (characters 9 and 14, respectively) have been assembled by recording every distinct shape of pronotum encountered (Figs 14, 15). The five types of antennal club (character 8, Figure 13) are combinations of several characters typically evolving together: longitudinal profile (character 7), accentuation of costa of the first club segment (character 11), curvation of suture of the 1st segment (character 21), size of the 1st and 2nd segments (character 19) and the number of segments visible on the posterior face of antennal club (character 18).

Results and discussion

Trees

We found 10,000+ equally parsimonious trees (1045 steps, CI = 0.06, RI = 0.46). The strict consensus tree was mostly unresolved (Figure 1 in Hulcr et al. 2007a). However, all nodes of the consensus tree were recovered in more than 50% of replications in the bootstrap analysis. The large number of spurious groups probably is caused by the unfavorable ratio of number of taxa vs. number of characters, by the substantial degree of homoplasy among characters, and perhaps by missing or ambiguous coding in a number of instances (4% of cells in the matrix). The weak support and lack of resolution indicate that the hitherto used set of characters is insufficient for a complete revision of Xyleborina genera. Hence, the addition of alternative characters is essential for development of a stable generic concept.

Characters

Characters were ranked according to their retention indices (Table 5). Generally only characters with ri of 0.6 and higher were phylogenetically informative and are discussed further. The most stable character is the enlarged metatibia and metatarsus in *Eccoptopterus* Motschulsky (ri = 1, character 1).

Three groups of characters are highlighted in the table: characters associated with pronotum shape, antennal club and elytra. Apparently characters from the former two groups often have high ri's, whereas elytral characters often have the lowest ri's. Thus most discussion pertains to pronotal and antennal characters, along with other informative characters.

States of the most useful characters have been formalized: antennal club type (Figure 13), lateral aspect of pronotum shape (Figure 14), and dorsal aspect of pronotum shape (Figure 15). The evolution of the antennal club probably progressed from the type 4 found in the outgroup and in *Sampsonius* Eggers, through type 3. Type 3 is the basal state of all the rest of Xyleborina. Derived antennal club types include type 2, which is most common among Xyleborina, and type 1 which is found mostly in *Xyleborinus* Reitter and in the clade that contains *Xylosandrus* Reitter and related genera. Type 5 is found only rarely, typically in *Amasa* Lea, and in a clade of a few species that represent the genus *Notoxyleborus* Schedl, a genus currently synonymised with *Xyleborus*.

The standard types of pronotum shape can be understood as a pattern of hypothetical diversification of the pronotum shape. The most common type of the lateral aspect of pronotum (Figure 14) is type 1, from which the pronotum was either prolonged (types 7 to b) or shortened (types 2 to 5), or assumed other rarer shapes (1, 6). The prolonged types of pronotum can be further distinguished by the extent to which the summit of the pronotum remained approximately median (7, a) or moved anteriorly, causing the anterior end of pronotum to bulge anteriorly and laterally (8 and especially b). (The forms of pronotum 'a' and 'b' are not given numbers 10 and 11, as would be expected logically. We decided to choose single-character names that can be readily used in cladistic software, where utility of two-character numbers is limited.)

The diversity of the topical aspects of the pronotum can be expressed as a combination of an increase of length/width ratio and the tendency of the anterolateral sides to bulge (Figure 15). The latter represents a gradual change from almost triangular to quadrangular shapes.

Another important phylogenetically-informative character is the scutellum (character 4). Even though highly consistent state definitions need further elaboration in future. For example, we suspect that a number of species are currently included in *Coptodryas* Hopkins because of their lack of an externally visible scutellum, however, some of these species possess a cone-shaped scutellum (state 3) concealed under the elytra. Unfortunately, this is impossible to examine without damage to specimens. The cone shaped scutellum and absence of a visible scutellum in many species may be linked to the presence of elytral mycangia (Beaver, 1975).

Although not used in any taxonomic analysis known to us, the presence and type of mycangia proved to be a reliable character. Xyleborine mycangia are conserved structures, as compared with other bark and ambrosia beetles (for example, Platypodidae), where the presence and type of mycangium varies between related species (Wood, 1993). Four types of mycangium are known to occur in Xyleborina: mandibular, prothoracic, mesothoracic, and elytral. (Francke-Grosmann, 1967; Beaver, 1989; Goto, 1998). Only the pronotal type is easy to recognize externally by the presence of a tuft of setae on the medio-posterior edge of pronotum. This mycangium is typical for the group of apparently related genera *Cnestus* Sampson, *Eccoptopterus, Hadrodemius, Xylosandrus* and the "*Anisandrus*" group of species. The setae presumably collect fungal spores from tunnel walls. It must be emphasized that in the present work the tuft has been scored, not the presence/absence of mycangium. The tuft may often be absent even though the mycangium is present, which is perhaps the case in some species of *Cnestus*. Conversely, several species have posterior pronotal vestiture resembling the mycangial tuft, although the presence of a pronotal mycangium has not been proved. Thus, the character "pronotal mycangial tuft" may be more homoplastic than the actual presence/absence of mycangia, which may be scored only after dissection of specimens.

The tufts of setae occurring from the mesonotum and from the anterior margin of the elytra (character 9) are presumably also associated with mycangia. owever, it is sometimes unclear whether the mycangium is of the mesothoracic or elytral type. It is also unclear whether the mycangia in some *Cryptoxyleborus* Schedl that have openings on the outer surface of the elytra are homologous to the general elytral mycangia, or represent yet another type. Mycangial characters will likely be more informative following future study, and will be especially helpful for resolution within and between the genera *Cryptoxyleborus*, *Coptodryas*, *Pseudowebbia* Browne, *Schedlia* Browne, *Taphrodasus* Wood and *Xyleborinus*.

Character 11 "elytral l/w ratio" is the only elytral-associated character appearing relatively consistent. Rather than an elytral feature, this ratio describes the shape of the whole abdomen. It is probably for that reason that it is phylogenetically more stable than other elytral characters.

The third state of the character 16 "pronotal disc surface/asperities" (asperities covering most of the pronotal surface) is mentioned in most keys as diagnostic for *Ambrosiodmus* Hopkins (Wood, 1986; Maiti & Saha, 2004). Wood (1986) and Beaver (2004) mentioned several species of *Ambrosiodmus* that have the asperities confined only to the anterior parts of pronotum, as in other Xyleborine species (e.g. *A. apicalis* (Blandford), *A. funereus* (Lea)). These species share characters with other genera of Xyleborina. This finding suggests the removal of these species from *Ambrosiodmus*, but, with the exception of *A. apicalis*, this is not undertaken here pending further investigations.

In character 19 "posterolateral costa of elytral declivity" it seems that the states 1 (no costa) and 2 (small costa present) are not consistent across Xyleborina, but state 3 (costa reaching beyond the 7th interstriae, often encircling the whole elytral declivity) has arisen only a few times. There are problems with coding this third state, however, because it is unclear whether costa, carina, and elevated row of teeth/serrations are all homologous traits. Presently, only costa and carina have been scored as the 3rd state, which causes inconsistency in some groups, for example *Webbia* Hopkins s.str.

Of the three states of character 21 "pronotal anterior edge serration", only the third (two prominent teeth on the front edge of pronotum) seems to be phylogenetically informative. It is a typical feature of *Sampsonius*, and of the group of the four closely related genera *Cnestus*, *Eccoptopterus*, *Hadrodemius* and *Xylosandrus*, only rarely appearing elsewhere.

According to the distribution of character states for character 22 "elytral end shape" on the tree, the plesiomorphic state is apparently a rounded end. The derivations are abundant and often inconsistent with other characters, but within some groups, derived character states are often stable and diagnostic. This is the case for *Cryptoxyleborus*, which has attenuated elytra, *Streptocranus* Schedl with emarginate elytra, *Amasa* Lea, *Pseudowebbia* and *Webbia* with truncated elytra, and *Dryocoetoides* Hopkins with angulate elytra. It may be noted here that Schedl appears to have based his classification of Xyleborina to a large extent on the shape and sculpture of the elytral declivity (Schedl, 1963, 1977). However, characters associated with the elytral declivity are the least phylogenetically informative for generic level relationships.

Character no. 26 “geographical distribution” was included in the analysis even though it is not genetically heritable and its phylogenetic utility may be questioned. However, history of distribution of taxa and centres of speciation, both of which provide continuity of lineages through space and time, are often of great value for a systematist, especially in groups of which history has been shorter than that of continents. Geography was also one of the crucial features used by Wood to delimit the contemporary genera of xyleborines. Our analysis showed that geography is among the less decisive characters for generic level phylogeny.

Most of the original descriptions of Xyleborina genera and species were published in the pre-phylogenetic era of taxonomy, and as such often lack sufficient information on the descriptive characters (e.g., Lea, 1893; Sampson, 1911; Hopkins, 1915). Contemporary authors usually provide extensive discussion of characters, but the definitions of characters and especially their states may not be comparable between authors. We suggest that future descriptions of species of Xyleborina should refer to the set of phylogenetically most informative characters identified in the presented analysis, namely the pronotum shape types (Figures 14 & 15), antennal club types (Figure 13), scutellum and mycangial tufts. To assure consistency between descriptions, we suggest use of the formalized states presented here. Adoption of such a set of characters, and descriptions of their states, will increase the clarity of descriptions and provide greater justification for taxonomic changes within this group.

Taxonomy

The majority of characters used, hitherto, in the classification of Xyleborina do not support the generic concepts as defined by Wood & Bright (1992). Several monophyletic or stable paraphyletic groups were recovered in the present analysis. The following genera are supported: *Cnestus*, *Dryocoetoides*, *Eccoptopterus*, *Xylosandrus*, *Schedlia*, *Sampsonius* and *Taurodemus* Wood. *Hadrodemius* would be likely supported as well, but unfortunately only one species was available for the analysis. Genera that appear not to be monophyletic are *Amasa*, *Ambrosiodmus*, *Arixyleborus* Hopkins, *Coptoborus* Hopkins, *Coptodryas*, *Cryptoxyleborus*, *Cyclorhipidion* Hagedorn, *Euwallacea* Hopkins, *Leptoxyleborus* Wood, *Taphrodasus*, *Theoborus* Hopkins, *Webbia*, *Xyleborinus,* and *Xyleborus*. Monophyletic subgroups of the following genera were consistently recovered: *Amasa anomalus* group, *Coptoborus mirabilis* group, *Coptodryas eucalyptica* group, *Coptodryas elegans* group, *Webbia trepanicauda* group and *Webbia dipterocarpi* group. We now discuss some of the monophyletic genera and species groups, and put forward taxonomic changes based on these discussions. It should be noted that in making generic transfers of species, we cite the current name of the species as given by Wood & Bright (1992) in their catalogue, and not the original genus in which the species was described. The latter information can be obtained from the catalogue.

Xyleborinus Reitter, 1913

The apparent non-monophyly of *Xyleborinus* in the present analysis is caused by the ambiguous positions of *Xyleborinus collarti* (Eggers), *Xyleborus angustior* Eggers and *Xyleborus ferox* Blandford. The holotype of *Xyleborinus collarti* (in the USNM) does not possess the cone–shaped scutellum and elytral mycangia, which define *Xyleborinus* uniquely, and evidently is incorrectly placed by Wood & Bright (1992). The holotype of *Xyleborus angustior* (in the USNM), on the other hand, does have the *Xyleborinus* type of scutellum, and therefore is transferred here to that genus. *Xyleborus ferox* was placed by Wood (1982) in a new subgenus (*Neoxyleborus*), but the four species included in the subgenus by Wood (1982) are listed in Wood & Bright (1992) under *Xyleborus*. The position of *Xyleborus ferox* within *Xyleborinus* requires further examination. Its position within the *Xyleborinus* clade is difficult to explain since it lacks most diagnostic characters of this genus. Except for these three species, *Xyleborinus* is a rather uniform genus and future revision will likely preserve its monophyly.

Nomenclatural changes resulting from examination of type material:

Xyleborinus angustior (Eggers) **comb.nov.** for Xyleborus angustior Eggers, 1925.

Xyleborus collarti Eggers is returned here to its original genus from its current placing (Wood & Bright, 1992) in *Xyleborinus*.

Cnestus Sampson, 1911 and related genera

A stable group containing *Cnestus*, *Eccoptopterus*, *Hadrodemius*, *Xylosandrus* and a group of species currently placed in *Ambrosiodmus, Cyclorhipidion* and *Xyleborus,* has been recovered. We propose to restore the genus *Anisandrus* Ferrari for the latter group of species. Species in this group of genera are defined by the short, stout body, antennal club shape (generally type 1 and very flat) and, most importantly, by the presence of a pronotal mycangium. In the present analysis, this assemblage is paraphyletic with respect to a morphologically uniform group of species of *Taurodemus* and a few other similar

Xyleborus species. These species are very similar to the previously mentioned paraphyletic group of genera, except that the mycangium has not been observed.

Anisandrus Ferrari, 1867

Anisandrus represents a paraphyletic but diagnosable assemblage of species within the clade just discussed. These species share the pronotal mycangial tuft, antennal features (antenna type 1, flattened), shape of tibia, conspicuous tibial denticles and overall body shape. The group shares many features with *Xylosandrus*, but unlike *Xylosandrus*, the procoxae of *Anisandrus* are contiguous. Although on the morphological evidence, the group is paraphyletic with respect to the rest of the clade, a preliminary molecular phylogeny reconstructed using rDNA 28S data showed *Anisandrus* to be monophyletic (Cognato *et al*., unpubl.), and thus the genus *Anisandrus* is resurrected here. An overview of the synapomorphies is given in Table 7.

Diagnosis. Body dark brown or black, up to 3.7 mm long, rather bulky, length: width ratio 2.0 – 2.3. Antennal club of type 1 – truncated, margin of segment 1 elevated into circular costa on the anterior face, no sutures on the posterior face; segment 2 visible on the anterior face, glabrous or soft; segment 3 normally unapparent; scape and funicle long and slender. Pronotum moderately short to very short, stout, robust, sometimes tall (types 0, 3, mostly 5); its anterior edge bearing either two conspicuous teeth, a row of equally sized teeth, or without teeth; disc dull, not shining, without asperities, with a median tuft of mycangial setae posteriorly; lateral margin convex, sometimes with a short carina. Scutellum triangular, flush with elytra. Elytra seriate-punctate, vestiture sparse and inconspicuous in most species, rarely long and dense; declivity rounded, without outstanding sculpture apart from small interstrial tubercles; declivital costa never reaching beyond 7th interstriae, never conspicuously elevated, sometimes absent. Legs relatively long, slender, often with denticles held in enlarged sockets. Procoxae contiguous.

Type species. Anisandrus dispar (Fabricius, 1792) (Figure 16). The type species was described first in *Apate* Fab., but this genus belongs in the family Bostrichidae. It was designated the type species of the genus *Anisandrus* by Ferrari (1867) but in subsequently has usually been considered as a member of the genus *Xyleborus.*

Nomenclatural changes associated with the resurrection of Anisandrus (asterisks mark species of which the holotype or a paratype was examined):

The following species listed under *Xyleborus* by Wood & Bright (1992) are here transferred to *Anisandrus*:

A. cornutus (Schaufuss, 1891)* **comb.nov.** (Lectotype (USNM) examined but not included in the analysis)

A. dispar (Fabricius, 1792)*

A. eggersi (Beeson, 1930) **comb.nov.** (specimen examined but not included in the analysis)

A. improbus (Sampson, 1913)* **comb.nov.**

A. longidens (Eggers, 1930) **comb.nov.** (specimens examined but not included in the analysis)

A. maiche Stark, 1936 (specimens examined but not included in the analysis)

A. obesus (LeConte, 1868)* **comb.nov.**

A. sayi Hopkins, 1915*

The following species listed under *Ambrosiodmus* by Wood & Bright (1992) is here transferred to *Anisandrus*:

A. apicalis (Blandford, 1894)* **comb.nov.**

The following species listed under *Cyclorhipidion* by Wood & Bright (1992) is here transferred to *Anisandrus*:

Anisandrus hirtus (Hagedorn, 1904) **comb.nov.**

Coptodryas Hopkins, 1915

In the present analysis *Coptodryas* is polyphyletic. However, two distinct monophyletic groups have emerged. The first is comprised of the species *Coptodryas elegans* (Sampson), *C. mus* (Eggers), *C. nudipennis* (Schedl), and *C. quadricostata* (Schedl). Although this group and the type species, *Coptodryas confusa* do not form a monophyletic group on the cladogram, they share all but a few minor characters, such as pronotal anterior serrations, the shape of the costa of the first antennal club segment and overall habitus. These species should thus remain in a single genus until more thorough analysis is performed.

Diagnosis. Body proportions variable, length to width ratio 1.6 – 2.8. Antennal club variable, but never of type 1, ranging from obliquely truncate with segment 1 dominant on both anterior and posterior faces, with elevated and continuous costa, to not truncate with segment 1 smaller than segment 2 anteriorly; marginal costa of first segment usually procurved, sometimes straight; weak or obscured by setae in some species; second segment usually corneous on the anterior side, sometimes soft, always visible on posterior face, where sometimes also corneous. Pronotum of variable shape, most often slightly shorter and taller than the basic type, rarely longer or more robust, rounded; never of extreme shape, nor bulging conspicuously anterolaterally; rounded laterally, sometimes with elevated blunt costa, but no carina; serrations on anterior edge of pronotum variable; usually with a dense tuft of setae at base of pronotum, and always with a distinct tuft of setae on mesonotum and/or at bases of elytra. Scutellum conical, normally invisible, rarely visible as a pointed process almost hidden under the bases of elytra. Elytral bases typically costate or carinate, sometimes procurved; striae and interstriae sometimes forming ridges and furrows; declivital costa absent or short and inconspicuous; declivital sculpture normally consisting only of tubercles; elytral apex usually rounded, rarely truncate or slightly angulate; declivital vestiture variable, from almost none to dense, long hair. Legs of usual xyleborine type, procoxae almost always contiguous, except in several species with narrow separation. – This variable genus is characterised by the scutellum concealed beneath the elytra, and by the usually conspicuous vestiture on the mesonotum and elytral bases, associated with elytral mycangia. Such tufts of setae can be also found in *Pseudowebbia*, which can be distinguished by the truncate elytra, and in *Microperus*, but the latter genus has type 1 antennae, whilst *Coptodryas* has type 2, 3 or 4.

Type species. Coptodryas confusa Hopkins (1915)

Microperus Wood, 1980

A second monophyletic subgroup of species currently placed by Wood & Bright (1992) in *Coptodryas* is represented in our analysis by *C. huangi* (Browne), *C. intermedia* (Eggers), *C. eucalyptica* (Schedl), *C. myristicae* (Schedl) and *Xyleborus kadoyamaensis*

Murayama . These species differ from the type species *Coptodryas confusa* in many characters (Table 8), especially antennal characters and prolonged body shape. The species share characters and general appearance with *Xyleborinus*, but the small, conical scutellum is concealed by the elytra, and the elytral bases are not or very slightly incurved on either side of the scutellum. *C. myristicae* includes as one of its synonyms *Xyleborus theae* Eggers (Wood, 1989). The latter species was designated the type species of the genus *Microperus* Wood (Wood, 1980). Therefore this genus name is resurrected to include the species listed above in the second monophyletic group.

Diagnosis. Small with elongate body, 1.5 – 2 mm long and 0.5-0.7 mm wide. Antennal club of type 1, marginal costa of segment 1 continuous, segment 1 often covering most of the anterior face of the club, always completely covering posterior face which lacks sutures; segment 2 on the anterior side soft or barely distinguishable; segment 3 barely or not visible. Pronotum of the basic shape (type 0), slightly prolonged anteroventrally especially if seen from dorsal aspect; anterior margin almost never with a distinct row of serrations; lateral margin with a blunt elevated costa, but no carina; disc dull or shining; mycangial tuft never present, mesonotal or elytral mycangial tuft always present. Scutellum cone-shaped but normally hidden beneath the elytra. Elytral bases sometimes procurved, often costate; disc seriate–punctate, but punctures sometimes confused on declivity; declivity with elevated costa or carina laterally; the costa never extending beyond 7th interstriae, surface not strongly sculptured, but almost always coarse and matt, contrasting with smooth, shining elytral disc; declivital vestiture variable from almost absent to distinct, long and dense. Legs of the usual type, not inflated; procoxae contiguous. – The genus is very similar to some small *Coptodryas*, the main difference being the form of the antennal club which is of type 1 in *Microperus*, but type 3 or 4 in *Coptodryas* (see Table 8). *Microperus* is also closely related to *Xyleborinus*, but in *Microperus* the cone-shaped scutellum typical of *Xyleborinus* is hidden under the elytra, the elytral bases tend to be costate, and the elytral declivital costa is more developed than in most *Xyleborinus*.

Type species. *Xyleborus theae* Eggers (synonym of *Xyleborus myristicae* Schedl; Figure 17).

Nomenclatural changes associated with resurrection of *Microperus*:

The following species listed under *Coptodryas* by Wood & Bright (1992) are here transferred to *Microperus*:

Microperus myristicae (Schedl, 1939)* **comb.nov.**

M. eucalypticus (Schedl, 1938)* **comb.nov.**

M. huangi (Browne, 1983)* **comb. nov.**

M. intermedius (Eggers, 1923)* **comb.nov.**

The following species listed under *Xyleborus* by Wood & Bright (1992) is here transferred to *Microperus*:

Microperus kadoyamaensis (Murayama, 1934) **comb.nov.**

According to preliminary study of characters not used in this analysis (absolute size, details of elytral punctuation, details of scutellum) and according to similarity of general appearance, it is likely that number of smaller *Coptodryas* species shall be eventually transferred to *Microperus*.

Pseudowebbia Browne, 1961

Species placed in the genus *Webbia* by Wood & Bright (1992) fall into two distinct, stable groups which we consider represent two genera, *Webbia* and *Pseudowebbia* Browne. Wood (1983) synonymized *Pseudowebbia* with *Webbia* because the two type species, *W. dipterocarpi* Hopkins and *P. trepanicauda* Browne belonged to the same "species group", but no characters were given to support this suggestion. In our opinion, *Pseudowebbia* shares more characters with some species of *Coptodryas* than with *Webbia* s.str. (e.g. shape of pronotum, antennal club, body vestiture, especially the tuft which is likely associated with a mesothoracic mycangium; see Table 9). The main characters shared by *Webbia* and *Prowebbia* are the concealed scutellum, and the truncate elytral declivity. The former character is also characteristic of *Coptodryas* species, and the shape of the elytral declivity is a character with little phylogenetic information. Thus, *Pseudowebbia* is resurrected for the clade that includes *W. trepanicauda* and three other species.

Diagnosis. Body somewhat variable in proportions, up to 3.3 mm long, length to width ratio 2.1 – 2.7, generally covered with sparse vestiture, never glabrous. Antennae of type 3 or 4, not truncate, costa of segment 1 often discontinuous, obscured by hair, procurved (convex) on the anterior face of the club; segment 2 corneous and glabrous on anterior side or both sides of the club, segment 3 visible on both sides. Pronotum dorsally of type 7, rarely 2 or 3, never bulging or conspicuously quadrate or prolonged; laterally costate or rounded, without a carina; anterior margin of pronotum without a distinct row of serrations; surface of pronotal disc dull; mesonotum and bases of elytra of most species with a tuft of setae, possibly associated with a mycangium; in rare cases vestiture resembling mycangial tuft also present on posterior end of pronotal disc. Scutellum invisible externally. Elytra always sharply truncate; declivity encircled by declivital costa, sometimes armed with prominent teeth, declivital surface often rugose; declivital setae often transformed to flattened scales, vestiture sometimes rather sparse. Legs of the usual type, flattened; procoxae contiguous. – The genus is characterised by the antennal club of type 3 (type 4 in *P. squamatilis*), the slightly prolonged shape of pronotum (type 7 both laterally and dorsal, in *P. trepanicauda* the pronotum may be shorter, resembling types 2 or 3); scutellum not visible externally, and truncate elytra. A tuft of setae associated with the mycangium is usually present. The genus superficially is similar to *Webbia*, differing mainly in antennal characters, protibiae and pronotum shape (Table 9).

Type species. *Xyleborus trepanicauda* Eggers, 1923 (Figure 18).

Nomenclatural changes associated with resurrection of *Pseudowebbia*:

The following species listed under *Webbia* in Wood & Bright (1992) are here transferred to *Pseudowebbia* (asterisks mark species for which holotype or paratype was examined):

P. armifer (Schedl, 1942)* **comb.nov.**

P. seriata Browne, 1963*

P. squamatilis (Schedl, 1955)* **comb.nov.**

P. trepanicauda (Eggers, 1923)

The following species listed under *Xyleborus* in Wood & Bright (1992) is here transferred to *Pseudowebbia*:

P. curvatus (Browne, 1986)* **comb.nov.** (species examined but not included into the analysis)

Webbia Hopkins 1915

Diagnosis. Body cylindrical, usually with abruptly truncate elytra; very little or no vestiture. Length to width ratio 2.4 – 3.1. Antennae rather short, antennal club often wider than long; costa of first segment pronounced and continuous; segment 2 anteriorly mostly corneous, rarely soft; posterior side largely covered by corneous segment 1 with soft segment 2 visible above the edge of segment 1. Pronotum of a very characteristic shape – prolonged, quadrate from dorsal view, slightly bulging frontally and fronto-laterally; no distinct row of serrations on the frontal margin; laterally with long costa, sometimes transformed to sharp carina; disc and sides uniformly chagrinate; no vestiture. Scutellum invisible externally or visible only as pressed to the anterior slope of elytral bases. No vestiture associated with mycangia. Elytra of most species abruptly truncate, sometimes obliquely truncate or rounded or even angulate; elytral disc with seriate or confused punctures; declivity usually armed with prominent teeth, or conspicuous rugosities, or ridges and furrows; declivital costa from blunt or unapparent, to long, encircling the whole declivity; vestiture sparse or absent. Protibiae not flattened, but stick-like; procoxae contiguous. – The genus is characterised by the antennal club of type 1 or 2, the elongate, quadrate, densely chagrinate pronotum of type "a" (both dorsal and lateral views) strongly bulging frontally and fronto-laterally, truncate elytra, and stick-like protibiae. Distinguishing characters from *Pseudowebbia* are given in Table 9.

The *Webbia* s. str. clade also contains *Taphrodasus penicillatus* (Figure 1 in Hulcr et al. 2007a). *Taphrodasus* is represented by only two species in our analysis, but these two species were never recovered as a monophyletic group. Although *T. percorthylus* is affiliated with *Coptodryas*, *T. penicillatus* always appears within *Webbia*. The most important characters shared between *T. penicillatus* and *Webbia* species are the antennal club type 2 and prolonged quadrangular pronotum bulging anteriorly and laterally. Additional characters and further analyses are needed to evaluation the taxonomic status of *Taphrodasus*.

Streptocranus Schedl, 1939

Species placed in the genus *Coptoborus* by Wood & Bright (1992) appear scattered throughout the cladogram, with the exception of a group of extremely elongate African and Asian species. This group is distinct from the remaining *Coptoborus* species, which are mostly shorter species, and of American origin. Wood (1980, 1986) synonymised the genus *Streptocranus* with *Coptoborus* without giving any reason for his action. In the present analysis, the type species of *Coptoborus* (*C. vespatorius* (Schedl)), and the other New World species have not been recovered within the highly autapomorphic group of the Old World species. Since this group includes the type species of *Streptocranus* (*S. mirabilis* Schedl 1939), the genus *Streptocranus* is resurrected.

Diagnosis. Extremely elongate species, with length to width ratio 3.8 – 4.1. Antennae always obliquely truncate, types 1 or 2, with segment 1 dominant on both sides; costa of segment 1 always clearly formed, generally enclosing the club on its anterior face, its anterior part usually recurved (concave); segment 2 mostly soft, sometimes corneous on the anterior face, barely or not visible on the posterior face. Pronotum always extremely long, types a (lateral) and b (dorsal view); anterolateral margin sometimes bulging, making pronotum almost rectangular; laterally always emarginate, concave, in rare cases with a long sharp carina; anterior margin without conspicuous serrations; dorsally glabrous, shining; pronotum without any vestiture associated with mycangia. Elytrae always long, declivity deeply emarginate, emargination sometimes extending into the anterior half of elytra; declivital costa none to very long, encircling the whole declivity; margins of declivity often armed with teeth; surface of declivity smooth, with few setae. Protibiae typically slender, stick-like; procoxae contiguous.

Type species. *Streptocranus mirabilis* Schedl, 1939 (Figure 19).

Nomenclatural changes associated with resurrection of *Streptocranus*:

The following species included in *Coptoborus* by Wood & Bright (1992) are here transferred to *Streptocranus*.

Streptocranus bicolor Browne, 1949*

S. bicuspis (Eggers, 1940)* (holotype of synonym, *S. recurvus* Browne, 1949, examined)

S. capucinulus Schedl, 1942* (holotype of synonym, *S. penangensis* Browne, 1950, examined)

S. forficatus (Schedl, 1957)* comb. nov.

S. fragilis Browne, 1949*

S. longicauda Browne, 1960*

S. longispinis Browne, 1986*

S. mirabilis Schedl, 1939*

S. usagaricus (Eggers, 1922) **comb.nov.**

The following species included in *Ambrosiodmus* by Wood & Bright (1992) is here transferred to *Streptocranus*:

Streptocranus sexdentatus (Eggers, 1940)* **comb.nov.** (type examined but not included in the analysis)

Coptoborus Hopkins 1915

Diagnosis. Medium-sized, often elongate species from the New World tropics, almost always light brown or yellowish, length to width ratio 2.8 – 3.5. Antennal club of types 2 or 3, almost always obliquely truncate, with segment 1 dominant on both sides and its costa elevated; segment 1 is smaller than segment 2 in some species, its costa less pronounced; posterior side always with segment 2 visible, sometimes also segment 3. Pronotum prolonged but never extremely long, types 7 or 8, its dorsal side sometimes slightly concave (type 6); anterior edge almost always with inconspicuous or lacking serration; lateral sides often concave, emarginate from lateral view, sometimes with a short or long carina. Scutellum flush with elytra, no vestiture associated with mycangium. Elytra usually slightly elongate, their apices attenuated or emarginate, rarely rounded; declivital costa mostly inconspicuous, but sometimes long and elevated forming an emarginate declivity; prominent teeth or other structures absent, declivital surface may be densely rugose; vestiture mostly sparse. Legs of usual xyleborine shape, very rarely thinner. Procoxae contiguous. Characters which distinguish the genus from *Streptocranus* are given in Table 10.

The position of *Coptoborus melas* (Eggers, 1927) from the Philippines is yet to be investigated in detail. Although only a damaged specimen was available the species probably belongs in *Xyleborus*. Although the *Streptocranus* clade contains *Xyleborus cylindromorphus*, this species lacks the important diagnostic character, slender protibia, and thus is not included in *Streptocranus*.

Conclusion

This study is the first to examine xyleborine taxonomic characters in a cladistic framework. Although many generic relationships were unresolved, this analysis identified morphological characters that supported monophyletic species groups, which guided revision and resurrection of some genera. An obvious solution for the resolution of generic relationships is the inclusion of additional morphological (those unsampled, Table 6) and DNA data. Current research is underway to identify cladistically-informative nucleotide characters sampled from nuclear and mitochondrial genomes (Cognato *et al.*, unpubl.). Past and preliminary data (Jordal *et al.,* 2000; Jordal, 2002) suggest that these data will aid this effort. Current attempts to construct the phylogeny using molecular DNA sequences of several genes lend support for groups defined by the presence and type of mycangia (e.g., the group of *Anisandrus* and related genera, Cognato *et al.*, unpubl.). The data matrix used for the analysis was implemented in an on-line, multiple-entry illustrated electronic key at www.scolytid.msu.edu.

Table 5: Characters used in the analysis, references to literature, retention index (ri), and character states. Dark grey – antennal characters, light grey – elytral characters, black – pronotal characters.

#	Character	ri	Author	state 1	state 2	state 3
1	enlarged metatibia and metatarsus	100	Wood, 1986	normal size	exceedingly large metatibiae and metatarsi	
2	pronotum l/w ratio	80	This study.	1st third of the range	2nd third of the range	3rd third of the range
3	2nd club segment posteriorly	75	This study.	corneous	soft or undecided	not visible
4	scutellum	75	Wood, 1986	flush	invisible or visible only on the slope of elytral base	process-like
5	pronotal mycangial tuft	74	This study.	absent	present	
6	antennal club type (see Figure 13)	74	This study.	truncated, circle closed anteriad	circle closed posteriad	not truncated, 1st segment convex, 2nd prominent
7	antennal club profile	72	Wood, 1986	truncate	unclear	whole
				state 4	state 5	
				1st segment anteriad smaller than 2nd, both convex	sutures merged	
8	pronotum type - dorsal (see Figure 15)	69	This study.	See Figure 15 for character states.		
9	elytral mycangial tuft, hair on mesonotum/elytra associated with mycangium	69	This study.	no tuft	tuft present	
10	costa of the 1st club segment	68	Wood, 1986	weak, obsolete, obscured by hair	continuous	

Table 5 (cont'd).

11	elytra l/w ratio	67	This study.	1st fifth of the range	2nd fifth of the range	3rd fifth of the range
				state 4	state 5	
				4th fifth of the range	5th fifth of the range	
12	length of pronotal asperities/pronotal summit position	66	This study.	asperities/summit extending to posterior half, or unclear	asperities/summit confined to the anterior half	
13	2nd club segment anteriorly	66	Maiti & Saha, 2004; Wood, 1986	corneous, glabrous	soft, unclear	hardly or not visible
14	posterior face of antennal club	64	Wood, 1986	posterior face covered by 1st segment	comb of overreaching pubescence visible from back	one segment visible on the posterior side
				state 4	state 5	
				two segments visible on the posterior side	segments merged	
15	pronotum type - lateral (see Figure 14)	63	This study.	See Figure 14 for character states.		
16	pronotal disc surface/asperities	63	Wood, 1986	shining, puncturation may be present	dull, fine reticulation	asperities of about the same size as on the frontal slope
17	extent of apex of the 1st club segment	63	Wood, 1986	less than 1/3 of the club height	about 1/3	more than 1/3
18	pronotal lateral subacute elevation/costa (not carina)	60	Wood, 1986	none or short, pronotum generally rounded	long costa (elevated rim), exceeding 2/3 of length	
19	posterolateral costa of elytral declivity	59	Maiti & Saha, 2004; Wood, 1986	no elevated costa	costa not reaching beyond 7th interstriae	costa reaching over 7th interstriae, or encircling the whole declivity

Table 5 (cont'd).

20	declivity surface – teeth, outward structures	59	This study.	no prominent outward structures	prominent teeth or other structures	
21	pronotal anterior edge serration	58	Wood, 1986	none, first row of asperities distant from edge, or serration does not differ from pronotal asperities	two conspicuous teeth	conspicuous row of more less equal teeth
22	elytral end shape	58	Wood, 1986	rounded or unclear	attenuated	emarginate
				state 4	state 5	
				truncated	angulate	
23	central portion of the apical margin of the 1st club segment	57	Wood, 1986	convex	straight or unclear	concave
24	protibia secondary tubercles	57	Wood, 1986	absent	present	
25	pronotum anterolateral angle from sideview	56	This study.	less than 90 degrees	more than 90 degrees, bulging	unclear, about 90
26	geographical distribution	56	Wood, 1986	Eurasia, Australasia	Africa, Madagascar	Americas
27	protibia type	53	Wood, 1986	rounded	triangular	stick-like, inflated, or otherwise modified
28	vestiture inside declivity	51	Wood, 1986	declivity bald or almost so	few setae	long and/or dense setae
29	declivity surface – rugged surface	51	This study.	surface flat, smooth (may have tubercles or teeth)	densely rugged surface	
30	pronotal lateral edge emargination	50	Wood, 1986	convex	straight or unclear	concave, emarginate
31	declivity extent seen from above	48	Wood, 1986	reaching beyond posterior half of elytra	confined to posterior half	only structures (ridges, rugosities,..) extended anteriad

Table 5 (cont'd).

32	declivity surface - furrows and ridges	45	Wood, 1986	surface flat	ridges, furrows	
33	pronotum bulging, quadrate	45	This study.	normal	unclear, bulging at sides, semiquadrate	bulging frontally
34	gular-pregular sutures joint	44	Wood, 1986	impressed	flat	
35	procoxae	43	Wood, 1986	contiguous	narrowly separated	widely separated, gap wider than scapus
36	punctures on elytral disc	41	Wood, 1986	punctures seriate	punctures confused	
37	pronotal lateral acute carina	38	Wood, 1986	no carina	short carina	long carina exceeds 2/3 of pronotum width
38	2nd segment of funnicle	12	Hopkins, 1915	shorter than 1st	same length or longer than 1st	
39	elytral horizon anterior to declivity/elytral disc horizon	11	This study.	flat or convex	concave, saddle–shaped	

Table 6: Characters used by other authors but not used in the present analysis.

#	Character	Author	Reason
41	mesocoxal distance	Wood, 1986	Most specimens in Schedl's collection have been glued on the ventral side, thus preventing analysis of ventral characters.
42	antennal funicle segments number	Wood, 1986	Unobservable in many museum specimens, but should be used in future analyses.
43	basal segment of labial palpus cylindrical, same size as 2nd segment	Wood, 1986	Required damage to specimens.
44	ornamental setae on labial palpus	Wood, 1986	Required damage to specimens.
45	prolonged labium	Hagedorn, 1912	Required damage to specimens.
46	small oval ligula	Hagedorn, 1912	Required damage to specimens.
47	relative size of the segments of labial palpi	Hagedorn, 1912	Required damage to specimens.
48	maxilla's mala attenuate towards apex	Hagedorn, 1912	Required damage to specimens.
49	shapes of segments of labial palps	Hagedorn, 1912	Required damage to specimens.
50	ventral margin of metafemur angulate, rounded or flat	Wood, 1986	Character states gradually change across species and are difficult to score without making arbitrary decisions.
51	metatibial groove for reception of tarsus	Wood, 1986	Character states, as defined by the author, are not observed in most species.
52	number of denticles on protibia	Wood, 1986	Character states are variable within some species. Moreover, it is unclear whether it is continuous, meristic, or discrete character and it is difficult to determine homology of individual denticles.

Table 6 (cont'd).

53	number of denticles on metatibia	Wood, 1986	See reason for character 52.
54	denticles on protibia confined to less than half/more than 3/4	Wood, 1986	Character states, as defined by the author, are not observed in most species. May be used in future analyses after reevaluation.
55	declivity broad, flat	Wood, 1986	Character states gradually change across species and are difficult to score without making arbitrary decisions
56	spaces between striae - dull or shining	Wood, 1986	Character states gradually change across species and are difficult to score without making arbitrary decisions. In some species, both surface types occur on various parts of the elytra of a single specimen.
57	eye emargination	Wood, 1986	Character states gradually change across species and are difficult to score without making arbitrary decisions

Table 7: Synapomorphies of *Anisandrus*, and comparison to other genera.

	Anisandrus	Xyleborus	Xylosandrus	Ambrosiodmus
first segment of antennal club	forming circular costa mostly visible on the anterior face	variable	forming circular costa mostly visible on the anterior face	not forming circular costa on the anterior side
antennal club type	1	variable	1, 2	2,3
posterior face of antennal club	segm 2 & 3 not visible, segm. 1 covering the whole face	variable	segm 2 & 3 not visible, segm. 1 covering the whole face	segm. 2 always visible, segm. 3 mostly visible on the posterior face of antennal club
pronotal mycangial tuft	present	absent	mostly present	absent
procoxae	adjacent	adjacent	more or less apart	adjacent
pronotum type, dorsal profile	0,1	variable	1, 2	variable
pronotum type, lateral profile	0, 3, 5	variable	0, 1, 5	variable, mostly 4, 7
elytral end shape	rounded	variable	mostly rounded but often truncated or other shapes	variable

Table 8: Characters distinguishing *Microperus* from *Coptodryas*. *C. confusa* is the type species of *Coptodryas* and is thus used for the comparison.

	Coptodryas confusa	majority of other *Coptodryas*	Microperus
antennal club type (Figure 14)	4	3,4	1
pronotum shape type	2	varied, mostly 0	0 (7 in M. kadoyamaensis)
antennal club profile	rounded	rounded (truncated in C. gorontalosus)	truncated
extent of the 1st segment of antennal club anteriad	less than 1/3 of the club height	less than 1/3, rarely about 1/3 or more	exceeding 1/3 of the club height
cental portion of the apical margin of 1st club segment anteriad	convex	convex or straight	concave, straight in *M. eucalyptica*
costa of the 1st antennal segment	weakly defined or obscured	varied	pronounced
2nd club segment anteriad	corneous	mostly corneous	soft or hardly distinguishable
2nd club segment posteriad	corneous	varied, mostly soft	not visible
posterior face of antennal club	2nd and 3rd segments visible	varied	covered by 1st segment
pronotal vestiture resembling mycangial tuft	present	varied	absent
vestiture on elytral declivity	sparse	mostly sparse	often rich, either dense setae or scales, except sparse in *M. eucalyptica*
body shape	short, robust	varied	never conspicuously robust

Table 9: Comparison of characters of *Pseudowebbia* and *Webbia*.

	Pseudowebbia	Webbia
antennal club type	3 or 4	2 or 1
protibia	normal, flattened	stick-like, rounded
pronotum type lateral aspect	2, 7	very distinct, autapomorphic pronotum type b
pronotum type dorsal aspect	2, 7	distinctly prolonged, quadrangular, type a, c
antennal club profile	not truncated, oval	truncated
anterior costa of the 1st segm. of antennal club	convex	concave or straight
costa of the 1st segm. of antennal club	sometimes obscured by hair laterally or posteriad, discontinuous, merged to the soft parts	distinct costa running at both posterior and anterior faces, sometimes almost entirely on the anterior face
posterior face of antennal club	segments 2 and 3 visible	at most segm. 2 visible, often completely covered by corneous segm. 1
pronotal summit, reach of pronotal asperities	asperities cover more than the anterior half of the pronotum, summit in typical position	asperities confined to the anterodorsal half of pronotum, summit pushed anteriad
vestiture inside declivity	most often scale-like flattened setae	sparse hair-like setae

Table 10: Comparison of characters of *Coptoborus* and *Streptocranus*.

	Streptocranus	Coptoborus
antennal club type	1, 2, (3 seen in a dried-out specimen of *S. usagaricus*)	mostly 3; 2 in *C. vespatorius*
protibia	stick-like or inflated	normal, flattened
pronotum type lateral aspect	type 14, conspicuously prolonged	types 9 or 11 – mildly prolonged
pronotum type dorsal aspect	b,c – conspicuously prolonged, often quadrangular frontally	2, 7, 8, 9
costa of the 1st segment of antennal club	concave or flat	convex or flat
2nd segment of antenanl club on the posterior face	almost never visible	almost always visible
posterior face of antennal club	mostly only comb of pubescence visible reaching over the otherwise fully corneous 1st segm, rarely 2nd segment visible	mostly 2nd and 3rd segments, sometimes only 2nd segment visible
pronotum bulging	pronotum fronto-laterally bulging except in *S. forficatus*	pronotum not bulging frontally
surface on pronotal disc	always shining	mostly opaque, shinig in *C. tolimanus*
reach of pronotal asperities (position of pronotal summit)	asperities reaching less than ½ of pronotal length	asperities reaching beyond ½ of pronotal length (unclear in *C. catulus*)
elytral declivity shape	always emarginate	ranging from angulate to emarginate
elytra l/w ratio	2.15-2.4	1.65-2.07
pronotum l/w ratio	1.42-1.92	1.11-1.33

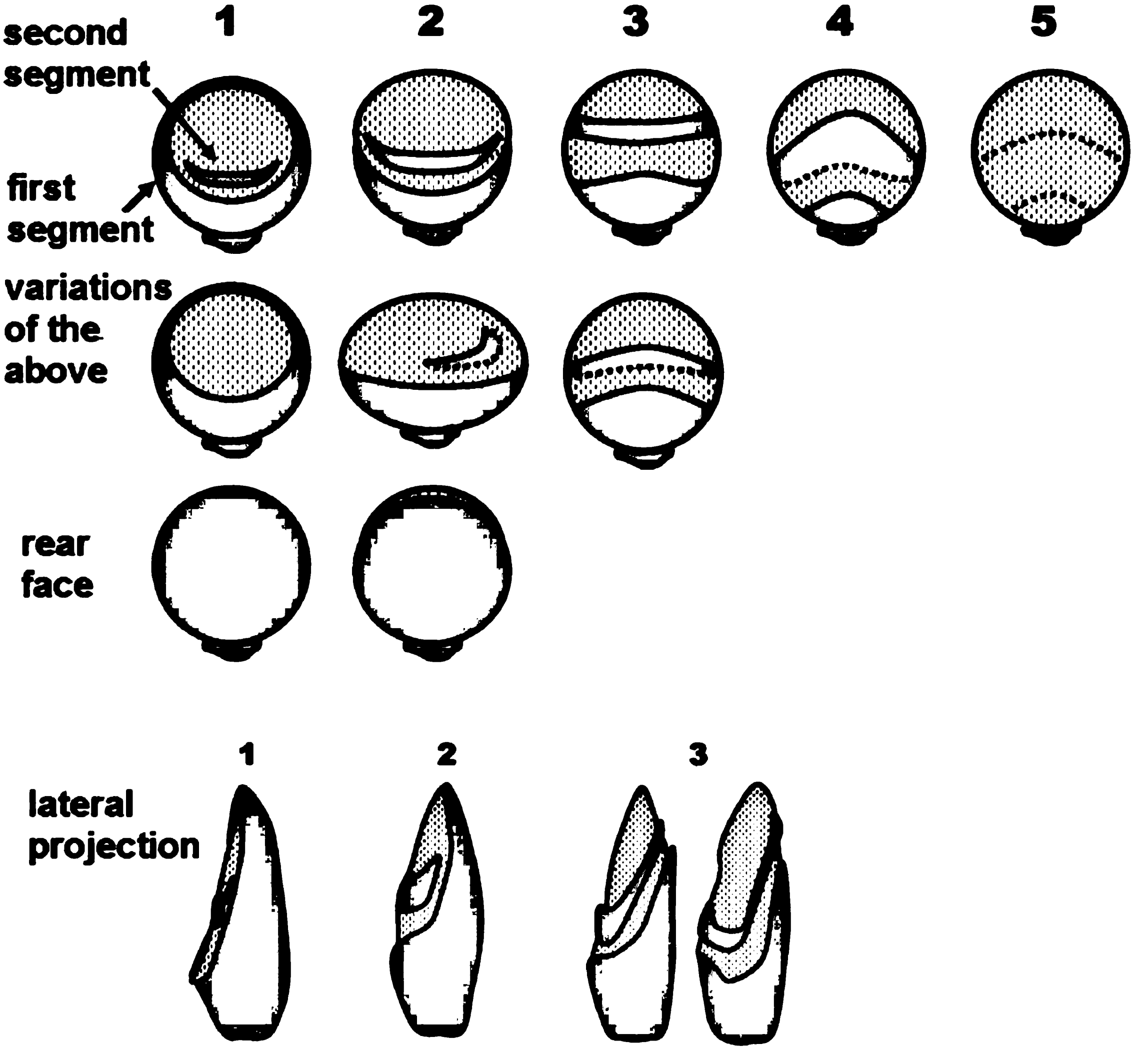

Figure 13: Types of antennal club in Xyleborina. Upper row - 5 basic types; second row - variations of the types 1-3; third row - posterior face of the club of types 1 and 2; fourth row - lateral view of types 1-3.

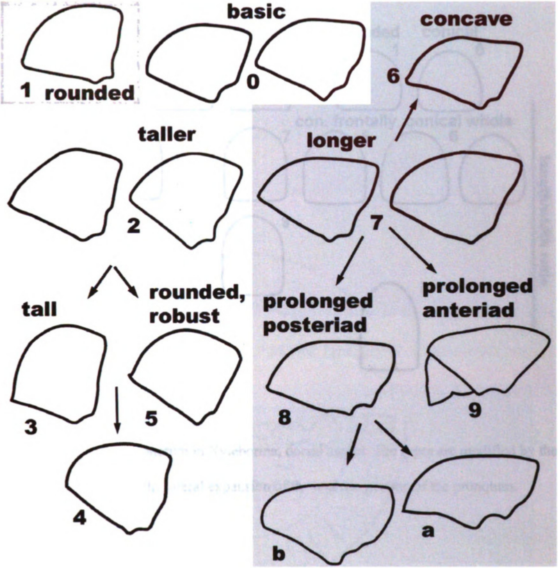

Figure 14: Types of pronotum in Xyleborina, lateral aspect. The types are modifications of the basic shape (0) and are modified into relatively taller shapes (left side) or relatively longer shapes (right side).

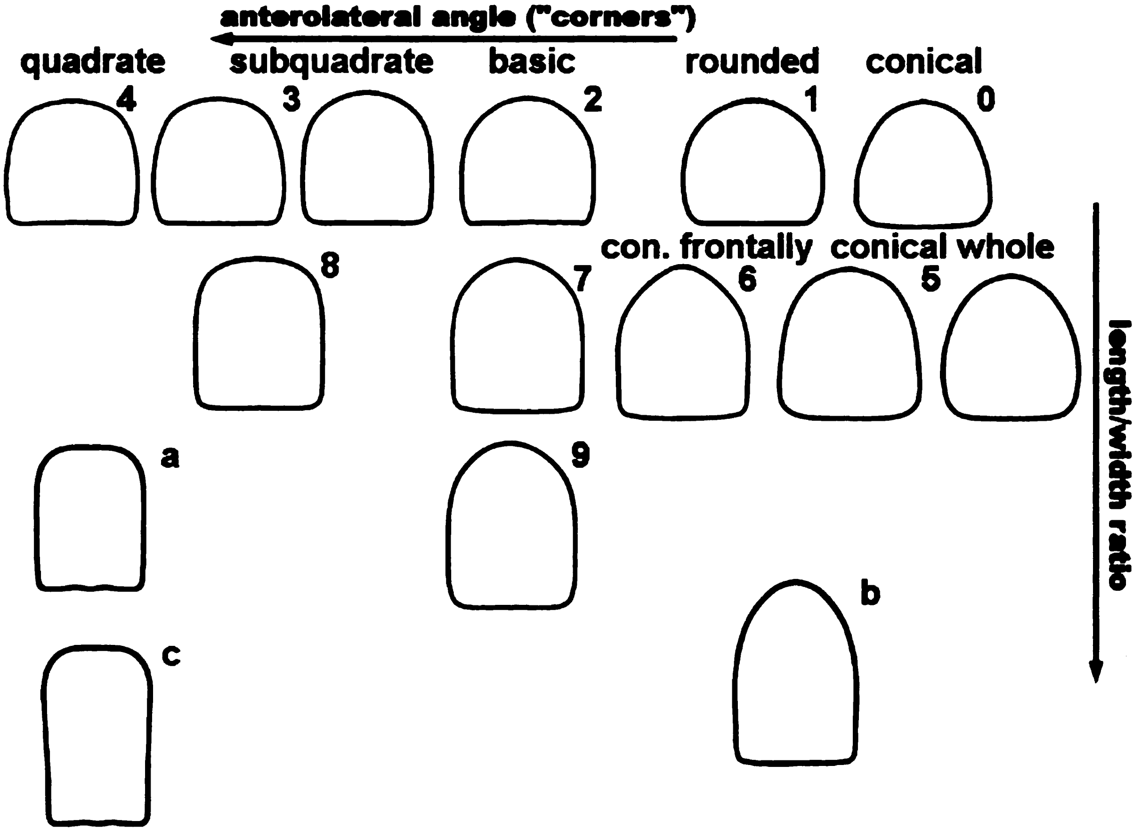

Figure 15: Types of pronotum in Xyleborina, dorsal aspect. The types are modified by the length/width ratio and the lateral expansion of the anterior portion of the pronotum.

Figure 16 *Anisandrus dispar* (Fabricius), 3.25 mm. Type species of *Anisandrus* Ferrari.

Figure 17: *Microperus myristicae* (Eggers), 1.55 mm. Type species of *Microperus* Wood.

Figure 18: *Pseudowebbia trepanicauda* (Eggers), 2.50 mm. Type species of *Pseudowebbia* Browne.

Figure 19: *Streptocranus longispinis* Browne, 2.15 mm. A characteristic member of *Streptocranus* Schedl.

CHAPTER 4

Monograph of Xyleborina of New Guinea

Abstract

To revise the genus- and species-level classification of Xyleborina (Coleoptera, Curculionidae: Scolytinae) from New Guinea and neighboring islands, we examined over 44,000 representatives of 281 putative species of Xyleborina, including 263 type specimens. Cladistic analysis was used to infer phylogenetically informative morphological characters, which were used to improve the genus-level classification of Xyleborina occurring in New Guinea. Eight new genera are defined (*Anceps, Emarginatus, Fortiborus, Immanus, Planiculus, Stictodex, Truncaudum, Wallacella*), 52 new combinations are given. Nine new species are described: *Amasa knizeki, Ambrosiophilus mogia, Arixyleborus simplicaudus, Beaverium rugipunctus, Biuncus niger, Cyclorhipidion artedilatatum, Planiculus rodmanculus, Wallacella andreae, Xyleborus devexipennis.* For the first time, operational species concept of Xyleborina is explicitly addressed. Many previous species were found to be delimited by uninformative characters, 87 new synonymies are given. The monograph is complemented by photographs of all species and multiple-choice keys to all species and genera, both available on-line. Because all genera and many species occurring in New Guinea also occur throughout Eastern Paleotropic region, the presented re-classification is significant for Xyleborina taxonomy on much larger geographical scale, in many cases for world-wide classification.

Introduction

Xyleborina are one of the most diverse and abundant groups of scolytine beetles worldwide. Many species of Xyleborina also belong among the world's most invasive and pestiferous insect species. At least 8 exotic Xyleborina species are now established in the U.S., some of them causing unprecedented damage to the local ecosystems or forest and orchard industry (Haack, 2006). Despite their importance, there are very few comprehensive monographic works dealing with xyleborine beetles, or of scolytines including xyleborines, for any particular area (Schedl 1962, Bright 1968, Wood 1982, Maiti and Saha 2004, Rabaglia et al. 2006). Of these, only two refer to tropical areas – the core area of their diversity, and the source of most invasive species (India: Maiti and Saha 2004, and Africa: Schedl 1962). No comprehensive treatment exists for the area where the xyleborine fauna is the most diverse - SE Asia and Oceania. K. E. Schedl worked on the fauna of PNG in the 1970's, and intended to produce a monograph of Scolytidae and Platypodidae of the islandic area from PNG to New Caledonia (Schedl 1972i). His plans never materialized.

The combination of xyleborine material accumulated during our collecting in Papua New Guinea and obtained via our collaboration with other collections and museums allowed us to obtain specimens of almost all species collected in New Guinea. For many species, we could compare multiple specimens (up to thousands), which allowed us to study within-species morphological variation. Further, more than 44,000 PNG xyleborine specimens of 128 species or morphospecies have been stored as a material for DNA, facilitating the use of DNA sequences for testing generic classification of the group and, in some instances, species boundaries (Cognato et al., 2009).

Methods

Photographs and keys

Two significant and inseparable parts of this work are presented as on-line internet resources: a comprehensive set of photographs of all available Xyleborina species, and a set of multiple-entry electronic keys for all genera and all recognized species. These photographs and keys can be found at: http://www.scolytid.msu.edu/PNG_Xyleborina .

Taxonomic procedures

The basis for the generic concept of Xyleborina was taken from Wood (1989). This is currently the most widely used generic concept of Xyleborina, and served as the basis of the most authoritative compendium of taxonomic information on scolytine beetles, the Catalog of Scolytinae and Platypodinae (Wood and Bright 1992) with its two supplements (Bright & Skidmore 1999, 2002). The initial list of NG Xyleborina was constructed from this Catalog, and augmented by species 1) from personal collection, 2) from museum collections worldwide, and 3) reported in original literature.

It was not possible to cover all species which have been historically reported from New Guinea. In some instances, no representative of many of the published species have been located in any museum (p. 184). Another common reason was, that it has been impossible to validate many of the published doubtful records of species from New Guinea. As each of the early prolific authors used largely private collections to identify world-wide specimens, alternative names or identification mistakes abound in published locality records. Also, Wood and Bright (1992) list a number of species from NG, records of which could not be verified either in museum collections or in literature.

However, the chance that any of these omissions represent an important species is low. The work is based on more than 100,000 specimens collected by the authors in many localities, and on material from museum collections worldwide, with special attention to collections with large amount of material from New Guinea (NHMW, BMNH, FICB, Bishop Museum, the Binatang Research Center in Madang, and others). Thus there is very small chance of missing any other than very rare species.

A common problem in the taxonomy of Xyleborina have been the numerous transfers of species between genera with different nomenclatural gender. Some Xyleborina taxonomists obeyed the requirement of the ICZN code and regularly adjusted the gender of the specific epithet of their transferred species, but more commonly, authors kept the original species name regardless of the new genus gender. This created large amount of confusion in general, and especially a lot of inconsistency between various catalogs and databases. This issue has been repeatedly addressed by weevil taxonomists (Oberprieler et al. 2007). In this publication, we attempted to prevent more confusion by creating new genera of the same gender as the species they contain.

In the descriptions of individual species or genus, we indicate the unique number of ech entity in the database of New Guinea Scolytinae and Platypodinae maintained by J. H. Since these codes are not changeable and are tied to physical specimens, they may in some cases be more stable reference than a taxonomic name.

Terminology

The terminology for details of beetle morphology varies among beetle groups and taxonomists. Here we define several terms commonly used in this work which are inconsistent in scolytine literature. Terms for cuticle surface, from the smoothest to the most rugose: shining; shagreened (dull surface, smooth, individual grains of the mosaic not apparent under regular binocular microscope); alutaceous (engraved reticulation, smoother than coriaceous); coriaceous (skin-like, rugged texture, individual grains of the mosaic discernible under regular binocular microscope); rugose or granulate (covered with granules). Antenna is composed of scapus, pedicel, funicle and club (i. e., pedicel is not considered a part of the funicle as in a some other works). The ventral part of the head which is surrounded by V-shaped sutures is termed pre-gula by Wood (1989), but Lyal (1995) showed that it is in fact submentum. We use the term submentum here.

Below is a list of abbreviations of collection or institutions which have been visited during this project, and/or PNG-related xyleborine material has been loaned from them.

AMNH - American Museum of Natural History, New York

ANIC - Australian National Insect Collection, Canberra

B. H. Jordal – Dr. Bjarte H. Jordal private collection, Bergen, Norway

BBM - Bernice P. Bishop Museum, Honolulu

BMNH - Natural History Museum, London

FICB - Forest Research Institute, Lae, Papua New Guinea

FMNH - Field Museum of Natural History, Chicago, IL

H. Gebhardt – Dr. Heiko Gebhardt's personal loan, Germany

IRSNB - Institut Royal de Sciences Naturelles de Belgique, Brussels

IZM - Institute of Zoology, Moscow

MCG - Museo Civico Genova, Genova

MNB - Museum fur Naturkunde der Humboldt University, Berlin

MSUC - A. J. Cook Arthropod Research Collection at MSU, East Lansing, MI

NHMW - Naturhistorisches Museum, Wien

NSMT - National Science Museum, Natural History, Tokyo

R. Rabaglia - Robert Rabaglia's private collection, Washington, D.C.

RAB - Roger A. Beaver's private collection, Chiang Mai, Thailand

RMNH - Naturalisk, Leiden

SAM - South Australian Museum, Adelaide

SLW - S. L. Wood's collection, Provo, UT

SMTD - Staatliches Museum fur Tierkunde, Dresden

UCD - Bohart Museum of Entomology, UC Davis, Davis, CA

USNM - Smithsonian Institution, National Museum of Natural History, Washington, D.C.

UZMC - Universitets Zoologisk Museum, Copenhagen

Zhu Hongbin - Zhu Hongbin, Chinese Quarantine Office

Other examined collection not referenced by an abbreviation: the Binatang Research Center in Madang, PNG; Dr. S. L. Wood's collection at the Brigham Young University, Provo, UT; Forest Research Commission collection in Sepilok, Sabah, Malaysia; Texas A&M Department of Entomology Insect collection, College Station, TX.

Species concept

Cladistic revision of Xyleborina is challenging for many reasons. Because of regular inbreeding (intensified by possible outbreeding depression (Peer & Taborsky, 2005)), separation between genetic lineages is blurred and lineage sorting is slower than in outbreeding species. As a result, distributions of many morphological characters appear continous among lineages (i.e., species) and do not co-vary with biogeographical regions. Further, the xylem borer lifestyle probably imposes significant constraints on diversification of certain morphological features, thus limiting the number of characters which are actually variable. Most importantly, while there is a large number of described "species" of Xyleborina, many of them are known from a single or a very few individuals, which prevents an analysis of within-lineage morphological variability.

The paucity of synapomorphies and an abundance of homoplastic characters make delimitation of species and genera difficult. In such cases, traditional taxonomists often guided their decision strategies by their "gestalt", or by their non-explicit position on the gradient between "splitters" and "lumpers". However, even in complicated taxonomic cases, decision-making can be greatly aided by employing a hypothetico-deductive approach. In general, rather than examining data first and then inducing a hypothesis based on them, it is more appropriate to first propose hypotheses, and test them with the available data. The general form of a hypothesis used in alpha taxonomy is an *a priori* formulated species concept. Many different species concepts exist, which is a result of the variability of barriers (or their absence) to gene flow in different organisms, which resulted in variable patterns of discontinuity of similarity among related populations. This implies that a species delimitation concept and its rationale should be ideally declared anytime a species-level systematic work is conducted, especially in group with unusual reproduction strategies.

Most species concepts can be classified as either separating species based on processes in nature, or based on patterns in occurrence of characters. The first class is represented by perhaps the most widely recognized and the most intuitive species concept, the Biological species concept (Coyne and Orr, 2004). Broadly speaking, according to the BSC, populations are considered separate species if they don't have the ability to interbreed. The applicability of this concept to Xyleborina remains unexplored, and may not be useful because of the overwhelming frequency of inbreeding in this group.

An example of a pattern-based species concept is the Phylogenetic species concept, perhaps the second most widely accepted one. According to the PSC, species are ''the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states" (Wheeler and Platnick, 2000). Because for majority of Xyleborina species, no other information is available than their morphological characters, no species concept is applicable other than the phylogenetic species concept.

The potential pitfall of the PSC approach in hypervariable and largely clonal groups like Xyleborina is, that the number of "smallest diagnosable aggregations" is a function of the number of specimens (clones) examined. Xyleborina taxonomists frequently remark on the increase of the number of different combinations of characters with increased number of examined representatives of a lineage (R. A. Beaver, D. E. Bright, M. Knizek, pers, comm). Thus the "top-down" process of splitting groups into smaller ones based on shared synapomorphies has to be complemented by a "bottom-up" process of lumping variants that are unlikely to represent geographically and ecologically separate clades. Compared to synapomorphy-driven splitting of groups, identifying minor variants and subsequent lumping is more difficult, since it depends on distinguishing which characters are variable and which are not, information that can be gained only from examination of intra-group morphological variability. Only after examination of large numbers of related individuals from different localities, one has an opportunity to separate homoplastic characters from synapomorphies. Although a formal cladistic analysis to distinguish homoplasies from synapomorphies was performed for only several species complexes (e. g., Figure 21), it was possible to identify the classes of characters, which are plastic in most groups, and downweigh these in treatment of groups where such knowledge was not available.

It is questionable whether "species" as unique interbreeding populations exist in Xyleborina, mainly due to the largely clonal reproduction in this group. Thus rather than clustering morphotypes according some arbitrary level of variation considered a species level, our goal was to reconcile the splitting of clades and lumping of minor variants in such a manner that the recognized entities are testable, useful, predictive, and form a stable classification. Such entities may not be delimitable as true species according to any species concept, but they are nevertheless interesting or predictive groupings, which, if nothing else, bear record of the spectacular diversity of the group. Thus our operational *a* *priori* species concept is less an algorithm to delimit true species, and more a sequence of steps in 1) distinguishing informative co-varying characters from highly homoplastic characters, 2) identifying groups of individuals sharing the informative characters and thus diagnosable as "species", and 3) recognizing groups of these "species" with unique combinations of the informative characters, and thus constituting genera.

One of many futher advantages of an explicit hypothesis of species limits is, that it also allows us to discern situations when there is not enough data for any decision. When several groupings are in conflict given an incongruent distribution of characters among lineages, it is clear that more data need to be obtained, or a decision would be arbitratry.

Generic concept

All presented genera are defined by synapomorphic characters or unique combinations of homoplastic characters, and are intended to represent monophyletic or at least paraphyletic groups. Genera designated by previous authors where monophyly or paraphyly was not supported by molecular or morphological characters were dissolved and their constitutive species regrouped. Where grouping of species in genera by previous authors appeared to defy monophyly, and where true monophyletic groups were not obvious either from the molecular phylogeny (Cognato et al., 2009) or from shared synapomorphies (based on Hulcr et al. 2007a), a cladistic analysis of variable morphological characters was conducted (Figs. 48-50).

Cladistic Analyses

Each matrix of morphological characters was submitted to the New Technology Search in TNT (Goloboff et al. 2003), using driven search with initial level 60, set to find minimal length 10 times. The resulting sets of shortest trees were summarized using Combinable component consensus implemented in TNT. This way of consensing has the advantage to both Majority rule and Strict consensus in retaining the greatest number of truly recovered nodes and at the same time identifying "floating" taxa. Due to the small number of characters, of which many contained substantial homoplasy, Bootstrap analysis always yielded very small support values, which are consequently not reported.

Characters

The summary of characters reported for each taxon (genus or species) is not an exhaustive description. Instead, only characters useful in distinguishing the taxon from others on the same taxonomic level are given. For example, characters typical for a given genus are rarely reported in individual species descriptions. For even more detailed lists of characters and their associations with species and genera, we encourage the reader to refer to the on-line keys.

For the antennal club structure and pronotum shape, two phylogenetically very informative characters, the formalized character states ("types") from Hulcr et al. (2007a) are referenced throughout the text (Figs. 14-16).

Although the phylogenetic signal of characters vary across taxa, several character classes are homoplastic within most genera. If such character were the only character differing between individuals, it was not considered sufficient for defining a species boundary. Among these were for examples setae-associated characters. Setae abundance and patterns are very variable and also subject to loss due to trapping methods (e.g. Sticky traps) or age. Setal characters have often been mistakenly used because of their visual prominence to the researcher. Different length or slope of setae can make two beetle individuals appear very different, even though they are identical in all other characters (a common problem in genera with abundant vestiture such as *Cyclorhipidion*, *Coptodryas*, *Microperus*, etc.).

One of the most variable intraspecific features in Xyleborina is body size. Especially the size of conspecifics from different altitudes can differ as much as 1.5x. The size variation correlated with altitude has been noted by others (e.g., Beaver, (1976), and references therein). Body length was measured between the anterior edge of pronotum and the apex of elytra. Head was not included, as it can be hidden inside pronotum or exposed far beyond it, depending on the way the specimen was preserved. For cladistic analysis, only the median of the observed sizes in each species was taken.

Body proportions ratio (length to width ratio) is often an informative character on the species level. However, this ratio represents a continuum of change where interspecific variability is regularly overlapping with intraspecific variation. Thus, the character was usually coded verbally (as two states – robust versus slender, and illustrated in the key), rather than giving exact measurements and providing a false impression of clear boundaries between species. It was noted that measurements of beetles in original descriptions by K. E. Schedl are often inaccurate.

Another feature that varies with altitude within species is color. Several species characteristic for their light colors in low elevations have montane morphs which are completely black (*Biuncus papatrae*, *Planiculus aries*, etc.). In many other cases, however, color seems to contain significant phylogenetic information. For example, most *Biuncus* tend to be light brown or orange, most *Planiculus* have bicolored (black and yellow) pronotum, most representatives of the *Anisandrus*-clade (*Anisandrus*, *Hadrodemius*, *Eccoptopterus, Cnestus*) are black, while many *Cnestus* have also transparent elytra giving the impression of whitish (testaceous) patches. On the other hand, exceptions to the overall color pattern within groups are also frequent, make it difficult to use this character both in phylogenetic analyses as well as in keys. Also, as in most beetles, specimen color changes significantly with age from yellow in callow individuals to full color (usually dark) in mature adults. Further, in museum pinned specimens the color changes unpredictably over time. Many specimens of scolytines from New Guinea deposited in the NHMW were collected from sticky traps, these tend to be dark brown or black, regardless of the original color.

Although antennal club contains some of the most phylogenetically informative characters in Xyleborina, in some genera antennal club seems to vary more than other characters. For example, *Microperus* spp. from different parts of the Eastern Paleotropical region can be virtually identical, but their antennae range from type 1 through type 3 (Figure 13). The variability of antennae in some Xyleborina groups was noted by Browne (1950b).

Male characters are not considered in this work. In many species males have never been collected, in others they are extremely morphologically variable even within a single brood (Browne 1958).

Discussion

Xyleborina in New Guinea

With 139 species in 31 genera, Xyleborina are probably the most species-rich group of scolytine beetles in New Guinea. (Prior to this work, there were 181 putative species and 18 genera reported from PNG; Wood & Bright, 1992, Bright & Skidmore, 1996, 2002).

Schedl (1975f) remarked on the large proportion of PNG fauna represented by endemic species, not shared by either the islands to the East, nor with continental Asia to the West. However, with the accumulation of new records, and especially following many necessary synonymies, the percentage of species unique to PNG has decreased. The actual number of species endemic to New Guinea is not possible to estimate due to the un-revised fauna of the surrounding islands and continents. On the level of genus and higher, the assemblages of Xyleborina (or Scolytinae in general) throughout the whole Eastern Paleotropic are not divided by any major biogeographic boundary, such as many other organisms. There is no known Xyleborine genus in New Guinea which would not also occur in continental SE Asia. This not only contradicts the paradigm of biogeographical isolation of New Guinea, but also broadens the geographical utility of the presented monograph.

Beaver and Browne (1978) classified Eastern Paleotropic scolytine fauna into several biogeographical assemblages, such as the Eastern Palearctic Element, Indian Element, Malaysian Element, etc. (fauna of PNG was not the focus of their study). The authors mentioned many species from the Malaysian, Indomalaysian and Circumtropical Element having their ranges extended to New Guinea. However, biogeographical classification is contingent on the completeness of the knowledge of individual species distributions. With the accumulation of discoveries of many species in PNG which were previously known only from continental Asia, such hypothetical boundaries are becoming less clear. Any biogeographical analysis of Paleotropical scolytines will be only tentative until a comprehensive taxonomic and faunistic revision is carried out for any given group.

The history of species concept in Xyleborina classification

Most of the junior synonyms declared in this work had been originally mistakenly described as distinct species for one of two reasons. One obvious reason, and a common one in early taxonomy of insect, is the authority-driven taxonomy, where authors may not have consulted type collections of colleagues before describing unknown species (S. L. Wood, pers. comm.). Possibly for this reason, many clearly identical lineages have been described independently by K. E. Schedl, F. G. Browne or H. Eggers, presumably because of the difficulties in exchanging specimens.

The other, more methodical reason, is the absence of species concept in traditional Xyleborina systematics, combined with under-appreciation of intra-clade variability. For these reasons, the species level classification of Xyleborina has been dominated by splitting and inflating the number of putative "species", distinguished by minute differences in highly variable characters.

The traditional taxonomy, having inherited the typological view of diversity, can be characterized as one having a null hypothesis of a species such that a deviation from the type indicates a distinct species. Traditionally, new species could be erected based on a deviation in any character, without any knowledge of its phylogenetic value.

Unfortunately, hypothetical species boundaries so proposed convey no biologically meaningful information, and are not relevant for further research, conservation, or applied purposes.

Modern evolutionary theory assumes large variation in natural populations (Hendrick, 2005). This variation is further expected to increase with, among others, the size of a population, and with decrease in randomness of mating. Xyleborina are often some of the most abundant and widespread tropical beetle species (Jordal et al., 2000), and display dramatic deviation from panmixia (due to their geographic spread as well as largely inbred reproduction, Peer & Taborsky, 2005). Thus morphological differences between even closely related individuals can in fact be expected.

Using phylogenetic analysis of character information content, we inferred that many characters used by early Xyleborina taxonomists to delimit species are highly homoplastic (e. g., body size, declivital tubercle size, or patterns of declivital tubercles position). Most of these authors rarely referred to phylogenetically informative characters such as the antennal club, mycangia, or ventral characters, or combinations of characters. The two authors most prolific in describing Xyleborina from New Guinea, K. E. Schedl and F. G. Browne, almost never characterized the antennal club in their species description, and glued the ventral side of specimens to a mounting board. (There are exceptions, such as early Schedl's description of genus-level characters, e.g., Schedl 1937e). Although these authors were aware of the large morphological variation seen in larger series of Xyleborina conspecifics, and occasionally discussed its impact on the group's classification (e.g., Browne 1966, Schedl 1960h), they did not implement it into their taxonomic practice.

The predictive nature of each species hypothesis was considered key. When circumscribing a species, we are hypothesizing that the features used to characterize the species are not random, but shared within the population. As such, these characters are predictive, i.e., seeing a characteristic feature of a species, it is reasonable to predict that other characteristic features will be also present. For example, a conformation of denticles on elytral declivity characteristic for *Ips typographus* (a non-xyleborine outcrossing species) on an unknown specimen predicts, that the bearer is probably a spruce-specialist, occurs in Eurasia, and falls in the same place of the *Ips* phylogeny as other specimens with the same declivity. Unfortunately, this not true for Xyleborina and many of their characters traditionally used for species delimitation. For example, K. E. Schedl, the most prolific scolytine taxonomist, based his classification of Xyleborina almost entirely on the structure of elytral declivity. In *Amasa*, a group with variable elytral declivity, he described almost 20 species. However, nearly every combination of declivital characters of *Amasa* can be found in most biogeographical regions from Australia to India (declivital suture elevated or not, suture diverging at the end, the end bulging or not, striae impressed or not, size of tubercles, surface smooth, shagreened, hairy or scaly, etc.). Further, these characters don not correlate with the more phylogenetically conserved characters (such as antennal club, coxae, prosternal processes, protibiae shapes, etc., Figure 21). In other words, we cannot say that *Amasa* with elevated granulate declivital interstriae is from a certain region, since this phenotype has been found in many other regions, neither we can predict other charactres with which this declivity will co-occur.

On the other hand, there are cases in Xyleborina when even minute morphological differences have been confirmed to be indicative of ecologically unique lineages. For example, *Xyleborinus artestriatus* and *X. saxeseni* cannot be distinguished by any categorical differences beyond vague dissimilarity in body shape and elytral tuberculation, and their identification requires direct comparison of specimens. Ecologically however, the species are extremely different. *X. artestriatus* is a rare species confined to the tropics of SE Asia and the highlands of New Guinea. On the other hand *X. saxeseni* is a temperate species (i.e., adapted to freezing) and is one of the most widespread invasive beetles worldwide. We cannot exclude the possibility that some of the dubious species synonymized in this work were in fact representing monophyletic lineages with unique ecological features. However, given the paucity of data, it is impossible to discern these cases. Since there is a very large evidence against the assumption that minute differences correlate with ecological niche or standard genetic markers, the parsimonious solution of such ambiguity is a synonymy of the dubious species accompanied with a record of the observed variation.

Generic concept

Since Linnaeus described the first five species of scolytine beetles in 1758 (as *Dermestes* spp.), various subsequent authors produced about 20 different classifications of the whole group (Choo 1983). The first to recognize Xyleborina as their own group was LeConte (1876), introducing the subtribe Xylebori. So far the classification of Xyleborina that was most strongly evolution-based and character-explicit was that of Wood (1989). Wood's generic classification with its subsequent modifications (Wood & Bright, 1992, Bright & Skidmore, 1996, 2002) was used as the basis for this work.

Until recently, the subjective and/or phenetic approach to Xyleborina classification hindered the inferrence of a phylogenetic hypothesis and establishment of a stable generic concept. Already Browne (1961c) feared that "No real improvement [in Xyleborina taxonomy] can be expected until a world revision of the whole tribe becomes possible. [...] For this reason, we shall regard Xyleborus as a collection of numerous species-groups or subgenera, bearing in mind that many of them may eventually be recognized as distinct genera". In his unwillingness to split the large genus *Xyleborus*, where all Xyleborina had been placed, Browne recognized a very important aspect of the Xyleborina diversity – the continuous variation of morphological characters across large biogeographical regions.

However, with the introduction of phylogenetic perspective in Xyleborina classification (Wood, 1986), and especially with the newly available phylogenetic methods and molecular datasets (Cognato et al., 2009), the generic classification is reaching stability. This stability is evident in the presented generic re-classification because most of the genera delimited by Wood (1989) are retained, and the presented genera are consistent with recent phylogenies of xyleborine species (Hulcr et al., 2007, Cognato et al., 2009).

All genus-level groups in this work are designated as monophyletic, with the single exceptin of *Xyleborus s. l.* Species in this group differ significantly from each other, and the group is clearly polyphyletic. However, the true phylogenetic relationships of the constituent species were not discovered in this work. All the species were originally designated as *Xyleborus*. The suffix "*s. l.*" is given to distinguish these species from *Xyleborus s. str.*, a group which is based on several synapomorphies and is believed to be monophyletic (Figure 20, 22).

Introducing a number of new genera (one of them monotypic), in combination with synonymizing a large number of species, may result in oversplitting the group. However, Xyleborina of New Guinea are not an oversplit group with 4.9 species per genus on average, compared to some of the best studied beetle taxa such as the Carabidae of Britain (350 species, 90 genera = 3.9 species per genus on average, Luff 2008). Most importantly, the species/genus ratio will dramatically increase if the genera presented here are accepted and more species are transferred into them (J. Hulcr, unpublished data).

Notes on Xyleborina biology

In our previous work, we have shown that ambrosia beetles in New Guinea lowlands display almost no species turnover with distance (beta diversity, Hulcr et al. 2007c). Collection data in this monograph confirm, that a large proportion of the whole island fauna can be collected at a single locality, given sufficient sampling effort. Several collectors, namely Roberts, Gray, Wyllie and Shanagan, who carried out a large trapping of scolytine beetles in logging areas near Bulolo (near Wau), Morobe Province, collected 47% of all New Guinean species of Xyleborina. Bulolo is a middle-elevation locality, thus both lowland and highland species were intercepted. Even more - 54% - of total New Guinea species was collected during our collecting and rearing program in Ohu and Wannang villages, Madang Province, between 2002 and 2006.

On the other hand, community composition changes dramatically with altitude. Our samples from low elevation sites across the whole northern part of Papua New Guinea share only about 5% of species with our samples from the high elevation Chimbu province (1,200 m a. s. l.).

Surprisingly, Xyleborina are commonly found in extracts from the rainforest litter. In PNG, I have collected dozens individuals of *Eccoptopterus spinosus* and *Leptoxyleborus concisus* from ground emergence traps. Browne (1966) hypothesized that these beetles emerge after a maturation period akin to the temperate zone aestivation, or that they are individuals in the dispersal phase, resting in the litter. Emergence of beetles in ground traps many days or weeks after the trap has been installed refutes the latter hypothesis.

Although the shape of gallery varies widely in Xyleborina, the beetles never make individual larval chambers, a habit present in many other groups of ambrosia beetles (*Camptocerus* spp., *Scolytoplatypus* spp., *Scolytodes unipunctatus*, many Platypodinae and Corthylina). In species where individual larval cells (=cradles) do occur, they are initiated by the female as egg niches, and then extended by each larva during maturation. This sequence is very similar to the behavior of the majority of phloem feeding non-ambrosia scolytines, where females create egg niches and larvae extend their own galleries. Thus in ambrosia species where each larva occupies its own cradle, the larval cradles are most likely only a reduced tendency of the larvae to extend their own tunnel, rather than a de-novo specialized construction behavior. If this is the case, than the communal brood chambers and tunnels of Xyleborina are probably yet more evolutionarily derived behavior. In *Ozopemon* sp., the likely ancestors of Xyleborina (Jordal 1996), the phloem-feeding larvae display an intermediate behavior where they form irregular system of interconnected tunnels during foraging under bark; neither individual tunnels, nor a communal space (Hulcr, pers. obs.).

Checklist of Xyleborina confirmed for New Guinea

Amasa **Lea (1893)**

Amasa anomalus (Schedl, 1955)

Amasa knizeki Hulcr & Cognato **sp. n.**

Amasa resectus (Eggers, 1927)

Amasa schlichi (Stebbing, 1914)

Amasa similis (Eggers, 1923) **comb. n.**

Ambrosiodmus **Hopkins (1915)**

Ambrosiodmus asperatus (Blandford, 1895)

Ambrosiophilus **Hulcr & Cognato (2009)**

Ambrosiophilus atratus Eichhoff (1875)

Ambrosiophilus mogia Hulcr et al. **sp. n.**

Ambrosiophilus restrictus (Schedl, 1939)

Ambrosiophilus semicarinatus (Schedl, 1942)

Ambrosiophilus sexdentatus (Eggers, 1940)

Anisandrus **Ferrari (1867)**

Anisandrus ursa (Eggers, 1923)

Anceps **Hulcr & Cognato gen. n.**

Anceps puer (Eggers, 1923) **comb. n.**

***Arixyleborus* Hopkins (1915)**

Arixyleborus abruptus Schedl (1975)

Arixyleborus canaliculatus (Eggers, 1923)

Arixyleborus grandis (Schedl, 1942)

Arixyleborus minor (Eggers, 1940)

Arixyleborus puberulus (Blandford, 1896)

Arixyleborus scabripennis (Blandford, 1896)

Arixyleborus simplicaudus Hulcr & Cognato **sp. n.**

***Beaverium* Hulcr & Cognato (2009)**

Beaverium insulindicus Eggers (1923)

Beaverium perplexus Schedl (1969)

Beaverium rugipunctus Hulcr & Cognato **sp. n.**

Beaverium sundaensis Eggers (1923)

Beaverium venustulus Schedl (1969)

***Biuncus* Hulcr & Cognato (2009)**

Biuncus adossuarius Schedl (1951)

Biuncus conidens Eggers (1936)

Biuncus duodecimspinatus Schedl (1936)

Biuncus gorggae Schedl (1973)

Biuncus haberkorni Eggers (1920)

Biuncus justus Schedl (1931)

Biuncus mesoleiulus Schedl (1979)

Biuncus niger Hulcr & Cognato **sp. n.**

Biuncus papatrae Schedl (1972)

Biuncus quadrispinosulus Eggers (1923)

***Cnestus* Sampson (1911)**

Cnestus aterrimus (Eggers, 1927)

Cnestus bimaculatus (Eggers, 1927)

Cnestus mutilatus (Blandford, 1894)

Cnestus triangularis (Schedl, 1975)

***Coptodryas* Hopkins (1915)**

Coptodryas bella (Sampson, 1921)

Coptodryas pubifer (Schedl, 1972) **comb. n.**

***Cryptoxyleborus* Schedl (1937)**

Cryptoxyleborus acutus (Schedl, 1975)

Cryptoxyleborus subnaevus Schedl (1937)

Cryptoxyleborus vestigator (Schedl, 1973)

***Cyclorhipidion* Hagedorn (1912)**

Cyclorhipidion apicipenne (Schedl, 1974)

Cyclorhipidion artedilatatum Hulcr & Cognato **sp. n.**

Cyclorhipidion bituberculatum (Eggers, 1923)

Cyclorhipidion multipunctatus (Browne, 1980)

Cyclorhipidion perpilosellum (Schedl, 1935)

Cyclorhipidion repandus Schedl (1942) **comb. n.**

Cyclorhipidion superbus (Schedl, 1942) **comb. n.**

Cyclorhipidion sus Schedl (1973) **comb. n.**

***Eccoptopterus* Motschulsky (1863)**

Eccoptopterus limbus Sampson (1911)

Eccoptopterus spinosus (Olivier, 1795)

***Emarginatus* Hulcr & Cognato gen. n.**

Emarginatus cyclopus Schedl (1940) **comb. n.**

Emarginatus emarginatus Eichhoff (1878) **comb. n.**

Emarginatus fallax Eichhoff (1878) **comb. n.**

Emarginatus latecornis Schedl (1969) **comb. n.**

Emarginatus pumilus Eggers (1923) **comb. n.**

Emarginatus spinicornis Schedl (1975) **comb. n.**

***Euwallacea* Hopkins (1915)**

Euwallacea destruens (Blandford, 1896)

Euwallacea wallacei (Blandford, 1896)

***Fortiborus* Hulcr & Cognato gen. n.**

Fortiborus anisopterae Browne (1983) **comb. n.**

Fortiborus indigens (Schedl, 1955) **comb. n.**

Fortiborus major (Stebbing, 1909) **comb. n.**

Fortiborus pilifer Eggers (1923) **comb. n.**

Fortiborus sulcinoides (Schedl, 1974) **comb. n.**

***Hadrodemius* Wood (1980)**

Hadrodemius globus (Blandford, 1896)

***Immanus* Hulcr & Cognato gen. n.**

Immanus acanthurus (Lea, 1910) **comb. n.**

Immanus colossus (Blandford, 1896) **comb. n.**

***Leptoxyleborus* Wood (1980)**

Leptoxyleborus sordicauda (Motschulsky, 1863)

***Microperus* Wood (1980)**

Microperus chimbui (Schedl, 1973) **comb. n.**

Microperus corporaali (Eggers, 1923) **comb. n.**

Microperus diversicolor (Eggers, 1923) **comb. n.**

Microperus fragosus (Schedl, 1942) **comb. n.**

Microperus intermedius (Eggers, 1923)

Microperus parva (Lea, 1893) **comb. n.**

Microperus perparva (Samps, 1923) **comb. n.**

Microperus pometiana (Schedl, 1939) **comb. n.**

Microperus popondettae (Browne, 1970) **comb. n.**

Microperus recidens (Sampson, 1923) **comb. n.**

***Planiculus* Hulcr & Cognato gen. n.**

Planiculus aries Schedl (1969) **comb. n.**

Planiculus bicolor (Blandford, 1894) **comb. n.**

Planiculus immersus Schedl (1972) **comb. n.**

Planiculus limatus (Schedl, 1936) **comb. n.**

Planiculus rodmanculus Hulcr & Cognato **sp. n.**

***Pseudowebbia* Browne (1961)**

Pseudowebbia armifer (Schedl, 1942)

Pseudowebbia curvatus Browne (1986) **comb. n.**

Pseudowebbia squamatilis (Schedl, 1955)

***Schedlia* Browne (1950)**

Schedlia brownei Bright (1980)

Schedlia praeusta (Eggers, 1923)

Schedlia sumatrana (Hagedorn, 1908)

Schedlia usitata (Schedl, 1942)

***Stictodex* Hulcr & Cognato gen. n.**

Stictodex cuspidus (Schedl, 1975) **comb. n.**

Stictodex dimidiatus (Eggers, 1927) **comb. n.**

***Streptocranus* Schedl (1939)**

Streptocranus bispinus (Schedl, 1979) **comb. n.**

Streptocranus longispinis Browne (1986)

***Truncaudum* Hulcr & Cognato gen. n.**

Truncaudum agnatum (Eggers, 1923) **comb. n.**

Truncaudum impexus Schedl (1942) **comb. n.**

Truncaudum longior (Eggers, 1923) **comb. n.**

Truncaudum truncaticauda Browne (1984) **comb. n.**

Truncaudum truncatiformis (Eggers, 1923) **comb. n.**

Truncaudum tuberculifer (Eggers, 1923) **comb. n.**

***Wallacella* Hulcr & Cognato gen. n.**

Wallacella andamanensis (Blandford, 1896) **comb. n.**

Wallacella andreae Hulcr & Cognato **sp. n.**

Wallacella densatus Schedl (1979) **comb. n.**

Wallacella fornicatus (Eichhoff, 1868) **comb. n.**

Wallacella funereus (Lea, 1910) **comb. n.**

Wallacella piceus (Motschulsky, 1863) **comb. n.**

Wallacella similis Ferrari (1867) **comb. n.**

Wallacella striatulus Browne (1980) **comb. n.**

Wallacella timidus Schedl (1973) **comb. n.**

***Webbia* Hopkins (1915)**

Webbia pabo Sampson (1922)

***Xyleborinus* Reitter (1913)**

Xyleborinus andrewesi (Blandford, 1896)

Xyleborinus artestriatus (Eichhoff, 1878)

Xyleborinus exiguus (Walker, 1859)

Xyleborinus perpusillus (Eggers, 1927)

Xyleborinus saxeseni (Ratzeburg, 1837)

***Xyleborus* Eichhoff (1864)**

Xyleborus s. str. affinis Eichhoff (1868)

Xyleborus s. str. bispinatus Eichhoff (1868)

Xyleborus s. str. devexipennis Hulcr & Cognato **sp. n.**

Xyleborus s. str. perforans Wollaston (1857)

Xyleborus* s. *l.

Xyleborus s. l. bidentatus (Motschulsky, 1863)

Xyleborus s. l. cinctipes Schedl (1979)

Xyleborus s. l. declivispinatus (Schedl, 1969) **comb. n.**

Xyleborus s. l. granulosus Schedl (1975)

Xyleborus s. l. judenkoi (Schedl, 1959) **comb. n.**

Xyleborus s. l. metacuneolus Schedl (1940)

Xyleborus s. l. papuanus Blandford (1896)

Xyleborus s. l. pileatulus Schedl (1975)

***Xylosandrus* Reitter (1913)**

Xylosandrus compactus (Eichhoff, 1875)

Xylosandrus crassiusculus (Motschulsky, 1866)

Xylosandrus discolor (Blandford, 1898)

Xylosandrus hulcri Dole & Cognato (2009)

Xylosandrus mixtus (Schedl, 1979)

Xylosandrus morigerus (Blandford, 1894)

Xylosandrus rotundicollis (Browne, 1984)

Xylosandrus russulus (Schedl, 1942)

Synonymized species

Amasa cylindriformis (Schedl, 1942) synonymized with *Amasa similis* (Eggers)

Amasa fulgens (Schedl, 1975) synonymized with *Amasa resectus* (Eggers)

Amasa nakazawai (Browne, 1984) synonymized with *Amasa anomalus* (Schedl)

Amasa striatotruncatus (Schedl, 1936) synonymized with *Amasa schlichi* (Stebbing)

Amasa tereticollis (Schedl, 1951) synonymized with *Amasa similis* (Eggers)

Amasa umbratulus (Schedl, 1975) synonymized with *Amasa schlichi* (Stebbing)

Ambrosiodmus funestus (Schedl, 1979) synonymized with *Cyclorhipidion bituberculatum* (Eggers)

Ambrosiodmus incertus (Schedl, 1969) synonymized with *Ambrosiophilus restrictus* (Schedl)

Arixyleborus cariniceps Schedl (1975) synonymized with *Arixyleborus canaliculatus* (Eggers)

Arixyleborus guttifer (Schedl, 1955) synonymized with *Arixyleborus scabripennis* (Blandford)

Arixyleborus iriani Browne (1983) synonymized with *Arixyleborus abruptus* Schedl

Arixyleborus morio (Eggers, 1923) synonymized with *Arixyleborus puberulus* (Blandford)

Arixyleborus trux Schedl (1975) synonymized with *Arixyleborus minor* (Eggers)

Cnestus pseudosuturalis Schedl (1964) synonymized with *Cnestus aterrimus* (Eggers)

Coptodryas artegrapha (Schedl, 1942) synonymized with *Microperus recidens* (Sampson)

Coptodryas atava (Schedl, 1979) synonymized with *Microperus diversicolor* (Eggers)

Coptodryas docta (Schedl, 1975) synonymized with *Microperus popondettae* (Browne)

Coptodryas extensa (Schedl, 1955) synonymized with *Microperus recidens* (Sampson)

Coptodryas nitella (Browne, 1984) synonymized with *Microperus intermedius* (Eggers)

Coptodryas pubipennis (Schedl, 1974) synonymized with *Microperus parva* (Lea)

Cyclorhipidion anoplum (Schedl, 1975) synonymized with *Cyclorhipidion apicipenne* (Schedl)

Cyclorhipidion canarii (Browne, 1984) synonymized with *Cyclorhipidion bituberculatum* (Eggers)

Cyclorhipidion delicatum (Schedl, 1955) synonymized with *Truncaudum agnatum* (Eggers)

Cyclorhipidion revocabile (Schedl, 1942) synonymized with *Cyclorhipidion bituberculatum* (Eggers)

Cyclorhipidion subagnatum Wood (1992) synonymized with *Truncaudum agnatum* (Eggers)

Eccoptopterus gracilipes (Eichhoff, 1886) synonymized with *Eccoptopterus spinosus* (Olivier)

Eccoptopterus sagittarius Schedl (1939) synonymized with *Eccoptopterus spinosus* (Olivier)

Euwallacea filiformis (Schedl, 1975) synonymized with *Planiculus bicolor* (Blandford)

Euwallacea laevis (Eggers, 1923) synonymized with *Planiculus bicolor* (Blandford)

Euwallacea procerrimus (Schedl, 1969) synonymized with *Euwallacea destruens* (Blandford)

Euwallacea subemarginatus (Eggers, 1940) synonymized with *Planiculus limatus* (Schedl)

Euwallacea subparallelus (Eggers, 1940) synonymized with *Planiculus limatus* (Schedl)

Euwallacea talumalai (Browne, 1966) synonymized with *Wallacella andamanensis* (Blandford)

Euwallacea tumidus (Schedl, 1975) synonymized with *Planiculus bicolor* (Blandford)

Leptoxyleborus ceramensis (Schedl, 1937) synonymized with *Anceps puer* (Eggers)

Leptoxyleborus concisus (Blandford, 1894) synonymized with *Leptoxyleborus sordicauda* (Motschulsky)

Microperus myristicae (Schedl, 1939) synonymized with *Microperus diversicolor* (Eggers)

Schedlia convexa Bright (1980) synonymized with *Schedlia usitata* (Schedl)

Schedlia paraconvexa Bright (1980) synonymized with *Schedlia usitata* (Schedl)

Webbia denticulatus Browne (1983) synonymized with *Pseudowebbia squamatilis* (Schedl)

Webbia quadricinctus Schedl (1972) synonymized with *Webbia pabo* Sampson

Xyleborinus ankius (Schedl, 1975) synonymized with *Xyleborinus exiguus* (Walker)

Xyleborinus perexiguus (Schedl, 1971) synonymized with *Xyleborinus exiguus* (Walker)

Xyleborus abbreviatipennis Schedl (1973) synonymized with *Cyclorhipidion bituberculatum* (Eggers)

Xyleborus annexus Schedl (1973) synonymized with *Beaverium insulindicus* (Eggers)

Xyleborus apiculatus Schedl (1942) synonymized with *Biuncus justus* (Schedl)

Xyleborus aplanatideclivis Schedl (1942) synonymized with *Beaverium sundaensis* (Eggers)

Xyleborus approximatus Schedl (1951) synonymized with *Biuncus haberkorni* (Eggers)

Xyleborus australis Schedl (1980) synonymized with *Ambrosiophilus restrictus* (Schedl)

Xyleborus biuncus Browne (1984) synonymized with *Biuncus papatrae* (Schedl)

Xyleborus brevicollis Browne (1984) synonymized with *Biuncus mesoleiulus* (Schedl)

Xyleborus canarivorus Browne (1986) synonymized with *Truncaudum longior* (Eggers)

Xyleborus ciliatoformis Schedl (1953) synonymized with *Biuncus justus* (Schedl)

Xyleborus ciliatus Eggers (1940) synonymized with *Biuncus justus* (Schedl)

Xyleborus circumspinosus Schedl (1972) synonymized with *Truncaudum impexus* (Schedl)

Xyleborus cognatus Blandford (1896) synonymized with *Xyleborus perforans* Wollaston

Xyleborus cruciatus Schedl (1973) synonymized with *Stictodex dimidiatus* (Eggers)

Xyleborus cylindricus Eggers (1927) synonymized with *Emarginatus pumilus* (Eggers)

Xyleborus decumans Schedl (1953) synonymized with *Stictodex dimidiatus* (Eggers)

Xyleborus dentatulus Browne (1981) synonymized with *Truncaudum impexus* (Schedl)

Xyleborus depressurus Browne (1985) synonymized with *Beaverium insulindicus* (Eggers)

Xyleborus devius Schedl (1979) synonymized with *Ambrosiophilus restrictus* (Schedl)

Xyleborus falcarius Schedl (1942) synonymized with *Truncaudum impexus* (Schedl)

Xyleborus fastigatus Schedl (1935) synonymized with *Emarginatus fallax* (Eichhoff)

Xyleborus flavipennis Schedl (1979) synonymized with *Cyclorhipidion bituberculatum* (Eggers)

Xyleborus flavopilosus Schedl (1936) synonymized with *Cyclorhipidion bituberculatum* (Eggers)

Xyleborus glabratulus Browne (1983) synonymized with *Planiculus bicolor* (Blandford)

Xyleborus granulipes Schedl (1973) synonymized with *Wallacella timidus* (Schedl)

Xyleborus gratiosus Schedl (1975) synonymized with *Truncaudum agnatum* (Eggers)

Xyleborus hashimotoi Browne (1986) synonymized with *Planiculus immersus* (Schedl)

Xyleborus hopeae Browne (1986) synonymized with *Truncaudum tuberculifer* (Eggers)

Xyleborus immitatrix Schedl (1975) synonymized with *Xyleborus judenkoi* Schedl

Xyleborus ipidia Schedl (1972) synonymized with *Emarginatus pumilus* (Eggers)

Xyleborus mucronatoides Schedl (1975) synonymized with *Biuncus papatrae* (Schedl)

Xyleborus multipunctulus Browne (1984) synonymized with *Cyclorhipidion multipunctatus* (Browne)

Xyleborus nitens Browne (1984) synonymized with *Ambrosiophilus semicarinatus* (Schedl)

Xyleborus opulentus Schedl (1975) synonymized with *Emarginatus latecornis* (Schedl)

Xyleborus platyurus Browne (1984) synonymized with *Beaverium perplexus* (Schedl)

Xyleborus protii Browne (1984) synonymized with *Truncaudum longior* (Eggers)

Xyleborus pseudopilifer Schedl (1936) synonymized with *Fortiborus pilifer* (Eggers)

Xyleborus putputensis Browne (1986) synonymized with *Truncaudum impexus* (Schedl)

Xyleborus siclus Schedl (1936) synonymized with *Fortiborus major* (Stebbing)

Xyleborus subcostatus Eichhoff (1869) synonymized with *Xyleborus bidentatus* (Motschulsky)

Xyleborus subdentatulus Browne (1986) synonymized with *Truncaudum impexus* (Schedl)

Xyleborus tunggali Schedl (1936) synonymized with *Stictodex dimidiatus* (Eggers)

Xyleborus vernaculus Schedl (1975) synonymized with *Truncaudum impexus* (Schedl)

Xyleborus viaticus Schedl (1974) synonymized with *Truncaudum longior* (Eggers)

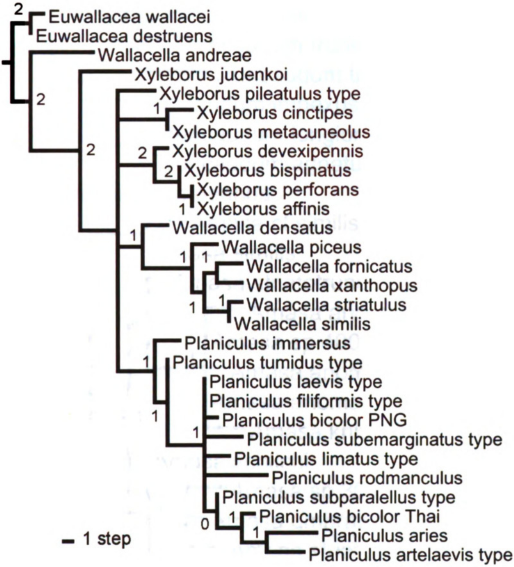

Figure 20: A morphology-based cladistic analysis of species previously placed in *Euwallacea*, *Xyleborus*, and several similar species of unclear affiliation. Combinable-component consensus of 33 most parsimonious trees (97 steps), 25 characters (8 additive), search in TNT (Goloboff et al., 2003) using driven search with initial level 60, set to find minimal length 10 times. Numbers at nodes indicate Bremer support.

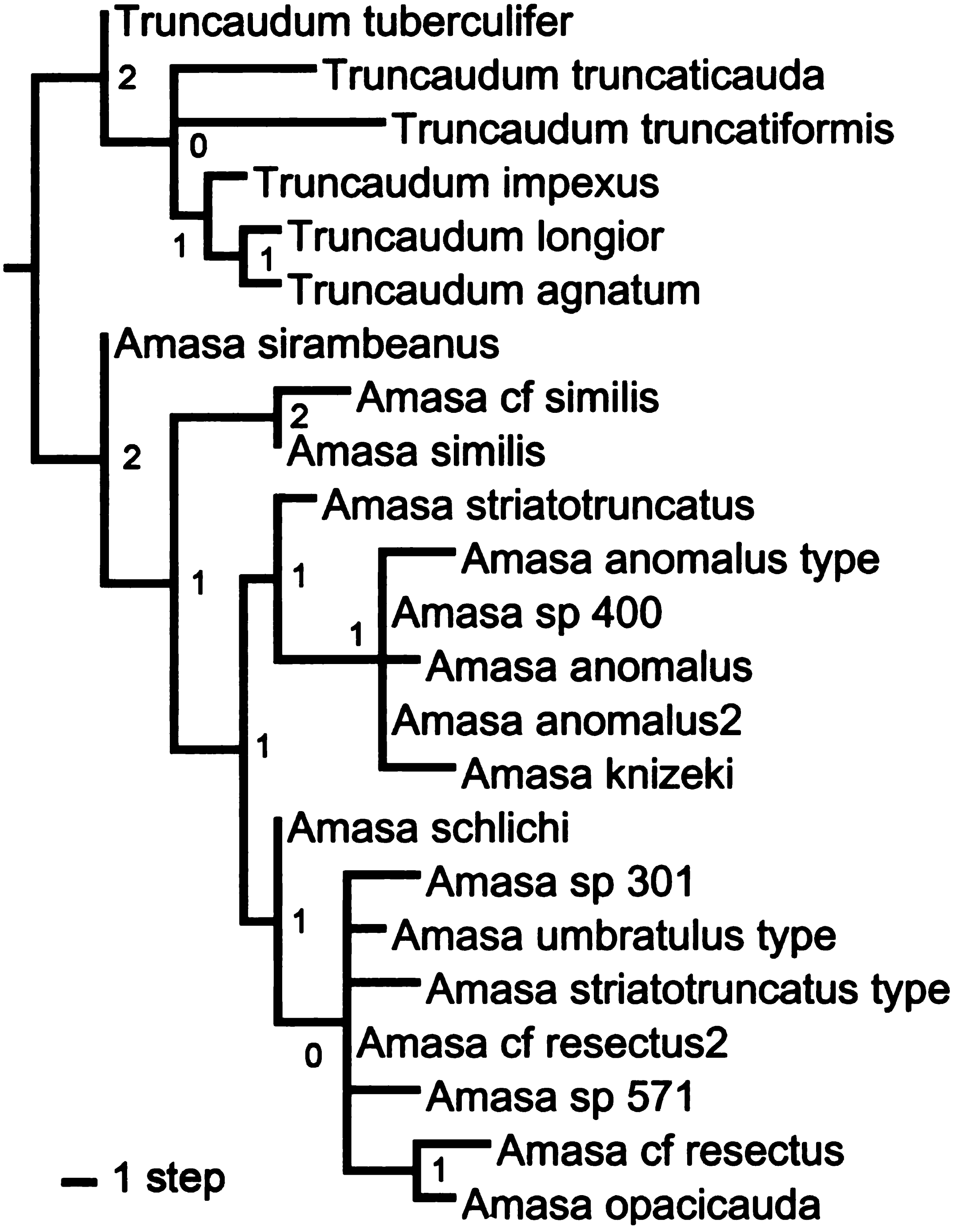

Figure 21: A morphology-based cladistic analysis of species previously placed in *Amasa,* Cyclorhipidion, Xyleborus, and similar species of unclear affiliation. Combinable-component consensus of 240 most parsimonious trees (60 steps), 21 characters (1 ordered), search in TNT (Goloboff et al., 2003) using driven search with initial level 60,

set to find minimal length 10 times. The large number of MP trees is almost entirely due to the lack of resolution among *Amasa* spp., illustrating to the paucity of synapomorphic characters in these species. Numbers at nodes indivate Bremer support.

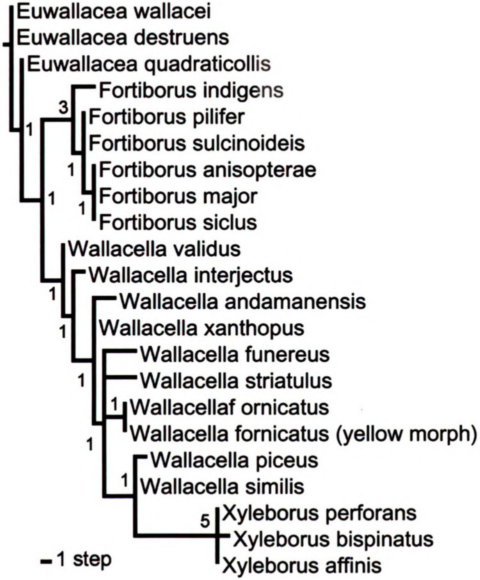

Figure 22: A morphology-based cladistic analysis of similar species previously placed mostly in *Euwallacea, Xyleborus* "*major*-group", and other genera. Combinable-component consensus of two most parsimonious trees (46 steps), 19 characters

(unordered), search in TNT (Goloboff et al., 2003) using driven search with initial level 60, set to find minimal length 10 times. Numbers at nodes indicate Bremer support.

DIVERSITY AND SYSTEMATICS OF AMBROSIA BEETLES (CURCULIONIDAE: SCOLYTINAE, PLATYPODINAE) WITH EMPHASIS ON XYLEBORINA

VOLUME II

By

Jiri Hulcr

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Entomology

2009

Taxonomic treatment

Genus *Amasa* Lea (1893)

J.H. database code: Scol 800

Type species: *Amasa thoracica* Lea (= *Tomicus truncatus* Erichson).

Redescription: Eyes deeply emarginate, sometimes almost disjunct, upper portion of eyes smaller than lower part. Antennal club more-less circular shape, club type four (first segment small, second and third prominent on both sides), or five (all pubescent, sutures obscured). First segment of club convex, small, margin of the first segment appears softer and pubescent on posterior side, or the margin is all soft, pubescent. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only, or corneous on both sides of club, but not strictly circular. Third segment of club clearly visible and dominant on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. In some species, mandibular mycangia are visible as bulges on the epistoma. Frons above epistoma mostly smooth, alutaceous, with minor punctures. Submentum deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum mostly with distinct row of serrations. Pronotum from lateral view of basic shape (type 0), or prolonged, with low summit (type 7), or with disc distinctly prolonged (type 8). From dorsal view it is basic, short, parallel-sided, rounded frontally (type 2), or prolonged basic shape with rounded frontal margin (type 7). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum obliquely costate. Procoxae contiguous or narrowly separated, prosternal posterocoxal process short, conical or flat, inconspicuous, or tall and pointed. No setose mycangial openings either in mesonotum or in elytral bases. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat, punctures on elytral disc in strial lines. Elytral declivity sharply truncated, mostly with costa or elevated carina on the edge. Declivital vestiture variable - mostly devoid of hair, sometimes with few setae or scales, or covered with adherent flat setae or scales. Circumdeclivital costa all of declivity. Declivital surface greatly variable but always devoid of major processes or other structures, except small uniform granules. First interstriae are parallel on the elytral disc, often distinctly broadened towards the apex of elytra. Protibiae with evenly rounded edge, or obliquely triangular, broadest in 2/3 of the length, or very slender, slightly broader only at the distal end. Posterior side of protibia flat, with setae only, or appears inflated, often with several granules. Protibial denticles small, bases of the denticles not enlarged or only slightly elevated, usually between 6 and 8 protibial denticles present. Metatibiae of regular size. Body length between 2.1-3.7 mm. Color uniformly light brown or reddish or uniformly dark brown, rarely uniformly black, pronotum commonly lighter than elytra, sometimes starkly contrasting (yellow pronotum, black elytra).

Discussion

As compared the most closely related genus *Truncaudum* gen. n., *Amasa* differs by deep eye imagination, antenna type 4 or 5 (as opposed to 3), short body including pronotum, no vestiture on elytral disc, elytral declivity surrounded with costa, not with denticles, interstriae inside the declivity largely devoid of any tubercles (except interstria 1).

Browne (1961c) related the "truncatus group" (=*Amasa*) to *Pseudoxyleborus*, but retained *Amasa* spp. in *Xyleborus*. *Amasa* is closely related to *Truncaudum* gen. n., supported by molecular and morphology-based phylogenies (Figure 21) (Cognato et al., 2009). The placement of species in either *Amasa* or *Truncaudum* remains uncertain, as many morphological characters are homoplastic in the group (i.e., *Truncaudum tuberculifer* (Eggers) from New Guinea, or *Amasa sirambeanus* (Eggers) from Sumatra). Consensus of the MP trees (Figure 21) illustrates that most of the homoplasy occur within the *Amasa* s. str. clade, which is almost entirely collapsed. This lack of congruence among morphological characters in *Amasa* (both traditional characters and the newly designed) indicates that either morphological characters are inadequate in establishing monophyletic species in *Amasa*, or that most contemporary *Amasa* spp. are in fact only variants of species with hypervariable morphology.

Previously synonymized genera: *Pseudoxyleborus* Eggers, *Anaxyleborus* Wood.

Biology: Browne (1958) notes that although representatives of this genus (as truncatus-group) are not host specific, *X. uniseriatus* Egg. (now *Amasa schlichi*) is allegedly found specialized to Fagaceae. Most known *Amasa* excavate short tunnel leading to often large flat longitudinal brood cavity.

Figure 23: *Amasa resectus*, a typical representative of the genus *Amasa*. Size: 2.6 mm.

Amasa anomalus (Schedl, 1955)

J.H. database code: Scol 590

Compared to holotype in NHMW

Redescription: Antennae type 5 (sutures obscured, all pubescent, appearing soft). Deeply emarginate eyes, upper portion of eyes very small. Protibia more triangular than crescent-like; narrow, rear side flat or only slightly inflated, not granulated. Declivity flat, abruptly truncated, surrounded by elevated costa, covered with dense miniature scales (broadened flattened erect setae). Scales may be missing in rare cases.

Length: 3.0-3.4 mm.

Diagnosis: According to Schedl (1955b), the species is similar to *Amasa* (as *Xyleborus*) *orbicaudatus*, with minor differences in elytral declivity surface. The holotype of *Amasa*

(*Xyleborus*) *nakazawai* (Browne) was found to be nearly identical to the holotype of its senior synonym *A. anomalus*. *Amasa dasyurus* (Browne, type seen in BMNH), also has short adhering scales on declivity.

New junior synonym(s): *Amasa nakazawai* (Browne)

Examined material: New Guinea, (FICB); New Guinea, Morobe Province, Bulolo, (MSUC); New Guinea, (holotype, NHMW); New Guinea, Morobe Province, Bulolo, (NHMW); PNG: Chimbu Prov. (1), J. Hulcr 2002-2006.

Amasa cylindriformis **syn. n. (Schedl, 1942)**

Synonymized with: *Amasa similis (Eggers)*

J.H. database code: Scol 591

Compared to holotype in NHMW

Length: 2.1 mm.

Discussion

Schedl (1942c) suggested that, despite the superficial similarity of the species to *Webbia*, it is more similar to *X. longior* Egg., now included in *Truncaudum*. Both assertions were incorrect, perhaps due to an exaggerated emphasis on elytral shape. The species was synonymized with *A. similis* (Eggers, 1923) by Schedl (1980d) as subjective junior synonym. The synonymy was not recorded in Wood & Bright (1992) for unknown reason. The holotype of *A. similis* was not available for examination, but comparison of holotypes of the two species was carried out by R. A. Beaver, who confirmed the synonymy (Beaver, unpubl.).

Previously synonymized species: *Xyleborus circulicauda* Browne

Examined material: New Guinea, Morobe Province, Bulolo, (MSUC); New Guinea, (holotype, NHMW); New Guinea, Morobe Province, Bulolo, (NHMW).

Amasa fulgens **syn. n. (Schedl, 1975)**

Synonymized with: *Amasa resectus (Eggers)*

J.H. database code: Scol 592

Compared to holotype in NHMW

Length: 3.0 mm.

Discussion

According to Schedl (1975f), the species is similar to *Amasa resectus* (as *Xyleborus resectus*), and can be distinguished by the slightly larger size, more impressed striae on the declivity, coarser strial punctures, subshining interstriae (not opaque), with numerous small punctures bearing rather long inclined setae. The holotype (the only known representative of *A. fulgens*) is nearly identical to the earlier described *A.* (as *Xyleborus*) *opacicauda* (Eggers, 1940a), including the exact structure of antennal club, the protibiae, and minutiae such as the abundance and directions of setae on the elytral declivity. *A. opacicauda* is currently considered a synonym of *A. resectus* (Kalshoven, 1959b).

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

Amasa knizeki **sp. n. Hulcr & Cognato**

J.H. database code: Scol 349

Diagnosis: Uniquely among *Amasa* spp., the margin of elytral declivity of *A. knizeki* is not abrupt and costate, but oblique, bearing numerous minute granules and asperities. The species is only known from montane cloud forests in Chimbu province.

Description: Antennal club type 5 - densely pubescent, segment 1 reduced, not corneous, all sutures reduced. Pronotum dark, short (type 1 laterally), with a short row of serrations. Procoxae discontiguous, ante-and posterocoxal prosternal processes also separate. Protibia flat, not granulate posteriad, narrow, edge rounded (not triangular), with around 7 small socketed denticles. Elytral disc black, with faint, almost obscured strial and interstrial punctuation. Elytral end truncated but unlike other *Amasa*, the declivity is not surrounded by elevated costa. Instead, the edge is blunt, oblique. Surface of elytral declivity densely coriaceous and granulate, declivital edges with numerous minute confused granules. Strial punctures entirely absent.

Length: 3.1 mm.

Discussion

Holotype deposited in USNM, paratypes in MSUC, BMNH, and NHMW.

Biology: Larval cavity perpendicular to short entrance tunnel. Mostly in branches, in montane rainforests.

Examined material: PNG: Chimbu Prov. (17), J. Hulcr 2002-2006.

Etymology: Named in recognition of Milos Knizek's contribution to scolytine taxonomic knowledge.

Figure 24: *Amasa knizeki sp. n.* Size: 3.1 mm.

Amasa nakazawai **syn. n. (Browne, 1984)**

Synonymized with: *Amasa anomalus (Schedl)*

J.H. database code: Scol 744

Compared to holotype in BMNH

Length: 3.0 mm.

Discussion

Transferred to *Amasa* by Beaver (1995). Described by Browne (1984a) from New Britain. The author related it to *A.* (as *Xyleborus*) *anomalus*, and differentiated it by more glabrous elytral disc with not all striae impressed. In our comparison of this species to the holotype of *A. anomalus* we noticed a slightly less impressed declivital area, but the overall pattern of striae inside the declivital circle was identical (disc nearly all flat, interstria 1 elevated, especially towards the apex). The two species also share the same appressed pointed scales covering the declivital interstriae, including the direction of the scales (medially on the sides, posteriad in the middle). The two species also probably share the antennal club type 5 (all pubescent, sutures absent or obscure). The holotype is missing both antennal clubs, but a non-type identified by R. A. Beaver as *A. nakazawai* from Gulf province has antennal club type 5. No character was found to reliably distinguish the two entities.

Examined material: New Guinea, Madang Province, Baiteta, (B. H. Jordal); New Guinea, New Britain, "near Watergum", (holotype, BMNH); New Guinea, Gulf Province, Ivimka, (UCD), R. A. Beaver det..

***Amasa resectus* (Eggers, 1927)**

J.H. database code: Scol 64

Compared to non-types in NHMW

Redescription: Elytral declivity varies considerably, but can be broadly described as having the first interstria usually elevated and granulate, towards the declivital apex, the declivital surface dull, often shagreened, often with small setae-bearing granules. The opaque, often pubescent and tuberculate surface of declivity is the only character distinguishing this morph from *A. schlichi*. The antenna is of type 4 (small, convex, corneous segment 1, larger and mostly corneous segments 2 and 3, apparent on both sides of the club), which is shared with *A. schlichi* but differs from *A. anomalus* (which has fully pubescent antennal club type 5).Color and size vary greatly, although the most common coloration is yellow pronotum and head, and contrasting dark brown elytra. Individuals from Borneo have often smoothly shagreened elytral declivity with no granules or setae. *A. nakazawai* is similar but covered with flattened setae.

Length: 2.5-2.9 mm.

Discussion

Amasa (as *Xyleborus*) *resectus* is a nomen novum proposed in 1927 for *X. abruptus* 1923 by Eggers, as *X. abruptus* was preoccupied. Kalshoven (1959b) synonymized *X. opacicauda* with *X. resectus*, indicating that they are "identical". The synonymy is however not based on a comparison of holotypes. No discussion of characters is given. The holotype of *X. resectus* is allegedly lost (Wood & Bright, 1992). Lectotype from USNM and non-types of *X. resectus* identified by Kalshoven were examined and the synonymy with *A. resectus* is confirmed. Antennal clubs and the coarse declivital surfaces are identical. The only difference between the lectotype of *A. opacicauda* and most of *A. resectus* is that the declivity of *A. opacicauda* bears faint sparse setae. *Amasa kenchington* Beaver is very similar, has unusually large antennal clubs, only few punctures in declivity, non-type seen in USNM. Examination of the lectotype of *Xyleborus glaber* Eggers (holotype seen in USNM, now synonymized with *Amasa* *schlichi*) revealed that the holotype has clearly dull declivity, thus should have been synonymized with *A. resectus*.

Previously synonymized species: *Xyleborus opacicauda* Eggers, *Xyleborus abruptus* Eggers

New junior synonyms: *Amasa fulgens* (Schedl)

Examined material: Indonesia, Java, Batoerrad, (BMNH, 2 indiv.); Indonesia, Java, Mt. Gede, (NHMW); Malaysia, Sabah, Danum Valley, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Mallotus sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Danum Valley, Nauclea orientalis trunk, (Hulcr coll.); PNG: Madang Prov. (140), Oro Prov. (2), West Sepik (5), J. Hulcr 2002-2006.

***Amasa schlichi* (Stebbing, 1914)**

J.H. database code: Scol 776

Compared to co-type in NHMW

Redescription: *A. schlichi* is an amalgamation of many morphotypes of *Amasa*, distinguished from other *Amasa* spp. broadly by two characters: antennal club type 4 (small, convex, corneous segment 1, larger and mostly corneous segments 2 and 3, prominent on both sides), and by the shining truncated declivity with three shallowly punctuated striae. All other characters are greatly variable and mutually incongruent, thus failing to delimit clades. *Amasa schlichi* is greatly variable in body size, color of individual body parts (from uniformly light brown, to yellow pronotum and dark elytra, to uniformly black), the first interstria on declivity (raised and granulated or not), the size, density and depth of elytral punctures, etc. The size of elytral punctures often differs within and between individual striae. Even the elytral surface (shining, with no punctures) is variable, and many intermediate forms exist between this species and *A. resectus*, which has coarse, shagreened or coriaceous surface of declivity. Declivity can be opalescent in A. schlichi, which may be mistaken for shagreened surface.

Length: 3.1-3.7 mm.

Previously synonymized species: *Xyleborus brevipennis* Schedl, *Xyleborus verax* Schedl, *Xyleborus uniseriatus* Eggers, *Xyleborus glaber* Eggers, *Acanthotomicus truncatus* Stebbing

New junior synonym(s): *Amasa striatotruncatus* (Schedl), *Amasa umbratulus* (Schedl)

Biology: Browne (1958) notes that although representatives of the whole genus (as truncatus-group) are not host specific, *X. uniseriatus* Egg. (now *Amasa schlichi*) is allegedly specialized to Fagaceae. Unfortunately, no supporting data are given. Gallery consists of a radial tunnel leading to large and irregularly shaped brood chamber (Beaver & Browne 1978).

Examined material: Australia, Brisbane, (MSUC); no label, (co-type, NHMW); Thailand, Pong Yaeng N. P., (Hulcr coll.), R. A. Beaver det.; PNG: Madang Prov. (8), J. Hulcr 2002-2006.

Amasa similis **comb. n. (Eggers, 1923)**

J.H. database code: Scol 661

Previous genus: *Webbia*

Compared to holotype in ZMHB (RAB)

Redescription: Small *Amasa* with more slender body than other spp. Antenna type 4 (first segment of antennal club small, convex, corneous, second segment also corneous, broad, prominent, both second and third segments prominent on the posterior face of club). Pronotal disc prolonged compared to the anterior sloped part, giving the whole specimen slender appearance. Very small or no serrations on the frontal edge of pronotum. Protibiae very slender, almost stick-like. Declivity broadly impressed along first stria, which can be sometimes composed of conspicuous punctures, other striae mostly inconspicuous. Declivity shining, no tubercles except a row of small granules on each of the interstriae 1 close to the apex. The first (sutural) interstria on elytral declivity can be parallel along its whole length, or greatly diverged at the apex.

Length: 2.1-2.4 mm.

Discussion

Transferred from *Xelyborus* (sic!) to *Webbia* by Browne (1963). Type in Berlin museum, is partly destroyed. The type was not available for examination, but R. A. Beaver kindly provided an analysis of characters. The analysis suggests that *Xyleboricus* (as *Webbia* in Wood & Bright 1992) *similis* should be transferred to *Amasa*. It has a well-developed scutellum and antennae resembling those in some species of *Amasa*. Similar is *A. cilindriformis* (type in NHMW seen; synonymized with *A. circulicauda* from Fiji, also seen in BMNH) but it has a rather flat declivity (less prominent bulges along edges).Similarly long is *Amasa* (*Xyleborus*) *eugeniae* (Eggers) (Egger's non-types in USNM from India seen), but its eyes are smaller, and has a row of serrations on the frontal edge of pronotum.

Previously synonymized species: *Xyleborus obscurus* Schedl, *Xyleborus circulicauda* Browne

New junior synonyms: *Amasa cylindriformis* (Schedl), *Amasa tereticollis* (Schedl)

Examined material: New Guinea, Gulf Province, Ivimka, (UCD); West Papua, Hunsteinspitze, 1350 feet, (holotype, MNB).

Amasa striatotruncatus syn. n. (Schedl, 1936)

Synonymized with: _Amasa schlichi (Stebbing)_

J.H. database code: Scol 300

Compared to holotype in NHMW

Discussion

Type (unclear status) in BMNH has fewer interstrial punctures than most speicmens from New Guinea, almost no granules at the tip, yellow pronotum, and dark brown elytra. Highly variable morphotype from diverse locations, sharing all important characters with *A. schlichi*, mainly antennal club type 4, inflated and granulated protibiae, shining declivital surface. It is highly variable in size, color and declivital punctuation.

Examined material: Malaysia, Batu Laham, (holotype, NHMW); Malaysia, Sarawak, Gunung Buda, (R. A. Beaver det., UCD); Malaysia, Sabah, Danum Valley, Mallotus sp. branches, (Hulcr coll.); New Guinea, Chimbu Province, Mt. Wilhelm, (BBM); New Guinea, Morobe Province, Bulolo, (Schedl det., MSUC); New Guinea, Upper Manki, (Schedl det., MSUC); PNG: Madang Prov. (2), J. Hulcr 2002-2006.

Amasa tereticollis syn. n. (Schedl, 1951)

Synonymized with: *Amasa similis (Eggers)*

J.H. database code: Scol 595

Compared to holotype in NHMW

Discussion

The holotype and series of non-types of *Amasa* (*Xyleborus*) *tereticollis* were compared to the holotype and a series of non-types of *A.* (*X.*) *cylindriformis*. The two species are identical in all characters: identical structure of antennal club (type 4), very narrow ("stick-like") protibia, elongated body shape including long pronotal disc (type 8), bulging inner margins of declivital surface, suppressed strial punctuation and vestiture inside the declivity, elevated and granulate interstria 1. *Amasa. cylindriformis* is a junior synonym of *A. similis*, thus *A. tereticollis* becomes junior subjective synonym of *A. similis*.

Examined material: Indonesia, Sumatra, (holotype, NHMW); New Guinea, (FICB); New Guinea, Morobe Province, Bulolo, (NHMW).

***Amasa umbratulus* syn. n. (Schedl, 1975)**

Synonymized with: *Amasa schlichi (Stebbing)*

J.H. database code: Scol 597

Compared to holotype in NHMW

Discussion

The original description (Schedl, 1975g) mentioned dark reddish-brown color. Schedl (1975g) relates the species to Amasa (as Xyleborus) concitatus Schedl from Taiwan.

Amasa umbratulus is an example of a morphotype with mixture of homoplastic characters that is difficult to place in any species-group. All characters fall into the broad definition of A. schlichi, including the most important two - antennal club of type 4, and the opalescent but smooth declivity with only minor tubercles in interstria 1. Examined material: New Guinea, Western Province, Wavoi, (FICB); New Guinea, West New Britain, Dagi R., (holotype, NHMW).

Genus *Ambrosiodmus* Hopkins (1915)

J.H. database code: Scol 799

Type species: *Xyleborus tachygraphus* Zimmermann.

Redescripotion: Eyes shallowly emarginate, "bean shape", upper portion of eyes smaller than lower part. Antennal club more-less circular shape, club type four (first segment small, second and third prominent on both sides), or five (all pubescent, sutures obscured). First segment of club convex, small, margin of the first segment mostly soft, pubescent. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only, or corneous on both sides of club, but not circular (not making antenna tall, or "telescopic"). Third segment of club clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum slightly impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view low and rounded (type 1). From dorsal view it is basic, short, parallel-sided, rounded frontally (type 2). Pronotal disc of the genus is unusual in that it is covered with asperities resembling those on the frontal slope. Lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process tall and pointed, or conical and slightly inflated. Tuft on pronotal basis associated with mesonotal mycangium absent, also setae on elytral bases associated with elytral mycangium absent. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat slightly convex, punctures on elytral disc in strial lines. Lateral profile of elytral declivity steep, especially towards the apex, dorsal profile of elytral end rounded, or broadened laterally. Elytral declivity with few setae or scales, not conspicuously pubescent. Circumdeclivital costa ending in 7th interstriae. The inner part of declivity has no tubercles in interstria 1 (sutural), and several tubercles in interstriae 2, 3 and beyond. Striae and interstriae on the upper part of declivity mostly flat, striae sometimes impressed. First interstriae are parallel (sometimes slightly broadened towards elytral summit). Protibiae with evenly rounded edge. Posterior side of protibia flat, with setae only. Protibial denticles large, distinctly longer than wide, bases of the denticles not enlarged, protibial margin rounded, usually between 6 and 8 protibial denticles present. Metatibiae of regular size. Color uniformly dark brown or uniformly black. Length: 2.6-2.8 mm. (most non-New Guinean species larger).

Figure 25: *Ambrosiodmus asperatus*, the only confirmed Ambrosiodmus in New Guinea.

Size: 2.7 mm.

Ambrosiodmus asperatus **(Blandford, 1895)**

J.H. database code: Scol 285

Compared to holotype in BMNH

Redescription: The only *Ambrosiodmus* species from New Guinea, similar to *Ambrosiophilus* spp. (of which many species were previously included in *Ambrosiodmus*). The main differences are the rugose asperities distributed throughout the pronotum, and the distinctly rounded lateral profile of pronotum. Elytral declivity is broad and steep, interstriae 2 and 3 elevated, making the declivity appear impressed longitudinally along stria 1. Sparse long setae. Holotype is 2.8 mm..

Length: 2.6-2.8 mm.

Discussion

Holotype of *X. asperatus* Blandford has the same grossly punctured elytral disc, but smoother declivity than most PNG specimens. Also, it has only two pairs of declivital tubercles, though they are of the same size and in the same position as most other individuals. Wood (1989, 6761) synonymized *X. citri* Beeson and *X. cristatuloides* Schedl with this species. *Xyleborus nepotulomorphus* Blandford from Java was correctly synonymized by Schedl (1959a) (R. A. Beaver, pers. comm.). Surprisingly, Browne (1961c) includes the species among the *Euwallacea*-group (before *Euwallacea* was given official genus status).

Previously synonymized species: *Xyleborus cristatuloides* Schedl, *Xyleborus nepotulomorphus* Eggers, *Xyleborus citri* Beeson, *Xyleborus nepotulus* Eggers

Examined material: India, Ceylon, (holotype, BMNH); Sri Lanka, Sabargamuva, (NHMW); PNG: Madang Prov. (3), Oro Prov. (7), West Sepik (1), J. Hulcr 2002-2006.

Ambrosiodmus funestus syn. n. (Schedl, 1979)

Synonymized with: _Cyclorhipidion bituberculatum (Eggers)_

J.H. database code: Scol 598

Previous genus: *Ambrosiodmus*

Compared to holotype in NHMW

Discussion

Schedl relates the species to *Wallacella* (as *Xyleborus*) *funereus*, but notes that it is much larger, more slender, the basal area of the pronotum is densely and moderate finely punctured, the elytral declivity is shorter and obliquely convex. In reality, all characters of the holotype are those of genus *Cyclorhipidion*, and the species is a synonym of *Cyclorhipidion bituberculatum*.

Examined material: New Guinea, (holotype, NHMW).

Ambrosiodmus incertus **syn. n. (Schedl, 1969)**

Synonymized with: *Ambrosiophilus restrictus (Schedl)*

J.H. database code: Scol 599

Previous genus: *Ambrosiodmus*

Compared to holotype in ANIC

Discussion

Holotype of *A. incertus* from NG highlands is nearly identical to the representatives from SE Asia, including the rather larger size and more apparent declivital tubercles. The only difference is that the available individuals of *A. incertus* have slightly irridescent declivital surface. Schedl hypothesized that *A. incertus* may be a local variant of *A. consimilis* (Eggers) from SE Asia. Schedl labeled one male and one female as Type. All known individuals are from the same locality - presumably an artifact of Schedl's identification, whereby he overlooked similar specimens from other localities, identified as other species.

Examined material: New Guinea, Western Highlands, Jimi Valley, (allotype of male, ANIC); New Guinea, Western Highlands, Jimi Valley, (holotype, ANIC); New Guinea, Western Highlands, Jimi Valley, (paratype, FICB, 4 indiv.); New Guinea, Western Highlands, Jimi Valley, (paratype, NHMW).

Genus *Ambrosiophilus* Hulcr & Cognato (2009)

J.H. database code: Scol 835

Type species: *Ambrosiodmus restrictus* (Schedl) 1939.

Diagnosis: Similar to the related genus *Ambrosiodmus*, from which it differs by the absence of asperities on pronotal disc, the disc is flat, not rounded. Ecologically, many species of *Ambrosiodmus* are mycocleptic, which is not know for any *Ambrosiodmus*. Another similar genus is *Stictodex* (onle one species in New Guinea is similar – *S. dimidiatus*), from which *Ambrosiophilus* differs by the antennal club type 3, the club being approximately rounded (not broad), flat frons, parallel striae 1 (as opposed ot divergent), and steep elytral declivity.

Description: Eyes shallowly emarginate, upper portion of eyes smaller than lower part. Antennal club more-less circular shape, club type three (with first segment straight or convex). First segment of club straight (may be slightly concave or convex) on anterior face, margin of the first segment mostly costate, may appear softer on posterior side. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only, or corneous on both sides of club. Third segment of club clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma mostly smooth, alutaceous, with minor punctures, or rugged, coarsely punctate. Submentum flat, flush with genae, or slightly impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (at most serrations that don't differ from those on the pronotal slope). Pronotum from lateral view sometimes of basic shape (type 0), but mostly tall (type 2), flat on the disc and rounded or bulging on the frontal slope (type 4). From dorsal view it is basic, short, parallel-sided, rounded frontally (type 2). Pronotal disc densely and evenly punctured, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous, or tall and pointed, or conical and slightly inflated. Tuft on pronotal basis associated with mesonotal mycangium absent, setae on elytral bases associated with elytral mycangium absent. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat, elytral disc with distinct punctures in strial lines. Lateral profile of elytral declivity mildly flat or rounded, sometimes steep or very steep. Dorsal profile of elytral end rounded, often broadened laterally. In one species (*A. sexdentatus*) the declivity is excavated. Elytral declivity with few setae or scales, not conspicuously pubescent. Circumdeclivital costa ending in 7th interstriae. The inner part of declivity has no tubercles in interstria 1 (sutural), and several tubercles in interstriae 2, 3 and beyond. First interstriae are parallel (sometimes slightly broadened towards elytral summit). Protibiae with evenly rounded edge, or obliquely triangular, broadest in 2/3 of the length. Posterior side of protibia flat, with setae only. Protibial denticles large, distinctly longer than wide, bases of the denticles not enlarged or only slightly enlarged, usually between 6 and 8 protibial denticles present. Metatibiae of regular size. Body length between 2.4 and 3.2 mm. Mostly black, sometimes dark brown.

Discussion

The genus represents either a sister group or a subgroup of *Ambrosiodmus* Hopkins. Most of its species were in fact until recently included in *Ambrosiodmus* (Wood & Bright, 1992). Their sister-clade relationship to *Ambrosiodmus* is also supported by a five-gene molecular phylogeny (Cognato et al., 2009). There are two main reasons for separation of the two genera. First one is the inconsistent morphological definition of contemporary *Ambrosiodmus*. *Ambrosiodmus* has traditionally been defined by an autapomorphic asperate surface of pronotal disc. In many species, including the type species *A. tachygraphus* (Zimmermann), the pronotum truly looks unlike in most other genera of Xyleborina, both in terms of its surface and its very globular shape. However, number of species up to now included in the genus lacked the asperities and were included presumably based on superficial resemblance. On the other hand, a number of other species were included only because of this one character, while other characters contradicted it. The transfer of several such species from *Ambrosiodmus* into *Ambrosiophilus* in this work will hopefully help to alleviate this ambiguity, and will provide a direction creating *Ambrosiodmus* and *Ambrosiophilus* monophyletic and easily distinguishable in the future. The second reason to separate the two genera is the special ecological adaptation seen in many (not all) *Ambrosiophilus* spp. but never observed in *Ambrosiodmus* s. str. - mycocleptism.

Ambrosiophilus atratus **Eichhoff (1875)**

J.H. database code: Scol 507

Previous genus: *Xyleborus*

Compared to unspecified type in BMNH

Diagnosis: Superficially resembles some *Anisandrus* spp., but has no pronotal tuft, and the antennae and protibiae are not flat and type 1, but oblique, type 3. Conspicuous punctuation on pronotum. It differs from most other *Ambrosiophilus* by having less steep elytral declivity with virtually no tubercles, but the declivital stria 1 is impressed.

Length: 3.0-3.2 mm.

Discussion

In a Bayesian multi-gene phylogeny (Cognato et al 2009) the species falls within the *Ambrosiophilus* clade with 100% support. Superficially it resembles *Ambrosiodmus*, but it has key *Ambrosiophilus* characters. The species is transferred in the latter genus based on the absence of pronotal asperities and the overall shape of pronotum, which is not globular but has a flat disc. Transferred to *Ambrosiophilus* by Hulcr & Cognato (2009).

Biology: The Wood and Bright (1992) catalog lists the species as occurring in New Guinea, but its presence here is unclear at best. No verifiable record has been found. The species is native to temperate and subtropical East Asia and has been recently introduced to North America (Rabaglia et al. 2006). It is considered a species not occurring in New Guinea and is treated here only for the sake of completeness. The species does not employ the mycocleptic strategy; each individual female creates her own independent gallery.

Examined material: Japan, (BMNH, 5 indiv.); Japan, (unspecified "type", BMNH); USA, MI, Clinton Co., RoseLake Wildlife Res. Area. 21.ix.2006. (9) A.Cognato coll.; USA, MI, Cassopolis, *Acer*, (Hulcr coll. 2007, 3 indiv.); USA, MI, Cassopolis, *Fagus grandifolia*, (Hulcr coll. 2007); USA, MI, Ionia State Park, *Carya* sp., (Hulcr coll. 2007, 28 indiv.). Additional distribution records in Wood & Bright, 1992, and Rabaglia et al., (2006).

Ambrosiophilus mogia **sp. n. Hulcr & Cognato**

J.H. database code: Scol 335

Diagnosis: The elytral declivity is much more gently punctured than in most *Ambrosiophilus*, all declivital tubercles are minute. Of all *Ambrosiophilus* this species is most closely similar to *A. semicarinatus*, but *A. mogia* is more slender, darker (regularly black), the declivital interstriae are not covered with minute tubercles uniformly such as in *A. semicarinatus*, the circumdeclivital costa is not circular, but rather angulate at the elytral tip. *A. mogia* has been only collected in highlands, while *A. semicarinatus* is widespread in lowland rainforests. It is also similar to *Ambrosiophilus restrictus*, but with smaller antennal club, the first segment of antennal club larger and concave, declivity rounded rather than flat, clear declivital carina present, only few tubercles in elytral interstriae.

Description: Robust, most specimens black, some brown, whole surface with sparse erect setae. The first segment of antennal club small, concave, segments 2 and 3 larger, pubescent. Eyes shallowly emarginate. Submentum very shallowly impressed. Pronotum of basic shape, rounded frontally, without a notable row of serrations on the edge, flat on the disc, smoothly coriaceous but without asperities. Procoxae contiguous, posterocoxal prosternal process slightly inflated, pointed. Protibiae flat, slender in the proximal half, rounded in the distal half, with robust denticles in only slightly enlarged sockets.

Scutellum small, shining, flush with elytra. Elytral disc with evenly spaced parallel rows of strial punctures. Elytral declivity rounded from lateral view, not flat, the first stria is flush with surface, rather than impressed. No tubercles in interstria 1, three larger tubercles in each int. 2, smaller in 3 & 4. Declivity surrounded by elevated carina reaching up to the 7th interstria.

Length: 3.1-3.2 mm.

Discussion

Etymology: Mogia is a common traditional name of the Sinebare people. It is used here to acknowledge the many years of our collaboration with Martin Mogia, a parataxonomist from Chimbu province, now and expert on New Guinean scolytine beetles. Holotype deposited in USNM, paratypes deposited in MSUC, BMNH, NHMW.

Biology: Short branching tunnel. Probably strictly mycocleptous associate of *Beaverium perplexus* in New Guinea highlands, regularly collected in Chimbu province.

Examined material: New Guinea, Morobe Province, Gumi, (FICB); PNG: Chimbu Prov. (33), J. Hulcr 2002-2006.

Figure 26: *Ambrosiophilus mogia* n. sp. Size: 3.1 mm.

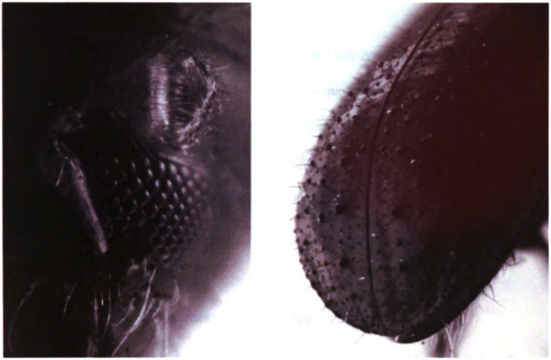

Figure 27: *Ambrosiophilus mogia*, antenna and elytral declivity (not to scale).

Ambrosiophilus restrictus **(Schedl, 1939)**

J.H. database code: Scol 390

Compared to lectotype in NHMW

Redescription: Robust body shape, antenna notably large, yellow, of type 4 with the first segment unusually small and convex. Elytral declivity steep, flat, with elevated circumdeclivital carina, two pairs of robust tubercles in interstria 3, smaller ones in 4 and 5, in rows, wide flat space between them (striae 1 impressed, interstriae 1, 2 without major tubercles) except a pair of blunt tubercles in upper part of interstria 2. Individuals from New Guinea often have iridescent surface of declivity and reduced size of declivital tubercles. Transferred to *Ambrosiophilus* by Hulcr & Cognato (2009).

Length: 2.0-2.6 mm.

Discussion

Representatives collected in Borneo are identical to (non-type) specimens in BMNH. They are larger and have larger declivital denticles than New Guinean representatives from lowlands, but are nearly identical to those from NG highlands. Specimens identified as *Xyleborus cristatulus* by Cox seen at FRC Sabah, Malaysia, fall within the variation span of *A. restrictus*. However, the holotype was not examined.

New junior synonym(s): *Xyleborus devius* Schedl, *Xyleborus australis* Schedl, *Ambrosiodmus incertus* (Schedl)

Biology: Associated with Bornean *Beaverium* spp., mostly *B. latus*.

Examined material: Indonesia, Java, Batoerrad (lectotype, NHMW); Malaysia, Sabah, Danum Valley (18), JH coll. vii.2006; New Guinea, Wisselmeren Enarotadi, (BBM).

Ambrosiophilus semicarinatus **(Schedl, 1942)**

J.H. database code: Scol 252

Previous genus: *Ambrosiodmus*

Compared to holotype in NHMW

Diagnosis: Antennal club of type 2 or 3, first corneous segment rather small, with straight and slightly pubescent margin, segments 2 and 3 large and all pubescent. Very steep and rounded declivity, few uniform scattered tubercles in interstriae 1, 2 and 3, prominent elevated semicircular costa.

Length: 2.4-2.8 mm.

Discussion

Schedl (1942c) mentioned its similarity to *X. tuberculifer*, with declivital carina reaching half of the declivity, with no tubercle on declivity. *X. tuberculifer* however belongs to a different genus, *Truncaudum*. Transferred to *Ambrosiophilus* by Hulcr & Cognato (2009).

New junior synonym(s): *Xyleborus nitens* Browne

Biology: Commonly found parasitizing on fungal gardens of *Beaverium insulindicus* throughout New Guinea.

Examined material: New Guinea, (holotype, NHMW); PNG: Oro Prov. (23), J. Hulcr 2002-2006.

Ambrosiophilus sexdentatus (Eggers, 1940)

J.H. database code: Scol 250

Previous genus: *Ambrosiodmus*

Compared to holotype in USNM

Redescription: Middle size. Antenna type 4- 5. posteriorly prolonged pronotum. Prolonged elytra, declivity impressed along suture, surrounded by an elevated sulcus from elevated interstriae 2 and 3, The sulcus reaches almost to the bases of elytra, and is armed with conspicuous teeth. The species is variable in size.

Length: 2.8-3.2 mm.

Discussion

Placement of this species in the *Ambrosiophilus* subgroup of *Ambrosiodmus* has 100% support in a multi-gene Bayesian phylogenetic analysis (Cognato et al., 2009).The holotype from Java has the same arrangement of teeth and striae. It is slightly shorter (5-10%), the declivital excavation is a little shallower and enclosed by less conspicuous wall. *Ambrosiophilus optatus* (which may eventually be transferred to *Ambrosiophilus*) from Australia closely resembles *A. sexdentatus*, but differs by shallowly excavated declivity. Both *A. sexdentatus* and *A. optatus* have mostly orange to light brown color.

Transferred to *Ambrosiophilus* by Hulcr & Cognato (2009).

Biology: Once recorded as associate of *Beaverium sundaensis*, but the record is uncertain (J.H., unpubl.).

Examined material: Indonesia, Java, Batoerrand, (holotype, USNM); PNG: Madang Prov. (8), Oro Prov. (2), J. Hulcr 2002-2006.

Genus *Anisandrus* Ferrari (1867)

J.H. database code: Scol 786

Type species: *Anisandrus dispar* (Fabricius 1792)

Redescription: Eyes shallowly emarginate or almost entire, only very slightly emarginate, upper portion of eyes smaller than lower part. Antennal club more-less circular shape, or taller than wide, club type one (truncated, first segment covering posterior side). First segment of club circular around the club, covering the entire posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club narrow, pubescent, visible on the anterior side only. Third segment of club absent from the posterior side of club. First segment of antennal funicle shorter than pedicel, or longer than pedicel, its base stalk-like, funicle composed of 4 segments, Scapus appears long and slender. Frons above epistoma rugged, coarsely punctate. Submentum slightly impressed, shaped as a distinct large triangle, or as a narrow slit, or a narrow triangle. Anterior edge of pronotum with two distinct flat denticles protruding anteriad. Pronotum from lateral view tall (type 3), or rounded and robust (type 5). From dorsal view it is conical (type 0), or rounded (type 1). Pronotal disc densely and evenly punctured, often with abundant setae, lateral edge of pronotum obliquely costate, often with a pointed shoulder. Procoxae narrowly separated, prosternal posterocoxal process short, conical or flat, inconspicuous. Tuft on pronotal basis associated with mesonotal mycangium often very distinct and dense; there are no setae on elytral bases associated with elytral mycangium. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc very short compared to the declivity, and usually convex. Punctures on elytral disc confused in New Guinean spesies, in straight lines in temperate species. Boundary between elytral disc and declivity distinct or indistinct, end of disc rounded and smoothly transitioning into declivity. Lateral profile of elytral declivity mildly flat or rounded, dorsal profile of elytral end rounded, or broadened lateraly. Elytral declivity covered with dense erect setae more abundant than strial punctures. Circumdeclivital costa absent or undefinable in tropical species. The inner part of declivity has no tubercles, or only uniform granules, the one species from New Guinea has several tubercles at the very end of elytral declivity. Protibiae obliquely triangular, broadest in 2/3 of the length, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles large, distinctly longer than wide, bases of the denticles distinctly enlarged, conical, between 6 and 8 protibial denticles present.

Metatibiae of regular size. Uniformly dark brown or black. Large species, robust, 4.3-4.3 mm.

***Anisandrus ursa* (Eggers, 1923)**

J.H. database code: Scol 149

Compared to lectotype in USNM

Diagnosis: Very similar to *Hadrodemius globus*, differing by the presence of scutellum and tubercles at the bottom of declivity. Also similar to *Cnestus* mutilatus, from which it differs by the elytra being longer than pronotum, and by the declivity not being as sharply truncated, with no circumdeclivital carina but with distinct tubercles at the elytral end.

Length: 4.3 mm.

Discussion

The only *Anisandrus* known from New Guinea. Transferred to *Anisandrus* by Dole & Cognato (2009) based on detailed character analysis. Holotype: 4.3 mm.

Examined material: New Guinea, Toricelli Mts., (SMTD); New Guinea, Haveri, (lectotype, USNM); PNG: Madang Prov. (57), Oro Prov. (8), West Sepik (1), J. Hulcr 2002-2006.

Figure 28: *Anisandrus ursa*, the only confirmed representative of Anisandrus in New Guinea. Size: 4.3 mm.

Genus *Anceps* gen. n. Hulcr & Cognato

J.H. database code: Scol 843

Type species: *Anceps puer* (Eggers, 1923).

Diagnosis: *Anceps* (specifically the single species *A. puer*) can be distinguished from other Xyleborina genera by its extremely flattened and prolonged elytra broadened posterolateraly, by large socketed denticles on all tibiae, by large and distinctly triangular submentum which is flush with genae, and by the pronotum which is extended anteriad, and lacks serrations on its edge.

Description: Eyes shallowly emarginate, upper portion of eyes smaller than lower part. Antennal club appear taller than wide, club type three (with first segment straight or convex). Edge of the first segment of club straight (may be slightly concave or convex) on anterior face, margin of the first segment clearly costate all around the antenna, or mostly costate, may appear softer on posterior side. Second segment of club visible on both sides of the club, with a narrow corneous part on the anterior side. Third segment of club clearly visible and dominant on both sides of the club. First segment of antennal funicle about as long as pedicel, its base stalk-like, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma mostly smooth, alutaceous, with minor punctures, or rugged, coarsely punctate. Submentum flat, flush with genae, shaped as a distinct large triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view low and rounded (type 1), or prolonged, with low summit (type 7). From dorsal view it is conical (type 0), or conical, long (type 5). Pronotal disc shining with small setae-bearing punctures; the shining part of the disc surrounded by asperate areas laterally. Lateral edge of pronotum obliquely costate. Procoxae narrowly separated, prosternal posterocoxal process tall and pointed. No signs of either mesonotal or elytral mycangia or associated tufts. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge. Elytral disc with punctures in strial lines. Elytral disc and declivity inseparable, the whole disc is rounded and smoothly transitioning into declivity. The elytral declivity very long and flat, slowly descending, distinctly broadened laterally and prolonged apically. Elytra covered with short abundant setae and flat scales. Circumdeclivital costa oblique and broad, ending in the 7th interstriae. There are no tubercles on elytra. Striae and interstriae on the upper part of declivity flat, first interstriae are parallel. Protibiae very slender, posterior side of protibia flat, with setae only. Protibial denticles large, distinctly longer than wide, bases of the denticles distinctly enlarged, conical, usually only 4 or 5 protibial denticles present. Pro- and metatibiae of regular size, also with large socketed denticles. Color uniformly light brown. Body length 2.9-3.2 mm.

Discussion

A genus characterized by a combination of characters of Xyleborina and Dryocoetina. Dryocoetina-like characters include the completely flat submentum, the ventral side of the head being long, almost resembling a short rostrum, narrow tibiae with few large tubercles in enlarged sockets, pronotum conical and dorsally flattened. The same characters however do not refute relatedness of the genus to Xyleborina because, except for the flat submentum, the exact shape of the tibiae, pronotal shape and antennal club are intermediate between Dryocoetina and Xyleborina. Strictly Xyleborina-like characters include the flat and broad elytral declivity (not known to occur in Dryocoetina). The antennal club is of limited information, since there is great overlap in this character between the two groups. It is not known to us whether *Anceps* is a phloem-feeder or a strict ambrosia beetle, which may be a decisive evidence for tribal placement of the genus (Jordal 2002a).

Etymology: (L) of two- natures, confusion. In reference to the intermediate status between Dryocoetina and Xyleborina.

Figure 29: *Anceps puer*, 3 mm.

Anceps puer comb. n. (Eggers, 1923)

J.H. database code: Scol 646

Previous genus: *Leptoxyleborus*

Compared to co-type in NHMW

Redescription: *Anceps puer* is the only known representative of this monotypic genus. The generic characters sufficiently describe and distinguish the species from other Xyleborina.

Length: 2.9-3.2 mm.

Discussion

Anceps (as *Xyleborus*) *puer* was included in *Leptoxyleborus* by Wood & Bright (1992). However, except the superficially similar flattened declivity and narrow protibiae, most of its distinguishing characters are unique to *Anceps*, not occurring in *Leptoxyleborus*.

Even the details of the protibiae and declivity vary substantially between the two. In *A. puer*, the protibiae resemble that of Dryocoetina, while the protibiae of *Leptoxyleborus* are simply a narrower example of Xyleborina protibiae. The elytra in *A. puer* are simple, evenly sloped, with uniform rows of punctures and setae. On the other hand, the elytra of *Leptoxyleborus* have rather complicated shape, convex disc and concave declivity, with the surface of declivity differing dramatically from that of elytral disc (declivity rugose, with dense star-like scales, disc shining, with variable punctuation).

New junior synonym(s): *Leptoxyleborus ceramensis* (Schedl)

Examined material: Indonesia, Sumatra, Sipora, (co-type, NHMW); Malaysia, Sarawak, Bako NP, (B. H. Jordal), 50m a.s.l., 1998, Beaver det.

Genus *Arixyleborus* Hopkins (1915)

J.H. database code: Scol 779

Type species: *Arixyleborus rugosipes* Hopkins (1915).

Redescription: Eyes shallowly or deeply emarginate, sometimes almost disjunct, upper portion of eyes smaller than lower part, or as large as the lower part. Antennal club more-less circular shape, often appears broader than tall and asymmetrical. Antennal club type two (obliquely truncated, second segment visible on posterior side). First segment of club circular around the club, covering the entire posterior face, or covering most of the posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club narrow, pubescent, visible on the anterior side only, or visible on both sides of the club, but soft, or the corneous part visible only on the anterior side. Third segment of club absent from the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma mostly smooth, alutaceous, with minor punctures, or rugged, coarsely punctate. Submentum deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope), or with a distinct row of serrations. Pronotum from lateral view of basic shape (type 0), or prolonged, with low summit (type 7). From dorsal view it is basic, short, parallel-sided, rounded frontally (type 2), or conical on the anterior part (type 6), or prolonged basic shape with rounded frontal margin (type 7). Pronotal disc densely and evenly punctured, or with dense setae, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous. Tuft of setae on pronotal basis associated with mesonotal mycangium absent, or similar tuft present but does not indicate mesonotal mycangium; setae on elytral bases associated with elytral mycangium also absent. Scutellum flat, flush with elytra, or regular size, impressed medially. Elytral bases straight, with oblique edge, or with slightly curved margin, even though there is no mycangium in the elytra. Elytral disc longer than declivity, flat, or slightly convex or bulging, punctures on elytral disc in strial lines (which may be difficult to discern), or confused. Boundary between elytral disc and declivity is distinct. Lateral profile of elytral declivity is mildly flat or rounded, or truncated, in some species with teeth or ridges on the edge. dorsal profile of elytral end rounded, or angulate. Elytral declivity with few setae or scales, or covered with dense setae which are more abundant than strial punctures. Circumdeclivital costa absent or indefinable, or ending in the 7th interstriae. The inner part of declivity has no tubercles, or only uniform granules, or there are tubercles on elevated ""wall"" around declivity. Striae and interstriae on the upper part of declivity are either entirely confused and covered with rugose tubercles, or form ridges and furrows, or bear teeth around the declivity. First interstriae are parallel (sometimes slightly broadened towards elytral summit), or parallel on disc but broadened towards the apex of elytra, where they sometime bear tubercles. Protibiae very slender, slightly broader only at the distal end. Posterior side of protibia flat, with setae only, or appears inflated, often with several granules. Protibial denticles small, usually between 6 and 8 present, bases of the denticles small, slightly elevated. Metatibiae of regular size. Color uniformly dark brown (pronotum sometimes slightly lighter), or uniformly black (pronotum sometimes slightly lighter). Length: 1.2-3.2 mm.

Discussion

Schedl (1958) proposed 3-segmented antennal funicle as the genus-distinguishing character, but Browne (1963) examined more species in more detail and determined that most species have a 5 segmented funicle. Browne (1955) examined larvae of two *Arixyleborus* species and found their morphology typical of that in *Webbia* larvae. Also the curved, coarse protibia with numerous denticles, and a cavity brood gallery, suggested relatedness of the two genera. Eggers regularly treated species of *Arixyleborus* as *Webbia* (e.g., Eggers 1927c). *Arixyleborus* has often been recognized as closely related to *Webbia* and *Schedlia*, in fact, the three genera have been commonly treated as representatives of their own tribe Webbini (e.g., Browne 1961c).

Biology: Some SE Asian species of *Arixyleborus* seem to be specialized on Dipterocarpaceae, while others (all New Guinea species) are generalists. Browne (1961c) attempts to attach phylogenetic meaning to these different strategies, however, nothing is known about the evolution of the group.

Figure 30: *Arixyleborus puberulus*, common and variable representative of *Arixyleborus* in New Guinea; 2.3 mm.

***Arixyleborus abruptus* Schedl (1975)**

J.H. database code: Scol 602

Compared to holotype in NHMW

Redescription: One of the smallest *Arixyleborus*. Differing from other *Arixyleborus* by the abruptly truncated declivity. The declivital apex appears constricted from above in some specimens. Slightly bulging tip of elytra.

Length: 1.5-1.9 mm.

Discussion

Individuals previously identified as *A. iriani* look superficially different due to the flat scales on declivity, and due to their smaller size. However, all other charactesr are nearly identical. Also, *A. medius* from Philippines (Eggers type seen in USNM) is similar in body shape, size, elytra but it has a much less truncated elytra, no flattened setae and only small tubercles on declivity.

New junior synonym(s): *Arixyleborus iriani* Browne

Examined material: New Guinea, Morobe Province, Bulolo, (MSUC), identified by Schedl; New Guinea, Morobe Province, Bulolo, (holotype, NHMW); New Guinea, Morobe Province, Bulolo, (NHMW).

Arixyleborus canaliculatus **(Eggers, 1923)**

J.H. database code: Scol 9

Compared to lectotype in USNM

Redescription: One of the most common *Arixyleborus* in New Guinea. It differs from other *Arixyleborus* mainly on the basis of its pronotum and elytrae. The pronotum is rounded anteriad, with a row of serrations on the anterior margin, not very prolonged posteriad, appearing slightly conical from a dorsal view. The basal part of elytral disc is shining, with shallow inconspicuous punctures, the posterior part of the disc has the same surface as the declivity: First 7 striae on each elytron are transformed into deep and prominently dull furrows, while the interstriae form elevated ridges. No other major rugosities are present, except small curved teeth on the interstrial ridges on the edge between disc and declivity. The extent of the furrow and ridges on the elytral disc is very variable. Individuals previously identified as *A. cariniceps* Schedl reach sizes up to 2.6 mm.

Length: 2.1-2.6 mm.

Discussion

Wood (1989) synonymized *X. subsimilis* Schedl with this species. *A. canaliculatus* (especially the slightly larger form described by Schedl (1975f) as *A. cariniceps*) is similar to and *A. grandis*, differing in smaller size, much more coarse asperities on the frontal slope of pronotum, shorter and more shining elytral disc. *A. canaliculatus* is very similar to *A. malayensis* Schedl, which has shining pronotal disc, and the strial ridges on its elytra reach only little beyond the declivital summit. However, a specimen identified as *A. canaliculatus* (R. A. Beaver det.) from Thailand bears intermediate state of these two characters. In the future, *A. malayensis* may become a junior synonym of *A. canaliculatus*.

Previously synonymized species: *Arixyleborus subsimilis* Schedl

New junior synonym(s): *Arixyleborus cariniceps* Schedl

Examined material: New Guinea, (FICB); New Guinea, Morobe Province, Bulolo, (FICB); New Guinea, Paumomu riv., (lectotype, USNM); New Guinea, Madang Province, Baitabag, (Hulcr coll., 2 indiv.); PNG: Madang Prov. (108), Oro Prov. (15), West Sepik (1), J. Hulcr 2002-2006.

***Arixyleborus cariniceps* syn. n. Schedl (1975)**

Synonymized with: *Arixyleborus canaliculatus (Eggers)*

J.H. database code: Scol 603

Compared to holotype in NHMW

Length: 2.6 mm.

Discussion

Schedl (Schedl, 1975f) did not provide differences between *A. cariniceps* and *A. canaliculatus* other than size. To our knowledge, only one specimen of *A. cariniceps* has ever been collected, the holotype. After detailed examination of the holotype of *A. cariniceps* and multiple specimens of *A. canaliculatus*, no consistent morphological difference was found.

Examined material: New Guinea, East Sepik, Wewak, (holotype, NHMW).

Arixyleborus grandis **(Schedl, 1942)**

J.H. database code: Scol 48

Compared to holotype in NHMW

Redescription: The largest *Arixyleborus* in New Guinea. The elytra are very similar as in the common *A. canaliculatus* - shallow parallel strial furrows and interstrial ridges, almost no hair. Ridges decreasing in height and disappearing towards elytral apex. Strial furrows shagreen, with punctures. Boundary between disc and declivity indiscernible, smoothly rounded (unlike A. canaliculatus). Punctures on pronotal disc largest at the pronotal base. Pronotal lateral edge distinctly costate, nearly carinate (blunt in *A. canaliculatus*).

Length: 3.2 mm.

Discussion

Browne's coll. in BMNH contains slightly variable specimens.

Biology: Male described from Java (Schedl 1971c).

Examined material: Indonesia, Java, Buitenzorg, (holotype, NHMW, 3 indiv.); PNG: Madang Prov. (1), J. Hulcr 2002-2006.

Arixyleborus guttifer syn. n. (Schedl, 1955)

Synonymized with: _Arixyleborus scabripennis (Blandford)_

J.H. database code: Scol 606

Compared to holotype in NHMW

Discussion

The holotype has the elytral sculpturing identical to that of *A. scabripennis*. The completely brushed-off pubescence appears to be the only difference compared to the *A. scabripennis* holotype . *A. scabripennis* is a very variable species, but all specimens have one row of tubercles per interstria (the tubercles themselves are of various shapes and sizes). *Arixyleborus guttifer* was described as *Xyleboricus guttifer* (Schedl, 1955b). Schedl (1955b) mentioned the similarity of his newly described *Xyleboricus guttifer* to *A.* (as *Xyleborus*) *canaliculatus*. He did not compare the species to any other *Arixyleborus*.

Examined material: New Guinea, (holotype, NHMW).

Arixyleborus iriani syn. n. Browne (1983)

Synonymized with: _Arixyleborus abruptus Schedl_

J.H. database code: Scol 295

Compared to holotype in BMNH

Discussion

The only difference between the holotypes of both species is the flattened setae on the declivity of *A. iriani*, which gives the beetle a different appearence. The holotype of *A. iriani* differs slightly from specimens from Eastern part of New Guinea except that interstria 1 is not elevated, and not bulging. Browne (1983b) mentions its similarity to *A. rugosipes*, and notes that the declivity of *A. iriani* is more abrupt and subtruncate.

Biology: Browne (1986b and 1983b) reports the species from West Papua.

Examined material: New Guinea, West Papua, Misool Isl., (holotype, BMNH), imported to Japan (Nagoya); PNG: Madang Prov. (4), Oro Prov. (6), J. Hulcr 2002-2006.

***Arixyleborus minor* (Eggers, 1940)**

J.H. database code: Scol 755

Compared to non-type

Redescription: One of the smallest *Arixyleborus*, with rather slender body and unique declivity. The declivity is composed of rugged and granulated interstrial ridges and dull strial furrows as in other *Arixyleborus* spp., but the second, fourth and fifth interstriae are reduced on the declivity, while the first and third interstriae are larger. The extent of this alternate expression is variable, though, and can be inconspicuous in some specimens. The pronotum is prolonged posteriad, dull, alutaceous.

Length: 1.2-1.4 mm.

Discussion

Holotype not in ZMA or in Leiden's (RMNH) Kalshoven's collection, probably in MZB (Museum Zoologicum Bogoriense, Cibinong, Java, Indonesia). Non-type specimens available in Leiden, although not from the type locality. Malaysian specimens slightly shorter, but morphologically identical.

New junior synonym(s): *Arixyleborus trux* Schedl

Examined material: Indonesia, Java, (NHMW, 2 indiv.), males, one of them allotype; Malaysia, Selangor, Kepong, (BMNH, 2 indiv.); Malaysia, (BMNH); New Guinea, Morobe Province, Bulolo, (MSUC); New Guinea, Morobe Province, Bulolo, (NHMW).

Arixyleborus morio syn. n. (Eggers, 1923)

Synonymized with: _Arixyleborus puberulus (Blandford)_

J.H. database code: Scol 76

Compared to lectotype in USNM

Discussion

The type specimen of *Arixyleborus morio* lies on the end of a continuum of a variation of the elytra seen in *Arixyleborus puberulus*. In *A. morio*, the shagreened tubercles on discal interstriae are smaller and more neatly aligned in two rows than in most other representatives of *A. puberulus*. Transferred to *Arixyleborus* from *Xyleborus* by Browne (1955).

Examined material: Malaysia, Sabah, Danum Valley, Parashorea malaanonan trunk, (Hulcr coll.); New Guinea, Morobe, (BBM); New Guinea, Watut valley, (FICB); New Guinea, (FICB); New Guinea, Malu, (lectotype of Xyleborus morio Eggers, USNM);

New Guinea, (Hulcr coll., 2 indiv.); PNG: Madang Prov. (91), Oro Prov. (17), West Sepik (6), J. Hulcr 2002-2006.

***Arixyleborus puberulus* (Blandford, 1896)**

J.H. database code: Scol 319

Compared to holotype in BMNH

Redescription: Declivital disc of this species varies in three characters: the size of the tubercles, the evenness of the tubercles, and the width of the interstrial ridges as compared to the strial furrows. The tubercles vary from small to large, from evenly sized (small or large) to being of variable size. The width of elytral ridges varies from 1) prominent interstriae with large tubercles and small, often hard to discern striae, to 2) narrow interstrial ridges with small tubercles and easy-to-follow smoother furrows. The size and organization of tubercles on the elytral base vary widely among representatives of the species, but the size of the tubercles increases and the clarity of striation decreases towards the elytral apex in all individuals, so the tubercles on the declivital slope are universally large and confused. These different morphs do not seem to follow any geographic pattern, and are likely just random variation of declivital surface which is universally plastic in Xyleborina.

Length: 2.2-2.6 mm.

Discussion

There are two principal differences between the puberulus complex and other similar *Arixyleborus*: 1) the presence of two or more rows of tubercles on the elytral interstriae and 2) the absence of conspicuously larger tubercles on the disc-declivity boundary.

Intermediates exist (e.g., the row of tubercles is irregular, and may be regarded as two), but are rare, and do not warrant more synonymies at this time. Another difference from several SE Asian species with similar elytral sculpturing is the absence of a prominent row of pronotal serrations. Individuals from higher elevations tend to be longer than those from lowlands, but maintain the same body width.

The holotype of *A. puberulus* from Blandford's collection in BMNH has the declivital tubercles organized by rows on the declivital disc, tubercles are larger and less aligned at the posterior part of elytra; tip of elytra bulging. Asperities on the frontal slope of pronotum covering part of disc behind summit. Some specimens from PNG highlands have notably longer abdomen than the holotype and have a pair of small bulges with big tubercles at the tip of declivity. A non-type specimen identified by Browne as *A. puberulus* from PNG (Gumi) is very similar to these specimens. Transferred to *Arixyleborus* from *Xyleborus* by Browne (1955).

New junior synonyms: *Arixyleborus morio* (Eggers)

Examined material: Malaysia, Sarawak, (holotype, BMNH); Malaysia, Sabah, Danum Valley, (BMNH); New Guinea, Chimbu Province, Ialibu Mt., (FICB, 5 indiv.); New Guinea, (Hulcr coll.); PNG: Chimbu Prov. (197), J. Hulcr 2002-2006.

***Arixyleborus scabripennis* (Blandford, 1896)**

J.H. database code: Scol 447

Compared to holotype in BMNH

Redescription: Most of the elytral surface rugged except shiny around scutellum. The ridges are tuberculate along most of their length, one line of tubercles on each stria. Most representatives have the largest tubercles on the disc-declivity boundary. The tubercles are usually large, regularly spaced, interspersed with small, irregularly spaced tubercles, but the exact size and extent of tuberculation vary extensively. Slope of declivity vary.

Length: 2.1-2.2 mm.

Discussion

Transferred to *Arixyleborus* from *Xyleborus* by Browne (1955). Browne (1980b) reported this species as imported on a log to Japan from New Guinea.

New junior synonym(s): *Arixyleborus guttifer* (Schedl)

Biology: It is unclear whether the record of this species from PNG is valid. *Arixyleborus scabripennis* is mentioned as occurring in PNG by Wood and Bright (1992), but the present authors did not discover the primary reference. The species is common in SE Asia (Beaver & Browne 1978; Hulcr, unpubl.).

Examined material: Malaysia, Sarawak, (holotype, BMNH); Malaysia, Sabah, Danum Valley, Mallotus sp. branches, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Danum Valley, Ficus sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Parashorea malaanonan branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Parashorea malaanonan trunk, (Hulcr coll., 6 indiv.).

Arixyleborus simplicaudus **sp. n. Hulcr & Cognato**

J.H. database code: Scol 350

Diagnosis: This species differs from other *Arixyleborus*, by a number of characters, most important among them is the slender body shape, the flat protibia (not slender and inflated posteriad), and the unusually inconspicuous surface of elytra. The elytral disc is shining and regularly striate-punctate, rather than opaque or rugose as in other *Arixyleborus*. The elytral declivity surface is flat, matt but not rugose, interstriae with several minor granules.

Description: Antennal club asymmetrical (typical for *Arixyleborus*). The first segment strongly corneous, with conspicuous semicircular costa around almost the whole club, segment 2 much less conspicuous, only slightly corneous or not, barely visible on the posterior side, segment 3 greatly reduced. Eyes deeply emarginate. Submentum deeply impressed, with rounded margin. Pronotum short, basic type, with no conspicuous serrations on the anterior edge, shagreened on the disc. Procoxae contiguous, posterocoxal prosternal process short, pointed. Protibia flat, slightly shagreened and almost no granules on posterior side. Scutellum small, flush with elytra. Mesonotal or elytral mycangium not visible. On elytral disc, the slightly impressed striae are not shagreen, surface as shiny as interstriae. Elytral disc long and straight, rather sharply descending to declivity. Declivity shagreen, with minor sharp tubercles, this surface extend only marginally to otherwise smooth disc. Striae 4, 5, 6 and 7 merge sequentially with the stria 3 on the declivity.

Length: 2.6 mm.

Discussion

Etymology: The specific epithet refers to the simple and inconspicuous surface of declivity, an unusual character in *Arixyleborus* where in most species the elytral surface is greatly modified into furrows, ridges and dense tubercles. Holotype deposited at USNM, paratypes at MSUC, BMNH and NHMW.

Examined material: PNG: Chimbu Prov. (24), J. Hulcr 2002-2006.

Figure 31: ***Arixyleborus simplicaudus sp. n.*** **Size: 2.6 mm.**

Figure 32: *Arixyleborus simplicaudus*, a typical *Arixyleborus*-like antenna, but atypical flat protibia. Not to scale.

***Arixyleborus trux* syn. n. Schedl (1975)**

Synonymized with: *Arixyleborus minor (Eggers)*

J.H. database code: Scol 608

Compared to holotype in NHMW

Length: 1.2 mm.

Discussion

The holotype of *A. trux* Schedl has the same unique structure of elytral declivity as the earlier described *A. minor*. Schedl (1975f) likened the species to *A. canaliculatus*, with the exception that only alternate interstriae are costate and granulate on the declivity. However, later he identified nearly identical specimens as *A. minor* which supports the synonymy of *A. trux*.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW), of A. trux, Wylie & Shanagan 1972 coll., sticky trap.

Genus *Beaverium* Hulcr & Cognato (2009)

J.H. database code: Scol 811

Type species: *Beaverium insulindicus* (Eggers, 1923).

Diagnosis: *Beaverium* spp. can be distinguished from most other Xyleborina by the large size, very robust, rounded elytral disc and distinctly flattened elytral declivity broadened posterolaterally. The genus is unique in Xyleborina in that the posterolateral declivital costa ends in 5th interstriae. The most similar genus is *Fortiborus*, from which *Beaverium* can be distinguished by the lack of tubercles on declivity, and by the continuous elevated carina on the anterior edge of pronotum (in most species).

Description: Eyes deeply emarginate, sometimes almost disjunct, upper portion of eyes as large as the lower part, or conspicuously large. Antennal club more-less circular shape, club type three (with first segment straight or convex), or four (first segment small, second and third prominent on both sides). First segment of club straight (may be slightly concave or convex) on anterior face, or convex, small, margin of the first segment mostly costate, may appear softer on posterior side. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only, or corneous on both sides of club, but sinuate, not strictly circular (not making antenna tall, or "telescopic"). Third segment of club clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, sometimes longer than pedicel with its base stalk-like.

Funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum slightly impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum usually with short continuous elevated recurved carina, in one species the edge is blunt. Pronotum from lateral view tall (type 2), or rounded and robust (type 5). From dorsal view it is conical (type 0), or rounded (type 1), or subquadrate (type 3). Pronotal disc densely and evenly punctured, often with asperities resembling those on the frontal slope, lateral edge of pronotum obliquely costate, often with distinctly elevated shoulder. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous, or conical and slightly inflated. No signs of mesosternal or elytral mycangia or the associated setae. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity and slightly convex or bulging, or impressed, "saddle-like". Punctures on elytral disc in strial lines, but the lines disappear and punctures become confused on the declivity. Boundary between elytral disc and declivity distinct, or indistinct, end of disc rounded and smoothly transitioning into declivity. Lateral profile of elytral declivity slowly descending or steep, flat or excavated, dorsal profile of elytral end broadened laterally, or shallowly emarginate. Elytral declivity with few setae or scales, not conspicuously pubescent. Circumdeclivital costa ending in 5th interstriae, a unique feature of the genus. The inner part of declivity has no tubercles, or only uniform granules. Striae and interstriae on the upper part of declivity even. First interstriae are parallel. Protibiae obliquely triangular, broadest in 2/3 of the length, or distinctly triangular, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles can be small but mostly are large and distinctly longer than wide, bases of the denticles slightly elevated, or distinctly enlarged, conical, protibial denticles present usually between 6 and 8. Metatibiae of regular size. Large to very large species, robust, 3.8-7.5 mm. Mostly uniformly dark brown or black, pronotum sometimes lighter.

Discussion

Etymology: The genus is named in honor of Roger A. Beaver, one of the most prominent contemporary bark beetle taxonomists, whose assistance and material was indispensable during this project. Gender masculine (masculine English origin, ICZN Code 30.2.).

Schedl (1942c) includes the following species into the "insulindicus-sweyzeyi" species-group: insulindicus, sweyzeyi Beeson, sundaensis, aplanatideclivis. According to Beeson's (1929) illustration of *X. swezei*, the species clearly belongs to the genus *Beaverium*. Early authors describing various species of this genus often used the declivital punctuation as an important character, and distinguished "confused punctures" from "punctures in likes". In reality, the strial punctures are always aligned, while interstrial punctures are almost never aligned and rarely present as only one row per interstria. Thus, the above mentioned distinction actually describes different sizes of strial and interstrial punctures, where 1) if interstrial punctures are small, strial punctures stand out and the elytrae appear striato-punctate, while 2) if interstrial punctures are as large as strial ones, the whole surface appears confused. Furthermore, upon examination of many specimens of various forms previously ascribed to various species, this character actually forms a continuum of variation which transcends specific boundaries and often doesn't co-vary with other characters.

Figure 33: *Beaverium insulindicus*, type species and the most common representative of the genus in New Guinea. Size: 6 mm.

Beaverium insulindicus Eggers (1923)

J.H. database code: Scol 30

Previous genus: *Xyleborus*

Compared to lectotype in USNM

Diagnosis: Pronotal margin rounded, with elevated recurved carina. The boundary between elytral disc and declivity unclear, continuously rounded. Declivital posterolateral margins broadened and flattened, but not beyond the apparent width of elytra, elytra only slightly (or not at all) constricted before the broadened end. Declivital punctures small, numerous, confused. End of declivity varied, from rounded to small emargination. Varied body length.

Length: 5.3-6.2 mm.

Discussion

The synonymy of the junior name *Xyleborus glaberrimus* Schedl is confirmed (the holotype of *X. glaberrimus* examined in NHMW). According to Schedl (1942c), *X. glaberrimus* differs from *X. insulindicus* by steeper slope and more dense punctuation of declivity, which are some of the most very plastic characters in this genus. Transferred to *Beaverium* by Hulcr & Cognato (2009).

Previously synonymized species: *Xyleborus glaberrimus* Schedl

New junior synonym(s): *Xyleborus depressurus* Browne, *Xyleborus annexus* Schedl

Biology: Short branching gallery.

Examined material: New Guinea, Morobe Province, Bulolo, (B. H. Jordal), identified as *X. annexus* by Beaver ex desc.; New Guinea, Fiume Purari, (MCG); New Guinea, Paumomufluss, (lectotype, USNM); PNG: Madang Prov. (9), Oro Prov. (38), J. Hulcr 2002-2006.

Beaverium perplexus **Schedl (1969)**

J.H. database code: Scol 241

Previous genus: *Xyleborus*

Compared to lectotype in ANIC

Diagnosis: Pronotum without prominent elevated carina on the anterior margin, pronotal disc with faint asperities. Broadly rounded apex of elytra, unlike *B. insulindicus*, where elytral end is usually flat or even slightly emarginate. Declivital punctures mostly in rows, confused at elytral apex, but not completely confused as in other *Beaverium*. The costa at the posterolateral edges of declivity is unusually elevated, almost broader than the rest of elytrae, creating conspicuously large declivital plane. Transferred to *Beaverium* by Hulcr & Cognato (2009).

Length: 4.8-5.1 mm.

Discussion

Schedl (1969b) mentioned its similarity to *B. insulindicus* (as *Xyleborus*). Browne (1984f) also mentioned the similarity of this species to *Beaverium* (as *Xyleborus*) *insulindicus*, and distinguished it by more dense punctures on declivity, the punctures are said to be more confused, not strictly following striae. This seems to be the reverse of what can be seen on the holotypes, however. The species differs from *B. insulindicus* very little, and no doubt eventually intermediate forms will be found. In this work, two consistent difference were found: absence of pronotal anterior elevated carina, and the declivital plane is broader than the rest of elytra, appears more flat. Pronotum often appears taller, but not always. The Catalog of Scolytidae and Platypodidae (Wood & Bright, 1992) indicate that the holotype of *X. perplexus* Schedl was collected in Kerevat, New Britain. The holotype is from Mt. Hagen, Western Highlands District, Papua New Guinea.

Transferred to *Beaverium* by Hulcr & Cognato (2009).

New junior synonym(s): *Xyleborus platyurus* Browne

Biology: Probably a strictly montane species. All known records come from Chimbu or Western Highland Provinces.

Examined material: New Guinea, Western Highlands, Mt. Hagen, (unspecified "type", ANIC); PNG: Chimbu Prov. (64), J. Hulcr 2002-2006.

Beaverium rugipunctus **sp. n. Hulcr & Cognato**

J.H. database code: Scol 340

Diagnosis: The species differs from among *Beaverium* spp. with its subquadrate pronotum, bulging on its anterolateral corners, devoid of any elevated carina or serrations on its anterior edge, and by the large punctures on elytral declivity, intensely shagreened and opalescent. Elytral punctures in other *Beaverium* spp. are also often shagreen, but never so large that the whole declivital surface appears opaque.

Description: Antenna type 2, with corneous first segment with concave margin, and soft and pubescent segments 2 and 3, which are clearly visible on the posterior side of the club. Eyes large, shallowly emarginate. Submentum obliquely impressed. The species is perhaps most characteristic with its subquadrate pronotum, bulging on its anterolateral corners. There is no carina or row of serrations on the anterior margin of pronotum. Pronotum faintly shagreen. Procoxae adjacent, posterocoxal prosternal process large, slightly inflated. Protibiae narrow at the proximal part, broadened and triangular at the distal part with 6 denticles in slightly enlarged sockets. Scutellum visible. Elytra rounded, almost globular in their profile, flattened only at the end of declivity. Declivital surface covered with large broadened elytral punctures with conspicuously shagreened internal surface. The punctures are slightly confused, and so large, that the whole declivity seems coarse. Only a minute emargination on the declivital apex.

Length: 4.5-4.8 mm.

Discussion

The subquadrate pronotum, in combination with other more typical *Beaverium* features (large eyes, stalk-like first segment of antennal funicle), indicates a possible phylogenetic relationship of this species to *Euwallacea* s. str. However, the posterolateral elytral costa ends in the 5th, not 7th interstria, the overall shape of elytra is that of *Beaverium*, the punctures on elytra are rather confused, not aligned as in *Euwallacea*, and the protibia has much smaller socketed denticles than *Euwallacea*, though it is also notably triangular at its apex.

Holotype deposited in USNM, paratype deposited in MSUC.

Examined material: PNG: Oro Prov. (1), West Sepik (2), J. Hulcr 2002-2006.

Figure 34: *Beaverium rugipunctus sp. n.* Size; 4.6 mm.

Beaverium sundaensis **Eggers (1923)**

J.H. database code: Scol 243

Previous genus: *Xyleborus*

Compared to lectotype in USNM

Diagnosis: Smallest representative of the genus in PNG, but size variable. Pronotum with elevated recurved carina on the frontal margin. Long and broad declivity, but notably narrower than in other *Beaverium* spp., attenuated towards the end. The costa around declivital end is blunt costa. Punctures on declivity are of variable size, usually small and completely confused, however in some specimens the strial punctures are larger than the interstrial ones, creating an impression of more aligned declivital surface. Little or no emargination of the end of elytra. Flat or rather concave elytral horizon.

Length: 3.8-4.8 mm.

Discussion

Non-types of rufobrunneus from Philippines seen in BMNH and FICB are almost the same. Their strial and interstrial punctures on the whole declivity vary, usually all of the same size and confused. Pronotum and colors the same. *X. rufonitidus* from Java also has a concavity on elytral disc. Browne (1961c) placed the species among the "major group", with *X. pseudopilifer*, *X. latus*, and so on, which however seem to belong to different genera. Transferred to *Beaverium* by Hulcr & Cognato (2009).

New junior synonym: *Xyleborus aplanatideclivis* Schedl

Examined material: Indonesia, Java, Poerwakarta, (lectotype, USNM); PNG: Madang Prov. (6), Oro Prov. (2), J. Hulcr 2002-2006.

***Beaverium venustulus* Schedl (1969)**

J.H. database code: Scol 718

Previous genus: *Xyleborus*

Compared to paratype in NHMW, FICB

Diagnosis: *X. venustulus* (paratype in NHMW seen) is the largest *Beaverium* in New Guinea. Usually dark colored. Pronotal margin with elevated recurved carina. Elytral disc flat or slightly concave, saddle-like. The end of declivity mostly shallowly emarginate, but this character seem to vary within *Beaverium* spp. Transferred to *Beaverium* by Hulcr & Cognato (2009).

Length: 6.7-7.5 mm.

Discussion

Schedl (1969b) mentioned the similarity of this species to *B.* (as *Xyleborus*) *insulindicus*, and notes the following differences: *B. venustulus* is more slender, the heart-like depression of elytral declivity more developed (unclear), distinctly separated from the disc, the punctuation is coarser. The only consistent difference between the examined series of *B. venustulus* and that of *B. sundaensis* (including types of both species) is the body size. The larger specimens currently designated as *B. venustulus* have all been collected in the highlands, while most of the smaller *B. sundaensis* are from the lowlands. The tendency of body size to increase with elevation is common in Xyleborina, thus *B. venustulus* and *B. sundaensis* may be just two size forms of the same lineage, and intermediates will likely be found.

Examined material: New Guinea, Western Highlands, Jimi Valley, (paratype, FICB); New Guinea, Moroka, (MCG); New Guinea, Western Highlands, Jimi Valley, (paratype, NHMW).

Genus *Bluncus* Hulcr & Cognato (2009)

J.H. database code: Scol 783

Type species: *Biuncus papatrae* (Schedl, 1972).

Diagnosis: Although the overall appearance of *Biuncus* is unique among Xyleborina, there are rather few characters that unambiguously distinguish the genus. With its bulky, light-colored body, it may resemble some *Xylosandrus* spp., but can be distinguished by contiguous procoxae. From most other Xyleborina, it can be distinguished by a very robust pronotum usually with two serrations pointing forward on the pronotal anterior edge, by the flattened antennal club of type 1, slender protibiae (in most species), and most importantly by its short elytral disc and very long, flat, broad, and laterally costate elytral declivity, usually with one or two pairs of denticles on its upper part.

Description: Eyes shallowly emarginate, "bean shape", upper portion of eyes smaller than lower part. Antennal club more-less circular shape or slightly asymmetrical, taller than wide, always very flat. Antennal club type one (truncated, first segment covering posterior side). First segment of club circular around the club, covering the entire posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club narrow, pubescent, visible on the anterior side only. Third segment of club absent from the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick, or appear long and slender. Frons above epistoma mostly smooth, alutaceous, with minor punctures. Submentum flat, flush with genae, or slightly impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with two distinct flat denticles protruding anteriad. Pronotum from lateral view rounded and robust (type 5), exceptions are rare. From dorsal view it is rounded (type 1). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous, or tall and pointed. No sign of mesonotal or elytral mycangial opening. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat, or longer than declivity and slightly convex or bulging, punctures on elytral disc in strial lines (which may be difficult to discern). Elytral disc almost always short, often convex, elytral declivity flat, gently sloped, conspicuously broadened and costate along its posterolateral edges, the edges bearing carina, which ends in 7th interstriae. Each of second and third interstriae often bears a tooth or a pointed hook on the summit of declivity, which is the most important diagnostic character of individual species. Elytral declivity with few setae or scales, not conspicuously pubescent, except for small appressed setae in several species. Circumdeclivital costa ending in 7th interstriae. The inner part of declivity has no tubercles. Striae and interstriae on the upper part of declivity even, or bearing teeth around the declivity. First interstriae are parallel (sometimes slightly broadened towards elytral summit), or parallel on disc but broadened towards the apex of elytra, where they often bear tubercles. Protibiae sometimes obliquely triangular, broadest in 2/3 of the length, but mostly very slender, slightly broader only at the distal end. Posterior side of protibia flat, with setae only. Protibial denticles large, distinctly longer than wide, bases of the denticles slightly elevated, or distinctly enlarged, conical, fewer than 6 protibial denticles present. Metatibiae of regular size. Uniformly yellow, orange, light brown or reddish species, pronotum often much lighter (yellow or orange) than elytra. However, some species display a drastic change of color between the lowland and highland populations, with the lowland beetles being yellowish to brown, often bicolored, while the montane forms are typically black. Length: 1.4-3 mm. Length: 1.4-3 mm.

Discussion

Morphologically this genus is rather uniform. Within the genus, the main distinguishing feature of many *Biuncus* spp. is the size and constellation of elytral denticles and granules. At the same time, in many cazes the size of many of these cuticular processess seems to be correlated, suggesting a single quantitative genetic mechanism. For example, *Biuncus haberkorni* and *Biuncus conidens* are both distinguished from other *Biuncus* spp. by having two pairs of equal-sized denticles on the elytral declivity (as opposed to a single pair, or two pairs of unequal size). Between each other, they differ by the size of the declivital denticles, the size of granules on the tip of declivity, and the size of denticles on the edges of tibiae. All these are larger in *B. conidens*. However, it is possible that the size of denticles all over the body is driven by a single genetic mechanism, thus all these above mentioned differences are in fact just a single character. It is thus possible that these two species simply occupy different parts of a continuum of morphological change and may be synonymized (as many other *Biuncus*). Browne (1961c) includes species of *Biuncus* into the "*mucronatus* group".

Biology: The genus is mostly of SE Asian and Melanesian distribution, with one species (*Xyleborus clerodendronae*, unpublished data) reaching Africa. Browne (1961c) provides brief notes on ecology of several Malaysian species, but doesn't mention any co-occurrence with a potential parasitized species. Species are found in all sizes and decay states of wood, from dry twigs to humid trunks.

Figure 35: *Biuncus papatrae*, the type species of the genus and a rather common representative in New Guinea. Size: 2.3 mm.

Biuncus adossuarius **Schedl (1951)**

J.H. database code: Scol 746

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: Two small recurved spines on each elytron. Declivity surface shagreen, dull, interstriae often slightly elevated, each with a line of minute granules. Elytral disc surrounding the teeth tends to be flat or concave (impressed). Declivity with minute appressed setae.

Length: 2.3-2.5 mm.

Discussion

Named by Eggers, but name, description, and illustration were published by Schedl (1951n). Schedl (1951n) relates the species to *X. dossuarius* Eggers (Vietnam, Philippines), but mentioned its larger size, longer elytral disc, shorter declivity and the presence of fine pubescence. Wood & Bright (1992) indicate the year of description as 1952, however to our knowledge the description was published in 1951. Transferred to *Biuncus* by Hulcr & Cognato (2009).

Biology: Described and until now known only from Philippines.

Examined material: New Guinea, Owen Stanley Range, Goilala, (BBM); Philippines, Luzon, (holotype, NHMW); Philippines, Luzon, (paratype, NHMW); Philippines, Luzon, (co-type, USNM).

Biuncus conidens **Eggers (1936)**

J.H. database code: Scol 69

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Diagnosis: Short but relatively slender-looking *Biuncus*, the appearance cause mainly by the prolonged pronotum. Two pairs of dominant spines on the declivity, forming shallow elevation, and a pair (or a group) of tubercles at the tip of elytra. The second spine is almost half-way down the declivity, unlike in most other *Biuncus*, where both spines tend to occur close to declivital summit. Individuals from New Guinea are markedly more slender than the holotype from India. Large tibial spines on all legs. Transferred to *Biuncus* by Hulcr & Cognato (2009).

Length: 1.5-2.0 mm.

Examined material: India, Mysore, Wynaad, (holotype, BMNH); India, Karnataka, Sringeri, (compared to type, BMNH); Malaysia, Sabah, Rhino Ridge, Danum Valley, Burseraceae sp. twigs, (Hulcr coll.); PNG: Madang Prov. (4), West Sepik (2), J. Hulcr 2002-2006.

Biuncus duodecimspinatus **Schedl (1936)**

J.H. database code: Scol 3

Previous genus: *Xyleborus*

Compared to lectotype in NHMW

Diagnosis: One of the largest *Biuncus*, with the most conspicuous elytral armature. The circumdeclivital costa surrounds the posterolateral broadened margin of elytra as an elevated carina, but on the upper part of declivity it is continued in each interstria as a pointed tooth with flattened base. The teeth are relatively equal in size, except for the tooth in interstria 3, which is greatly enlarged. The declivity is conspicuously broadened laterally, nearly concave. In live specimens, the elytra are usually darker than the pronotum. Transferred to *Biuncus* by Hulcr & Cognato (2009).

Length: 3.0 mm.

Biology: Common mycocleptic associate of *Hadrodemius globus* throughout New Guinea. Galleries often contain several males of very different sizes.

Examined material: New Guinea, Oro Province, Mt. Lamington, (lectotype, NHMW); PNG: Madang Prov. (213), Oro Prov. (13), J. Hulcr 2002-2006.

Biuncus gorggae Schedl (1973)

J.H. database code: Scol 751

Previous genus: *Xyleborus*

Compared to holotype in ANIC

Diagnosis: Very similar to *Biuncus* duodecimspinatus, except a few differences in the elytral armature. In *B. gorggae*, the interstriae 4-6 do not bear teeth, only interstriae 2 and 3, of which the tooth in interstria 2 is minute, the tooth in interstria 3 is large. The declivity is conspicuously broadened laterally, nearly concave. Its surface is unusual in that it isn't shining, but matt, softly shagreen.

Length: 2.4-2.6 mm.

Discussion

Schedl (1973e) compared the species to *Biuncus* (as *Xyleborus*) *duodecimspinatus*, and notes the missing teeth on the interstriae 4, 5, and 6.The islands of New Ireland and New Britain are the only localities of occurrence known to us. Transferred to *Biuncus* by Hulcr & Cognato (2009).

Examined material: New Guinea, New Ireland, (holotype, ANIC); New Guinea, New Britain, Gazelle Peninsula, (BBM); New Guinea, West New Britain, Wilelo, (paratype, NHMW).

Biuncus haberkorni Eggers (1920)

J.H. database code: Scol 421

Previous genus: *Xyleborus*

Compared to lectotype in USNM

Diagnosis: Extremely variable in size. All observed individuals orange to light brown, elytra darker than pronotum. Distinguishable from other *Biuncus* by two pairs of equal, medium-size teeth in interstriae 2 and 3, the pair in the third interstria is positioned lower towards the middle of declivity, the teeth are tubercle-like, with broad base, not spine-like. Interstriae 4, 5, 6 on upper part of declivity sometimes with rows of small serrations (minute in the lectotype specimen). The declivital surface vary widely, from flat surface to surface with impressed striae, from bald and shining to covered with dense appressed pubescence or opaque, from smooth to covered with minute interstrial spines. Other characters either do not vary (characters associated with head, sternal parts, tibiae).*Biuncus haberkorni* is very similar to *Biuncus conidens*, and differs by the absence of granules or tubercles on the elevated end of interstria 1 and by much smaller tibial denticles. It is also very similar to *Biuncus quadrispinosulus*, in which case the declivital teeth in striae 2 and 3 are minute, sharply pointed, recurved, and both pairs positioned at the very summit of declivity. However, it is clear that such species splits based on these very plastic characters are artificial, and probably do not define monophyletic lineages.

Length: 1.5-2.5 mm.

Discussion

Often identified as the junior synonym *Xyleborus approximatus*. Transferred to *Biuncus* by Hulcr & Cognato (2009).

New junior synonym(s): *Xyleborus approximatus* Schedl

Biology: Beaver and Browne (1978) noted that galleries of this species in Penang, Malaysia, were started in close proximity to those of *Xylosandrus mancus*. Though the species is commonly found creating galleries next to other ambrosia species in the typical mycocleptic fashion, it is also sometimes found apparently unassociated with any other species. The strictness of its mycocleptic habit is unclear. The variation may stem from the fact that the 'species' as determined here by the plastic characters is unlikely to be monophyletic.

Examined material: Africa, D. O. Afrika, Amani, (lectotype, USNM); Malaysia, (USNM); Malaysia, Sabah, Danum Valley, Ficus sp. branches, (Hulcr coll.); New Guinea, Morobe Province, Bulolo, Castanopsis, (FICB, 62 indiv.); Thailand, Khao Sok NP, Rambutan branch, (S. Dole); unknown locality, (BMNH); unknown locality, (BMNH); locality not recorded, (BMNH); PNG: Oro Prov. (2), J. Hulcr 2002-2006.

***Biuncus justus* Schedl (1931)**

J.H. database code: Scol 266

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: Very small species, considerably variable in body proportions. The length to width ration varies continuously from 1.5/0.7 mm. (robust) to 2.4/1.0 mm. (less robust). The holotype of *Biuncus* justus lies approximately in the middle of the continuum, lectotypes of the now synonymized *Xyleborus* ciliatus *Xyleborus* ciliatoformis and *Xyleborus* apiculatus are more slender, but also varied (1.6/0.75; 1.7/1.1and 2.0/0.8, respectively). The difference is attributable almost entirely to the relative length of elytral disc; the shape of pronotum and the shape and slope of elytral declivity are relatively constant. Pronotum is always robust and rounded, type 5 in lateral view. Elytra color varies between black to yellow. Declivity surface usually covered with rows of appressed setae directed backwards and towards the elytral median suture, but the pubescence is frequently absent. The elytral declivity usually has 1) an The most characteristic feature of the species is the complete lack of denticles on elytral declivity, and the broad and smooth depression traversing from the summit of interstria 1 to the apex in interstria 3, creating a bulge at the upper part of declivity. Transferred to *Biuncus* by Hulcr & Cognato (2009).

Length: 1.4-2.4 mm.

New junior synonym(s): *Xyleborus apiculatus* Schedl, *Xyleborus ciliatoformis* Schedl, *Xyleborus ciliatus* Eggers, *Xyleborus marginicollis* Schedl

Biology: Kalshoven (1960) first reported the tendency of this species to create tunnels next to entrance holes of other ambrosia beetles species, which is now know to be mycocleptism. Two larger representatives of *B. justus* were found associated with *Amasa resectus* in New Guinea and in Borneo.

Examined material: Indonesia, Java, Buitenzorg, (holotype, NHMW); Malaysia, (BMNH); Malaysia, (BMNH); Malaysia, Sabah, Danum Valley, (Hulcr coll.); New Guinea, Morobe Province, Bulolo, (FICB); PNG: Madang Prov. (9), Oro Prov. (1), West Sepik (1), J. Hulcr 2002-2006.

***Biuncus mesoleiulus* Schedl (1979)**

J.H. database code: Scol 693

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: Unusually shaped *Biuncus* - long elytra, short declivital costa, no vestiture, completely black, elytra all polished, and most notably, there are no tubercles or spines on the elytra. Elytral spines are also absent in *B. justus* (Schedl), which also can have slightly prolonged elytra. However, *B. mesoleiulus* is considerably longer (especially the very long elytra relative to the regular pronotum), and the declivital impression is absent. All examined specimens are black.

Length: 2.5 mm.

Discussion

Schedl (1979g) placed the species among his Xylebori solitari, and indicated that it is easily recognizable by its smooth shining surface and very delicate punctuation. Transferred to *Biuncus* by Hulcr & Cognato (2009).

New junior synonym(s): *Xyleborus brevicollis* Browne

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW); PNG: Chimbu Prov. (1), J. Hulcr 2002-2006.

Biuncus niger **sp. n. Hulcr & Cognato**

J.H. database code: Scol 352

Diagnosis: Above-average size *Biuncus*, brown to black. Distinguishable form other *Biuncus* primarily by a single miniature spine in each interstria 2, while interstriae 3 do not have any spines. The black body coloration distinguishes this species from all known lowland *Biuncus*, but montane forms of many species are also melanic.

Description: Scapus slender, first segment of antennal funicle slender but shorter than pedicel. Antennae type 1, antennal club slightly asymmetrical, taller than wide, very flat, first corneous segment with circular margin, covering the entire rear side, segments 2 and 3 visible only anteriad, pubescent. Shallowly impressed submentum. Frons alutaceous. Eyes of regular size, emarginate, upper part smaller than lower part. Pronotum type 5, rounded, robust. Pronotal edge bear two conspicuous medial serrations. Pronotal disc softly punctate, alutaceous. Procoxae contiguous, pronotal posterocoxal process slender, tall, pointed. Protibiae narrow along the whole length, slightly broader at the distal end, with 5 slender spines in slightly enlarged sockets. Scutellum visible, small. No sign of mesonotal or elytral mycangial opening. Elytral disc as long as elytra, with shining punctate surface. Elytral declivity flat, gently sloped, conspicuously broadened along its posterolateral edges, the edges bearing carina, which ends in 7th interstriae. Body largely devoid of noticeable vestiture, except for dense small appressed setae on elytral declivity.

Length: 2.4-2.5 mm.

Discussion

Holotype deposited in USNM, paratypes deposited in MSUC and BMNH.

Biology: Another example of melanism correlated with high altitudes in Xyleborina. All collected specimens were mycocleptic associates of *Xylosandrus russulus*.

Examined material: PNG: Chimbu Prov. (4), J. Hulcr 2002-2006.

Figure 36: *Biuncus niger sp. n.* Size: 2.5 mm.

Biuncus papatrae **Schedl (1972)**

J.H. database code: Scol 245

Previous genus: *Xyleborus*

Compared to holotype in FRI Lae

Diagnosis: One of the most common *Biuncus* in New Guinea. Most representatives have very characteristic coloration - orange or light brown pronotum and much darker brown elytra. The coloration is however often lost in museum specimens. Notably, individuals from high elevations are entirely black. Distinguishable from other *Biuncus* primarily by the single prominent recurved spine in each interstria 3 at the declivital summit. Otherwise the elytra are usually entirely smooth, without other tubercles or granules, shining. The circumdeclivital elevated carina is very conspicuous, elytral declivity is notably broad, appearing angulate from apical view.

Length: 2.1-2.5 mm.

Discussion

Schedl (1872i) compared the species to *Xyleborus approximatus* and suggested several distinguishing characters, among them the single spine on each elytron. Wood & Bright (1992) indicate that a type specimen is housed in ANIC (as CSIRO), however, it is currently absent from ANIC. Only a paratype from NHMW was available.

New junior synonym(s): *Xyleborus biuncus* Browne, *Xyleborus mucronatoides* Schedl

Biology: Ubiquitous mycocleptic associate of *Anisandrus ursa*, often also found with *Xylosandrus crassiusculus*.

Examined material: New Guinea, West New Britain, Pagi R., (FICB); New Guinea, New Ireland, Rapontamon, (paratype, NHMW); PNG: Chimbu Prov. (1), J. Hulcr 2002-2006.

***Biuncus quadrispinosulus* Eggers (1923)**

J.H. database code: Scol 422

Previous genus: *Xyleborus*

Compared to non-type in BMNH

Diagnosis: One of the smallest *Biuncus*, often very pale, appearing fragile compared toother *Biuncus* spp. Minute, almost invisible tubercles or hooks in interstriae 2 and 3. Vestiture inconspicuous, appressed. Feebly elevated strial ridges on declivity, almost invisible, only when dry. The impression across striae 2 and 3 and the resulting inflation of the anterolateral surface of declivity present but feeble.

Length: 1.4-2.0 mm.

Discussion

Holotype of *X. quadrispinosus* was not available. Instead, we examined non-types from Schedl's collection in NHMW and from Browne's collection in BMNH identified as *X. quadrispinosulus* (Eggers), and a holotype of *X. parvispinosus* Schedl from NHMW (junior synonym of *B. quadrispinosulus* (Eggers)). Transferred to *Biuncus* by Hulcr & Cognato (2009).

Previously synonymized species: *Xyleborus parvispinosus* Schedl, *Xyleborus parvispinosus palembangensis* Schedl

Biology: Kalshoven (1960) reported the tendency of this species to create tunnels next to entrance holes of other ambrosia beetles species, which is now know to be mycocleptism. In New Guinea, it is has been found associated with *Eccoptopterus spinosus*, *Cnestus bimaculatus*, and *Biuncus duodecimspinatus* (= also a mycocleptic species).

Examined material: Indonesia, Java, (type of *X. parvispinosus*, NHMW); Indonesia, Java, (NHMW); Indonesia, Java, (NHMW, 2 indiv.); Malaysia, Selangor, (BMNH); Malaysia, Sabah, Danum Valley, *Ficus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Ficus* sp. branches, (Hulcr coll.); PNG: Madang Prov. (14), Oro Prov. (13), J. Hulcr 2002-2006.

Genus *Cnestus* Sampson (1911)

J.H. database code: Scol 794

Type species: *Cnestus magnus* Sampson.

Rediscription: Eyes shallowly emarginate, upper portion of eyes as large as the lower part. Antennal club more-less circular shape, or appears broader than tall, or very flat, club type one (truncated, first segment covering posterior side). First segment of club circular around the club, covering the entire posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club narrow, pubescent, visible on the anterior side only, or corneous, visible on the anterior side only, or visible on both sides of the club, but soft, or the corneous part on the anterior side only. Third segment of club absent from the posterior side of club, or partly visible on the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, or 2 or 3 segments. Scapus appears long and slender. Frons above epistoma mostly smooth, alutaceous, with minor punctures. Submentum deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with two distinct flat denticles protruding anteriad, sometimes the whole margin extends anteriad forming a distinct "hood" over the head. Pronotum from lateral view of basic shape (type 0), or rounded and robust (type 5). From dorsal view it mostly rounded (type 1), sometimes conical (type 0) or basic, short, parallel-sided, rounded frontally (type 2), or conical on the anterior part (type 6). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum carinate. Procoxae narrowly separated, prosternal posterocoxal process short, conical or flat, inconspicuous. Setae on pronotal basis associated with mesonotal mycangium present as a small but dense tuft; there are no setae on elytral bases, and no elytral mycangium. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity and slightly convex or bulging, or short compared to the declivity and sometimes convex, punctures on elytral disc in strial lines. Boundary between elytral disc and declivity indistinct, end of disc rounded and smoothly transitioning into declivity. Lateral profile of elytral declivity can be flat, but is mostly rounded, slowly descending, rarely excavated. Dorsal profile of the elytral end rounded. Elytral declivity mostly devoid of setae or scales, only rarely pubescent. Circumdeclivital costa very short, or ending in 7th interstriae. The inner part of declivity has no tubercles, or only uniform granules. First interstriae are parallel (sometimes slightly broadened towards elytral summit). Protibiae obliquely triangular, broadest in 2/3 of the length, or distinctly triangular, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles small or large, distinctly longer than wide, bases of the denticles slightly elevated, or distinctly enlarged, conical, fewer than 6, or between 6 and 8 protibial denticles present. Metatibiae of regular size.

Pronotum always dark, mostly black, but elytra often with a whitish (semitransparent) patch. Body length: 1.9-3.7 mm.

Discussion

Described by Sampson (1911) with type species *C. magnus*. Based on *Cnestus magnus* from Ceylon, Sampson (1911) mentioned that the elytra are almost transparent except at the e

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the edges and along the suture, which is indeed a character present in several *Cnestus* spp. but not in all. In fact, the extent of the white elytral patches varies substantially among and within species of *Cnestus*. Sampson (1911) conjectured that the transparency of elytra was a sign of the specimen's immaturity, which is incorrect. Substantially re-described by Browne (1955). According to Browne (1955) who re-described *Cnestus* based on the three hitherto known species, it has 3-segmented funicle. This is true for only a subset of *Cnestus* spp. A 4-segmented antennal funicle has often been considered a generic character (e.g., Nobuchi 1983). It occurs in the most common *Cnestus* in PNG, *C. bimaculatus*, but not in others, thus it is not a valid genus-level identification character.

Previously synonymized genus: *Tosaxyleborus* Murayama (for *C. murayamai* Schedl)

Biology: Breeds almost universally in small branches or twigs. Some species create bifurcating gallery following the radial wood layers. Other species, namely *C. bimaculatus*, create almost no tunnels, but bore in the soft pith of twigs. Commonly these twigs are hollow, and *C. bimaculatus* creates the ambrosia garden simply on the inner surface of such twigs (Hulcr, pers. obs.).

Figure 37: *Cnestus bimaculatus*, a typical representative of the genus. Size: 3.2 mm.

Cnestus aterrimus (Eggers, 1927)

J.H. database code: Scol 610

Compared to holotype in NHMW

Diagnosis: The smallest *Cnestus* in New Guinea. All NG specimens known have more or less transparent patches on elytra (appearing white), which is however not true throughout the whole range of the species. These patches, the small size, and the 3-segmented antennal funicle distinguish this species from all New Guinean *Cnestus*, except *C. bimaculatus*, form which it can be distinguished by size and the more prolonged body shape.

Length: 1.9-2.2 mm.

Discussion

Eggers (1927b) relates the species to the vicinity of *X. ursus*; both species have been indeed moved to *Cnestus* recently (Dole & Cognato, 2009).

Previously synonymized species: *Cnestus nitens* Browne, *Xyleborus glabripennis* Schedl

New junior synonym(s): *Cnestus pseudosuturalis* Schedl

Biology: It is unclear whether the record of this species from PNG is valid. *C. aterrimus* is mentioned as occurring in PNG in the Wood & Bright (1989) catalog, but we did not discover the primary reference. The species is common in SE Asia (Beaver & Browne 1978).

Examined material: Indonesia, Sumatra, (holotype, NHMW).

Cnestus bimaculatus **(Eggers, 1927)**

J.H. database code: Scol 2

Compared to holotype in USNM

Diagnosis: Medium-sized species, most characteristic with the large pronotum, rounded body and a white semitransparent patch on each elytron. The white patches, the gently rounded elytra, and a three-segmented antennal funicle distinguish this species *Cnestus mutilatus*. *Cnestus triangularis* differs by the uniformly black and excavated elytra. *C. aterrimus* (=*pseudosuturalis* comb. nov.), is very similar to *C. bimaculatus*, including the white patches on elytra, but it is much smaller (less than 2.2 mm.). The extent of the white elytral patches is know to vary substantially among and within species of *Cnestus*, but seems to be fairly stable in *C. bimaculatus* form New Guinea.

Length: 3.2 mm.

Discussion

Type from Mindanao, Philippines. Eggers relates the species to the Australian *Cnestus* (as *Xyleborus*) *solidus* (Eich.), with differences in scutellum and elytra, primarily the semi-transparent elytra of C. *bimaculatus*.

Biology: Inhabits the smallest twigs at the very top of dead trees, mostly Moraceae. Often establishes fungus gardens inside hollow twigs, without creating a gallery.

Examined material: Philippines, Mindanao, Iligan, (holotype, USNM); PNG: Madang Prov. (18), Oro Prov. (4), J. Hulcr 2002-2006.

***Cnestus mutilatus* (Blandford, 1894)**

J.H. database code: Scol 498

Compared to allotype, lectotype of *X. bajoewangi* in BMNH, NHMW

Diagnosis: Differs from all similar species (*Hadrodemius globus* and *Anisandrus ursa*) by a distinct carina along the side of pronotum and around the bottom part of elytral declivity.

Length: 3.5 mm.

Discussion

The authors have not seen representatives of this species from New Guinea. The Catalog of Scolytidae and Platypodidae report this species from PNG, however, the primary reference for this record has not been found. The occurrence of the species in NG cannot be confirmed, and may have been a result of misidentification of a similar species.

Previously synonymized species: *Xyleborus sampsoni* Eggers, *Xyleborus banjoewangi* Schedl, *Xyleborus taitonus* Eggers

Examined material: Indonesia, Java, Banyuwangi, (unspecified "type", NHMW); USA, Mississippi, Oktibbeha county, (Doug Stone, 3 indiv.); locality not recorded, (allotype of male, BMNH).

***Cnestus pseudosuturalis* syn. n. Schedl (1964)**

Synonymized with: *Cnestus aterrimus (Eggers)*

J.H. database code: Scol 43

Compared to holotype in NHMW

Length: 2.1-2.2 mm.

Discussion

Holotype: 2.1 mm. The holotype of *Cnestus* (*Xyleborus*) *pseudosuturalis* is virtually identical to the holotype of *C. aterrimus*, except for the elytral coloration. The only two discernable differences are a minute elevated short costa on the forehead of *C. suturalis*, and a slightly more impressed first stria along the elytral suture in the same species. The specimens from New Guinea resemble *C. pseudosuturalis* by their semitransparent and whitish patches on elytra bear a combination of characters of both, with some characters unique to themselves. The body shape of NG non-type specimens is slightly more elongated, less compact-looking, than both holotypes. The elytra are less rounded, most striae are impressed on the end of declivity creating a more rugged appearance. The frons have more pronounced short elevated costa, the white patch on each elytron is smaller and darker than in *C. pseudosuturalis* holotype, evidencing the fact that it is a variable character. The variaiton between these three forms prompted us to synonymize *C. pseudosuturalis* with *C. aterrimus*.

Examined material: Vietnam, Tonkin, Choganh, (holotype, NHMW); Vietnam, Tonkin, Choganh, (NHMW); PNG: Madang Prov. (35), J. Hulcr 2002-2006.

Cnestus triangularis **(Schedl, 1975)**

J.H. database code: Scol 612

Compared to holotype in NHMW

Diagnosis: *C. triangularis* differs from other *Cnestus* spp. by its unusually excavated elytra. Pronotum is distinctly longer than wide, apex drawn forward into an extension with two large median serrations and two smaller serrations at their side. It lacks a dense tuft mycangia-associated present on the pronotal basis of other *Cnestus* spp.

Length: 3.7 mm.

Discussion

Schedl (1975f) compared the species to *Cnestus* (as *Xyleborus*) *klapperichi* Schedl from China, and distinguished it by the triangular pronotal apex, smaller size and the absence of teeth on the declivital sulcus.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

Genus *Coptodryas* Hopkins (1915)

J.H. database code: Scol 788

Type species: *Coptodryas confusa* Hopkins (1915).

Redescription: Eyes deeply emarginate, almost disjunct, upper portion of eyes smaller than lower part. Antennal club appears broader than tall, club type four (first segment small, second and third prominent on both sides). First segment of club convex, small, margin of the first segment mostly costate, may appear softer on posterior side. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only, or corneous on both sides of club, but not circular (not making antenna tall, or "telescopic"). Third segment of club clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma mostly smooth, alutaceous, with minor punctures. Submentum flat, flush with genae, or slightly impressed, shaped as a distinct large triangle. Anterior edge of pronotum with two conspicuous flat serrations protruding forward. Pronotum from lateral view of basic shape (type 0), or rounded and robust (type 5). From dorsal view it is rounded (type 1), or basic, short, parallel-sided, rounded frontally (type 2). Pronotal disc shining or smoothly alutaceous, with small punctures, or with asperities resembling those on the frontal slope, always with dense setae. Lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous. Tuft on pronotal basis associated with mesonotal mycangium absent (though the abundant pronotal vestiture often resembles such tuft), but the setae on elytral bases associated with elytral mycangium are abundant and conspicuous. Scutellum not visible. Elytral bases curved, costate due to the presence of elytral mycangium. Elytral disc longer than declivity, flat, or longer than declivity and slightly convex or bulging, punctures on elytral disc confused. Boundary between elytral disc and declivity rounded, in some species smoothly transitioning into declivity. Lateral profile of elytral declivity mildly flat or rounded, or steep, especially towards the apex, or obliquely truncated. dorsal profile of elytral end rounded, or obliquely truncated. Elytral declivity covered with dense setae, often more abundant than strial punctures, the setae may be erect or appressed. Circumdeclivital costa absent or undefinable. The inner part of declivity has no tubercles. Striae and interstriae on the upper part of declivity even, not forming ridges and furrows. However, several species of *Coptodryas* from SE Asia have much richer declivital sculpturing, incliding large teeth, circumdeclivital carina, etc. Protibiae with evenly rounded edge, posterior side of protibia flat. Protibial denticles small, bases of the denticles not enlarged, protibial margin rounded, or slightly enlarged; more than 6, sometimes many more protibial denticles present. Metatibiae of regular size. Color uniformly light brown or reddish or uniformly dark brown, pronotum sometimes much lighter than elytra. New Guinean species are large and robust, between 3.8 and 4.6 mm.

Discussion

This group is a sister clade to *Microperus* (Cognato et al., 2009), but the species of these two genera living in New Guinea are morphologically different, sharing little but the presence of elytral mycangium and the suppressed scutellum. *Coptodryas* and *Micorperus* are currently poly- or paraphyletic with respect to each other, as even the available molecular data do not resolve the ambiguous positions of several species. In this work, the minute species with strial punctures in lines, and with slender body shape are transferred to *Microperus*, and only large species with confused strial and interstrial punctuation, and often with abundant vestiture are retained in *Coptodryas*. However, the reorganization of the whole group was not possible in this work, since the center of diversity of *Coptodryas* seems to be in Malaysia and Indonesia.

Biology: For some small species, Blandford (1961c) reports complex tunnel systems with multiple brood chambers and several entrances. This suggests the existence of communal breeding, such as that shown for the related *Xyleborinus*. The large and richly pubescent species of *Coptodryas* seem to prefer (or be specific to) hosts in the Dipterocarpaceae family in Indonesia and continental SE Asia. This may explain their rarity in New Guinea, where Dipterocarpaceae are not common.

Figure 38: *Coptodryas pubifer*, a typical representative of the genus. Size: 4.5 mm.

Coptodryas artegrapha syn. n. (Schedl, 1942)

Synonymized with: *Microperus recidens (Sampson)*

J.H. database code: Scol 773

Previous genus: *Coptodryas*

Compared to holotype in NHMW

Diagnosis: Holotype length: 1.9 mm.

Discussion

Smaller representative of *Microperus recidens*.

Examined material: Indonesia, Java, Mt. Gede, (holotype, NHMW); New Guinea, Morobe Province, Bulolo, (FICB).

Coptodryas atava syn. n. (Schedl, 1979)

Synonymized with: _Microperus diversicolor (Eggers)_

J.H. database code: Scol 617

Previous genus: *Coptodryas*

Compared to holotype in NHMW

Discussion

Except for its slightly larger size, the holotype of *Coptodryas atava* (as *Xyleborus*) doesn't differ from the holotype of *Microperus diversicolor*. In his description, Schedl (1979) related the species to *Xyleborus brevipilosus* Eggers (later synonymized with *Coptodryas myristicae*, which is synonymized with *M. diversicolor* here), and noted that it is larger, more slender, and the elytral declivity is more obliquely convex (characters which are very variable in this group of species).

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

Coptodryas bella (Sampson, 1921)

J.H. database code: Scol 496

Compared to holotype in BMNH

Diagnosis: One of two *Coptodryas* in New Guinea. Similar in body size, robustness, and rich vestiture. *C. bella* differs from *C. pubifer* by obliquely truncated (flat towards the end) declivity, and dense adherescent setae on declivital surface. Pronotum is usually lighter colored (oragnge or reddish-brown) than dark elytra.

Length: 3.8 mm.

Discussion

The large hairy representatives of *Coptodryas* were tentatively placed in a group *Kalshovenius* by Browne, with *C. bella* as the type species.

Biology: Males of both *Coptodryas* from New Guinea have conspicuoulsy enlarged and excavated pronotum with which they guards entrance tunnels of their galleries (Hulcr, pers. obs). The males of *C. bella* from Kuching, Sarawak, Malaysia, in Browne's collection (BMNH) are substantially smaller and have less developed pronotal armature than PNG males.

Examined material: Indonesia, Borneo, Mt. Matang, (holotype, BMNH); Malaysia, Sarawak, Kuching, (BMNH); Malaysia, Kelantan, (BMNH); New Guinea, Western Province, Wavoi, (FICB).

***Coptodryas docta* syn. n. (Schedl, 1975)**

Synonymized with: *Microperus popondettae (Browne)*

J.H. database code: Scol 619

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Previous genus: *Coptodryas*

Compared to holotype in NHMW

Length: 2.0 mm.

Discussion

The holotype of *C.* (as *Xyleborus*) *docta* is nearly identical to that of *C. popondettae*, only it is slightly smaller (2.0 mm.).According to Schedl (1975f), the species is similar to *Cyclorhipidion artedilatatum* (Schedl) (as *Xyleborus artedilatatus*), and can be distinguished by slightly smaller size, more strongly striate-punctate declivity, narrow, convex interstriae, each with a regular row of blunt branules bearing short semi-erect setae. The description doesn't mention tubercles and impressed striae on declivity, which are the main distinguishing character of the species.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

***Coptodryas extensa* syn. n. (Schedl, 1955)**

Synonymized with: *Microperus recidens (Sampson)*

J.H. database code: Scol 620

Previous genus: *Coptodryas*

Compared to holotype in NHMW

Discussion

Schedl (1955b) related the species to *Xyleborus minusculus* Eggers (now synonymized with *Coptodryas recidens*). *C. extensa* is said to be larger, more slender, with a larger bulge on declivity, and with the dots on the bulge barely visible. The holotype of *C. extensa* is nearly identical to the holotype of *C. recidens*.

Examined material: New Guinea, holotype (NHMW).

Coptodryas nitella **syn. n. (Browne, 1984)**

Synonymized with: *Microperus intermedius (Eggers)*

J.H. database code: Scol 242

Previous genus: *Coptodryas*

Compared to holotype in BMNH

Discussion

The holotype of *C. nitella* is virtually identical to *M. intermedius*, except for slightly longer elytra (1.1 mm. versus 0.95-1 mm.; but only 1.0 in a FICB paratype) and very small granules, further obscured by dense setae. Holotype of *C. nitella* does have antennal clyb type 1.*C. nitella* was included into *Microxyleborus*, along with *C. perparva*, *C. micrographus*, etc. by Browne. Moved to *Coptodryas* by Beaver (1995). According to Browne (1984d), the species is similar to *Coptodryas* (as *Xyleborus*) *nudibrevis* (Schedl) from Malaysia, no closer comparison given.

Examined material: New Guinea, (holotype, BMNH), from BMNH.One specimen of *M. intermedius* designated as homotype.; New Guinea, Morobe Province, Bulolo, (paratype, FICB).

Coptodryas pubifer **comb. n. (Schedl, 1972)**

J.H. database code: Scol 382

Previous genus: *Hadrodemius*

Compared to holotype in BMNH

Diagnosis: Very similar to *C. bella*, from which it differs by continuously rounded elytral profile, and erect setae on elytral declivity.

Length: 4.3-4.6 mm.

Discussion

The species is classified as *Hadrodemius* by Wood & Bright (1992). However, it has antennae of type 4 and elytral mycangia (rather than antennae of type 1 and a mesonotal mycangium) which are characteristics of *Coptodryas* Hopkins.*C. pubifer* vaguely resembles *C. punctipennis* (Schedl), which is smaller, has chagrenate and granualte elytra on the posterior half, and is less hairy. Another similar species is *C. muasi* (Browne), which is much longer and has bulging declivity with impressed striae.

Biology: Males have similar pronotal armature as in *C. bella.*

Examined material: Malaysia, Borneo, (holotype, BMNH); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 37 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 30 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 15 indiv.); Malaysia, Sabah, Danum Valley, (Hulcr coll., 9 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 15 indiv.); New Guinea, Kinuga, (BBM, 5 indiv.), males only; New Guinea, Western Province, Wavoi/Guavi, (FICB).

***Coptodryas pubipennis* syn. n. (Schedl, 1974)**

Synonymized with: *Microperus parva (Lea)*

J.H. database code: Scol 778

Previous genus: *Coptodryas*

Compared to paratype in NHMW

Discussion

The paratype of *Coptodryas* (*Xyleborus*) *pubipennis* from NHMW is a typical representative of *Microperus parva*. It has antennal club type 1 (truncated, first egment prominent, with semicircular costa), rather flat elytral disc (not notably convex), and each stria on elytral declivity has a dense row of minute recurved spines.

Examined material: Vietnam, Thai-Novyen, (paratype, NHMW).

Genus *Cryptoxyleborus* Schedl (1937)

J.H. database code: Scol 801

Type species: *Cryptoxyleborus naevus* Schedl.

Rediscription: Eyes shallowly emarginate or almost entire, upper portion of eyes as large as the lower part, or conspicuously large. Antennal club more-less circular shape, or appears broader than tall, club type four (first segment small, second and third prominent on both sides). First segment of club convex, small, margin of the first segment mostly costate, may appear softer on posterior side, or mostly soft, pubescent. Second segment of club corneous on both sides of club, but not circular (not making antenna tall, or "telescopic"). Third segment of club clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus

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regularly thick. Frons above epistoma mostly smooth, alutaceous, with minor punctures. Submentum slightly impressed, or deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope), or with distinct row of serrations. Pronotum from lateral view with disc distinctly prolonged (type 8), or long and "hooded" frontally (type A), or long, flat, bulging frontally (type B). From dorsal view it is conical on the anterior part (type 6), or prolonged basic shape with rounded frontal margin (type 7), or prolonged and quadrate or subquadrate (type 8). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous. Tuft on pronotal basis associated with mesonotal mycangium absent. All *Cryptoxyleborus* have a pair of elytral mycangia, but the setae on elytral bases associated with them may be absent. The openings of these mycangia may be very small, either on the anterior slope of elytral bases, or conspicuously on the top of elytra, next to scutellum. Scutellum visible on on the anterior slope of elytral bases. Elytral bases straight, with oblique edge, or curved, costate due to the presence of elytral mycangium. Elytral disc longer than declivity, flat, punctures on elytral disc in strial lines (confused in some SE Asian species). Boundary between elytral disc and declivity indistinct, end of disc rounded and smoothly transitioning into declivity. Elytral declivity in all *Cryptoxyleborus* is characteristically attenuated and pointed at the end. The declivity has only few setae, but the pointed end is often densely covered with minute setae. The declivity has no tubercles. First interstriae are parallel. Protibiae are very slender or narrowly arcuate. Posterior side of protibia distinctly inflated and granulate. Protibial denticles small, bases of the denticles not enlarged, fewer than 6 protibial denticles present. Metatibiae of regular size. Body length between 1.9-3 mm. Color uniformly yellowish, or light brown, rarely dark brown.

Discussion

Some morphological characters and the host specificity to Dipterocarpaceae led to the inclusion of *Cryptoxyleborus* in (now dissolved) separate tribe Webbini, along with *Webbia, Arixyleborus* and *Schedlia* (e.g., Browne 1961c).

Biology: Browne (1958) discusses specificity of representatives of this genus to trees from Dipterocarpaceae. Host plants of this genus in New Guinea are not known. All known species create short radial entrance tunnel and often large brood cavity (see Browne 1961c for illustrations).

Figure 39: *Cryptoxyleborus subnaevus*, a typical representativ eof the genus. Size: 2.6 mm.

Cryptoxyleborus acutus **(Schedl, 1975)**

J.H. database code: Scol 538

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Compared to holotype in NHMW

Diagnosis: Differs from other New Guinea *Cryptoxyleborus* by subquadrate pronotum.

Length: 1.9-2.0 mm.

Discussion

This species was described from a single specimen collected in Papua New Guinea (Schedl, 1975f). The holotype (NHMW), the only known specimen, has been examined. Contrary to Schedl's description, the elytra are 1.6 times as long as the pronotum, not 1.3 times. The species was placed without comment in the genus *Webbia* Hopkins by Wood and Bright (1992). However, the form of the antenna, combined with the strongly cuneiform elytra, place it in *Cryptoxyleborus*. Schedl (1975f) noted that the species was allied to *Cryptoxyleborus* vestigator (as *Xyleborus* vestigator).

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

***Cryptoxyleborus subnaevus* Schedl (1937)**

J.H. database code: Scol 767

Compared to lectotype in NHMW

Diagnosis: This species can be distinguished from the two other New Guinea *Cryptoxyleborus* by the mycangial openings exposed on the elytral bases.

Length: 2.5 mm.

Biology: Widespread, also in Australia.

Examined material: Malaysia, Borneo, (lectotype, NHMW); New Guinea, Western Highlands, Jimi Valley, (BBM); Philippines, Luzon, Aparri, (NHMW).

Cryptoxyleborus vestigator **(Schedl, 1973)**

J.H. database code: Scol 624

Compared to holotype photograph in NHMW

Diagnosis: *C. vestigator* can be distinguished from other PNG *Cryptoxyleborus* by the rounded frontal margin of pronotum and the absence of mycangial openings on the top of elytral bases.

Length: 2.6-3.0 mm.

Discussion

Schedl designated the species as *Platypus goilalae* (holotype in ANIC). Wood & Bright (1992) indicated that an erroneously identified *C. vestigator* individual was used as a type specimen for *Platypus goilalae* (type residing in NHMW). Beaver & Hulcr (2008) examined the type of *Platypus goilalae* and synonymized it with *C. vestigator*.

Biology: Type specimen was captured on a glue trap; nothing is known about the host specificity of this species.

Examined material: New Guinea, Morobe Province, Bulolo, (paratype, FICB); New Guinea, Morobe Province, Bulolo, (NHMW), Platypus goilalae, det. Schedl.

Genus *Cyclorhipidion* Hagedorn (1912)

J.H. database code: Scol 802

Type species: *Cyclorhipidion pelliculosum* Hagedorn.

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Redescription: Eyes often deeply emarginate, sometimes almost disjunct, upper portion of eyes as large as the lower part. Antennal club mostly appears broader than tall, club type three (with first segment straight or convex), or four (first segment small, second and third prominent on both sides). First segment of club straight (may be slightly concave or convex) on anterior face, or convex, small, margin of the first segment mostly costate, may appear softer on posterior side. Second segment of club corneous, visible on the anterior side only, or corneous on both sides of club, but not circular (not making antenna "telescopic"). Third segment of club clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate, rounded from lateral view. Submentum deeply impressed, shaped as a narrow slit, or a narrow triangle. Pronotal anterior edge with small elevated serrations or bare, never with prominent elevated costa with serrations. Pronotum from lateral view of basic shape (type 0), or tall (type 2), or bulging anteriad (type 4), or rounded and robust (type 5), or prolonged, with low summit (type 7). From dorsal view it is basic, short, parallel-sided, rounded frontally (type 2). Pronotal disc shining or smoothly alutaceous, with dense small punctures, always with dense setae, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous, or tall and pointed, or conical and slightly inflated. Neither pronotal nor elytral mycangium present, but the rich vestiture on pronotum may for a tuft simar as in species with mesonotal or elytral mycangium. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat, or longer than declivity and slightly convex or bulging, punctures on elytral disc sometimes in strial lines (which may be difficult to discern), but mostly confused. Boundary between elytral disc and declivity distinct or indistinct, end of disc rounded and smoothly transitioning into declivity. Lateral profile of elytral declivity mildly flat or rounded, or steep, especially towards the apex, or excavated, dorsal profile of elytral end rounded. All elytra pubescent, hair more abundant than strial punctures (if striae present). Circumdeclivital costa absent or undefinable, or very short, only in one species reaching beyond 5th interstriae, encircling most of declivity. The pattern of tuberculation on declivity very variable. The inner part of declivity may not have any tubercles, or only uniform granules, or no tubercles in interstria 2, and several tubercles in interstriae 1, 3 and beyond, or tubercles on elevated costa around declivity, or abundant and oblique tubercels in all interstriae. First interstriae are parallel (sometimes slightly broadened towards elytral summit), or parallel on disc but broadened towards the apex of elytra, where they sometime bear tubercles. Protibiae with evenly rounded edge. Posterior side of protibia flat, with setae only, or inflated and granulated. Protibial denticles small to minute, bases of the denticles not enlarged, protibial margin rounded, or only slightly elevated, usually between 6 and 8 protibial denticles present. Metatibiae of regular size. Variable body shapes, often bulky and rounded, body length between 2.2-5.5 mm. Color variable from uniformly light or dark brown to black. Most of the body covered with faint pubescence and very abundant, minute punctures, which gives *Cyclorhipidion* its characteristic look.

Discussion

Schedl (1960i) replaced the name *C. pelliculosum* with *X. parlaetus* when he synonymized *Cyclorhipidion* with *Xyleborus*. Wood & Bright (1992) reported an incorrect reference of this move. Instead of (Schedl, 1960h), the replacement was published in Schedl (1960i). Browne (1961c) separated some of the larger and hairy *Cyclorhipidion* spp. into the "*Xyleborus pruinosus* group".

Biology: Browne (1958) notes that many representatives of this genus (referred to as *punctatopilosus*-group) display preference for hosts from the tree family Fagaceae. The known species excavate a single short tunnel leading to often large terminal brood cavity.

Figure 40: Cyclorhipidion multipunctatus, a typical representative of the genus. Size: 3.7 mm.

***Cyclorhipidion anoplum* syn. n. (Schedl, 1975)**

Synonymized with: *Cyclorhipidion apicipenne (Schedl)*

J.H. database code: Scol 572

Compared to holotype in NHMW

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Junior synonym of *C. apicipenne*, based on similarity in all aspects, especially the gobulae and granulate elytral declivity. Schedl (1975f) mentioned its similarity to *C. punctatum* (misspelled *punctulus*) (Egg) from Asia.

Examined material: New Guinea, Morobe Province, Gumi, *Castanopsis*, (compared to type, FICB, 2 indiv.).

Cyclorhipidion apicipenne **(Schedl, 1974)**

J.H. database code: Scol 625

Compared to paratype in NHMW

Diagnosis: Small compared to other *Cyclorhipidion* spp. Antenna type 4. Pronotal anterior costa blunt, inconspicuous. Elytra prolonged, more slender than in most congeners, often ending in oblique hemispheric shape. Declivital costa only feeble at the very tip of elytra, with a few granules. Declivity usually densely covered with setae, with a few scattered pointed tubercles in various positions. Common is a pair of tubercles in the second interstriae in the middle of declivity, or a pair of tubercles at the posterior end of second or third interstriae.

Length: 2.2-2.4 mm.

Discussion

Holotype confirmed to be present in ANIC.Vaguely similar is *Xyleborus inarmatus* Egg., but it is larger, and has conspicuous punctures on elytra in rows, not minite and cofused granules as in *C. apicipenne*.

New junior synonym(s): *Cyclorhipidion anoplum* (Schedl)

Examined material: New Guinea, (paratype, FICB); New Guinea, Morobe Province, Bulolo, (MSUC); locality not recorded, (paratype, NHMW).

Cyclorhipidion artedilatatum sp. n. Hulcr & Cognato

J.H. database code: Scol 579

Diagnosis: Smaller than most *Cyclorhipidion* spp., rather bulky, with dense, often long, rather adherent vestiture. Each elytra bears a major tubercle in the center of declivity close to the suture, and several other smaller tubercles on declivity. Similar to *C. bituberculatum*, but significantly smaller, and with more prominent declivital spines closer to the suture. Similar to *C. apicipenne*, but bulkier, declivity more flat, surrounded by a carina.

Description: Frons densely punctate with median carina. Eyes emarginate, upper part slightly smaller than lower part. Antennal scapus and flagelum very stout, short, funicle 4-segmented. Antennal club type 4, flat, with segments 1-3 clearly visible on both sides and procurved, segments 1 and 2 costate anteriad, segment 1 less prominent than segment 2, convex. Submentum large, triangular, deeply impressed. Pronotum with no serrations on the anterior edge, only a row of setae-bearing granules. pornotal surface covered with minute asperities frontally, punctate on the disc, densely covered with semi-adherent setae. Prosternal precoxal and posterocoxal areas connected with a narrow costa, making procoxae narrowly separated. Femora of all legs have a robust appearance. All tibiae broadly curved on the distal edge, with numeorus minute socketed denticles (over 12 on protibiae). Mesothoracal and elytral mycangia absent. Elytral disc flat, with shagreen surface, strial punctures not visible, or faint and confused with interstrial punctures. Elytral declivity sligthly convex, with levated carina around declivital bottom. Declivital surface rugose, covered with granules especially laterally. Striae 1 and 3 bear several pairs of pointed tubercles, of which the pair in the middle of declivital stria 1 is conspicuous, and dominate the declivital surface. Declivital striae entirely obsolete. Body conspicuously hairy, uniform light brown pigmentation.

Length: 2.5 mm.

Discussion

A specimen labeled as a Holotype of *Xyleborus artedilatatus* resides in Schedl's collection in NHMW. However, description of this species could not be located by the authors, is also absent from the Wood & Bright (1992) catalog. Vaguely similar is *Xyleborus neivai* Egg. (S America), but it is about twice as large, has punctured arrayed in interstriae, pronotal lateral costa straight to almost concave, and more tuberlces on declivity.

One paratype deposited in UCD.

Examined material: New Guinea (designated as holotype by Schedl, NHMW); New Guinea, Gulf Province, Ivimka, (compared to holotype, UCD).

Cyclorhipidion bituberculatum **(Eggers, 1923)**

J.H. database code: Scol 626

Compared to holotype in NHMW

Diagnosis: Variable and relatively common *Cyclorhipidion*. The variability of its elytral declivital granules and the size variation of the two more prominent tubercles was probably the cause of numerous re-descriptions of this species (most synonymized in this work).

Length: 3.2-5.5 mm.

Discussion

Several non-types examined in BMNH identified as *C. bituberculatus* are good examples of the morphological variation of the species.

New junior synonym(s): *Cyclorhipidion revocabile* (Schedl), *Xyleborus flavopilosus* Schedl, *Xyleborus flavipennis* Schedl, *Xyleborus abbreviatipennis* Schedl, *Cyclorhipidion canarii* (Browne), *Ambrosiodmus funestus* (Schedl)

Examined material: New Guinea, Milne Bay, Agaun, (BBM); New Guinea, (FICB); New Guinea, (holotype, NHMW).

Cyclorhipidion canarii **syn. n. (Browne, 1984)**

Synonymized with: *Cyclorhipidion bituberculatum (Eggers)*

J.H. database code: Scol 628

Compared to holotype in BMNH

Length: 5.1 mm.

Discussion

Holotype of *C. canarii* is identical to the holotype and a large series of *C. bituberculatum*. Also the available literature suggests that the species is almost certainly a synonym of *Cyclorhipidion bituberculatum*. Beaver (1995) transferred the species to *Cyclorhipidion* . Browne (1984a) mentioned the similarity of this species to *Cyclorhipidion foersteri* (as *Xyleborus*)(Hagedorn), and noted that it differs in bearing a pair of tubercles on the elytral declivity, and having the apex of elytra granulate.

Biology: Described from individuals found on a log shipped from New Britain to Japan (Browne 1984a).

Examined material: New Guinea, New Britain, (holotype, BMNH).

Cyclorhipidion delicatum **syn. n. (Schedl, 1955)**

Synonymized with: *Truncaudum agnatum (Eggers)*

J.H. database code: Scol 629

Previous genus: *Cyclorhipidion*

Compared to holotype in NHMW

Discussion

Schedl (1995b) compared the species to *X. flavopilosus* Schedl, noting that it differs by the slightly larger and more slender body, and unspecified details of the declivity sculpturing. The holotype was re-examined, and which fits within the variation of *Truncaudum. agnatum*.

Examined material: New Guinea, (holotype, NHMW).

Cyclorhipidion multipunctatus **(Browne, 1980)**

J.H. database code: Scol 328

Compared to holotype in BMNH

Diagnosis: Sharp boundary between smooth shining elytral disc and rugged area of posterior disc and declivity. No tubercles on declivity. The lateral profile of elytra notablly rounded.

Length: 3.7-3.8 mm.

Discussion

Browne (1980b) described the species from Borneo, and mentioned that the species is similar to *Coptodryas bella* (as *Xyleborus*). According to character-based generic concept, the two species are not related. Beaver (1995) transferred the species to *Cyclorhipidion.*

New junior synonym(s): *Xyleborus multipunctulus* Browne

Examined material: Malaysia, Borneo, Tatau, (holotype, BMNH), imported to Japan (Nagoya); New Guinea, Kupa Range, (FICB, 2 indiv.); PNG: Chimbu Prov. (13), J. Hulcr 2002-2006.

***Cyclorhipidion perpilosellum* (Schedl, 1935)**

J.H. database code: Scol 492

Compared to lectotype in NHMW

Diagnosis: A smaller and bulkier *Cyclorhipidion* spp. Dense uniform pubescence nearly all around the body. Orange to red to brown color. Elytra uniformly covered with confused faint dense punctures, and usually has many small granules scattered on the declivity. The granules can bear the shape of forward-pointing miniature spines, or oblique granules, or can be nearly absent.

Length: 2.5-2.7 mm.

Discussion

Schedl (1935b) indicated the similarity of the species to *X. punctatulus*, and noted its stout body shape and dense pubescence. In Thailand, most representatives have declivital tubercles shaped as minute forward-pointed teeth, while Melanesian and Bornean representatives have blunt, oblique granules. Material from Luzon, Philippines, in Eggers' collection in USNM has both the procurved spines and tubercles. *C.* (*X.*) *improbus* (Sampson) in Browne's collection also has minute procurved spines.

Previously synonymized species: *Xyleborus punctatopilosum* Schedl

Biology: Occures in throughout SE Asia to Melanesia. In New Guinea the species seem to be rare, all records come from middle to high altitude regions. According to Browne (1961c), the species associated with Fagaceae.

Examined material: New Guinea, Morobe Province, Bulolo, (FICB, 2 indiv.); New Guinea, Morobe Province, Bulolo, (MSUC); Philippines, Luzon, Mt. Makiling, (holotype, NHMW); Thailand, (Hulcr coll., 8 indiv.), R. A. Beaver det.; PNG: Chimbu Prov. (2), J. Hulcr 2002-2006.

Cyclorhipidion repandus **comb. n. Schedl (1942)**

J.H. database code: Scol 707

Previous genus: *Xyleborus*

Compared to lectotype in NHMW

Diagnosis: Simiar to *C. perpilloselum*, but has stouter, shorter elytra, seems to be less hairy, declivity flat on large portion of the area, Although elytral disc has puncures confused, on declivity they follow striae. No tubercles on declivity. From *C. apicipenne* it differs predominantly by the flattened, obliquely truncated declivity and by overall more stout body.

Length: 3.5-4.1 mm.

Discussion

Schedl (1942c) mentioned its relatedness to *X. obtusus*, and mentioned its greater size and different declivity. The species name is misspelled as "*rapandus*" in Wood & Bright (1992); the primary description and label indicate"*repandus*". Type specimen label does not specify the type category, thus the specimen is designated a lectotype. *C. sisyrnophorum* Hag., is similar in size, and several elytral characteristics: obliquely truncated declivity, declivity covered with dense granules bearing adherent setae, rugose appearance; striae also apparent on declivity and confused on disc; and declivital apex bulging.

Examined material: New Guinea, label: Neu Guinea, (unspecified "type", NHMW); New Guinea, Gulf Province, Ivimka, (UCD).

Cyclorhipidion revocabile **syn. n. (Schedl, 1942)**

Synonymized with: *Cyclorhipidion bituberculatum (Eggers)*

J.H. database code: Scol 302

Compared to holotype in NHMW

Discussion

Schedl (1942c) mentioned relatedness of *C.* (as *Xyleborus*) *revocabile* species to *C.* (as *Xyleborus*) *foersteri* Hag., but noticed its shorter, steeper and more granulate declivity. The species is identical to *Cyclorhipidion bituberculatum* in many aspects: it is large, but variable in size; rather abruptly declining declivity, almost concave; two major and multiple minor tubercles on declivity; the larger pair in variable distance from suture, always in the third striae; tubercles along the posterior end of declivity, variable.

Examined material: New Guinea, (holotype, NHMW); PNG: Madang Prov. (6), Oro Prov. (1), J. Hulcr 2002-2006.

Cyclorhipidion subagnatum syn. n. Wood (1992)

Synonymized with: _Truncaudum agnatum (Eggers)_

J.H. database code: Scol 634

Previous genus: *Cyclorhipidion*

Compared to lectotype in NHMW

Discussion

Wood & Bright (1992) designated the lectotype for *Xyleborus subagnatus*, previously a nomen nudum of Eggers and Schedl; Schedl 1979c:239. The only difference between the lectotype of *C. subagnatum* Wood 1992 and that of *Truncaudum agnatum* is a slightly larger size of several declivital tubercles in *C. subagnatum*. This is clearly a small quantitaive difference in this particular character, and does not constitute a different species.

Examined material: New Guinea, West New Britain, (FICB); New Guinea, Morobe Province, Bulolo, (MSUC); Philippines, Tumigan(?), (lectotype, NHMW); Philippines, Luzon, Tayabas, (SMTD, 6 indiv.).

Cyclorhipidion superbus comb. n. (Schedl, 1942)

J.H. database code: Scol 615

Previous genus: *Coptoborus*

Compared to holotype in NHMW

Diagnosis: Easily distinguishable form other *Cyclorhipidion* spp. by its deeply excavated elytral declivity.

Length: 5.2 mm.

Discussion

Schedl (1942c) mentioned its relatedness to *X. sexspinatus* (now *C. sexspinatum*), the only indicated difference being a missing teeth on the edge of declivity. Though placed in *Coptoborus* by Wood & Bright (1992), it is a member of the genus *Cyclorhipidion*. *Coptoborus* is a South American genus with entirely different antennae, body proportions, leg features, etc.

Examined material: New Guinea, (holotype, NHMW).

Cyclorhipidion sus **comb. n. Schedl (1973)**

J.H. database code: Scol 315

Previous genus: *Arixyleborus*

Compared to holotype in NHMW

Diagnosis: Almost identical to *Cyclorhipidion multipunctatum*, except for the tubercles on elytral declivity. As in *C. multipunctatum*, the lateral profile of elytra is notably rounded, and the protibia is inflated and granulate posteriad.

Length: 3.7-4.0 mm.

Discussion

The species was transferred to *Arixyleborus* based presumably on the fact that it has more than one row of tubercles on protibia (several tubercles on the posterior face), which is a legitimate and often reliable genus-level apomorphy of *Arixyleborus*. However, the same character state is also seen in some *Cyclorhipidion*, notaby in the almost identical *C. multipunctatum* from New Guinea. All other characters suggest tha the species belong to *Cyclorhipidion* (shape of most body parts - pronotum, thick femora, shape of the abdomen; dense vestiture; antennae; small and numerous denticles on all tibiae; outer edges of all tibiae evenly convex). The species is also almost inseparable from *C. multipunctatum* in a molecular phylogeny (Cognato et al., 2009). Similar is *Arixyleborus multituberculatus* Beaver but smaller, and has fewer tubercles on the posterior end of elytra; elytra setose including the elytral disc. In the description of the species, Schedl (1973e) mistakenly relates it to *X. cancellatus* Eggers from Java based simply on the fact that both have granulated elytra. Following that, he placed the species in his "Xylebori granulosi", an unnatural group. Schedl (1979g) synonymizes *Arixyleborus varicus* Schedl with *A. sus*.

Previously synonymized species: *Arixyleborus varicus* Schedl

Examined material: New Guinea, Morobe Province, Bulolo, (FICB); New Guinea, Moroko, Loria, (holotype, NHMW); New Guinea, Morobe Province, Bulolo, (NHMW); PNG: Oro Prov. (32), J. Hulcr 2002-2006.

Genus *Eccoptopterus* Motschulsky (1863)

J.H. database code: Scol 793

Type species: *Eccoptopterus sexspinosus* Motschulsky (1863), (= *E. spinosus* Olivier).

Redescription: Eyes shallowly emarginate, upper portion of eyes smaller than lower part. Antennal club more-less circular shape, club type one (truncated, first segment covering posterior side). First segment of club circular around the club, covering the entire posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club narrow, pubescent, visible on the anterior side only, or corneous, visible on the anterior side only. Third segment of club absent from the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, Scapus appears long and slender. Frons above epistoma mostly smooth, alutaceous, with minor punctures. Submentum slightly impressed, or deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with two distinct flat serrations protruding anteriad. Pronotum from lateral view rounded and robust (type 5). From dorsal view it is rounded (type 1), or rarely basic, short, parallel-sided, rounded frontally (type 2). Pronotal disc shining or smoothly alutaceous, with small punctures, often with dense setae. Lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous. Tuft on pronotal basis associated with mesonotal mycangium often very conspicuous; no setae on elytral bases, no elytral mycangium. Scutellum miniature but visible. Ohno (1989) identified the genus by a missing scutellum, which is incorrect. Elytral bases straight, with oblique edge, elytral disc short compared to the declivity and sometimes convex, punctures on elytral disc confused. Elytral declivital impression extending almost beyond the middle of the elytra, often nearly to the base. Lateral profile of elytral declivity slowly descending, usually excavated, dorsal profile of the elytrla end rounded, or prolonged apically, attenuated. Elytral declivity with vairbale vestiture, rnaging from few setae, not conspicuously pubescent, to densely covered with adherent flat scales. Circumdeclivital costa absent or undefinable. The declivity is always surrounded by teeth or denticles, sometimes conspicuous ones. Protibiae obliquely triangular, broadest in 2/3 of the length. Posterior side of protibia flat, with dense pocket of setae for the tarsi. Protibial denticles large, distinctly longer than wide, but their bases are not enlarged, protibial margin mostly rounded; usually between 6 and 8 protibial denticles present. Metatibiae greatly extended, broadened, without denticles. Color always dark, from uniformly dark brown to black, legs often conspicuously white or yellow. Length extremely variable even within species, from 1.9 to 4.7 mm.

Discussion

The genus *Eccoptopterus* was first used by Motschulski for *E. sex-spinosus* (species later correctly synonymized with Olivier's 1795 *E. spinosus*). Eichhoff in 1886 erected genus *Platydactylus* for *P.* (as *Eccoptopterus*) *gracilipes*. The genus *Eccoptopterus* has a priority over *Platydactylus* (Blandford, 1893b). Browne (1955) notes that larvae of *Eccoptopterus* are different from typical larvae of *Xyleborus*, with no further detail. Due to its general appearance, remarkably different from most Xyleborina, *Eccoptopterus* has been occasionaly treated as its own tribe (e.g., Browne 1961c). Analysis of both morphological and molecular characters however place the genus firmly within Xyleborina, probably as a sister group to *Hadrodemius*, *Anisandrus* or *Biuncus*.Following this revision, there are five species of *Eccoptopterus* in the world: *E. drescheri* (Eggers), *E. limbus* (Sampson), *E. multispinosus* (Hagedorn), *E. spinosus* (Olivier) and *E. tarsalis* Schedl. Examination of hundreds of specimens from all major Paleotropical regions suggest that there are two main character sets distinguishing these species: the pattern of teeth on the declivital margin, and the declivital vestiture. As is usual in Xyleborina, both represent continuum of phenotypic variation, rather than discontinuous lineages. Characters such as color of femora, color of pronotum or elytrae, and tibial size may prove to be of use, but are not variable within PNG representatives and thus are beyond the scope of this work. (*E. drescheri* is unique in yet other characters, and will be discussed below). The declivital teeth occur on the convergence of interstriae and the declivital margin (the exact point of convergence of the interstria and declivital edge usually cannot be seen due to the confused punctuation of the elytra). The phenotypic variation across species seems to be produced by different expression of the teeth in different interstriae. As an example, by a superficial examination it appears that the second tooth in *E. spinosus* is positioned in various distance from the declivital summit - close to the first tooth or almost all the way at the end of elytra. In fact, these are different teeth, positioned either in the fifth, sixth, or some further interstria, which determines their position on the elytron in reference to the first tooth. In other words, the "second" tooth is in fact several non-homologous teeth, either expressed or not. *E. spinosus* is defined here by a tooth in the third, the fifth, and in one of the last interstriae, which gives the species the most characteristic phenotype with three teeth. The *E. multispinosus* phenotype (not known from PNG) can be defined as having large teeth in the third, and fifth interstriae, and small teeth in most of the following interstriae. In the *E. limbus* phenotype, we observe usually one large tooth in the third interstria, and a small tooth in each of the subsequent interstriae. Many of these interstriae however don't have the tooth expressed. The pattern of interstrial teeth expression is not correlated with the region of origin. *Eccoptopterus tarsalis* Schedl (holotype and male allotype examined) combines properties of both *E. spinosus* and *E. limbus*, but in a unique way, so it deserves species status. It is also remerkably larger (female holotype: 5.5 mm.) and more colorful than most other known forms of *Eccoptopterus* spp. There are several other large colored forms known from Borneo, but their species identity remains unclear.

Biology: Gallery of all species consists of short tunnels branching randomly into the xylem. It is sometimes observed that the female first excavates small cacity or a curved tunnel just under bark, from which it then proceeds to create the radial tunnel. The behavior has been observed in *E. limbus* and *E. spinosus* at some localities but not others.

Figure 41: *Eccoptopterus spinosus*, the type species of the genus. Size: 4 mm.

Eccoptopterus gracilipes **syn. n. (Eichhoff, 1886)**

Synonymized with: *Eccoptopterus spinosus* (Olivier)

J.H. database code: Scol 5

Discussion

E. gracilipes was described by Eichhoff as a single species in his new genus *Platydactylus* (currently not used) without any reference to other species in the already existing genus *Eccoptopterus*. Thus, *E. spinosus* and *E. gracilipes* have been deemed different not according to their original descriptions, but presumably since later workers wanted to separate the extremely variable forms of *Eccoptopterus spinosus* into smaller and larger forms, or forms with differing elytral armature. Holotype of *E. gracilipes* is probably lost (Wood & Bright, 1992), only a large number of individuals identified as *E. gracilipes* by several earlier authors are available. True to the hypervariable nature of the group, these identifications are often inconsistent. For example, specimens from lowland elevations are often much smaller than those from highland elevations, while other characters are similar. Specimens in FICB identified by H. Roberts or K. E. Schedl have evenly spaced elytral teeth and are large but are placed under the label *E. spinosus*, as is one specimen identified as *E. gracilipes* by D. E. Bright. Non-types in USNM identified by Kalshoven and Hopkins as *E. gracilipes* all have uneven distribution of strial teeth - the 2nd tooth closer to the last than to the first one. *E. gracilipes* is synonymized here with *E. spinosus*, as the two names represent only vaguely defined forms the same variable species.Wood (1989, 6761) correctly synonymized *E. collaris* (Eggers) with this species (lectotype in USNM examined).

Previously synonymized species: *Xyleborus collaris* Eggers

Biology: Large individuals were collected in Chimbu (highlands), small ones in Madang and other low-elevation provinces, middle-sized are common in FICB collection mostly from Bulolo, which is a middle-elevation locality.

Examined material: Australia, Cairns, (B. H. Jordal, 6 indiv.); Malaysia, Sabah, Rhino Ridge, Danum Valley, Burseraceae sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Ficus sp. branches, (Hulcr coll.); New Guinea, Madang, (B. H. Jordal); New Guinea, Morobe Province, Mt. Kaindi, (BBM); New Guinea, Madang Province, Baitabag, (Hulcr coll., 3 indiv.); Philippines, Mt. Banahao, (H. Gebhardt);, Morobe Province, Bulolo, (B. H. Jordal);, Morobe Province, Mt. Kaindi, (B. H. Jordal); New Guinea, Aseki, (H. Gebhardt); PNG: Chimbu Prov. (11), Madang Prov. (206), Oro Prov. (80), West Sepik (21), J. Hulcr 2002-2006.

***Eccoptopterus limbus* Sampson (1911)**

J.H. database code: Scol 397

Compared to holotype in BMNH

Diagnosis: The declivital armature consists of two large teeth closest to the suture on the declivital summit (on the convergence of the 3rd interstia and declivital edge), and a number of smaller, uniform-sized teeth around the declivital plane (on the convergence between other interstriae and declivital edge). The exact position of the teeth in relation to striae (even the large pair) is difficult to ascertain due to the largely confused punctuation on the elytra. The small teeth can be blunt, tubercle-like, or sharply pointed, uniform in size or slightly increasing in size towards summit. The declivity can vary greatly in vestiture. Inconspicuous vestiture is rare; most common are dense flattened scales. The single individual known from PNG (Chimbu province, 1200 m a. s. l.) has long and not medium-dense setae on the declivity. More commonly, especially in SE Asia, the declivity is covered with dense flattened scales. The scales sometimes reflect light inbright yellow to gold color. Even small differences in the density, shape or color of these scales or setae can cause dramatic differences in overall appearance between otherwise almost identical individuals, which probably caused the number of re-descriptions of this species. The species is also greatly variable in size. The one known PNG specimen is 3 mm long, but throughout SE Asia, the sizes vary between 1.9 mm. (specimens from Thailand) to 3.5 mm. (holotype of *X. squamulosus* var. *duplicatus* Eggers).

Length: 1.9-3.6 mm.

Discussion

Wood's (1989) synonymy with *squamulosus, squamulosus auratus*, and *squamulosus duplicatus* (Eggers' species) correct, lectotypes seen in USNM, they are middle-sized to large. *Eccoptopterus squamulosus* var. *auratus* has dense flattened setae giving the declivity a golden look.

Previously synonymized species: *Xyleborus squamulosus duplicatus* Eggers, *Xyleborus squamulosus auratus* Eggers.

Examined material: Indonesia, Sumatra, (holotype of E. squamulosus, H. Gebhardt); Malaysia, Sabah, Danum Valley, *Ficus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Ficus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll., 8 indiv.); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Ficus sp. branches, (Hulcr coll., 3 indiv.); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll.); Thailand, Pong Yaeng N. P., (Hulcr coll., 4 indiv.); PNG: Chimbu Prov. (1), J. Hulcr 2002-2006.

***Eccoptopterus sagittarius* syn. n. Schedl (1939)**

Synonymized with: *Eccoptopterus spinosus (Olivier)*

J.H. database code: Scol 723

Compared to paratype in NHMW

Discussion

No decisive character difference was found between the types of *E. sagittarius* from Philippines, a non-type from New guinea identified by Schedl, non-types of various origins in Browne's BMNH collection, and a large series of *E. spinosus*, except for the small size of the putative *E. sagittarius*. *E. sagittarius* has all essential features of *E. spinosus*, except it lies at the end of the size spectrum with (paratype: 2.3 mm.). More over, the small specimens are often less similar to each other (in elytral declivity shape and surface, etc.) than to other larger specimens *E. spinosus*, suggesting that size itself does not indicate monophyletic clades within *Eccoptopterus*. Thus *E. sagittarius* is synonymized here with *E. spinosus*.

Examined material: New Guinea, Morobe Province, Bulolo, (H. Gebhardt); Philippines, Luzon, Mt. Irid, (paratype, H. Gebhardt).

***Eccoptopterus spinosus* (Olivier, 1795)**

J.H. database code: Scol 4

Compared to non-types in collected in Java

Diagnosis: There are only two species of *Eccoptopterus* known from New Guinea: *E. spinosus* and *E. limbus*. The main differences between the two extremely variable and widespread species are the pattern of teeth around the elytral declivity and the declivital vestiture. In *E. spinosus*, there is a pair of large teeth close to the suture on the summit of declivity (in 3rd interstriae), and two or rarely three teeth along the declivital edge. The second (and equally unreliable) difference is pubescence. In most representatives recognized as *E. spinosus*, the declivity is devoid of pubescence, only in rare cases the pubescence is more prominent.

Length: 2.3-4.7 mm.

Discussion

Holotype from MNHN in Paris was not available. Several specimens from various regions were examined which can be considered intermediate forms between *E. spinosus* and *E. limbus*. In these, the declivital tooth set consists of a pair of large ones, two or three pairs of smaller ones (as in *E. limbus*), and several smaller ones scattered among them on the declivital edge (as in *E. limbus*). The size and vestiture of these vary. Therefore the boundary between the two species is not a strict phenotypic discontinuity. However, these intermediates are so rare that the distinction between the two species is justified on the ground of utility. Blandford synonymized the independently described *E. sexspinosus* Motsch. with *Xyleborus* (then *Platydactylus*) *abnormis* Eich. Beaver analyzed specimens of this species from several bioregions, and concluded that *Eccoptopterus eccoptopterus* (Schedl) falls within the range of variation of *E. spinosus*.

Previously synonymized species: *Xyleborus abnormis* Eichhoff, *Eccoptopterus sexspinosus* Motschulsky, *Eccoptopterus eccoptopterus* Schedl, *Eccoptopterus sexspinosus* var. *multispinosus* Hagedorn, *Eccoptopterus sexspinosus* var. *pluridentatulus* Sched

New junior synonym(s): *Eccoptopterus gracilipes* (Eichhoff), *Eccoptopterus sagittarius* Schedl

Examined material: Australia, Palmerston, (B. H. Jordal); India, Kerala, Munnar, (FMNH); Indonesia, Nias, (holotype of *E. sexspinosus* var. *multispinosus* Hag., H. Gebhardt); Malaysia, Sarawak, Lambir Hills, (B. H. Jordal); Malaysia, Taman Negara, (BMNH); Malaysia, Sabah, Danum Valley, Mallotus sp. branches, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll.); New Guinea, Morobe Province, Mt. Kandi, (B. H. Jordal), 2200 m asl; New Guinea, Madang Province, Baiteta, (B. H. Jordal, 8 indiv.); New Guinea, Morobe Province, Bulolo, (B. H. Jordal); New Guinea, Milne Bay, Astrolabe Bay, (H. Gebhardt), identified as E. gracilipes by Schedl; New Guinea, Madang Province, Ohu, *Artocarpus camansii* twigs, (Hulcr coll., 16 indiv.); Samoa, (paratype of E. eccoptopterus, H. Gebhardt); Samoa, Upolu, (paratype of Xyleborus eccoptopterus Schedl, H. Gebhardt); Thailand, Pong Yaeng N. P., (Hulcr coll.), R. A. Beaver det.; Uganda, Kibale Forest Reserve, (B. H. Jordal); PNG: Madang Prov. (21), Oro Prov. (29), J. Hulcr 2002-2006.

Genus *Emarginatus* gen. n. Hulcr & Cognato

J.H. database code: Scol 832

Type species: *Emarginatus* (*Xyleborus*) *emarginatus* (Eichhoff 1878).

Diagnosis: The essentialdiagnostic characters of the genus are the prolonged and flat pronotal disc, slender and triangular tibiae with few but large and long denticles, bulging prosternal posterocoxal process, and most notably the structure of elytral declivity. The declivity ranges from flat to excavated and emarginate, with first interstriae broadened to the point that strial punctures are displaced lateraly, and surrounded by tubercles or teeth. In many species, the declivity is surrounded by elevated wall and emarginate.

Description: Eyes shallowly emarginate, "bean shape", upper portion of eyes smaller than lower part. Antennal club more-less circular shape, club type two (obliquely truncated, second segment visible on posterior side). First segment of club circular around the club, covering most of the posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only. Third segment of club partly visible on the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum slightly impressed, shaped as a distinct large triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view with disc distinctly prolonged (type 8). From dorsal view it has prolonged basic shape with rounded frontal margin (type 7), or long, rounded anteriad (type 9). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum concave (pronotum very long), or obliquely costate. Procoxae contiguous, prosternal posterocoxal process large and bulging. Tuft on pronotal basis associated with mesonotal mycangium absent, setae on elytral bases associated with elytral mycangium absent. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat, punctures on elytral disc in strial lines (which may be difficult to discern). Elytral declivity with few setae or scales, not conspicuously pubescent. The details of structure of the elytral declivity is discussed below. Circumdeclivital costa ending in 7th interstriae, or reaching beyond 5th interstriae, encircling most or all of declivity. First interstriae are parallel, or distinctly broadened towards the summit of elytral disc, or parallel on disc but broadened towards the apex of elytra, where they sometime bear tubercles. Protibiae distinctly trinagular, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles small in small species, but mostly large, distinctly longer than wide. Bases of the denticles range from not enlarged to slightly enlarged, fewer than 6 protibial denticles present. Metatibiae of regular size. Body length 1.8 to 4.2 mm., mostly slender species, never very robust. Color varies from light brown to black, pronotum sometimes much lighter than elytra.The genus is named after its elytral declivity, which is usually emarginate and with characteristic tubercle pattern. There are several (around 3 pairs) or large tubercles in each interstria 1. However, the fact that these all originated in the first stria is not apparent, even counterintuitive at first, and can be seen only in some species and preferrably from the bottom side of elytra. This is due to the fact that the first striae are greatly broadened on the declivity, and the strial punctures have been displaced and reduced. The flat or excavate shape of elytra is in fact a greatly broadened interstria 1 and to a certain extent 2 and 3. The broad interstria 1 displaced strial lines. The dominant declivital tubercle appears to lie on or around the remnants of the first strial line, which is caused by the fact that the line is curved around the tubercle but the displaced strial punctues are not discernible. There are usually no tubercles in the second striae (though it often looks like the dominant ones in fact are in 2nd interstriae), there are smaller tubercles in striae 3 and beyond, creating tuberculated elevated wall surrounding the declivity.The greatly plastic declivity also provides the main identification characters of species within the genus - the shape of the circumdeclivital wall and the size of the paired declivital spines around and inside the declivity. The height of the wall and the spines are almost exactly correlated, suggesting a shared genetic mechanism. Simple two-dimensional extension or retraction of these created a whole array of declivital shapes (subsequently described as a slew of species by early taxonomists). The feature seems to be a encoded by a very plastic genetic mechanism. Anyone attempting identification of specimens in this clade is almost guaranteed to find intermediate forms. Also, because the differences between species are largely relative, identification by comparison to photographs or specimens is recommended over identification using descriptions only. Full range of the circumdelcivital costa extensions can be found in nearly every region where this group occurs, throughout SE asia to Melanesia. Whether each morph have colonized all the areas independently or whether the same range of modifications originated independently in each region is equally likely. Since the genetic background of the declivity is so easily modifiable, while the rest of the body is nearly immutable across majority of the morphs (except for body size), the authors are inclided to the later hypothesis of frequent emergence of similar declivital forms independently in each region. The great plasticity of the character can be illustrated by specimens which have different tooth pattern on each elytron. For these reasons, our occasional use of the declivital armature as a sole character for species delimitation may be disputable. However, very few other distinguishing characters have been found in this group, and in order to preserve the notion of the amazing morphological diversity in this clade we decided not to collapse all the species in one.The paired declivital spines are the principal generic character of the clade and deserve more attention. Nearly in every case, four of these spines can be found on each elytron. Their mediolateral position is relatively stable in reference to the striae and the circumdeclivital costa, but may be confusing due to the variable expression of these striae. The first tooth is always minute, positioned on the first stria on the summit of elytral disc. The second spine lies on the approximate boundary between elytral disc and declivity, it is positioned close to the first one, also seemingly on the first stria or within the first interstria. The third, always the largest spine, is in the middle of the declivital slope, anywhere between the first interstria to the lateral margin of declivity. The strial position of the last, usually very small spine, is unclear, but it always occurs near the very tip of the elytra. Small granules in the first interstria may or may not occur on the top of declivity or on the circumdeclivital wall. The relative position of the largest declivital spine and the circumdeclivital elevated costa may seem like a useful character (teeth inside the declivity or on the costa), but when sufficient number of individuals is examined, a full range of intermediates can be found in all species. The variable pattern of expression of homologous teeth around declivity is remarkably similar to that in *Eccoptopterus*; the teeth pattern may be governed by the same genetic mechanism.

Discussion

Browne (1961c) placed many *Emarginatus* spp. in a subjective typological group *Coptoborus*. However, *Coptoborus* was an unrecognized group designated by Hopkins

(1915) for unrelated Neotropical species. Wood (1980c) later elevated *Coptoborus* to the generic rank, and only included *Streptocranus* spp. from the Paleotropical fauna, no any *Emarginatus* spp. The genera *Emarginatus*, *Coptoborus* or *Streptocranus* are not closely related. Browne (1961c) remarked on the variability of many species, and the ambigious species boundaries.

Biology: Galleries of many species contain several irregular brood chambers. Often significant portion of the tunnel system is between the bark and the xylem core.

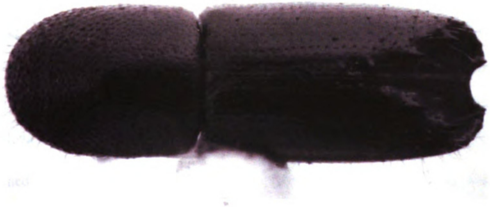

Figure 42: *Emarginatus emarginatus*, type species of the genus. Size: 3.5 mm.

***Emarginatus cyclopus* comb. n. Schedl (1940)**

J.H. database code: Scol 480

Previous genus: *Xyleborus*

Compared to holotype in BMNH

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Diagnosis: Extremely long posterolateral declivital processes, and deep emargination. The elytral processes appear constricted at their bases. Smooth surface of declivity, very few tubercles on the circumdeclivital costa except for the large spines and a few minute granules at the apex.

Length: 4.2 mm.

Discussion

Examined specimens from PNG are identical to the holotype. The species belongs in a group of similar species (or rather morphotypes), mostly from Malaysia. *X. amphicranoides latecavatus* is a similar species but larger, has shorter declivital teeth and less deep emargiantion, pronotal disc less shining, more punctures. Schedl (1940b) provides distinguishing characters from similar Asian species *X. amphicranoides* and *X. fischeri*. Similar to non-types of *Xyleborus* (*Emarginatus*) *amphicranoides* (Hagedorn) in USNM, which have slightly broader elytral emargination.

Examined material: New Guinea, Morobe, Wau, (BBM); New Guinea, Morobe, Wau, (BBM); New Guinea, West Papua, Cyclops Mts., Mt. Lina, (holotype, BMNH), 3500-4000 ft.; New Guinea, Morobe Province, Bulolo, (FICB); PNG: West Sepik (1), J. Hulcr 2002-2006.

Emarginatus emarginatus **comb. n. Eichhoff (1878)**

J.H. database code: Scol 80

Previous genus: *Xyleborus*

Compared to homotype in NHMW

Diagnosis: *E. emarginatus* is usually larger and darker than most *Emarginatus* spp. Representatives of *E. emarginatus* have very shallow declivital excavation and small declivital denticles compared to *E. latecornis*, and even less so compared to *E. fallax*. There is no clear boundary in morphological variation between the three species.

Length: 3.2-3.7 mm.

Discussion

Schedl (1954c) suggest close relationship between *X. emarginatus, X. fisheri* Hag., *X. excesus* (*sic!*) Blandf., *X. detritus* Egg., and *X. blandus* Schedl. *X. blandus* allegedly differs from others by the absence of tubercles on the lateral processes of elytra and differences in declivity shape and armature.Kalshoven (1959b) synonymized *Tomicus cinchonae* Veen with *E.* (as *Xyleborus*) *emarginatus*. He examined larger number of individuals from different localities identified by different authors as different species, and concluded that *E. emarginatus* varies in size (3.0-4.0 mm.) and in the development of the spines on the declivity. He also mentioned that *X. dentatus* Blandford appeared identical to *X. cordatus* Hagedorn, which was synonymized with *E. emarginatus* (Eggers, 1929). We have not seen these species, but *X. dentatus* should be compared to *E. emarginatus*. Schedl (1973e:92) suggested a synonymy of *Xyleborus exesus* with *E.* (as *Xyleborus*) *emarginatus* based on the fact that both *X. exesus* and an Asian (non-PNG) variant of *X. emarginatus* have shallow declivital emargination. Schedl subsequently described the PNG form (deeper emargination) as *Xyleborus emarginatus semicircularis* (synonymized again with *E. emarginatus* by Wood (1989)). We confirmed the similarity of all three forms, synonymy will be published elsewhere.

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Previously synonymized species: *Xyleborus emarginatus semicircularis* Schedl, *Xyleborus cordatus* Hagedorn, *Xyleborus cinchonae* Veen

Biology: Galleries (tunnels and chanbers) often between bark and xylem (Beaver & Browne 1978). Browne (1961c) remarked on the large geographical range of this species and consequently the variability. The distribution spans from India to New Guinea, occuring from the sea level to over 2100m a.s.l. The species is fairly common throughout its range.

Examined material: Indonesia, Sumatra, Bandar Baroe, (compared to type, NHMW); Indonesia, Java, Bandjar, (compared to type, NHMW, 2 indiv.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll., 5 indiv.); Malaysia, Sabah, Danum Valley, *Ficus* sp. trunk, (Hulcr coll., 5 indiv.); Malaysia, Sabah, Danum Valley, Parashorea malaanonan branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Parashorea malaanonan trunk, (Hulcr coll., 6 indiv.); New Guinea, (BBM, 20 indiv.); New Guinea, Ambunti, (BBM, 4 indiv.); New Guinea, (FICB); New Guinea, Gulf Province, Ivimka, (UCD), R. A. Beaver det.; Philippines, Laguna, Pangil, (compared to type, NHMW); Thailand, Pong Yaeng N. P., (Hulcr coll.); PNG: Madang Prov. (79), J. Hulcr 2002-2006.

Emarginatus fallax **comb. n. Eichhoff (1878)**

J.H. database code: Scol 117

Previous genus: *Xyleborus*

Diagnosis: Schedl (1954c) distinguishes *X. fallax* from other species of the same group by the equidistant mutual position of the three elytral teeth, deep apical emargination, and by comparatively slender body. The second tooth varies from long and slender, or almost as long the third, or much shorter than the third. The declivity width varies as well, and the apical edge of declivity may or may not bear a distinct tooth. Usually slightly bicolored, with light brown pronotum and dark brown elytra. Individuals from higher elevations tend to be larger and dark.

Length: 2.5-3.5 mm.

Discussion

The situation of a holotype of *E. fallax* is unclear. Wood & Bright (1992) indicate IRSNB as its depository. However, the museum personell reported to us that the holotype was never deposited there. Specimens from Borneo have on average more robust elytral armature than PNG specimens. Schedl (1954c) discusses the large variation in overall shape, in the relative sizes of the declivital teeth, and in the declivital emargination. Especially the position and size of the second tooth varies widely, with no obvious relation to biogeographical regions. Wood (1989) included *X. amphicranulus* Eggers 1923 as a synonymy which we confirmed.

Previously synonymized species: *Xyleborus amphicranulus* Eichhoff

New junior synonym(s): *Xyleborus fastigatus* Schedl

Biology: Short tunnel, flat vertical chamber; in Borneo - simple chaotic tunnels. *E. fallax* almost invariable creates at least part of its tunnel system in cambium, just under bark. *E. fallax* is probably the most common and widespread representative of the genus (Browne 1961c), and consequently displays large regional morphological variation.

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Examined material: Malaysia, Sabah, Danum Valley, (Hulcr coll.); Malaysia, Sabah, Danum Valley, (Hulcr coll., 8 indiv.); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, non-dipterocarp branches, (Hulcr coll., 3 indiv.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll., 5 indiv.); Malaysia, Sabah, Danum Valley, *Ficus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Ficus* sp. trunk, (Hulcr coll., 23 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* trunk, (Hulcr coll., 10 indiv.); New Guinea, Morobe Province, Bulolo, (B. H. Jordal); New Guinea, (BBM, 5 indiv.); New Guinea, Morobe Province, Bulolo, (MSUC), identified by Schedl as *X. latecornis* Schedl, but it resembles *E.* (as *X.*) *fallax* more than the type of *X. latecornis*; New Guinea, (Zhu Hongbin, Chinese Port Quarantine); Philippines, Luzon, Mt. Makiling, (holotype of *X. amphicranulus* Egg., synonymized with *X. fallax*, SMTD); Sulawesi, (BMNH); Thailand, Pong Yaeng N. P., (Hulcr coll., 2 indiv.); PNG: Madang Prov. (36), Oro Prov. (66), West Sepik (123), J. Hulcr 2002-2006.

Emarginatus latecornis **comb. n. Schedl (1969)**

J.H. database code: Scol 774

Previous genus: *Xyleborus*

Compared to holotype in NSMT

Diagnosis: There are three differences between *Emarginatus fallax* and *E. latecornis* which seem to be more or less stable: The surface of declivity and adjacent disc along the suture is distinctly shagreen (not apparent in wet or dirty specimens), the depth of the declivital excavation is less deep, somewhere between *E. fallax* and *E.emarginatus* (which can be difficult to realize if specimens of both species are not available), and the posterolateral processes of declivity are not flat or excavated, but slightly inflated. The holotype specimen differs further by having the second pair of declivital teeth unusually strongly recurved, but that is likely an idiosyncratic feature of that specimen. In reality, *E. latecornis* is probably a variation of the general *E. emarginatus* groundplan, rather than a distinct species, with the declivital emargination somewhere between *E. fallax* and *E. emarginatus*. However, the examined specimens are disctinct and we decided to preserve the name. *X. latecornis* is also very similar to *X. shoreae* (Stebbing) but the surface of declivity is not shagreen, emargination is less quadrate, and rather narrower. *X. exesus* from Japan is very similar, but the surface of declivity is not shagreen , it is 1.5x larger, and has slightly narrower emargination. *X. exesus* has shorter and more robust declivity and is synonymized with *E. emarginatus* above.

Length: 2.4-2.7 mm.

New junior synonym(s): *Xyleborus opulentus* Schedl

Examined material: New Guinea, Morobe Province, Bulolo, (NHMW); New Guinea, Gulf Province, Ivimka, (UCD); New Guinea, Gulf Province, Ivimka, (UCD); Philippines, Abulug, (paratype, NHMW); Philippines, Abulug, (holotype, NSMT); Sri Lanka, Kande-ella, (SLW); PNG: Oro Prov. (1), J. Hulcr 2002-2006.

***Emarginatus pumilus* comb. n. Eggers (1923)**

J.H. database code: Scol 26

Previous genus: *Xyleborus*

Compared to lectotype in USNM

Diagnosis: Smallest and most slender of all *Emarginatus* spp. in New Guinea. Declivity is only slightly excavated or entirely flat. End of elytra is usually flat, may be slightly emarginate. Declivital denticles are smaller than in other *Emarginatus* (except some *E. emarginatus*). Many specimens are bicolored, with orange to light brown pronotum, and dark brown to black elytra. Presence, absence and configuration of striae on declivity varies. In most specimens, several prominent punctures mark the remnant of stria 1 close to the major denticle; a row of small punctures marking the stria 2 may be present. Elytral sides vary from parallel to slightly concave.

Length: 1.8-2.0 mm.

Discussion

Egger's lectotype (from Sumatra) has a little less pronounced tubercles than specimens from PNG, both on and around declivity. The extent of the development of the declivital emargination and teeth is, as in all *Emarginatus*, a rather simple two-dimensional gradient, represented by species (from shortest to most produced) *E. pumilus* (Melanesia), *E. cylindricus*, *E. pseudocylindricus* and *E. fallax*. *X. cylindricus* is an intermediate between *E. pumilus* and *E. pseudocylindricus* in that it has broad and flat edge of declivity at the bottom, not rounded as in *E. pumilus*, but not yet emarginate as in *E. pseudocylindricus*. *E. pseudocylindricus* (Eggers) from Borneo shows emargination at the elytral tip, but not as deep as in *E. fallax*. No other significant differences between these forms have been found (except for size, which is however very variable).

New junior synonym(s): *Xyleborus ipidia* Schedl, *Xyleborus cylindricus* Eggers

Biology: Short tunnel, flat chamber. Beaver and Browne indicate strong association of this species to Moraceae, which Hulcr et al. (2007b) confirmed with numerous records form PNG.

Examined material: Indonesia, Sumatra, (lectotype, USNM); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll., 35 indiv.); Malaysia, Sabah, Danum Valley, *Ficus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Ficus* sp. trunk, (Hulcr coll., 30 indiv.); New Guinea, Morobe Province, Bulolo, (FICB); New Guinea, Gulf Province, Ivimka, (UCD), R. A. Beaver det.; PNG: Madang Prov. (960), Oro Prov. (20), West Sepik (370), J. Hulcr 2002-2006.

***Emarginatus spinicornis* comb. n. Schedl (1975)**

J.H. database code: Scol 77

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: Small species bearing unusually large spines on the declivity. The first as well as the third (apical) pair of declivital tubercles transformed into large and long teeth.

Length: 2.1-2.2 mm.

Discussion

In the description, Schedl (1975f) deposited the holotype in AMNH. However, the type resides in NHMW. Schedl (1975f) put the species in Xylebori emarginati, and distinguishes it by the very deep declivital cavity and very long and slender teeth, of which the one in the pair in the fifth interstriae and the pair at the postero-lateral process are bent towards the suture.

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Biology: Found in Oro in branches on the ground, most numerous in a moist branch in a creek. Short tunnel, flat chamber. Also occurs in West Papua (Browne 1983b).

Examined material: New Guinea, Bodem, (BBM, 2 indiv.); New Guinea, Milne Bay, Gwariu River, (holotype, NHMW); PNG: Oro Prov. (35), J. Hulcr 2002-2006.

Genus *Euwallacea* Hopkins (1915)

J.H. database code: Scol 798

Type species: *Euwallacea* (*Xyleborus*) *wallacei* (Blandford).

Redescription: Eyes shallowly emarginate, upper portion of eyes smaller than lower part, or as large as the lower part. Antennal club more-less circular shape, club type two (obliquely truncated, second segment visible on posterior side), or three (with first segment straight or convex). First segment of club circular around the club, covering most of the posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only, or corneous on both sides of club, but not entirely circular (not making the club "telescopic"). Third segment of club partly or clearly visible on both sides of the club. First segment of antennal funicle longer than pedicel, its base stalk-like. Funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum slightly impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view tall (type 2). From dorsal view it is subquadrate (type 3), or quadrate, robust (type 4).

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Pronotal disc densely and evenly punctured, lateral edge of pronotum concave (pronotum very long), or obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous, or tall and pointed, or conical and slightly inflated. Tuft on pronotal basis associated with mesonotal mycangium absent, also setae on elytral bases associated with elytral mycangium absent. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat or slightly convex, punctures on elytral disc in distinct strial lines. Boundary between elytral disc and declivity indistinct, end of disc rounded and smoothly transitioning into declivity. Lateral profile of elytral declivity slowly descending, often flat. Elytral end broadened and flattened lateraly. Elytral declivity with few setae or scales, not conspicuously pubescent. Circumdeclivital costa ending in 7th interstriae. Interstriae on declivity mostly with regularly spaced setae-bearing granules. These tubercles are small but abundant, making declivity appear rugose. First interstriae are parallel (sometimes slightly broadened towards elytral summit). Protibiae distinctly trinagular, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles large, distinctly longer than wide, bases of the denticles distinctly enlarged, conical, fewer than 6 protibial denticles present. Metatibiae of regular size. Large species, 3.9-5.7 mm. Color uniformly dark brown. Characters distinguishing *Euwallacea* from *Wallacella* gen. n.: upper part of eyes as large as the lower part (in *E. wallacei*), first segment of funicle slender, stalk-like, as long or longer than pedicel (except for *W. striatulus* which also has first segment of funicle long and slender); pronotum quadrate to subquadrate (overlapping character: *Walacella* have subquadrate to rounded pronotum); protibiae triangular, with 6 or fewer denticles, protibial spur (a single denticle positioned proximal to the body, separated from the other equidistant denticles) present; sockets of tibial denticles enlarged. Characters distinguishing *Euwallacea* and *Fortiborus* gen. n.: fisrt segment of antennal club concave, circular around the club (not recurved, convex); antennal club rounded or taller than wide (several (not all) *Fortiborus* with antennal club broader than long); anterior pronotal edge not elevated, lacking a row of serrations; protibiae triangular, with 6 or fewer denticles, protibial spur present.

Discussion

Gender masculine (named after a A. R. Wallace).The boundaries between *Euwallacea*, *Wallacella* and *Fortiborus* are not clear-cut. The close relation of the generea can be seen in a morphology-based phylogeny (Figure 22). For example, *Walacella* (previously *Euwallacea*) *interjectus* has most features of *Wallacella*, but also a quadrate pronotum without elevated anterior margin, typical for *Euwallacea*. On the other hand, *Euwallacea quadraticollis* has antennal club No. 4, characteristic for *Fortiborus* (all other characters place it in *Euwallacea*). If specimens from many bioregions are examined, it is possible that number of intermediate forms will be found.

Figure 43: *Euwallacea wallacei*, the type species of the genus. Size: 5.3 mm.

Euwallacea destruens **(Blandford, 1896)**

J.H. database code: Scol 59

Compared to syntypes in BMNH

Diagnosis: The major character distinguishing *E. destruens* from *E. wallacei* is the body dimensions. *E. destruens* spans lengths of 3.8-4.5 and widths 1.4-1.6, with an average l/w ratio of 2.76. Despite a considerable number of examined specimens from many localities and many different altitudes, no intermediates have been found within New Guinea. Further, *E. destruens* has smaller upper portion of the eye, and more slender protibiae with only 4 denticles.

Length: 3.9-4.5 mm.

Discussion

There are two specimens on a single holotype point. One of the two type specimens has conspicuously flat, almost concave declivity and very abrupt declivity-disc boundary, the other one is more akin to the common form of *E. destruens*. The latter specimen is possibly a synonym of Neotropical *Xyleborus discretus* Eggers. Beeson (1929) mentioned that Samoan individuals are smaller than Javanese ones.

Previously synonymized species: *Xyleborus barbatus* Hagedorn, *Xyleborus barbatulus* Schedl, *Xyleborus nandarivatus* Schedl, *Xyleborus pseudobarbatus* Schedl

New junior synonym(s): *Euwallacea procerrimus* (Schedl)

Biology: The name destruens refers to the occasional habit of this species as a pest in live trees. Mass attacks of this species on live trees have been recorded frequently, usually in cases where the trees have been planted artificially. *E. destruens* is especially pestiferous in plantations of teak (Tectona, Browne 1958). The authors observed a mass attacks of *E. destruens* on live and apparetnly healthy planted *Casuarina* sp. in Chimbu Province, PNG. Browne (1961c) claims that the total gallery length of *E. destruens* can reach up to 1.4 m. The gallery is primarily in one transversal plane, and several such transverse tunnel systems can be created parallel to each other, connected by longitudinal tunnels.

Examined material: Indonesia, Java, Gilolo, (syntype, BMNH, 2 indiv.); New Guinea, Morobe Province, Mt. Kaindi, (BBM), 2400m asl; New Guinea, New Britain, (BBM, 5 indiv.); New Guinea, Madang Province, Baiteta, (IRSNB); New Guinea, (Zhu Hongbin, Chinese Port Quarantine); PNG: Chimbu Prov. (15), Madang Prov. (100), West Sepik (9), J. Hulcr 2002-2006.

***Euwallacea filiformis* syn. n. (Schedl, 1975)**

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Synonymized with: *Planiculus bicolor* (Blandford)

J.H. database code: Scol 641

Previous genus: *Euwallacea*

Compared to holotype in NHMW

Length: 2.1 mm.

Discussion

Included in Xylebori submarginati by Schedl (1975f), among which it is allegedly unique by its very elongate and slender body. In reality, *X. filiformis* (*Euwallacea filiformis* in Wood & Bright, 1992) doesn't differ in any significant character from *Planiculus bicolor*, except for the slightly prolonged body. There is no evidence that such deviation in body shape is indicative of a unique and monophyletic genetic lineage. On the contrary, all three known specimens were collected in the same locality within the span of two years, thus likely representing local deviation of body shape from the typical *P. bicolor*.

Biology: All known individuals were found in Morobe or Oro province (Eastern parts of the island).

Examined material: New Guinea, Morobe Province, Bulolo, (FICB); New Guinea, Morobe Province, Bulolo, (holotype, NHMW); New Guinea, Morobe Province, Bulolo, (NHMW).

***Euwallacea laevis* syn. n. (Eggers, 1923)**

Synonymized with: *Planiculus bicolor* (Blandford)

J.H. database code: Scol 642

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Previous genus: *Euwallacea*

Compared to lectotype in USNM

Discussion

The holotype of *X. laevis* (*Euwallacea* in Wood & Bright, 1992 Catalog) is very similar to the holotype of the senior synonym *Planiculus* (*Xyleborus*) *bicolor*. Browne (1966) mentioned that the species size and declivital sculpture varies among different regions or islands. His Melanesian specimens were smaller than those from Malaysia.

Examined material: Indonesia, Java, (lectotype, USNM); Philippines, Luzon, (SMTD).

***Euwallacea procerrimus* syn. n. (Schedl, 1969)**

Synonymized with: *Euwallacea destruens* (Blandford)

J.H. database code: Scol 756

Compared to holotype in NSMT

Discussion

The holotype as well as a paratype are identical to a typical form of *Euwallacea destruens*.

Examined material: New Guinea, New Britain, (paratype, NHMW); New Guinea, New Britain, (holotype, NSMT).

***Euwallacea subemarginatus* syn. n. (Eggers, 1940)**

Synonymized with: *Planiculus limatus* (Schedl)

J.H. database code: Scol 317

Previous genus: *Euwallacea*

Compared to lectotype in USNM

Discussion

The lectotype of *Xyleborus* (*Euwallacea* in Wood & Bright, 1992) *subemarginatus* is a representative of the very variable morph of *Planiculus* with emarginate declivital apex, first described as *Xyleborus limatus*. Differences between *X. subemarginatus* and *P. limatus* are the less rugose declivity surface, less prominent circumdeclivital costa and more prominent tubercles in the end of interstria 1. All of these features are extremely variable in *Planiculus* species group. Thus *X. subemargiantus* is considered a synonym of *P. limatus*. *X. subemarginatus* is also virtually identical to *Xyleborus subparallelus* Eggers, with the exception of larger tubercles in the first interstria in the *X. subparallelus* lectotype. The patterns of tuberculation on elytral declivity cannot be used for species delimitation. The examined lectotype and paratypes of *X. subemarginatus* and the lectotype of *X. subparallelus* and many other representatives of these morphs display variable patterns of this declivital tuberculation. For example, both lectotypes of *X. subemarginatus* and *X. subparallelus* have one or two small tubercles in each interstria in the middle of the declivital slope and small granules on the top of declivity. The lectotype of *X. subemarginatus* lacks the pair of tubercles in the interstria 1 towards the apex of declivity, which is however present in both the paratypes of *X. subemarginatus* and in the lectotype of *X. subparallelus*. *X. subemarginatus* was transferred to *Euwallacea* from *Xyleborus* by Beaver (1998).

Examined material: Indonesia, Java, Bandjar, (NHMW, 2 indiv.); Indonesia, Java, Batoerraden, (paratype, NHMW, 3 indiv.).

Euwallacea subparallelus **syn. n. (Eggers, 1940)**

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Synonymized with: *Planiculus limatus (Schedl)*

J.H. database code: Scol 760

Previous genus: *Euwallacea*

Compared to lectotype in USNM. No reliable characters distinguishing this species from *P. limatus* and *P. bicolor* were found. It has a small notch at the apex of elytra (emarginated apex), which suggests closer relationship to *P. limatus*.

Examined material: Indonesia, Java, Batoerrad, (lectotype and a non-type, USNM, 2 indiv.); Malaysia, Sarawak, Mt. Dulit, (NHMW).

***Euwallacea talumalai* syn. n. (Browne, 1966)**

Synonymized with: *Wallacella andamanensis (Blandford)*

J.H. database code: Scol 53

Previous genus: *Euwallacea*

Compared to paratype in BMNH

Discussion

The specimens from PNG hitherto identified as *Euwallacea talumalai* are in fact smaller forms of *Wallacella andamanensis*. Except for size, all important characters are shared between all examined *E. talumalai* and the holotype of *W. andamanensis*, including the antennal club, tibiae, pronotal shape, declivital sculpturing, and the bluish iridescence on the elytra. Browne (1966) distinguished the species from other similar species (presumably *Wallacella* spp.) merely by the more evenly long and thick setae in the elytral striae. He also related the species to *E. andamanensis* (as *X. granulipennis*) and noted that it differed by its smaller size and by the more uniform granules across the elytral declivity.

Examined material: New Guinea, Morobe Province, Bulolo, (FICB); PNG: Madang Prov. (200), J. Hulcr 2002-2006.

Euwallacea tumidus **syn. n. (Schedl, 1975)**

Synonymized with: *Planiculus bicolor* (Blandford)

J.H. database code: Scol 645

Previous genus: *Euwallacea*

Compared to holotype in NHMW

Discussion

Schedl (1975f) relates *Xyleborus tumidus* (*Euwallacea tumidus* in Wood & Bright, 1992) to *Xyleborus conditus* Schedl from India, from which it can be distinguished by the smaller size, much finer sculpture of the declivity and the less steep declivity. No comparison to sympatric or more similar species is given. *X. tumidus* Schedl is nearly identical to *P. bicolor*, the only difference being the lack of declivital vestiture (likely an artifact of poor preservation) and the much smaller and uniform granules on the elytral declivity. Given the known variability in elytral tuberculation in *Planiculus* spp., this specimen (the holotype, the only representative of *X. tumidus* known) is a slightly differentiated individual or a local variant of the very plastic *Planiculus bicolor*.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

Euwallacea wallacei **(Blandford, 1896)**

J.H. database code: Scol 58

Compared to holotype in BMNH

Diagnosis: Largest *Euwallacea* in New Guinea, holotype: 57 mm. Distinguishable from *E. wallacei* from *E. destruens* is body dimensions. *E. wallacei* lengths range within 5.2-5.7 and width 2.0-2.4, with an average l/w ratio of 2.49. Despite a considerable number of examined specimens, no intermediates have been found in any altitude or any locality within New Guinea. Further, *E. wallacei* has much larger upper portion of eyes than *E. destruens*.

Length: 5.3-5.7 mm.

Discussion

Synonymy with *X. siporanus* Hagedorn is confirmed; the only difference between *E. wallacei* and *X. siporanus* lectotype is the opaque surface of declivity of *X. siporanus*.

Previously synonymized species: *Xyleborus wallacei indocorus* Schedl, *Xyleborus perakensis* Schedl, *Xyleborus ovalicollis* Eggers, *Xyleborus confinis* Eggers, *Xyleborus siporanus* Hagedorn

Examined material: Malaysia, (holotype, BMNH); New Guinea, Madang Province, Ohu, (B. H. Jordal); New Guinea, Morobe, Wau, (BBM, 4 indiv.); New Guinea, (FICB); New Guinea, Madang Province, Baiteta, (IRSNB); New Guinea, Gulf Province, Ivimka, (UCD); PNG: Madang Prov. (46), Oro Prov. (3), West Sepik (8), J. Hulcr 2002-2006.

Genus *Fortiborus* gen. n. Hulcr & Cognato

J.H. database code: Scol 834

Type species: *Fortiborus* (*Xyleborus*) *major* Stebbing, 1909.

Diagnosis: Some of the largest species of Xyleborina. Characters distinguishing *Fortiborus* from *Euwallacea*: margin of the first segment of antennal club concave, recurved (may appear straight); in several *Fortiborus* the antennal club is wider than long; anterior edge of pronotum produced anteriad, bearing a row of serrations (except. *F. anisopterae*); protibiae rounded (except in *F. indigens*), bearing seven or more denticles, protibial spur absent (a protibial spine separated from the row of equidistant tubercles). The rather similar genus *Immanus* can be distinguished by very robust protibiae with reduced denticles merged with a robust, irregular protibial edge; by asperate pronotal disc; by the antennal club which appear taller than broad, with second segment ring-like, semi-circular around the club, giving the club a "telescopic" look, and by the declivity which is entirely obliquely truncated and/or surrounded by a costa.

Description: Eyes shallowly emarginate, upper portion of eyes conspicuously large. Antennal club more-less circular shape, club type three (with first segment straight or convex), or four (first segment small, second and third prominent on both sides). First segment of club straight (may be slightly concave or convex) on anterior face, or convex and small; margin of the first segment mostly costate, may appear softer on posterior side. Second segment of club corneous on both sides of club, but irregularly sinuate, not ring-like. Third segment of club clearly visible on both sides of the club. First segment of antennal funicle longer than pedicel, its base stalk-like, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum slightly impressed, or deeply impressed, shaped as a narrow slit, or a narrow triangle.

Anterior edge of pronotum with distinct row of serrations, in most species conspicuously produced. Pronotum from lateral view tall (type 2), or rounded and robust (type 5). From dorsal view it is subquadrate (type 3), or quadrate, robust (type 4). Pronotal disc shining or smoothly alutaceous, with small punctures, or densely and evenly punctured, lateral edge of pronotum obliquely costate, usually with pointed shoulder. Procoxae contiguous, prosternal posterocoxal process conical and slightly inflated. Tuft on pronotal basis associated with mesonotal mycangium absent, setae on elytral bases associated with elytral mycangium absent. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge. Elytral disc longer than declivity and slightly convex or bulging, or impressed, "saddle-like". Punctures on elytral disc in strial lines. Boundary between elytral disc and declivity indistinct, end of disc rounded and smoothly transitioning into declivity, or 2. Lateral profile of elytral declivity mildly flat or rounded, or steep, especially towards the apex, excavated in one species. Dorsal profile of elytral end rounded, usually broadened lateraly. Elytral declivity with few setae or scales, not conspicuously pubescent. Circumdeclivital costa ending in 7th interstriae, in one species encircling most or all of declivity. The inner part of declivity has no tubercles, or only uniform granules, or no tubercles in interstria 1 (sutural), and several tubercles in interstriae 2, 3 and beyond, or tubercles on elevated costa around declivity. Tubercles in interstriae 1 absent, or minor granules (elytra excavated or other deviation), absent, or minor granules, or distinct, enlarged in interstriae 2, absent, or minor granules, or distinct tubercles in interstriae 3. Striae and interstriae on the upper part of declivity even, or bearing teeth around the declivity. First interstriae are parallel (sometimes slightly broadened towards elytral summit). Protibiae obliquely triangular, broadest in 2/3 of the length, or distinctly trinagular, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles small, bases of the denticles slightly distinctly enlarged, conical, usually between 6 and 8 protibial denticles present. Metatibiae of regular size. Very large species, 5.2-7 mm. Color uniformly dark brown or black.

Discussion

The closest genera to *Fortiborus* are probably *Euwallacea* and *Immanus*, all comprising large or very large species with similar antennal club structure, often with conspicuously large eyes, and modified procoxae. Putative relationships between *Euwallacea*, *Fortiborus* and other genera are illustrated is Figure 22.

Figure 44: *Fortiborus anisopterae*, a typical representative of the genus. Size: 5.2 mm.

Fortiborus anisopterae **comb. n. Browne (1983)**

J.H. database code: Scol 671

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Diagnosis: *F. anisopterae* differs from other *Fortiborus* spp. by having the anterior pronotal edge only slightly produced forward, armed with very small row of serrations.

Length: 5.2 mm.

Discussion

According to Browne (1983b), the species resembles *X. siclus*, but it has different sculpture on the elytral disc. Browne (1986a) mentioned similarity between males of *X. anisopterae* and *X. pseudopilifer*.

Examined material: New Guinea, West Papua, Fakfak, (compared to holotype, BMNH).

Fortiborus indigens **comb. n. (Schedl, 1955)**

J.H. database code: Scol 631

Previous genus: *Cyclorhipidion*

Compared to holotype in NHMW

Diagnosis: The species has unique elytral declivity. Unlike all other *Fortiborus* with declivity rounded, smoothly descending towards the apex, *F. indigens* has a large sulcus on each elytron topped with numerous small pointed tubercles, which makes the declivity appear deeply excavated. The declivity vaguely resembles that of *Stictodex* (previously *Taphrodasus* or *Xyleborus*) *cuspidus* or *Cyclorhipidion* (previously *Coptoborus* or *Xyleborus*) *superbus*.

Length: 7.0 mm.

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Discussion

Schedl (1955b) surprisingly claimed that the species is similar to *Eccoptopterus spinosus* (as *Xyleborus sexspinosus*).

Examined material: New Guinea, (holotype, NHMW).

Fortiborus major **comb. n. (Stebbing, 1909)**

J.H. database code: Scol 821

Previous genus: *Xyleborus*

Compared to homotype in NHMW

Diagnosis: Pronotal apical edge elevated, bearing short serrations. Conspicuously angulate end of elytra, the posterolateral costa elevated, making the declivity appear very broad and flat.

Length: 5.5 mm.

Discussion

X. major has not been reported from PNG, except a specimen identified as *X. siclus*.

New junior synonym(s): *Xyleborus siclus* Schedl

Biology: Common in continental Malaysia.

Examined material: India, Bengal, Buxa, (compared to type, NHMW).

Fortiborus pilifer **comb. n. Eggers (1923)**

J.H. database code: Scol 570

Previous genus: *Xyleborus*

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Compared to holotype in Berlin

Diagnosis: Larger than *E. wallacei*, steeper declivity. The difference between this species and *F. sulcinodis* is the absence of transversal impression on declivital disc, typical for *E. sulcinodis*. The diference between this species and *F. major* (or its synonym *Xyleborus siclus*) is the regularly shaped declivity, devoid of the conspicuosuly elevated lateral costa. Also, *X. pilifer* has larger (sometimes much larger) and much less dense tubercles on elytral declivity. Type: 6.4mm

Length: 6.0-6.3 mm.

New junior synonym(s): *Xyleborus pseudopilifer* Schedl

Examined material: Irian Jaya (D. N. Guinea), Maanderberg, (holotype, MNB).

Fortiborus sulcinoides **comb. n. (Schedl, 1974)**

J.H. database code: Scol 635

Previous genus: *Cyclorhipidion*

Compared to paratype in FICB

Diagnosis: Characteristic by its transversal "saddle-like" impression on elytral disc.

Length: 6.0-7.0 mm.

Discussion

Very similar to *F. pilifer*. Schedl (1974d) indicated its similarity to *X. kajangensis* Schedl (Malaysia). The type specimen is currently absent from ANIC. Paratype label (FICB) reads "*Xyleborus sulcinodis*", instead of sulcinoides.

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Examined material: New Guinea, Oro Province, Popondetta, (FICB); New Guinea, Morobe, (paratype, FICB); New Guinea, Western Porvince, Wavoi, (FICB, 2 indiv.); New Guinea, Western Province, Wavoi, (FICB); New Guinea, Western Province, Fly River, (MCG); New Guinea, Western Province, Fly River, (MCG); New Guinea, Morobe, (NHMW).

Genus *Hadrodemius* Wood (1980)

J.H. database code: Scol 795

Type species: *Hadrodemius globus* Blandford.

Redecription: Eyes shallowly emarginate, upper portion of eyes smaller than lower part. Antennal club more-less circular shape, or very flat, club type one (truncated, first segment covering posterior side). First segment of club circular around the club, covering the entire posterior face, or covering most of the posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club corneous, visible on the anterior side only, or corneous on both sides of club, but not circular (not making antenna tall, or "telescopic"). Third segment of club absent from the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick, or appear long and slender. Frons above epistoma rugged, coarsely punctate. Submentum slightly impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with two distinct flat denticles protruding anteriad. Pronotum from lateral view rounded and robust (type 5). From dorsal view it is rounded (type 1). Pronotal disc shining or smoothly alutaceous, with small punctures, or with dense setae, lateral edge of pronotum obliquely costate. Posterolateral corners of pronotum

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pronotum angulately produced. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous. Tuft on pronotal basis associated with mesonotal mycangium present and very conspicuous, setae on elytral bases associated with elytral mycangium absent. Scutellum visible only on the anterior slope of elytral bases, not visible form above. Elytral bases straight, with oblique edge. Elytral disc short compared to the declivity and convex, rounded, smoothly transitioning into declivity. Punctures on elytral disc confused. Lateral profile of elytral declivity steep, especially towards the apex, dorsal profile of elytral end rounded. Elytral declivity covered with abundant and long setae. Circumdeclivital costa ending in 7th interstriae. The inner part of declivity has no tubercles, or only uniform granules. Protibiae distinctly trinagular, slender on the upper part, very broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles large, distinctly longer than wide, bases of the denticles slightly or distinctly enlarged, conical, usually between 6 and 8 protibial denticles present. Metatibiae of regular size. Large species, robust, around 4.9 mm. long. Mature specimens are uniformly black.

Discussion

Several bulky representatives of *Anisandrus* (sensu Dole & Cognato, 2009) with miniature scutellum probably represent close relationship between *Anisandrus* and *Hadrodemius* (i.e., *A. pseudosolidus* (Schedl)); however all other charcters point to *Anisandrus*.

Figure 45: *Hadrodemius globus*, the only representative of the genus in New Guinea.

Size: 4.9 mm.

***Hadrodemius globus* (Blandford, 1896)**

J.H. database code: Scol 16

Compared to holotype in BMNH

Diagnosis: The only *Hadrodemius* in New Guinea. It could be potentially confused with *Anisandrus ursa*, from which it differs by the absence of scutellum and of the tubercels on the end of declivity of *A. ursa*.

Length: 4.9 mm.

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The characteristic rich vestiture is mostly lost from the type specimen. Specimens collected in continental Asia identified as *H. globus* often differ, and there may be significant molecular distance between these and PNG representatives (Cognato et al., 2009).

Previously synonymized species: *Xyleborus ursus fuscus* Eggers, *Xyleborus ursus* Eggers

Biology: Relatively common throughout its large range, which spreads across New Guinea, Philippines, Borneo, and continental SE Asia. Almost always breeds in small branches, between 1.5 to 10 cm, often appearing surprisingly large for the branch diameter.

Examined material: New Guinea, (holotype, BMNH); Philippines, Luzon, (SMTD, 7 indiv.); Philippines, Tayabas, (SMTD, 2 indiv.); Thailand, Pong Yaeng N. P., (Hulcr coll., 2 indiv.); PNG: Madang Prov. (109 indiv.), Oro Prov. (2), J. Hulcr 2002-2006.

Genus *Immanus* gen. n. Hulcr & Cognato

J.H. database code: Scol 830

Type species: *Immanus colossus* (Blandford, 1896).

Diagnosis: The genus contains some of the largest species of Xyleborina, all species are robust and display some extent of declivity truncation. Both species occuring in New Guinea are over 7 mm long and very robust. Most species (both species from New Guinea) have unusualy tall antennal club with well developed corneous segments 2 and 3 encircling the antennal club. Most species have reduced socketed denticles on protibiae, protibial edge is on the other hand robust, irregular. The rather similar genus *Fortiborus* can be disti

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can be distinguished by regular socketed denticles in protibiae, shining, not asperate pronotal disc; broad, rather than tall and "telescopic-looking" antennal club, and a rounded lateral profile of declivity, rather than truncated or surrounded by a costa (with the exception of *F. indigens*).

Description: Eyes shallowly emarginate, "bean shape", upper portion of eyes conspicuously large. Antennal club tall, "telescopic", club type four (first segment small, second and third prominent on both sides). First segment of club convex, small, margin of the first segment mostly soft, pubescent. Second segment of club ring like, corneous, encircling the whole antennal club, making it appear telescopic. Third segment of club clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum slightly impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with distinct row of serrations or with an elevated medial carina, sometimes with only a pair of pointed flat serrations. Pronotum from lateral view distinctly tall (type 3), or rounded and robust (type 5). From dorsal view it is rounded (type 1). Pronotal disc with asperities resembling those on the frontal slope, lateral edge of pronotum with distinct pointed shoulder. Procoxae contiguous, prosternal posterocoxal process conical and slightly inflated. No mycangia or associated tufts present on either pronotum, mesonotum or elytra. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc as long or shorter than declivity, convex or bulging or impressed, "saddle-like", punctures on elytral disc in strial lines or confused. Lateral profile of elytral declivity obliquely truncated, sometimes with costa or carina on the edge, sometimes excavated, dorsal profile of elytral end rounded, or broadened

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broadened laterally. Circumdeclivital costa encircling most or all of declivity. Declivity truncated, often armed with large teeth, or surrounded with robust elevated costa. Declivital surface in some species covered with short dense setae. In some species, striae and interstriae on the upper part of declivity bear teeth around the declivity. First interstriae distinctly broadened towards the summit of elytral disc. Protibiae distinctly triangular, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles reduced, merged with the rugose protibial edge, bases of the denticles uneven. Metatibiae of regular size. Uniformly dark brown or black, in some SE Asian species pronotum much lighter than elytra. Possibly the largest species of Xyleborina, 7.5-8.8 mm. long.

Etymology: (L)- monstrous.

Figure 46: *Immanus colossus*, type species of the genus. Size: 8.8 mm.

Immanus acanthurus **comb. n. (Lea, 1910)**

J.H. database code: Scol 745

Previous genus: *Xyleborus*

Compared to non-type in RAB

Diagnosis: Large beetle, 7.5 mm. long and 3.5 mm. wide. Declivity excavated and entirely surrounded by a circle of large teeth, one or more in each interstria.

Length: 7.5 mm.

Discussion

The type is not present in Victoria Museum, as indicated by Wood & Bright (1992), nor in SAM. Only a non-type specimen identified by R. A. Beaver was available.

Biology: Previously reported only from Australia, this is the first record from New Guinea.

Examined material: New Guinea, Madang Province, Baitabag, (B. H. Jordal), Kasbal coll. 1999, R. A. Beaver det.

Immanus colossus **comb. n. (Blandford, 1896)**

J.H. database code: Scol 477

Previous genus: *Ambrosiodmus*

Compared to holotype in BMNH

Diagnosis: Possibly the largest xyleborine species in the world, 8.5 mm. long and 4.5 mm. wide. Distinguishable form the only other *Immanus* in New Guinea (*I. acanthurus*) by the circumdeclivital costa without major teeth, and by the row of tubercles in each second interstria inside the declivity.

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Length: 8.8 mm.

Discussion

The synonymy of *X. szentivanyi* Schedl with *A. colossus* by Wood (1989) is confirmed. Schedl (1968e) distinguished them by only a few minor differences on declivity and size.

Previously synonymized species: *Xyleborus szentivanyi* Schedl

Biology: Collected regularly from *Celtis* sp.

Examined material: New Guinea, Morobe, Wau, (BBM); New Guinea, (holotype, BMNH); New Guinea, Madang Province, Ohu, *Celtis philippinensis*, (L. Cizek); PNG: Madang Prov. (17), J. Hulcr 2002-2006.

Genus *Leptoxyleborus* Wood (1980)

J.H. database code: Scol 797

Type species: *Leptoxyleborus* (*Phloeotrogus*) *sordicauda* Motschulsky.

Redescription: Eyes shallowly emarginate, "bean shape", upper portion of eyes smaller than lower part. Antennal club more-less circular shape, or taller than wide, club type two (obliquely truncated, second segment visible on posterior side), or three (with first segment straight or convex). First segment of club circular around the club, covering most of the posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only. Third segment of club clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, or longer than

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pedicel, its base stalk-like, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum slightly impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with distinct row of serrations. Pronotum from lateral view tall (type 2), with its anterior part extended. From dorsal view it is conical (type 0), or conical and long (type 5). Pronotal disc densely and evenly punctured, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process tall and pointed. Tuft on pronotal basis associated with mesonotal mycangium absent, also setae on elytral bases associated with elytral mycangium absent. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc short compared to the declivity and sometimes convex, punctures on elytral disc in strial lines, often impressed, ridge-like. Lateral profile of elytral declivity slowly descending, flat, very long compared to elytral disc. Elytral end distinctly broadened lateraly. Elytral declivity of the one species living in New Guinea has its declivity densely covered with star-like minute scales. Circumdeclivital costa elevated, carinate, ending in 7th interstriae. The inner part of declivity has no tubercles, or only uniform granules. First interstriae are parallel. Protibiae distinctly trinagular, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles large, distinctly longer than wide, bases of the denticles slightly elevated, or distinctly enlarged, conical, fewer than 6 protibial denticles present. Metatibiae of regular size. Body length between 2.8 to 3 mm. Color uniformly light brown or reddish or dark brown, pronotum much lighter (yellow or orange) than elytra. According to Browne (1961c), several species of the genus are elliptical on crossection, rather than cylindrical as other ambrosia beetles.

Discussion

Many species were transferred into the genus, based only on the presence of a flat declivity. This is a homoplastic character in Xyleborina, and the inclusion of several species in *Leptoxyleborus* needs re-examination. For example, *L. puer* does not share diagnostic characters of *Leptoxyleborus*, and the species represents a unique Xyleborina lineage, which is described in this study as a new genus *Anceps*.

Figure 47: *Leptoxyleborus sordicauda*, the type species of the genus. Size: 2.8 mm.

***Leptoxyleborus ceramensis* syn. n. (Schedl, 1937)**

Synonymized with: *Anceps puer* (Eggers)

J.H. database code: Scol 769

Previous genus: *Leptoxyleborus*

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Compared to holotype in NHMW

Discussion

Both examined specimens - the holotype and a specimen from New Guinea - are identical to the holotype of *Anceps puer* comb. nov. All characters (e.g.antennal club, entirely flat submentum, dorsally flattened pronotum, large and few socketed denticles on all tibiae with enlarged sockets) suggest synonymy with *A. puer*. Schedl (1937e) puts *Xyleborus ceramensis* in the "neighborhood" of *X. spathulatus* Blandford, now synonymized with *Leptoxyleborus punctatissimus* (Eichhoff).

Biology: Originally described from Borneo.

Examined material: Indonesia, Ceram, (holotype, NHMW); New Guinea, Morobe, Gabensis, (FICB).

Leptoxyleborus concisus syn. n. (Blandford, 1894)

Synonymized with: _Leptoxyleborus sordicauda_ (Motschulsky)

J.H. database code: Scol 857

Compared to holotype in BMNH

Discussion

Based on the examination of several hundreds of non-type specimens, the type of *L. concisus* in BMNH, and a photograph of the lectotype of *L. sordicauda* (from IZM kindly provided by Dr. A. Petrov). We confirm the synonymy of *L. concisus* with *L. sordicauda* (Schedl 1951i). Eggers (1927c) noted the similarity of *X. marginatus* and *L.* (as *Xyleborus*) *sordicauda*, and indicated a few minute differences. *X. concisus* was transferred to *Leptoxyleborus* by Maiti & Saha (1986). Wood (1989) included *Xyleborus incurvus* Eggers 1930 as a synonymy. Eggers (1927c) described another variant of the same species from a different part of the Philippines as *Xyleborus marginatus*, based on color differences. *X. marginatus* was also synonymized with *L. concisus* by Browne (1955).

Examined material: Japan, (holotype, BMNH).

Leptoxyleborus sordicauda (Motschulsky, 1863)

J.H. database code: Scol 17

Compared to lectotype photograph in IZM

Diagnosis: Pronotum long anteriad, almost conical, very tall from lateral perspective. Elytral disc short, ending in a conspicuously "humped"elytral summit. Declivity convex at the summit, but concave near the apex. The declviity is very flat, conspicuously broadened posterolateraly. Its surface is covered with a dense layer of minute scales in the shape of inflated stars.

Length: 2.8-3.0 mm.

Discussion

The only species of the genus confirmed in New Guinea. Described first as *Phloeotrogus sordicaudus* Motschulsky 1863, but in many collections identified as the junior synonym *Leptoxyleborus concisus* (Blandford, 1894). The IZM collection contains a lectotype and at least one paratype of *L. sordicauda*. The characteristic dense declivital vestiture is lost in these specimens, but the declivital surface bears dense puctures which mark absence of the missing scales.

Previously synonymized species: *Phloeotrogus attenuatus* Motschulsky, *Xyleborus sordicaudulus peguensis* Eggers, *Xyleborus incurvus* Eggers, *Xyleborus marginatus* Egger, *Xyleborus sordicaudulus* Eggers.

New junior synonym(s): *Leptoxyleborus concisus* (Blandford)

Biology: Remarkably widespread species, common from India throughout SE Asia to Melanesia. Beaver & Browne (1978) suggest that the species is particularly attracted to sap-rich hosts. No host specificity was detected in this species by Hulcr et al. (2007b) in PNG, except that it occurs predominantly in larger and humid logs, often those partly burried in ground.

Examined material: Malaysia, Sabah, Danum Valley, (Hulcr coll., 10 indiv.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Ficus* sp. trunk, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* trunk, (Hulcr coll., 2 indiv.); Thailand, Pong Yaeng N. P., (Hulcr coll.), R. A. Beaver det.; PNG: Madang Prov. (454), Oro Prov. (4), West Sepik (96), J. Hulcr 2002-2006.

Genus *Microperus* Wood (1980)

J.H. database code: Scol 787

Type species: *Xyleborus theae* Eggers (synonym of *M. diversicolor* (Eggers, 1923))

Redescription: Eyes shallowly emarginate, "bean shape", upper portion of eyes smaller than lower part. The structure of antennal club varies greatly, possibly even within a single lineage of *Microperus* from different locations. Antennal club more-less circular shape, or

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shape, or appears broader than tall, club type two (obliquely truncated, second segment visible on posterior side), or three (with first segment straight or convex). First segment of club circular around the club, covering most of the posterior face, or straight (may be slightly concave or convex) on anterior face, margin of the first segment clearly costate all around the antenna, or mostly costate, may appear softer on posterior side. Second segment of club narrow, pubescent, visible on the anterior side only, or corneous, visible on the anterior side only, or visible on both sides of the club, but soft, or the corneous part on the anterior side only. Third segment of club absent from the posterior side of club, or partly visible on the posterior side of club, or clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma mostly smooth, alutaceous, with minor punctures, or rugged, coarsely punctate. Submentum slightly impressed, or deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view prolonged, with low summit (type 7). From dorsal view it is short, parallel-sided, rounded frontally (type 2). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous. No tuft on pronotal basis associated with mesonotal mycangium absent, but setae on elytral bases associated with elytral mycangium present. Scutellum not visible. Elytral bases curved, costate due to the presence of elytral mycangium. Elytral disc longer than declivity, flat or slightly convex or even bulging, punctures on elytral disc in strial lines. Boundary between elytral disc and declivity may be indistinct when the disc is smoothly transitioning into declivity. Lateral profile of elytral declivity mildly flat or rounded, or steep, especially towards the apex, dorsal profile of elytral end rounded. Elytral declivity sometimes with few setae or scales, not conspicuously pubescent, but more often covered with dense setae more abundant than strial punctures. Circumdeclivital costa ending in 7th interstriae. The inner part of declivity has no large tubercles, but comonly does have abundant uniform granules or miniature recurved spines. Striae and interstriae on the upper part of declivity are flat or form ridges and furrows. First interstriae are parallel (sometimes slightly broadened towards elytral summit). Protibiae distinctly trinagular, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles small, bases of the denticles not enlarged, protibial margin rounded, usually between 6 and 8 protibial denticles present. Color uniformly light brown or reddish (pronotum often slightly lighter), rarely dark brown, pronotum is often much lighter (yellow or orange) than elytra. Minute species, length 1.1-2 mm., length beyond 2 mm. is very rare.

Discussion

This genus was previously synonymized with *Coptodryas* (Wood & Bright, 1992) but was recently resurrected (Hulcr et al. 2007). Individual species of *Microperus* in New Guinea are distinguishable primarily based on the type of antennae and the surface of elytral declivity. However, the species "limits" as proposed here are unlikely to be diagnostic for monophyletic groups, especially when used outside of the New Guinea region. External morphological characters are limited in number and extremely homoplastic in *Microperus*. During the revision of the smaller species of *Coptodryas* and *Microperus*, all of which are here included in *Microperus*, it was not always possible to avoid using a single character as delimitation of a species boundary. The *Microperus* group is a typical example of a contiguous landscape of variation in a very few characters, which produced a large number of morphological forms. These were described as nearly 50 different species. In reality, only a handful of these are geographically and morphologically identifiable forms and deserve a species rank. However, many dubious names have been preserved here, primarily to preserve and acknowledge the great morphological diversity of the clade. Further, the functional and genetic significance of this morphodiversity is unknown, and may indeed include a number of unique lineages.

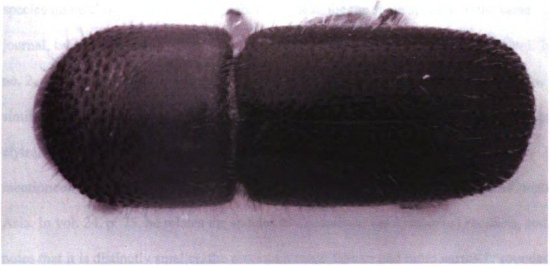

Figure 48: *Microperus diversicolor*, the type species of the genus. Size: 1.7 mm.

Microperus chimbui **comb. n. (Schedl, 1973)**

J.H. database code: Scol 618

Previous genus: *Coptodryas*

Compared to paratype in NHMW

Diagnosis: One of two species with major tubercles on the elytral declivity (with *M. fragosus*). Unlike *M. fragosus*, the tubercles are dispersed throughout interestriae, not connected to an elevated costa. The tubercles are also largest on the declivital summit, making the declivity seem obliquely abruptly truncated. The lateral profile of elytral disc is flat, not concave.

Length: 2.1 mm.

Discussion

Wood and Bright (1992) mention it as a synonymy of *Coptodryas rosselli*, which however appears to be an incorrect combination (see *C. roselli* below). Schedl used the species name chimbui three times, probably to describe the same species, in the same journal, twice in the same issue: Schedl 1973e, vol 24, no. 3, p. 91; Schedl 1973f, vol. 24, no. 2, p. 74; and Schedl 1973f, vol. 24, no. 2, p. 75. In (Schedl, 1973e) he mentioned its similarity to *Coptodryas* (as *Xyleborus*) *fragosus*, but distinguishes it by the more abrupt elytral declivity, and the granules on the elytral disc. In (Schedl, 1973f, p. 74), he mentioned its similarity to *Coptodryas* (as *Xyleborus*) *leprosulus* Schedl from continental Asia. In vol. 24, p. 75, he relates the species to *Coptodryas* (as *Xyleborus*) *recidens*, and notes that it is distinctly smaller, the pronotum more slender and more narrowly rounded at the apex, the interstriae on elytral declivity are shining, and the granules on alternating interstriae are comparatively larger. The descriptions from vol. 2, p. 74 and vol 3 are nearly identical, it is likely the Schedl described the same species. The description of elytra and declivity in vol. 2, p. 75 differs slightly, most notably in the absence of transversal impression on elytral disc. It is not clear which species is described here. Only a paratype was available for examination.

Previously synonymized species: *Xyleborus chimbui* Schedl

Examined material: New Guinea, Eastern Highlands, Arau, Kratke Mts., (paratype, NHMW).

Microperus corporaali **comb. n. (Eggers, 1923)**

J.H. database code: Scol 91

Previous genus: *Coptodryas*

Compared to lectotype in USNM

Diagnosis: The species represents a possible intermediate between *Microperus* and the larger *Coptodryas*. Its size is intermediate between the two groups. Orange to brown, hairy, only small granules on declivity, sometimes forming an array on posterolateral circumdeclivital costa, sometimes fused in a sharp carina. Antenna type 4, moslty pubescent, with small convex corneous first segment.

Length: 2.5-2.8 mm.

Discussion

Body shape and surface and the antennae are very similar to *Xylosandrus mixtus*, which however has mesonotal, not elytral mycangium, narrow tibiae with large socketed denticles, and other characters placing it in *Xylosandrus*.

Examined material: Indonesia, Kotangan an der Ostkusgte, (lectotype, USNM); New Guinea, Madang Province, Baiteta, (IRSNB); New Guinea, Gulf Province, Ivimka, (UCD); PNG: Madang Prov. (1), J. Hulcr 2002-2006.

Microperus diversicolor **comb. n. (Eggers, 1923)**

J.H. database code: Scol 823

Previous genus: *Coptodryas*

Compared to holotype in Dresden

Diagnosis: Antennae type 3 or 4 (first segment convex, second segment prominent, sometimes larger than the first, both second and third segments apparent on the posterior face of the club), uniform granules (not pointed) on declivity spaced as densely or more as strial punctures, elytral disc shape variable - straight to convex (humped). Inner surface of punctures sometimes shagreen (when dry), declivity surface shagreen as well, feebly.

Length: 1.6-2.1 mm.

Discussion

Non-types of *Coptodryas diversicolor* in BMNH are slightly different from the holotype or from New Guinean specimens (e.g., smaller elytral area with tubercles). In many collections, individuals indentical to the holotype of *M. diversicolor* are commonly identified as *Coptodryas* (or as *Xyleborus*) *myristicae*, with which it is now synonymized. *Coptodryas myristicae* is further a valid name for its junior synonym *Xyleborus theae* (synonymized with *Coptodryas myristicae* by Wood (1989)) which is the type species of the genus *Microperus*, designated by Wood (1980c). Thus *M. diversicolor* is now the type species for *Microperus*.

New junior synonym(s): *Coptodryas atava* (Schedl), *Microperus myristicae* (Schedl)

Biology: Browne (1948a) mentioned that the species is often a pest of timber, a very abundant and creating long and intricate tunnel systems. Several tunnel systems may interconnect.

Examined material: Malaysia, Kelantan, (BMNH); Malaysia, Sabah, Danum Valley, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Nauclea orientalis* trunk, (Hulcr coll.); New Guinea, (FICB); New Guinea, Madang Province, Baiteta, (IRSNB); New Guinea, Morobe Province, Bulolo, (MSUC), identified as Xyleborus pubipennis by Schedl; New Guinea, Gulf Province, Ivimka, (UCD); Philippines, Mindanao, Butuan, (unspecified "type", SMTD).

Microperus fragosus **comb. n. (Schedl, 1942)**

J.H. database code: Scol 135

Previous genus: *Coptodryas*

Compared to lectotype in NHMW

Diagnosis: A rare type of *Microperus* with prominent structures/teeth on elytra. The tubercles are largest on the declivital summit, making the declivity seem abruptly truncated. The lateral profile of elytral disc concave, "saddle-like". Unlike *M. chimbui*, the declivital summit bears a small elevated transverse costa (likely from enlarged and fused tubercles), (in *M. chimbui* the tubercles and teeth are solitary throughout the declivity).

Length: 1.9 mm.

Discussion

Lectotype designated by Schedl (1979c). *C. leprosulus* Schedl (type seen in NHMW, now *C. undulatus* Sampson, after Wood 1989) is similar, but the teeth and rugosities are largely confined only to declivity and the elytral disc is not concave. Wood (1989, 6761) synonymized *X. fragosus* Schedl and *X. nugax* Schedl. It was removed from synonymy by Beaver (1999d).

Examined material: Indonesia, Java, Buitenzorg, (lectotype, NHMW); New Guinea, West Sepik, Utai, (Hulcr coll.); PNG: Madang Prov. (1), West Sepik (1), J. Hulcr 2002-2006.

***Microperus intermedius* (Eggers, 1923)**

J.H. database code: Scol 56

Compared to lectotype in USNM

Diagnosis: Probably the most common *Microperus* in New Guinea. The main diagnostic characters of *M. interemedius* are: antennal club of type 1 (obliquely truncated, first segment dominant; the main difference from *M. diversicolor*), pronotum alutaceous, in some specimens with traces of minute asperities, elytral declivity with short continuous posterolateral carina, elytral disc convex, "humped"; and the minute blunt granules on declivity, instead of minute sharp spines (the main difference from *M. parva*). Many specimens have only negligible granules, such as specimens from Gulf Province. However, most of these characters are continuously variable in the genus and specimen of mixed characters should be expected.

Length: 1.6-1.8 mm.

New junior synonym(s): *Coptodryas nitella* (Browne)

Biology: Males have unchanged, maybe even enlarged pronotum, robust head and enlarged mandibles. Tiny eyes. Common in New Guinea and Philippines, rare in Malaysia (Browne 1961c).

Examined material: Malaysia, Sabah, Danum Valley, Nauclea orientalis trunk, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Nauclea orientalis branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Parashorea malaanonan branches, (Hulcr coll.); Philippines, Nagoya from Lianga, (NHMW); Philippines, Mindanao, (unspecified "type", SMTD); locality not recorded, (NHMW); PNG: Madang Prov. (999), Oro Prov. (30), West Sepik (5), J. Hulcr 2002-2006.

Microperus myristicae **syn. n. (Schedl, 1939)**

Synonymized with: *Microperus diversicolor (Eggers)*

J.H. database code: Scol 407

Compared to lectotype in NHMW. Type not in ZMA, probably in Kalshoven's collection in Leiden.

Discussion

Hulcr et al. (2007) transferred *Coptodryas myristicae* to *Microperus*, based on examination of non-type specimens identified by Browne. These specimens were identical to the holotype of *Coptodryas diversicolor* (Eggers, now transferred to *Microperus*), but had antenna of the type 1, instead 3. The antennae of Schedl's holotype of *Xyleborus myristicae* were examined, and were found to be of type 3. Thus Browne's specimens in BMNH were mis-identified and are *Microperus intermedius* (Eggers). Wood (1989, 6761) synonymized *Xyleborus brevipilosus* Eggers 1940, *Xyleborus* *cylindripennis* Schedl 1954, and *Xyleborus theae* Eggers with this species. Kalshoven (1959b) synonymized *X. brevipilosus* Eggers with *Xyleborus myristicae*, based on the similarity of description of both species, and by noting that Egger's and his own specimens, each set carrying a different name by different author, are from the same collection. Very similar is *Xyleborus theae* from Java, now synonymized with *M. myristicae* but *X. theae* has fewer and smaller granules, co-type has a nearly smooth elytral surface (apart from dense vestiture) and an inconspicuous declivital carina. *M. myristicae* non-type specimens from NHMW have a steeper declivity, more pronounced arrays of granules and larger strial punctures with a shagreen surface.

Previously synonymized species: *Xyleborus cylindripennis* Schedl, *Xyleborus brevipilosus* Eggers, *Xyleborus theae* Eggers

Examined material: Indonesia, Java, (NHMW); Indonesia, Sumatra, Solok, (lectotype, NHMW); Indonesia, Java, Maswati, (co-type, RMNH, 2 indiv.); Indonesia, Java, Buitenzorg, (RMNH, 2 indiv.), identified as Xyleborus theae by Kalshoven; New Guinea, Gulf Province, Ivimka, (UCD), R. A. Beaver det.

Microperus parva **comb. n. (Lea, 1893)**

J.H. database code: Scol 68

Previous genus: *Coptodryas*

Compared to holotype in SAM.

Diagnosis: One of two most common species of *Microperus* in New Guinea (along with *M. intermedius*). It is smaller than *M. intermedius*, elytral disc is much less convex ("humped"). Elytral interstriae bear minute pointed recurved spines, which are slightly larger on the end of elytral disc than on declivity. (*M. intermedius* has small blunt granules in elytral interstriae.). Antennal club of type 1, obliquely truncated, with the first corneous segment dominant on both sides.

Length: 1.4-1.9 mm.

Discussion

The holotype of *Microperus* (as *Xylopertha*) *parva* in SAM is slightly larger than most PNG specimens and has less abundant recurved denticles on declivity. Lectotype of *C. libra* from New Britain is identical to most New Guinean specimens, including the minute hooks on declivity, their slightly larger size on declivital summit, small elytral hump, and the clearly truncated antennal club. Paratype of *Xyleborus bismarcensis* Browne (1966) (synonymized with *Coptodryas libra* by Schedl (1971f)) doesn't have the curved sharp denticles on declivity and elytral disc. Browne (1966) distinguished *X. bismarcensis* only by the more slender body and more conspicuous pubescence on the declivity.

Previously synonymized species: *Xyleborus bismarcensis* Browne

New junior synonym(s): *Coptodryas pubipennis* (Schedl)

Biology: All *Microperus* seem to have flat chamber.

Examined material: Australia, N. S. Wales, (holotype, SAM); New Guinea, New Britain, (NHMW); PNG: Madang Prov. (791), Oro Prov. (17), West Sepik (40), J. Hulcr 2002-2006.

***Microperus perparva* comb. n. (Sampson, 1923)**

J.H. database code: Scol 238

Previous genus: *Coptodryas*

Compared to non-type in USNM

Diagnosis: Elytral costa not carinate, largely replaced by row of tubercles. Strial punctures on elytral summit and on declivity often enlarged and with shagreen inner surface. Individuals from Borneo markedly larger than those form New Guinea. The slope and surface of declivity is variable (Sampson's non-type series in USNM).

Length: 1.8-2.7 mm.

Discussion

Transferred to *Microperus* by Maiti and Saha (1986). The transfer is not recorded in Wood & Bright (1992).

Biology: Irregularly branching galleries with transverse brood chambers (Beaver & Browne 1978).

Examined material: Malaysia, Sabah, Danum Valley, (Hulcr coll.); New Guinea, Morobe Province, Bulolo, (FICB); PNG: Madang Prov. (1), Oro Prov. (11), West Sepik (1), J. Hulcr 2002-2006.

Microperus pometianus **comb. n. (Schedl, 1939)**

J.H. database code: Scol 265

Previous genus: *Coptodryas*

Compared to lectotype in NHMW

Diagnosis: One of the smallest *Microperus*. Antennal club type 3, first segment convex, second prominent, both second and third visible on posterior side. The elytral disc is flat, not convex. No spines or conspicuous rugosities on elytrae except few granules on declivity. Granules on declivity either absent, or small and dispersed, less frequent than strial punctures. The species is defined by absence of other characters, ratehr than by unique characters, and as such varies. For example, the holotype differs slightly from some specimens from New Guinea by less abrupt declivity-disc boundary, more angulate end of elytra and slightly narrower pronotum. A specimen from Sarawak has shorter circumdeclivital costa with tubercles.

Length: 1.1-1.6 mm.

Discussion

Transferred to *Coptodryas pometiana* by Beaver 1998c. Schedl (1939e) suggested that the species is related to *X. laevis*, but this species belongs to a very different and unrelated group in Xyleborina (transferred to *Planiculus* gen. n. here). Similarly Browne (1961c) included the species into the *Xyleborus subemarginatus* group. Both authors missed the significance of mycangium and antennal characters.

Examined material: Malaysia, Sarawak, Ng. Tekalit, (Schedl det., FMNH); Malaysia, Sel. Sg. Bulok, (lectotype, NHMW); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, (Hulcr coll.); New Guinea, Southern Highlands, Lk Kutubu, (BBM); New Guinea, East Sepik, Ambunti, (Schedl det., BBM); New Guinea, Madang Province, Ohu, (Hulcr coll. 2006); New Guinea, Gulf Province, Ivimka, (UCD), R. A. Beaver det.; PNG: Madang Prov. (2), Oro Prov. (6), West Sepik (2), J. Hulcr 2002-2006.

Microperus popondettae **comb. n. (Browne, 1970)**

J.H. database code: Scol 55

Previous genus: *Coptodryas*

Compared to holotype in BMNH

Diagnosis: Unlike other *Microperus* spp. *M. popondettae* has impressed striae and elevated tuberculate interstriae on elytral declivity, which creates a rugged appearance. Antenna type 3 (first segment convex, second segment prominent).

Length: 1.9-2.4 mm.

Discussion

Similar, but much shorter, is *X. semistriatus* Schedl from Malaysia (type seen in BMNH). Transferred to *Coptodryas* by Beaver (1995). It is similar to *M. nugax* (SE Asia), but without the transverse depression on the elytral disc and with much smaller rugosities on the elytral declivity.

New junior synonym(s): *Coptodryas docta* (Schedl)

Examined material: New Guinea, Oro Province, Popondetta, (holotype, BMNH); New Guinea, Morobe Province, Bulolo, (NHMW); PNG: Madang Prov. (5), Oro Prov. (34), West Sepik (4), J. Hulcr 2002-2006.

Microperus recidens **comb. n. (Sampson, 1923)**

J.H. database code: Scol 240

Previous genus: *Coptodryas*

Compared to holotype in BMNH

Diagnosis: Steep and flat declivity with very few small tubercles, a pair of slightly larger ones in interstria 3. Declivity surrounded by a costa or elevated carina around its bottom part. Antenna type 3 to 4. The size and the density of declivital pubescence vary.

Length: 1.8-2.0 mm.

Discussion

Synonymy of *Coptodryas minusculus* (Eggers) with *M. recidens* is confirmed). Browne (1955) included *X. crassitarsus* Schedl. Transferred to *Microperus* by Maiti & Saha (1986), but the combination was not recorded by Wood & Bright (1992). Wood (1989, 6761) included *Xyleborus minutissimus* Eggers. Beaver (1995) transferred *Xyleborus tuberculosus* Browne to *Coptodryas recidens.*

Previously synonymized species: *Xyleborus crassitarsus* Schedl, *Xyleborus minutissimus* Eggers, *Xyleborus minusculus* Eggers, *Xyleborus tuberculosus* Browne

New junior synonym(s): *Coptodryas artegrapha* (Schedl), *Coptodryas extensa* (Schedl)

Examined material: India, Lower Tondu, Khariabandar, (holotype, BMNH); New Guinea, (BBM, 25 indiv.); New Guinea, Morobe, Nauti Watut, (FICB), D. E. Bright det.; New Guinea, Morobe Province, Bulolo, (FICB); New Guinea, Morobe Province, Bulolo, (FICB); New Guinea, Madang Province, Baiteta, (IRSNB, 2 indiv.); PNG: Madang Prov. (1), J. Hulcr 2002-2006.

Genus *Planiculus* gen. n. Hulcr & Cognato

J.H. database code: Scol 839

Type species: *Xyleborus bicolor* (Blandford) 1894, (as *Euwallacea* in Wood & Bright, 1992).

Diagnosis: This genus can be confused with *Xyleborus* or *Wallacella*. It is distinguished from *Xyleborus* by the flattened, broadened elytral declivity with very few if any tubercles, smaller size and slender body, inconspicuous prosternal posterocoxal process, prolonged pronotal disc, and antennal club type 2 or 3. It is distinguished from some slender *Wallacella* spp. by the much smaller size (rarely over 2.5 mm), rounded frontal margin of the pronotum, and the very characteristic color pattern (the basal part of pronotum is often yellowish, lighter than its anterior part, and much lighter than the dark brown elytra), although variations exist.

Description: Eyes shallowly emarginate, "bean shape", upper portion of eyes smaller than lower part. Antennal club more-less circular shape, club type two (obliquely truncated, second segment visible on posterior side), or three (first segment straight or convex). First segment of club circular around the club, covering most of the posterior face, or straight (may be slightly concave or convex) on anterior face, margin of the first segment clearly costate all around the antenna. Second segment of club narrow, pubescent, visible on the anterior side only, or visible on both sides of the club, but soft, or the corneous part on the anterior side only. Third segment of club absent from the posterior side of club, or partly visible on the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus thicker and shorter than in most other genera. In some species, mandibular mycangia are visible as bulges on the epistoma. Frons above epistoma mostly smooth, alutaceous, with minor punctures. Submentum slightly impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view prolonged, with low summit (type 7), often with disc distinctly prolonged (type 8). From dorsal view it has prolonged basic shape with rounded frontal margin (type 7), or long, rounded anteriad (type 9). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum concave (pronotum very long), or obliquely costate. Procoxae contiguous, prosternal posterocoxal process conical and slightly inflated. Tuft on pronotal basis associated with mesonotal mycangium absent, setae on elytral bases associated with elytral mycangium absent. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat, punctures on elytral disc in strial lines (which may be difficult to discern). Boundary between elytral disc and declivity distinct in some species, but mostly indistinct with the end of disc rounded, smoothly transitioning into declivity. Lateral profile of elytral declivity mildly flat or rounded, or slowly descending, often flat, dorsal profile of elytral end broadened laterally, sometimes narrowly emarginate. Elytral declivity with few setae or scales, not conspicuously pubescent. Circumdeclivital costa ending in 7th interstriae. The inner part of declivity has no tubercles, or only uniform granules, or no tubercles in interstria 2, and several tubercles in interstriae 1, 3 and beyond. Striae and interstriae on the upper part of declivity flat, not forming ridges and furrows. First interstriae are sometimes parallel, but in many species broadened at the elytral end, slightly bulging, bearing several tubercles. Protibiae distinctly triangular, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles small, bases of the denticles slightly elevated, usually 6 denticles present. Metatibiae of regular size.

Color uniformly light brown or reddish, rarely dark brown, pronotum almost always much lighter (yellow or orange) than elytra. The genus includes mostly small to minute species, 1.4-2.5 mm, rarely up to 3.2 mm in montane species.

Discussion

The broadened declivital margin led Wood (1989) and Wood & Bright (1992) to include many species in *Euwallacea*. However, *Euwallacea* is an unrelated genus characterized with different suite of characters.

The lack of resolution on the cladogram (Figure 20) indicates that *Planiculus* spp. are virtually indistinguishable from each other. These "species" often represent multiple re-descriptions of the same species or morphs, rather than unique lineages, and a number of them are synonymized here. The characters most often used to distinguish new species by earlier authors were the pattern of granules on declivity, and the emargination of declivital apex. The variation in elytral emargination seems to occur independently of other patterns of characters variation. Specimens from the Moluccas and continental Asia often have slightly emarginate elytral apex, while in specimens from New Guinea the apex is usually rounded. Thus it is questionable whether such small and variable elytral emargination can be used to delimit species. The pattern of declivital tuberculation is known to vary tremendously in Xyleborina, and are used with caution in recognizing separate lineages. One major pattern observed in this genus (and other genera as well) is, that some species have larger tubercles expressed in interstria 1 and 3, while other species have small granules in all interstriae, including in. 2. The exact position of tubercles along these interstriae is very variable. Specimens from Thailand often have shagreen declivital interstriae.

The morphology-based phylogeny (Figure 20) illustrates the relationships between *Planiculus* and related genera, namely the closely related *Wallacella* and *Xyleborus* s. str. It also shows that *Euwallacea* inclusive of several *Planiculus* spp. as in Wood & Bright (1992) is polyphyletic.

Figure 49: *Planiculus bicolor*, the type species of the genus. Size: 1.7 mm.

Planiculus aries **comb. n. Schedl (1969)**

J.H. database code: Scol 324

Previous genus: *Xyleborus*

Compared to paratype in NHMW

Diagnosis: There are two sympatric morphological types. One is larger and completely dark, the other form is slightly smaller, with bicolored pronotum and light brown elytra. No intermediated have been discovered. Because color is the only difference, the two morphs are not considered different species. The dark morph is likely another example of melanism observed in some Xyleborines from high altitudes of New Guinea.

Length: 3.0-3.2 mm.

Discussion

Although this species does not share all features of typical *Planiculus*, the generic position of this species is confirmed by both morphological (Figure 20) and molecular analyses (Cognato et al., 2009). The habitus of the species resembles that of typical *Planiculus*, with the exception of the larger size which is expected given the species occurrence in higher altitudes. This species and the genus *Planiculus* (type species *P. bicolor*) share bicolored pronotum (in the light morph of *P. aries*), antennal club with the first segment anteriad straight or slightly convex, second segment clearly visible on the posterior side, third usually not visible but if so, then it is represented by a tuft of setae; rounded frontal side of pronotum; broadened lateral declivital costa, 1 to 3 pairs of tubercles in the first (sutural) and third declivital interstria. The small size of the first segment of antennal club, small and numerous protibial denticles, short pronotal disc, and the absence of the small granulate bulge at the apex of interstria 1 differentiate *P. aries* from the complex of typical *Planiculus* spp. *Planiculus tumidus* is a similar species, its shape, color, and antennae are identical, but the declivity is devoid of tubercles. The dark colored variants are identical to paratypes in NHMW, including details such as size, color, and shagreen surface of the punctures. Schedl (1969b) compared the species to *X. discrepans* Schedl from Africa, and not to any sympatric species.

Biology: Species encountered only in montane localities of New Guinea.

Examined material: PNG: Chimbu Prov. (50), J. Hulcr 2002-2006.

***Planiculus bicolor* comb. n. (Blandford, 1894)**

J.H. database code: Scol 51

Previous genus: *Euwallacea*

Compared to syntypes in BMNH

Diagnosis: Most individuals have slightly or greatly bicolored pronotum; elytral declivity gently sloped, with apex of interstria 1 elevated and with granules. The two characters distinguishing this species from other *Planiculus* spp. is the rounded, rather than slightly emarginate end of elytra, and the gently, rather than steeply rounded declivity. The pattern in declivital granules or tubercles is very variable, most often there are several larger tubercles in the first and third declivital interstria, and none or very small granules in the second interstria.

Length: 1.7-2.6 mm.

Discussion

Specimens of *Planiculus bicolor, Euwallacea laevis*, *E. artelaevis,* and similar forms have often been confused and misidentified. This was caused by 1) the variation of declivital tuberculation and subtle variations of declivity shape, which earlier authors used to delimit interspecific boundaries, and 2) the lack of communication between authors, because several holotypes of these species are virtually identical and represent multiple re-descriptions. The granules on interstriae 1 and 3 decrease or increase in size, thus producing patterns such as: small uniform granules on all interstriae, tubercles on the intrestriae 3, tubercles on interstriae 1 and 3, etc. The apical bulge/elevated and broadened end of interstria 1 varies independently of the rest of declivity, and forms a gradient ranging from flush and flat apex to apex bulging with a pair of prominent tubercles. The most common form in New Guinea features small tubercles on interstriae 1 and 3, and a slightly elevated apex of interstria 1 with several granules. The holotype of *X. laevis* is nearly identical to the holotype of *P. bicolor*, only less pigmented (bleached) and less flat elytra (= on pin, inflated). Also non-types of *X. laevis* in NHMW appear the same, including the few granules on slightly bulging elytral apex. Some non-types identified as *Xyleborus laevis* in BMNH have more elevated strial ridges on declivity, and less elevated declivital costa. Wood (1989) included the following species as synonymous: *Xyleborus bicolor unimodus* Beeson 1929, *Xyleborus rodgeri* Beeson 1930, and *Xyleborus rodgeri privatus* Beeson 1930. Beeson (1929) described a subspecies *X. bicolor unimodus* based on differences in uniform coloration, slightly more oblique declivity and somewhat larger declivital tubercles. Schedl (1940b) described *Xyleborus rameus* as closely similar to *X. laevis*, distinguished by several difference on the declivity - 'alternating interstices on the declivity' (unclear expression), apical sutural notch somewhat larger, the dorsal line more strongly convex, when viewed from the sides, the declivity longer and more oblique, somewhat aplanate. These are very plastic characters which are not considered here as valid for the separation of species. One exception is the 'apical sutural notch', which is here recognized as the putative distinguishing character of *Euwallacea limatus*. Thus *X. rameus* may have been synonymized with *E. limatus*, rather than with *P. bicolor*, which is supported by our examination of a specimen identified as *X. rameus* by Schedl in BMNH.

Previously synonymized species: *Xyleborus rameus* Schedl, *Xyleborus rodgeri privatus* Beeson, *Xyleborus rodgeri* Beeson, *Xyleborus subparallelus* Eggers, *Xyleborus bicolor unimodus* Beeson

New junior synonyms: *Euwallacea tumidus* (Schedl), *Euwallacea laevis* (Eggers), *Xyleborus glabratulus* Browne, *Euwallacea filiformis* (Schedl)

Biology: This and related species create galleries composed of frequently branching tunnels and multiple small brood chambers. Very common throughout SE Asia and Melanesia.

Examined material: Fiji, Namosi, (BMNH), identified as Xyleborus rameus by Schedl; Indonesia, Sulawesi, (BMNH); Malaysia, Sabah, Danum Valley, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Nauclea orientalis branches, (Hulcr coll.); New Guinea, New Britain, (FICB); New Guinea, Milne Bay, Mt. Dayman, (NHMW); Thailand, Pong Yaeng N. P., (Hulcr coll., 2 indiv.), R. A. Beaver det.; PNG: Madang Prov. (170), Oro Prov. (176), West Sepik (51), J. Hulcr 2002-2006.

Planiculus immersus **comb. n. Schedl (1972)**

J.H. database code: Scol 60

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: First segment of antennal club vary from mildly concave to mildly convex. Characteristic pattern of declivital tubercles (a single tubercle in each interstria 1 and two such tubercles in each intestria 3, forming a flat “X”), which at least within PNG seems to display little variability. Posterolateral margins of elytra broadened, creating the impression of angulate elytral end. Unlike in many *Planiculus*, elytral declivity of *P. immersus* is rather steep, flat, clearly distinguishable from the elytral disc. Perhaps because of the steep declivity, rather short pronotal disc, and only weak double coloration of the pronotum, the species can be confused with some *Xyleborus* s. str., namely *X. perforans*.

Discussion

Wood & Bright (1992) indicate that a type specimen of this species is in ANIC. However the type resides in the NHMW.

New junior synonym(s): *Xyleborus hashimotoi* Browne

Examined material: New Guinea, Madang Province, Baiteta, (IRSNB); New Guinea, East New Britain, Lakunai, (holotype, NHMW); PNG: Madang Prov. (540), Oro Prov. (1), West Sepik (23), J. Hulcr 2002-2006.

Planiculus limatus comb. n. (Schedl, 1936)

J.H. database code: Scol 643

Previous genus: *Euwallacea*

Compared to holotype in NHMW

Diagnosis: Typical *Planiculus* with antennae type 3, bicolored pronotum, flattened and gradually sloped elytral declivity, few and variable tubercles on the declivity. The main distinguishing character of the species is its emarginate declivital end.

Length: 1.8-2.3 mm.

Discussion

The representatives of this species collected by the first author in Borneo are markedly thinner, less emarginate, and extremely varied in size. Similar to *P. bicolor* with small tubercles in interstriae 1 and 3, except for the emarginated end of elytra. The phylogenetic significance of this emargination is however unclear, the two species may be eventually synonymized. Further, Schedl (1936h) notes the difference in size between individuals from lowlands and from highlands. While the holotype is 1.8 mm. long, specimens from higher elevations are allegedly up to 2.19 mm. long. The holotype is unfortunately very poorly mounted, with limited access to many characters.

New junior synonym(s): *Euwallacea subparallelus* (Eggers), *Euwallacea subemarginatus* (Eggers)

Examined material: Malaysia, Sabah, Danum Valley, *Artocarpus camansii* branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Nauclea orientalis* branches, (Hulcr coll., 25 indiv.); Malaysia, Sabah, Danum Valley, (Hulcr coll., 9 indiv.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Danum Valley, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Danum Valley, *Ficus* sp. branches, (Hulcr coll., 10 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* trunk, (Hulcr coll.); Philippines, Luzon, Mt. Makiling, (holotype, NHMW, 2 indiv.); PNG: Madang Prov. (1), J. Hulcr 2002-2006.

***Planiculus rodmanculus* sp. n. Hulcr & Cognato**

J.H. database code: Scol 255

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Diagnosis: The smallest, most slender *Planiculus*. Along with the minute size, the characters distinguishing this species from other *Planiculus* spp. are the antennal club type 2 (first segment concave, dominant, second segment apparent on the posterior side), minute evenly spaced tubercles in declivital striae 1, 2 and 3, posterolateral costa present but inconspicuous, elytral end angulate rather than rounded, elytral declivity steep, rather than gently rounded.

Description: Minute slender species. Antennal scapus, pedicel and funicle all short, robust. Antennal club asymmetrical, type 2 (first segment corneous, concave, dominant, second segment suppressed and pubescent, apparent on the posterior side). Submentum only feebly impressed, almost flush with genae. Eyes small, upper part smaller than antennal club. Frons alutaceous, not punctured. Pronotal anterior edge rounded, with only minor on no serrations on the margin, pronotal disc shining, prolonged (type 8 laterally, type 9 dorsally). Procoxae contiguous, posterocoxal prosternal process inflated but not bulging. Protibiae clearly triangular, with 6 socketed denticles concentrated on the distal end. Scutellum relatively small, flush with surface of elytra, no signs of mesonotal or elytral mycangium. Elytra relatively long, appearing strictly cylindrical, parallel sided almost to the end. Elytral declivity rather steep, flat, with small pointed tubercles in interstriae 1, 2, and 3. Posterolateral costa broad, making elytral end appear angulate; costa continuing to approximately 4th interstria, elevated carina ends in 7th interstria. Body mostly devoid of vestiture, only declivity with erect sparse setae. Body color light brown, with base of pronotum very light, almost yellow.

Length: 1.4 mm.

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Etymology. *Planiculus rodmanculus*, approximately translates as " Little Rodman, (the) little flat (one)". The species epithet honors Dr. Jim Rodman for his influential directorship of the NSF program for Partnerships for Enhancing Expertise in Taxonomy and his sincere support of PEET applicants, awardees and panel reviewers. The diminutive latinization of Rodman acknowledges the remarkable small size of this species.

Holotype deposited in USNM, paratypes deposited in MSUC, BMNH, NHMW.

Examined material: PNG: Oro Prov. (17), J. Hulcr 2002-2006.

Figure 50: *Planiculus rodmanculus sp. n.* Size: 1.4 mm.

Genus *Pseudowebbia* Browne (1961)

J.H. database code: Scol 791

Type species: *Pseudowebbia trepanicauda* (Eggers, 1923).

Diagnosis: Eyes deeply emarginate, sometimes almost disjunct, upper portion of eyes smaller than lower part. Antennal club more-less circular shape, club type four (first segment small, second and third prominent on both sides). First segment of club convex, small, margin of the first segment mostly costate, may appear softer on posterior side, or mostly soft, pubescent. Second segment of club corneous on both sides of club, but not circular (not making antenna tall, or "telescopic"). Third segment of club clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma mostly smooth, alutaceous, with minor punctures, or rugged, coarsely punctate. Submentum flat, flush with genae, or slightly impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view of basic shape (type 0), or low and rounded (type 1). From dorsal view it is basic, short, parallel-sided, rounded frontally (type 2). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous. Tuft on pronotal basis associated with mesonotal mycangium absent, but the setae on elytral bases associated with elytral mycangium abundant. Scutellum not visible. Elytral bases straight, with oblique edge, or curved, costate due to the presence of elytral mycangium, elytral disc longer than declivity, flat, or impressed, "saddle-like", punctures on elytral disc confused. Elytral declivity sharply truncated, with teeth or ridges around the edge. Circumdeclivital costa completely encircling the declivity. All known species have their declivital surface covered with conspicuous thick scales. The shape of the scales vary between erect and pointed to flat or cushion-like. The scales can be clearly white from a certain angle, while entirely transparent from other angles. The inner part of declivity has tubercles on elevated costa around declivity, their assignment to interstriae is difficult. First interstriae are parallel (sometimes slightly broadened towards elytral summit). Protibiae with evenly rounded edge. Posterior side of protibia flat, with setae only. Protibial denticles small, or large, distinctly longer than wide, bases of the denticles not enlarged, usually 7 or more protibial denticles present. Metatibiae of regular size. Color uniformly light brown or reddish, or uniformly dark brown (pronotum sometimes slightly lighter). Length: 1.8-3.2 mm.

Discussion

According to Browne (1963), *Pseudowebbia* is distinguished from *Webbia* by having pronotal broad granules, having a more convex pronotum, different form of the antennal club - compressed, rather than truncated, and antennal funicle 5-segmented (however, the number of funicular segments is known to vary in *Webbia*). *Pseudowebbia* was synonymized with *Webbia* by Wood (1983a) based on his comparison of type species of both genera. S. L. Wood asserted that "[*Webbia*] *dipterocarpi* and [*Pseudowebbia*] *trepanicauda* both represent the same species group within the genus", but no further explanation was given. Based on an analysis of approximately 40 morphological characters by Hulcr et al. (337), several species of *Pseudowebbia* including the type were found to be not closely related to *Webbia*, and the genus was resurrected.

Figure 51: *Pseudowebbia trepanicauda*, the type species of the genus. Size: 2.1 mm.

Pseudowebbia armifer **(Schedl, 1942)**

J.H. database code: Scol 655

Compared to holotype in NHMW

Length: 2.6-2.8 mm.

Discussion

Schedl (1942c) groups the species close to *X. obtusus* (now *Cyclorhipidion circumcisum*) with no discussion on characters. *Xyleborus spinachius* Schedl was included under *P. armifer* as a putative synonym (Wood & Bright, 1992). In the original description of *X. spinachius*, Schedl (1955b) noted its similarity to *P. armifer* (as *Xyleborus armifer*). To our knowledge, only the holotype of each species is known, making it impossible to judge the intraspecific variation. The holotypes are very similar. *X. spinachius* has smaller, more numerous, and more evenly distributed circumdeclivital teeth. The holotype of *P. armifer* has a prominent tooth in the middle of each elytron's declivity. Besides these characters (which are very plastic in Xyleborina at large), no other difference is apparent. Thus the synonymy is considered warranted. In reality, the variation in most examined species of *Pseudowebbia* except *P. percorthylus* is completely continuous. *P. armifer, P. curvatus, P. squamatilis*, and *P. trepanicauda* vary in three characters - the depth of the depression on elytral disc, presence or absence of a pair of teeth on the declivity, and the shape of declivital scales. All these characters are known to vary considerably in other groups of Xyleborina. Unfortunately, *Pseudowebbia* spp. are extremely rare in collections (and presumably in the nature), and series of individuals are not available to test the species limits.

Previously synonymized species: *Xyleborus spinachius* Schedl

Examined material: New Guinea, (holotype of *Pseudowebbia spinachiu*, NHMW), label: D. Neu Guinea, Burgers 1912; New Guinea, (holotype of *Pseudowebbia armifer*, NHMW), label: Neu Guinea.

Pseudowebbia curvatus **comb. n. Browne (1986)**

J.H. database code: Scol 495

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Diagnosis: Second largest *Pseudowebbia*, characteristic with its deeply concave elytral disc. Other *Pseudowebbia* spp. have disc flat, or only mildly impressed. It has characters typical of *Pseudowebbia* - no scutellum, mycangial openings on anterior slope of elytra, and the pronotum is of basic type, not prolonged and cylindrical as in *Webbia*.

Length: 3.1-3.2 mm.

Discussion

In the holotype of *X. curvatus* Browne, the array of teeth around the declivity is discontiguous on the summit. The array is complete in other specimens from New Guinea. Browne (1986a) mentioned the similarity between *Pseudowebbia curvatus* (Browne) and *Pseudowebbia* (as *Xyleborus* or later *Taphrodaus* by Wood) *percorthylus* (Schedl). *P. seriata* Browne is similar but smaller, has normal convex elytral disc, only several granules around declivity. The declivity is also flat and covered with flat or star-like setae.

Examined material: New Caledonia, Fakfak to Nagoya, Japan, imported, (holotype, BMNH); New Guinea, Western Province, Wavoi, (FICB).

***Pseudowebbia squamatilis* (Schedl, 1955)**

J.H. database code: Scol 663

Compared to holotype in NHMW

Diagnosis: Smaller than other NG *Pseudowebbia*, circular declivity seems less broad than elytra as a whole (appears constricted), the surface is densely covered by peculiarly broadened and inflated scales, no denticles present inside the declivity.

Length: 2.1 mm.

Discussion

Described as *Xyleborus* (Schedl, 1955b), included in *Webbia* (Wood & Bright, 1992), and transferred to *Pseudowebbia* by Hulcr et al. (2007). Schedl (1955b) mentioned its similarity to *P. trepanicauda* (as *Xyleborus*), and noted that *P. squamatilis* is slightly smaller and that the elytral declivity lacks punctate striae and tubercles. These differences appear inconclusive, unfortunately, the holotype of *P. trepanicauda* was not available for examination.

New junior synonym(s): *Webbia denticulatus* Browne

Examined material: New Guinea, (holotype).

Genus *Schedlia* Browne (1950)

J.H. database code: Scol 790

Type species: *Schedlia sumatrana* (Hagedorn).

Redescription: Eyes deeply emarginate, sometimes almost disjunct, upper portion of eyes as large as the lower part. Antennal club more-less circular shape, club type four (first segment small, second and third prominent on both sides). First segment minor, convex or bisinuate, second segment chitinous, glabrous, prominent, third segment clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum deeply impressed, shaped as a distinct large triangle. Anterior margin of pronotum flat or concave, densely asperate, the anterior edge of pronotum with distinct row of serrations, the posterior edge (base) of pronotum broadly concave-emarginate, posterior shoulders angulately produced. Pronotum from lateral view bulging anteriad (type 4). From dorsal view it is subquadrate (type 3), or quadrate, robust (type 4). Pronotal disc with asperities resembling those on the frontal slope. Lateral edge of pronotum obliquely costate, with produced costate shoulder. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous. Tuft on pronotal basis associated with mesonotal mycangium absent, but setae on elytral bases associated with elytral mycangium abundant. Scutellum not visible. Elytral bases broadly sinuate to accommodate openings of elytral mycangia. Elytral disc longer than declivity, flat, punctures on elytral disc irregular. Declivity markedly separated from the disc. Lateral profile of elytral declivity obliquely truncated and steep, especially towards the apex, dorsal profile of elytra obliquely truncated with rounded apical margin. Elytral declivity with few setae or scales, not conspicuously pubescent, or covered with dense setae. Circumdeclivital costa absent or indefinable. Declivity coarsely granulated, the inner part of declivity can have a pair of long projections in some species, one on each elytron (not seen in New Guinea). Striae and interstriae on the upper part of declivity bearing teeth around the declivity. Protibiae with evenly rounded edge, posterior side of protibia appears inflated and densely granulated. Protibial denticles small and numerous, bases of the denticles not enlarged. Metatibiae of regular size. Large species, robust, 3.4-5.2 mm. Color uniformly light brown or uniformly dark brown.

Length: 3.4-4.8 mm.

Discussion

Some species originally among Schedl's "Xylebori discoidale", but Browne (1950b) noted the many characters in common with *Webbia*, and erected *Schedlia* as a separate genus with mainly pronotum distinguishing it from his group Webbinae. Wood (1980c) listed the genus as a tentative, but Bright (1980) supported the recognition of *Schedlia* . Bright (1980) lists five species from New Guinea: *S. brownei*, *S.* convexa, *S.*

paraconvexa, *S.* praeusta, and *S.* usitata, two of which are synonymized here. Bright (1980) provided a key to all species .

Biology: As all members of the group historically called Webbinae, *Schedlia* is a true xylomycetophagous genus, i.e., larvae assist in extending the gallery, which results in a flat chamber (Beaver & Browne 1978). Browne (1958) notes the specificity of this genus to trees from the family Dipterocarpaceae. In New Guinea, Dipterocarpaceae are species-poor and rare, and the diet of dipterocarp-feeding xyleborines is unknown.

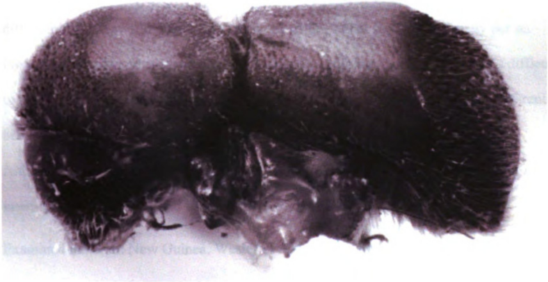

Figure 52: *Schedlia usitata*, a typical representative of the genus. Size: 3.7 mm.

***Schedlia brownei* Bright (1980)**

J.H. database code: Scol 647

Compared to holotype in AMNH

Diagnosis: Elytral declivity sharply truncate, unlike convex in *S. usitata*, all covered with prominent dense granules decreasing in size towards elytral tips. Tubercles in the 7th interstria are enlarged, forming a row around the lower third of the declivital margin.

Length: 4.7 mm.

Discussion

As compared to *S. usitata s. l.* (including its junior synonyms *S. convexa* and *S. paraconvexa*), the difference in density in pronotal asperities is minor, fully within variation seen in other species of Xyleborina where larger series are available. It also differs in the extent of the area with dense asperities, rather than in the density per se. Pronotal antero-lateral sides are indeed slightly less bulging, but the difference is difficult to recognize unless representatives are directly compared. The only significant difference between *S. brownei* and *S. usitata s. l.* is the flat truncated declivity in *S. brownei*. Although it is possible that this is no more than a variant of a very plastic character, no intermediates are known and thus the species status is upheld.

Examined material: New Guinea, Western Province, Fly River, (holotype, AMNH).

***Schedlia convexa* syn. n. Bright (1980)**

Synonymized with: *Schedlia usitata (Schedl)*

J.H. database code: Scol 648

Compared to holotype in AMNH

Discussion

According to Bright (1980), the species is similar to *S. brownei* and *S. paraconvexa*. It differs from *S. brownei* in having posterior part of the pronotal surface more densely asperate; elytral declivity rounded, impressed along the costa between disc and declivity; granules on the upper part large and dense, smaller on the lower part of declivity. There are several enlarged pointed granules along the lower part of declivity. The holotype of the species was compared to the holotype of *S. usitata* (Schedl). There are several other differences between the individuals, such as the relative size of declivital tubercles (especially those in the 7th interstria which form a row of larger tubercles under the declivity in *S. convexa*, but are rather inconspicuous in *S. usitata*), or the slope of declivity, but all these characters are known to be greatly variable within species of Xyleborina. The distinguishing feature between the species suggested by Bright (1980) is the smaller size of the holotype of *S. usitata* (3.5 mm., vs. 4.7 mm.). Although appreciable, this size difference in no greater than what is observed in other species of Xyleborina (*Eccoptopterus*, *Cyclorhipidion* or *Biuncus* spp. display almost twofold difference in size within a single lineage). Thus *S. convexa* is considered a junior synonym of *S. usitata*.

Examined material: New Guinea, Milne Bay, Sudest (Tagula) Island, (holotype, AMNH).

Schedlia paraconvexa **syn. n. Bright (1980)**

Synonymized with: *Schedlia usitata (Schedl)*

J.H. database code: Scol 649

Compared to holotype in AMNH

Length: 4.8 mm.

Discussion

According to Bright (1980), it differs from *S. brownei* in round and convex, not truncated declivity. Pronotal disc more densely granulated than in both. Granules on the upper part of declivity are smaller than in *S. convexa*. The main reported difference is a faint longitudinal carina above weakly impressed epistoma, the carina is said to be as absent in both *S. convexa* and *S. brownei*. Upon a close re-examination we did not locate the supraepistomal costa. There are differences in the surface micro-sculpturing between the holotypes of *S. convexa* and *S. paraconvexa*, some of them resembling faint longitudinal impressions or elevated costae, but variations on these are present in all species of Xyleborina whenever several conspecifics are compared. No other differences between the holotypes were found. The holotype was compared to the holotype of *S. usitata*. Except for a difference in size and in details of tuberculation on the elytral declivity, no characters were found that would suggest a species boundary. Thus *S. paraconvexa* Bright is considered a junior synonym of *S. usitata*.

Examined material: New Guinea, Milne Bay, Rossel Island, (holotype, AMNH).

***Schedlia praeusta* (Eggers, 1923)**

J.H. database code: Scol 650

Compared to holotype in Berlin

Diagnosis: *S. praeusta* can be distinguished from the other *Schedlia* species recorded from PNG by its two pairs of prominent teeth on the surface of the elytra. One pair is near the top edge, second pair on the lateral side of declivity. Other species reported from PNG differ by having no major tooth on the upper part of declivity (*S. brownei*, and *S.*

usitata) or having only one pair of large teeth and no row of larger tubercles under the declivity (7th interstria, *S. sumatrana*). Declivity is convex, rounded, not truncated.

Length: 4.8-5.2 mm.

Examined material: Irian Jaya (D. N. Guinea), Sabron, Cyclops Mts., (compared to type, NHMW); Irian Jaya (D. N. Guinea), Kaiserin Angustafluss, (MNB).

Schedlia sumatrana **(Hagedorn, 1908)**

J.H. database code: Scol 445

Compared to cotype in NHMW

Diagnosis: The species differs from other *Schedlia* species by having a single pair of large spines on the upper part of declivity and by the absence of a row of enlarged tubercles in the 7th interstria below declivity, present in other species.

Length: 5.2 mm.

Discussion

Transferred to *Schedlia* from *Xyleborus* by Browne (1950b), upon erecting the genus *Schedlia*. Wood & Bright (1992) indicated that *S. sumatrana* occurs in New Guinea but without a reference to the record. We could not confirm the occurrence of this species in New Guinea because the original record was not located in the literature. It is included here for the sake of completeness.

Examined material: Indonesia, Sumatra, (co-type, NHMW); Malaysia, Sabah, Danum Valley, Parashorea malaanonan branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Parashorea malaanonan branches, (Hulcr coll.).

***Schedlia usitata* (Schedl, 1942)**

J.H. database code: Scol 652

Compared to holotype in NHMW

Diagnosis: Smaller than other *Schedlia* species from PNG (around 3.4 mm.). Basal (posterior) half of the pronotum is densely punctate, not granulate. There are no major projections on or around the elytral declivity, which is evenly granulated with granules decreasing in size or disappearing towards the elytral tips.

Length: 3.4-4.7 mm.

Discussion

Transferred to *Schedlia* by Browne (1950b).

New junior synonym(s): *Schedlia paraconvexa* Bright, *Schedlia convexa* Bright

Examined material: New Guinea, (holotype).

Genus *Stictodex* gen. n. Hulcr & Cognato

J.H. database code: Scol 829

Type species: *Stictodex dimidiatus* (Eggers, 1927).

Diagnosis: The group closely resembles some species of *Ambrosiophilus*. Differences between the two genera include: *Stictodex* have a distinct antennal club shape - very broad, with first segment procurved (convex), appearing similar to that of *Webbia*; antennal club in *Ambrosiophilus* varies, but is mostly typical type 3 - rounded, with first segment nearly truncated, both second and third segment visible on both faces. The frons is conspicuously spherical in *Stictodex*, mildly rounded to flat in *Ambrosiophilus*. Pronotum is not inflated alongside the head, appearing tight around the head, while it is inflated (sometimes mildly) in *Ambrosiophilus*. *Stictodex* spp. have conspicuous punctuation all around the body including the last abdominal segment, *Ambrosiophilus* have only faint punctures. In *Stictodex*, the first and second striae on declivity are divergent (sometimes creating large declivital sulci), while in *Ambrosiophilus* they are parallel. Most species of *Ambrosiophilus* have the typically impressed first declivital stria, which does not occur in *Stictodex* spp. In *Stictodex*, the declivity is gently sloped (except for the elevated sulci), while in *Ambrosiophilus* it is almost always steep. *Stictodex* are self-reliant ambrosia beetles, while many species of *Ambrosiophilus* parasitize other ambrosia beetle's gardens (not all species).

Also *Ambrosiodmus* species are mostly black and densely punctured, and may possibly be mistaken for *Stictodex*. *Stictodex* differs from *Ambrosiodmus* by shining or shagreen pronotal disc, which is not asperate; the pronotal disc is flat and prolonged, and not rounded, and by the inflated posterior side of protibiae.

Description: Eyes deeply emarginate, sometimes almost disjunct, upper portion of eyes smaller than lower part. Antennal club appears broader than tall, sometimes much broader, club type two (obliquely truncated, second segment visible on posterior side), or three (with first segment straight or convex). First segment of club straight (may be slightly concave or convex) on anterior face, margin of the first segment clearly costate all around the antenna. Second segment of club corneous, visible on the anterior side only, or visible on both sides of the club, the corneous part on the anterior side only. Third segment minor, absent from or partly visible on the posterior side of club. The antennal club resembles the antennal club of *Arixyleborus*. First segment of antennal funicle shorter than rounded, heavily punctured. Submentum deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view prolonged, with low summit (type 7). From dorsal view it has prolonged basic shape with rounded frontal margin (type 7). Pronotal disc densely and evenly punctured, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process conical and slightly inflated. Tuft on pronotal basis associated with mesonotal mycangium absent, setae on elytral bases associated with elytral mycangium absent. Scutellum very small, appears embedded in between the elytra. Elytral bases sinuate, with curved margin even though elytral mycangia are absent. Elytral disc longer than declivity, flat, with clearly delineated striae marked with large punctures, shiny interstriae. Declivity flat, separated from disc either by simple angulate boundary, or surrounded by a large elevated wall with large teeth. Elytral declivity with few setae or scales, not conspicuously pubescent. Circumdeclivital costa ending in 7th interstriae, or reaching beyond 5th interstriae, encircling most or all of declivity. The tuberculation of declivity variable, from the inner part of declivity having tubercles in all interstriae, or no tubercles in interstria 1 (sutural) and several tubercles in interstriae 2, 3 and beyond, or tubercles on elevated costa around declivity. The most variable feature in the genus are the second elytral interstriae, which vary from a simple, flat form indistinguishable from other interstriae, through a form when on the declivity boundary the interstriae are elevated and deviate outwards, to large elevated wall around the declivity armed with teeth. Striae and interstriae on the upper part of declivity even, or forming ridges and furrows, or bearing teeth around the declivity. The first interstriae distinctly broadened towards the summit of elytral disc, or parallel on disc but broadened towards the apex of elytra, where they sometime bear tubercles. Second interstriae often also broadened on elytral disc, inflated. Protibiae obliquely triangular, broadest in 2/3 of the length. Posterior side of protibia inflated, may be slightly granulate. Protibial denticles small, bases of the denticles slightly elevated, usually between 6 and 8 protibial denticles present. Metatibiae of regular size. Mature specimens uniformly black. Length: 2.5-4.1 mm. Overall appearance - black color, mostly bald, most of the body surfaces are shiny black (may be softly shagreen) with conspicuous equidistant punctures.

Etymology: *Stictodex* (G) = punctured wood worm, denoting the abundant and conspicuous punctures covering the entire body.

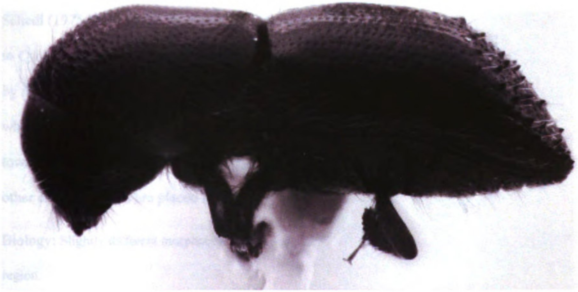

Figure 53: *Stictodex dimidiatus*, type species of the genus. Size: 3 mm.

***Stictodex cuspidus* comb. n. (Schedl, 1975)**

J.H. database code: Scol 471

Previous genus: *Taphrodasus*

Compared to holotype in NHMW

Diagnosis: Steep declivity, its summit surrounded by conspicuously elevated costa armed with large teeth in interstriae 2 and 3. The position of the teeth in relation to the costa is variable, ranging from the teeth being on top of the costal edge, to being almost entirely inside the costal margin. The excavated elytra are a result of broadening of interstriae 1-3 on the apex of elytral declivity, which is typical for *Stictodex* spp. Antennal club typical for the genus, with the club segment 2 always corneous, long and narrow.

Length: 3.9-4.1 mm.

Discussion

Schedl (1975f) placed the species in his Xylebori subadjuncti. He mentioned its similarity to *Cyclorhipidion* (as *Xyleborus*) *indigens*, from which it can allegedly be distinguished by much smaller size, more elongate pronotum, and the armature of the declivital sulcus which, apart from numerous pointed tubercles, bears a pair of large teeth pointing towards the suture (Schedl, 1975f). However, the two species are dissimilar in many other characters, and are placed in separate genera in this work.

Biology: Slightly different morphotypes of the species can be found throughout the Australasian region.

Examined material: Malaysia, Sabah, Danum Valley, (Hulcr coll., 7 indiv.); New Guinea, Morobe Province, Bulolo, (B. H. Jordal), 1100m a.s.l., New Guinea, Morobe Province, Bulolo, (holotype).

Stictodex dimidiatus **comb. n. (Eggers, 1927)**

J.H. database code: Scol 842

Previous genus: *Xyleborus*

Compared to holotype in USNM

Diagnosis: Easily recognizable from the only other *Stictodex* in New Guinea by relatively simple, flat elytral declivity.

Entirely black or dark brown (museum specimens may be lighter), mostly devoid of setae except for sparse long setae on forehead, pronotum and the declivital slope. Antennal club is also typically *Stictodex*-like: broader than tall, with the first segment corneous and dominating on both sides, completely covering the rear side, but with straight or convex margin in the anterior side. Second segment can be corneous or soft, pubescent. The antennal club is wider than tall, and resembles antennal club of *Arixyleborus*. Protibia slightly to distinctly inflated. Pronotum brown, elytra black, shining. Declivity flat, disc-declivity boundary rather abrupt, accentuated by the fact that the upper tubercles are a little larger than those below. Characteristic feature of *Stictodex* is the broadened first interstria and impressed, groove-like second stria around the summit of elytral declivity. In *S. dimidiatus*, the first interstria has one or more tubercles on the summit, all other interstriae bear a row each of sparse but prominent pointed tubercles.

Length: 2.5-3.2 mm.

Discussion

Based on superficial similarity, Browne (1961c) placed both *Xyleborus dimidiatus* and *Xyleborus decumans* in a non-monophyletic group "*Xyleborus artestriatus* group", composed mostly of *Xyleborinus* and *Coptodryas* spp.

New junior synonyms: *Xyleborus decumans* Schedl, *Xyleborus cruciatus* Schedl, *Xyleborus tunggali* Schedl

Examined material: Malaysia, Perak, (holotype, USNM).

Genus *Streptocranus* Schedl (1939)

J.H. database code: Scol 796

Type species: *Streptocranus mirabilis* Schedl (1939).

Redescription: Eyes shallowly emarginate, "bean shape", upper portion of eyes smaller than lower part. Antennal club more-less circular shape, or taller than wide, club type two (obliquely truncated, second segment visible on posterior side). First segment of club circular around the club, covering most of the posterior face, margin of the first segment mostly soft, pubescent. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only. Third segment of club absent from the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma mostly smooth, alutaceous, with minor punctures. Submentum flat, flush with genae, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with short continuous elevated carina. Pronotum from lateral view long, "hooded" frontally (type A). From dorsal view it is long and rounded anteriad (type 9), or long and conical anteriad (type B). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum concave due to the extended pronotum. Procoxae contiguous, prosternal posterocoxal process shortly conical. Tuft on pronotal basis associated with mesonotal mycangium absent, setae on elytral bases associated with elytral mycangium also absent. Scutellum miniature but visible, or flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat, punctures on elytral disc in strial lines (which may be difficult to discern). Boundary between elytral disc and declivity indistinct, flat or slightly convex disc smoothly transitioning into flat declivity. Lateral profile of elytral declivity slowly descending, flat, dorsal profile of elytral end emarginate. Elytral declivity with not pubescence. Circumdeclivital costa absent or indefinable. The inner part of declivity has no tubercles. All species have a pair of more or less elongated processes on the elytral lateral apices. The curvature and length of these processes is the only diagnostic character of most of the putative species. First interstriae are parallel (sometimes slightly broadened towards elytral summit), or parallel on disc but broadened towards the apex of elytra. Protibiae very slender, slightly broader only at the distal end. Posterior side of protibia flat. Protibial denticles large, distinctly longer than wide, bases of the denticles not enlarged, or slightly enlarged, fewer than 6 protibial denticles present. Metatibiae of regular size. Body color mostly very light, yellow or light brown, or pronotum much lighter (yellow or orange) than elytra. Some of the smallest and most slender species, those living in New Guinea are around 2 mm. long.

Discussion

The only feature that varies between several putative "species" of *Streptocranus* is the length and curvature of the posterolateral elytral processes. Characters such as the size and shape of elytral processes are the most plastic morphological features in Xyleborina. Furthermore, descriptions of all *Streptocranus* spp. are based on single individuals and do not consider intraspecific morphological variability. At present there is not enough material to examine the significance of these characters in delimiting monophyletic lineages of *Streptocranus*.

Biology: The genus occurs throughout the whole Paleotropic region, but representatives are always rare. The gallery consists of several short, often parallel tunnels (Browne 1961c).

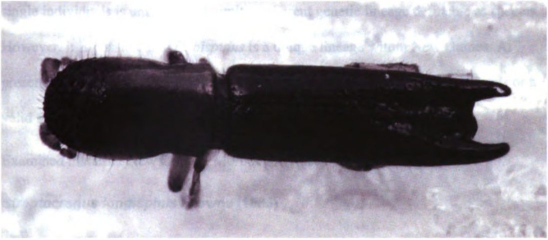

Figure 54: *Streptocranus longispinis*, a typical representative of the genus. Size: 2 mm.

Streptocranus bispinus **comb. n. (Schedl, 1979)**

J.H. database code: Scol 613

Previous genus: *Coptoborus*

Compared to holotype in NHMW

Diagnosis: *S. bispinus* differs from *S. longispinis* in the shape of the posterolateral processes, which are sharply pointed and curved upwards.

Length: 2.1 mm.

Discussion

Schedl (1979g) related the species to *Streptocranus* (as *Xyleborus*) *bicuspis* (Egg.), and noted that it was smaller, the elytral declivity was more clearly separated from the elytral disc, the declivity was very oblique, transversely flattened, coarsely punctured, and the apical "horns" widened at the tip. After re-examination of the holotype (the only specimen known), the only unique difference found between this species and other *Streptocranus* spp. is the curvature of the processes. This single deviation of declivity in a single individuals is unlikely to delimit a coherent genetic lineage definable as species. However, it is possible that *C. bispinus* is a unique lineage within New Guinea. At present it is not possible to decide whether *S. bispinus* is a synonym of *S. bicuspis* or a valid species.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

***Streptocranus longispinis* Browne (1986)**

J.H. database code: Scol 154

Compared to holotype in BMNH

Diagnosis: Posterolateral elytral processes is long and blunt. Some specimens have several minute tubercles in the interstria 3 on elytral declivity. There are a few shallow longitudinal furrows on elytral sides towards the apex (impressed striae 5 - 8).

Length: 2.0 mm.

Discussion

It was recently resurrected from *Coptoborus* (Wood & Bright, 1992) and restored to its original genus (Hulcr et al. 2007a). Browne (1986a) relates the species to *S. longicauda* Browne from SE Asia, and distinguishes it by its more slender and acute elytral spines. The species is very similar to *Streptocranus bicuspis* (Eggers). The only notable difference is that the posterolateral processes on declivity are less curved and less pointed. The impressed striae 5-8 and the granules in interstria 3 are almost certainly very plastic. At present there is not enough material to explore the variability of the posterolateral processes and their significance for delimiting monophyletic lineages in *Streptocranus*.

Examined material: New Guinea, West Papua, Fakfak, (holotype), imported to Japan (Nagoya); PNG: Madang Prov. (3), Oro Prov. (1), West Sepik (1), J. Hulcr 2002-2006.

Genus *Taphrodasus* Wood (1980)

J.H. database code: Scol 785

Type species: *Xyleborus percorthylus* Schedl.

Discussion

Wood (1980c) erected this genus for *Xyleborus percorthylus.* Three more species were later transferred to it: *Webbia divisus* Browne, *Xyleborus penicillatus* Hagedorn, and *Xyleborus cuspidus* Schedl. The type species *T.* (as *Xyleborus*) *percorthylus* belongs to *Pseudowebbia* and is transferred here. *T. cuspidus* is not related to any of the other putative *Taphrodasus*, it is transferred here to *Stictodex*. The remaining species, *T. divisus* and *T. penicillatus* fit within the generic concept of *Webbia*, and will be transferred there in an upcoming publication (returned, in case of *T. divisus*; Hulcr, unpubl.). Thus the genus *Taphrodasus* is not considered available. Browne (1972) indicated that *Taphrodasus penicillatus* (as *Webbia*) is a part of a distinct group in *Webbia*, in which the elytral declivity is slightly depressed and its acute lateral margins are acutely produced forward above the suture. He also indicated that *T.* (as *Webbia*) *divisus* is the only other species belonging to that group.

Genus *Truncaudum* gen. n. Hulcr & Cognato

J.H. database code: Scol 789

Type species: *Truncaudum impexus* (Schedl).

Diagnosis: The genus is most characteristic by its abruptly truncate elytral declivity, often surrounded by denticles. *Truncaudum* differs from *Amasa*, another genus with truncated declivity, by having the declivity surrounded by denticles, by usually rich vestiture on most of the body surface, prolonged pronotal disc, and antennal club type 2. The unusual *Truncaudum agnatum*, the only *Truncaudum* without truncated declivity, can be mistaken with *Xyleborus s. str.*, however *T. agnatum* has more abundant vestiture over its body, its declivity is not surrounded by costa posteriad, and its prosternal posterocoxal process is slender and pointed.

Description: Eyes shallowly to deeply emarginate, upper portion of eyes smaller than lower part. Antennal club more-less circular shape, club type two (obliquely truncated, second segment visible on posterior side). First segment of club circular around the club, covering most of the posterior face, margin of the first segment clearly costate all around the antenna, or mostly costate, may appear softer on posterior side. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only. Third segment of club absent from the posterior side of club, or partly visible on the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view prolonged, with low summit (type 7). From dorsal view it has prolonged basic shape with rounded frontal margin (type 7). Pronotal disc shining or smoothly alutaceous, with small punctures, and often richly pubescent. Lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process tall and pointed. Tuft on pronotal basis associated with mesonotal mycangium absent, setae on elytral bases associated with elytral mycangium absent. Scutellum flat, flush with elytra, or miniature, but always visible. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat, punctures on elytral disc in strial lines (which may be difficult to discern). The description of elytral declivity differs for *T. agnatum*, the most common *Truncaudum* in New Guinea, and all other *Truncaudum* species. In *T. agnatum*, the lateral profile of elytral declivity is mildly flat or rounded, dorsal profile of elytral end rounded. Elytral declivity usually richly pubescent, often appearing rugose, densely granulate of punctured. Circumdeclivital costa is absent or indefinable in *T. agnatum*. The inner part of declivity has no tubercles in interstria 2, but several tubercles in interstriae 1 and 3, these are often very dense, or in the form of spines. Striae and interstriae on the upper part of declivity are flat, not in the form or circumdeclivital costa or carina. The first interstriae are parallel on disc but broadened towards the apex of elytra, where they sometimes bear tubercles. In other members of the genus, the characteristic feature is the often sharply truncated elytral declivity. Most *Truncaudum* spp. have small pointed granules or large tubercles surrounding the elytral declivity, and small tubercles inside the declivity in interstriae 1 and 3. The inner surface of declivity varies from shining and opalescent to coriaceous, granulate and conspicuously rugged. As in *T. agnatum*, the first interstriae are parallel on disc but broadened towards the apex of elytra, where they sometime bear tubercles. The rest of the description applies to all species. Protibiae with evenly rounded edge, posterior side of protibia flat, with setae only. Protibial denticles small, bases of the denticles not enlarged or slightly enlarged, usually between 6 and 8 protibial denticles present. Metatibiae of regular size. Most species are colored in varied shades of reddish brown, darkening towards abdomen. The whole body is often richly pubescent. Length: 1.7-3.4 mm.

Discussion

Gender: neuter. The gender-specific endings of many species names in this group of Xyleborines have been uncertain since Wood & Bright (1992) moved a number of them from *Xyleborus* (masculine) to *Cyclorhipidion* (neuter). Although the new combinations were not explicitly published, the neuter names from the Catalog (Wood & Bright 1992) have now been disseminated more broadly than the masculine ones from the original publications. It is thus suitable to transfer these species into a genus with neutral gender.

Truncaudum is phylogenetically related to *Amasa*, nevertheless it differs significantly in its morphology (Figure 21, Cognato *et al.*, 2009).

Browne (1961c) remarked on the unclear position of this group (in his work represented by a single species, *T.* (as *Xyleborus*) *circumcisus*), and suggested its phylogenetic position between the group "Webbini" and the rest of Xyleborines. Browne attempted to organize similar species, of which some are now included in *Truncaudum*, into his "*Xyleborus agnatus* group". For example, *Xyleborus truncaticauda* was included upon its description (Browne, 1984d). Schedl placed many similar *Truncaudum*-like species in two groups (the distinction between them is not clear): 1) Xylebori truncatipenni, including *X. obtusus* Eggers 1923 (synonymized with *X. circumcisum* Sampson 1921), *X. pilosulus* Eggers 1927, *X. pilipennis* Eggers 1940, *X. tuberculifer* Eggers 1923, *X. umbratus* Eggers 1941, *X. agnaticeps* Schedl 1957, *X. artiflex* Schedl 1942, *X. polyodon* Eggers 1923, *X. truncatipennis* Schedl 1961 (as *Xyleborinus* in Wood & Bright, 1992), *X. obliquesectus* Eggers 1927, *X. obtusitruncatus* Schedl 1948 (as *Dryocoetoides* in Wood & Bright, 1992), and 2) Xylebori circumcincti, including *X. falcarius* Schedl 1942, *X. circumspinosus* Schedl 1972, *X. vernaculus* Schedl 1975, and *X. impexus* Schedl 1942. Those species available for examination during this work have been found to be extremely similar, and transferred to *Truncaudum*. Importantly, Schedl, Eggers, and other authors erected a number of these species based on minute differences, and as such these are unlikely to constitute valid species in contemporary sense. Several synonymies are proposed in this publication, greater number of synonymies is probable when more material is available for examination. The earliest described species of those transferred here to *Truncaudum* is *T. agnatum*. However, it is not a very characteristic representative of the new genus, thus *T. impexus* is chosen as the type species.

Biology: The known species excavate a single short tunnel leading to often large terminal brood cavity.

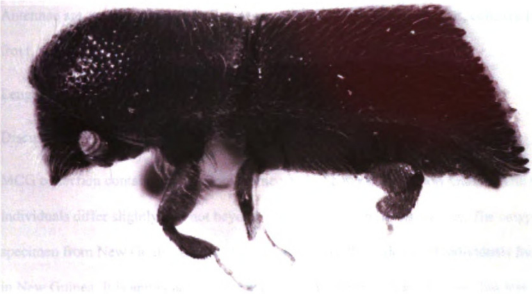

Figure 55: *Truncaudum impexus*, the type species of the genus. Size: 2.3 mm.

Truncaudum agnatum **comb. n. (Eggers, 1923)**

J.H. database code: Scol 61

Previous genus: *Cyclorhipidion*

Compared to holotype in MCG

Diagnosis: Probably the most common *Truncaudum*, one of the most variable, and also the only species without sharply truncated declivity. However, all other characters as well as a molecular phylogeny (Cognato et al., 2009) place this species unambiguously within *Truncaudum*. Extremely variable in body size and the shape of elytral declivity, which varies from obliquely rounded to nearly truncated. As most *Truncaudum* spp., *T. agnatum* has small pointed granules or tubercles surrounding the elytral declivity, and small tubercles inside the declivity in interstriae 1 and 3. The surface of declivity is often coriaceous, with variable-sized and very dense interstrial punctures, and abundant setae. This combination of features gives the declivity a conspicuously rugged appearance. Antennae are typically of type 2 (first segment of club dominant, corneous, concave in front, second and third segments reduced, pubescent).

Length: 2.0-3.0 mm.

Discussion

MCG collection contains "type" from Borneo and a "cotype" from New Guinea. The two individuals differ slightly, but not beyond the variation seen in this species. The cotype specimen from New Guinea is a good representative of the majority of individuals found in New Guinea. It is appreciably larger than the type specimen form Borneo, has less flat declivity, less abruptly truncated. Antennae and ventral side are not available for examination. The "type" from Borneo has obliquely truncated declivity, supporting the inclusion of this species in *Truncaudum*. Wood & Bright (1992) indicate existence of another "type" in USNM. This type should be ideally designated a lectotype, however it was not available for this study.

Previously synonymized species: *Xyleborus nutans* Schedl, *Xyleborus borneensis* Eggers

New junior synonym(s): *Cyclorhipidion delicatum* (Schedl), *Cyclorhipidion subagnatum* Wood, *Cyclorhipidion nutans* (Schedl), *Xyleborus gratiosus* Schedl

Examined material: Malaysia, Sarawak, (unspecified "type", MCG); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Ficus* sp.

trunk, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* trunk, (Hulcr coll.); New Guinea, (FICB); New Guinea, Western Province, Wavoi, (FICB); New Guinea, Hatam, (co-type, MCG); PNG: Madang Prov. (111), Oro Prov. (5), West Sepik (33), J. Hulcr 2002-2006.

Truncaudum impexus **comb. n. Schedl (1942)**

J.H. database code: Scol 248

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: The most common *Truncaudum* in New Guinea. Antenna type 2 (dominant, corneous segment 1 with concave or straight costa, segment 2 and three soft, pubescent, segment 2 visible on the posterior side of club, segment 3 may or may not be visible). Pronotum prolonged posteriad (lateral type 7 or 8), rounded frontally, no serrations on its front edge. Protibiae crescent-shaped, rounded on the outer edge with more than 8 small denticles. Protibiae contiguous, posterocoxal prosternal process short, pointed, slightly inflated. Elytrae brown, with parallel lines of strial punctures on disc, with faint but abundant vestiture, abruptly truncated, declivity surrounded with conspicuous serrate costa. The serration is very variable, often differing between bottom and upper margin of declivity. The upper part serration size ranges from very small tubercles to large conspicuous pointed teeth. Inner side of declivity with parallel rows of punctures, interstria 1 often elevated and broadened towards the end, mostly bearing one or more pairs of small tubercles, interstria 3 also often with tubercles. Declivital surface variable, shining, or hairy, or shagreen, often bluish opalescence.

Length: 1.9-2.6 mm.

Discussion

Schedl (1942c) states that the species (along with *X. falcarius*) is related to *X. trepanicauda* based on elytral characters. However, all other characters point clearly to its relatedness to *Truncaudum*. According to Schedl, it differs from *X. falcarius* by the absence of the prominent tooth in the first interstria on the edge of declivity. The variation of declivital armature in this species is extraordinary. The circumdeclivital teeth vary in size from minute granules to large sharp teeth. Molecular analysis confirms that these forms belong to a single lineage. The sequence of the 28S ribosomal gene of the form with large teeth is identical to one of the examined sequence of *T. impexus s. str.* (small teeth), while the difference between two sequences of randomly selected individuals of *T. impexus s. str.* (small teeth) was 0.001 (one substitution per 1000 bp). The p-distances to other members of the genus (*T. longicaudum* and *T. agnatum*) was 0.008 and 0.005, respectively. Differences between sequences of the CO1 mitochondrial gene, usually used for insect species delimitation, are less conclusive due to the enormous variation regularly seen in Xyleborina. The difference among randomly chosen *T. impexus* s. str. including the large-teeth form is between 0.109 and 0.116 (nearly all substitution in 3rd codon sites). Although large, the difference is still lower than the average between-species difference among *Truncaudum* spp. is 0.147 (almost never below 0.130).

New junior synonym(s): *Xyleborus dentatulus* Browne, *Xyleborus circumspinosus* Schedl, *Xyleborus subdentatulus* Browne, *Xyleborus falcarius* Schedl, *Xyleborus vernaculus* Schedl, *Xyleborus putputensis* Browne

Biology: Gallery in the form of a flat larval communal chamber, sometimes with multiple entrances.

Examined material: New Guinea, (B. H. Jordal); New Guinea, (B. H. Jordal); New Guinea, (FICB); locality not recorded, (holotype, NHMW); PNG: Madang Prov. (8), Oro Prov. (30), West Sepik (4), J. Hulcr 2002-2006.

***Truncaudum longior* comb. n. (Eggers, 1923)**

J.H. database code: Scol 309

Previous genus: *Cyclorhipidion*

Compared to lectotype in lectotype in NHMW, USNM

Diagnosis: Circumdeclivital costa rather oblique, not carinate, nor tuberculate. Only few circumferential tubercles, confined to the apical end of declivity. Multiple tubercles within the declivity, few (often 2) in interstria 1 and a few more (often 4) in interstria 3. Surface smooth.

Length: 2.0-2.2 mm.

Discussion

The Wood & Bright (1992) catalog indicates a specific epithet *longius*, instead of *longior*.

New junior synonym(s): *Xyleborus canarivorus* Browne, *Xyleborus viaticus* Schedl, *Xyleborus protii* Browne

Biology: Flat chamber deep in xylem.

Examined material: New Guinea, Japen, (BBM); New Guinea, Madang Province, Baiteta, (IRSNB); New Guinea, Maifluss, (lectotype, USNM); PNG: Madang Prov. (9), J. Hulcr 2002-2006.

Truncaudum truncaticauda comb. n. Browne (1984)

J.H. database code: Scol 717

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Diagnosis: Small *Truncaudum*. There are two main differences between this species and most *Truncaudum* spp.: The declivital surface is rugose, densely shagreen; strial punctures are obsolete and fused into continuous furrows; interstriae are transformed into rows of robust short tubercles; the circumdeclivital costa is armed with several small adjacent denticles in each interstria. Holotype length: 1.8 mm.

Length: 1.7-1.8 mm.

Discussion

Browne (1984d) included the species into his "*Xyleborus agnatus* group", which also contained some other species of *Truncaudum*. According to Browne, the clear division of the elytra to the shiny and the matt surfaces identifies the species. However, this character is also found in other *Truncaudum* spp.

Examined material: New Guinea, Morobe Province, Gumi, (holotype, BMNH); New Guinea, Morobe Province, Gumi, (paratype, FICB).

Truncaudum truncatiformis comb. n. (Eggers, 1923)

J.H. database code: Scol 596

Previous genus: *Amasa*

Compared to holotype in MCG

Diagnosis: The species is hairy, not very dense but abundant erect vestiture, especially on declivity. It has unusually large eyes, antenna type 2 or 3 (first segment corneous, rather prominent, its margin straight or slightly concave, segments 2 and 3 also prominent, corneous). In some specimens the elytral end appears slightly constricted. Declivity is concave, circular costa rugged, thick, with minute tubercles on the margin. Protibia is triangular rather than crescent-shaped.

Length: 3.4 mm.

Discussion

Vaguely similar species include *Cyclorhipidion* (probably *Truncaudum*) *obtusus* and *Cyclorhipidion* (probably *Truncaudum*) *pilosulus*, but both have smaller eyes and bulging, not concave, declivity. Lectotypes of *C. obtusus* and *C. pilosulus* were examined.

Examined material: New Guinea, Moroka, (unspecified "type", MCG); New Guinea, Gulf Province, Ivimka, (UCD); PNG: Madang Prov. (1), J. Hulcr 2002-2006.

Truncaudum tuberculifer **comb. n. (Eggers, 1923)**

J.H. database code: Scol 636

Previous genus: *Cyclorhipidion*

Compared to lectotype in MCG

Diagnosis: The species is characteristic with its unusually large eyes, short row of serrations on the anterior margin of pronotum, very narrow, sickle-like protibiae, and the structure of the declivity. The upper half of declivity is surrounded with angulate costa (not carina), and the edge bears several small tubercles in each interstria. The tubercles are also present in interstriae inside the declivity, close to the upper declivital edge, and decreasing in size towards the apex. The declivity is shining, flat.

Discussion

While most characters place this species in *Truncaudum* (Figure 20), the large eyes, serrate margin of pronotum and narrow protibiae resembles species of *Amasa*.

Length: 3.2 mm.

New junior synonym(s): *Xyleborus hopeae* Browne

Examined material: New Guinea, Bujakori, (unspecified "type", MCG).

Genus ***Wallacella*** gen. n. Hulcr & Cognato

J.H. database code: Scol 833

Type species: *Wallacella fornicatus* (Eichhoff 1868).

Diagnosis: Rather variable genus, sharing few synapomorphies such as the subquadrate pronotum, antennal type 3, protibial margin curved, and the expanded posterolateral sides of elytra. Characters distinguishing *Wallacella* from *Euwallacea*: first segment of funicle shorter than pedicel, not conspicuously slender (except *W. striatulus*); upper part of eye smaller than the lower part; pronotum rounded frontally, or if subquadrate (slightly inflated along posterolateral side), then prolonged and rectangular, rarely subquadrate and short, not quadrate with inflated sides as in *Euwallacea* (an overlapping character); the sockets with tibial denticles are not enlarged; protibiae rounded, with more than 7 denticles; rarely longer than 4 mm (*Euwallacea* is almost always longer than 4 mm.). Characters distinguishing *Wallacella* from *Fortiborus*: first segment of funicle shorter than pedicel, not unusually slender and stalk-like (except *W. striatulus*); upper part of eye smaller than the lower part; pronotal anterior edge not produced (although in many species it bears a row of serrations); the sockets with tibial denticles are not enlarged; rarely longer than 4 mm (*Fortiborus* is always longer than 5 mm.).

Description: Eyes shallowly emarginate, "bean shape", or deeply emarginate, sometimes almost disjunct, upper portion of eyes smaller than lower part. Antennal club variable, more-less circular shape, or taller than wide, club type two (obliquely truncated, second segment visible on posterior side), or three (with first segment straight or convex). First segment of club circular around the club, covering most of the posterior face, or straight (may be slightly concave or convex) on anterior face, margin of the first segment clearly costate all around the antenna, or mostly costate, may appear softer on posterior side. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only, or corneous on both sides of club, but never strictly circular (not making antenna tall, or "telescopic"). Third segment of club partly visible on the posterior side of club, or clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, only in one species longer than pedicel. Funicle composed of 4 segments, scapus regularly thick. Frons above epistoma mostly smooth, alutaceous, with minor punctures, or rugged, coarsely punctate. Submentum slightly impressed, or deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations or with distinct row of serrations. Pronotum from lateral view of basic shape (type 0), or tall (type 2), or prolonged, with low summit (type 7). From dorsal view it is subquadrate (type 3), or prolonged and quadrate or subquadrate (type 8). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process tall and pointed, or conical and slightly inflated. Tuft on pronotal basis associated with mesonotal mycangium absent, setae on elytral bases associated with elytral mycangium absent. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity and slightly convex or bulging, punctures on elytral disc in strial lines (which may be difficult to discern). Boundary between elytral disc and declivity indistinct, end of disc rounded and smoothly transitioning into declivity. Lateral profile of elytral declivity slowly descending, often flat, dorsal profile of elytral end broadened laterally. Elytral declivity with few setae or scales, not conspicuously pubescent. Circumdeclivital costa ending in 7th interstriae. The tuberculation of declivity is never very conspicuous, but the pattern is very variable. The inner part of declivity has often no tubercles or only uniform granules, but can have several tubercles in interstriae 2, 3 and beyond and no tubercles in interstria 1 (sutural), or no tubercles in interstria 2, and several tubercles in interstriae 1, 3 and beyond. In most species the upper part of declivity is flat, only in W. striatulus the striae and interstriae form ridges and furrows. First interstriae are parallel in most bulky species, or parallel on disc but broadened towards the apex of elytra in more slender species, in which case the broadened end of interstria 1 often bears granules or tubercles.

In almost all species, protibiae have evenly rounded edge, protibial denticles small, bases of the denticles not enlarged, usually between 6 and 8 protibial denticles present. In *W. andamanensis*, protibiae are obliquely or distinctly triangular, slender on the upper part, broad and denticulate on the lower part, protibial denticles are large, distinctly longer than wide, bases of the denticles distinctly enlarged, fewer than 6 protibial denticles are present. Posterior side of protibia is flat in all species. Metatibiae of regular size. Body length between 1.8 and 4.4 mm. Color varies from uniformly light brown or reddish to dark brown or black.

Discussion

The antennal club type may not be entirely consistent throughout the whole range of the group. Several Bornean representatives of *Xyleborus semirudis* Blandford (synonymized with *Wallacella xanthopus* (Eichhoff) by Wood 1989, but the synonymy is questionable) were found to have antennal type No. 4, i.e., with small and procurved first segment. Earlier authors used the surface of elytral declivity as a species-specific character. Unfortunately, this seems to be the most plastic of all morphological characteristics in this group, varying even within one geographical population (e.g., substantial variation in tubercle size, striae impression, etc, seen in *E. fornicatus* in lowland PNG).

Most representatives of *Wallacella* were placed in *Euwallacea* (Wood 1989, Wood & Bright 1992). However, many of these do not share some of the diagnostic features of *Euwallacea* as defined by Wood (1989), and are more closely related to species of *Xyleborus* (Figure 20, 22). Classification of this large group is still not entirely resolved, as evidenced by the low resolution on both morphological phylogeny (Figure 20, 22) and molecular phylogeny (Cognato et al., 2009).

Figure 56: *Wallacella fornicatus*, the type species of the genus. Size: 2.3 mm.

Wallacella andamanensis comb. n. (Blandford, 1896)

J.H. database code: Scol 638

Previous genus: *Euwallacea*

Compared to holotype in BMNH

Diagnosis: *W. andamanensis* differs from other similar *Wallacella* spp. by a relatively slender protibia with only 5 large protibial denticles in enlarged sockets and by the absence of a row of serrations on the anterior edge of pronotum. Specimens from New Guinea are more slender than the holotype, but bearing all the important characters (pronotum edge, antennae, protibiae, slightly convex elytral end, interstriae with rows of granules, elytral declivity with often distinct bluish opalescence). Holotype length: 3.2 mm.

Length: 2.7-3.2 mm.

Discussion

Light-colored *Wallacella fornicatus* individuals from PNG are often misidentified as *Wallacella* (as *Euwallacea* or *Xyleborus*) *andamanensis*. Maiti and Saha (1986) transferred *Xyleborus andamanensis* to *Euwallacea*. Wood (1989) included the following species as synonyms: *Xyleborus granulipennis* Eggers 1930, *Xyleborus intextus* Beeson 1930 and *Xyleborus senachalensis* Beeson 1930. A non-type of *X. noxius* Samps. from India and the lectotype of *E. siobanus* (Eggers) (both currently synonymized with *W. andamanensis*) in USNM are nearly identical to the slightly more slender specimens from New Guinea, including the iridescent elytral surface.

Previously synonymized species: *Xyleborus siobanus* Eggers, *Xyleborus senchalensis* Beeson, *Xyleborus intextus* Beeson, *Xyleborus granulipennis* Eggers, *Xyleborus noxius* Sampson, *Xyleborus burmanicus* Beeson

New junior synonym(s): *Euwallacea talumalai* (Browne)

Biology: Deep tunnels without chambers (Beaver & Browne 1978).

Examined material: India, Andaman, (holotype); New Guinea, Vogelkopf, (BBM), identified by S. L. Wood as *Xyleborus senchalensis*; PNG: Madang Prov. (60), Oro Prov. (18), West Sepik (7), J. Hulcr 2002-2006.

Wallacella andreae sp. n. Hulcr & Cognato

J.H. database code: Scol 341

Compared to holotype in USNM

Diagnosis: A number of characters distinguish this species from most *Wallacella* spp. It has a long, stalk-like first segment of funicle (as in *Euwallacea*), flat and clearly triangular submentum, rather than impressed and narrow. The antennal club is type 4, rather than 2 or 3. Internal mandibular mycangia are visible as bulges on the epistoma. *W. andreae* is also significantly larger than most *Wallacella* spp.

Description: Large species with idiosyncratic combination of characters, tentatively placed in *Wallacella*, with which it shares the overall appearance and several characters. Uniformly dark brown, with sparse vestiture. Antennae: first segment of funicle prolonged, stalk-like; antennal club type 4: first segment of antennal club small, with straight or slightly convex edge; second segment prominent, corneous, both second and third segments clearly visible on the posterior face of club. Eyes moderately large, mildly emarginate. Submentum large, nearly flush with surface. Mandibular mycangia visible as bulges on the epistome. Pronotum extended frontally (summit moved posteriad); no row of serrations on the frontal edge; pronotal asperities small, very small asperities extending also on the softly alutaceous pronotal disc. pronotal sides parallel, not inflated, thus pronotum appearing rounded frontally, not quadrate. Procoxae contiguous, mesosternal posterocoxal process narrow, flat. Protibiae rounded, not triangular, with 9 minute socketed denticles, sockets not enlarged. No mycangial opening on either pronotum or on elytral bases. Abdomen long, elytra gradually sloped, covered with parallel rows of inconspicuous punctures. Interstriae on declivity with numerous but not dense setae-bearing granules. Declivity mildly impressed along striae 1 and 2.

Length: 4.4 mm.

Discussion

Etymology: Named in recognition of Andrea Lucky. The phylogenetic position of this species in relation to *Euwallacea* and *Wallacella* is unclear (Figure 20). It is superficially similar to *Euwallacea* spp., but doesn't share many synapomorphies with these species; several distinguishing characters suggest it has acloser relationship with *Wallacella*.

Holotype deposited in USNM, paratypes deposited in MSUC, BMNH, NHMW.

Examined material: PNG: Chimbu Prov. (91), J. Hulcr 2002-2006.

Figure 57: *Wallacella andreae sp. n.* Size: 4.4 mm.

***Wallacella densatus* comb. n. Schedl (1979)**

J.H. database code: Scol 680

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: From other *Wallacella* it can be distinguished by large submentum, triangular shape of protibia with only 6 socketed denticles, the presence of rows of flattened erect scales in all elytral interstriae, and the smoothly concave elytral declivity. The broad and slightly impressed declivity with rows of flat setae vaguely resembles *Leptoxyleborus* spp.

Length: 1.8-2.0 mm.

Discussion

In many ways, *W. densatus* is an idiosyncratic member of the genus *Wallacella*, and future analyses may transfer it elsewhere. Elytra vaguely resemble those of *Leptoxyleborus*, but other characters differ. The characters which support its placement in *Wallacella* are the antennal club of type 2, slightly inflated sides of pronotum, but not bulging, thus pronotum broadened but not quadrate frontally, slightly extended anterior part of pronotum, slightly inflated mesosternal posterocoxal process; short and broad elytra, rounded and broadened laterally at the end.

Examined material: New Guinea, Morobe Province, Bulolo, (FICB); New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

Wallacella fornicatus **comb. n. (Eichhoff, 1868)**

J.H. database code: Scol 36

Previous genus: *Euwallacea*

Compared to neotype in NHMW

Diagnosis: Differs form other *Wallacella* by subquadrate or rounded, rather than quadrate frontal margin of pronotum, by protibiae with more than 7 socketed denticles which are small, and their sockets are also small, not conical and enlarged, and by the lack of conspicuous structures on declivity (such as furrows or enlarged denticles).

Length: 2.2-2.6 mm.

Discussion

Correctly synonymized with *E. fornicatior* Eggers. Wood (1989) included the following species as synonyms: *Xyleborus perbrevis* Schedl 1942, *Xyleborus tapatapaoensis* Schedl 1951, *Xyleborus whitfordiodendrus* Schedl 1942. Beaver (1991) examined large series of this species from the Old World tropics and found it somewhat variable. Wood (1989) and Beaver (1991) nearly simultaneously included *Xyleborus schultzei* Schedl 1958. Similar species: *E. fraternus* Blanford type specimen from Ceylon: declivity not concave, slightly convex even at the apex. Almost flat protibiae, without a recurved bottom margin. *E. asperipennis* has longer declivity and flatter disc. *Wallacella andamanensis* has 4-5 socketed teeth on protibia, subquadrate pronotum, and longer straight portion of elytral disc, more conspicuous tubercles on declivity, and no carina on anterior edge of pronotum. Very similar is *X. malloti* Eggers from India - similarly sloped elytra, but more bulky, and has subquadrate pronotum, and 8, not 6 socketed teeth. Schedl (1959a) mentioned the African *Wallacella* (as *Xyleborus*) *xanthopus* and the Oriental *X. fraternus* are almost identical to *E. fornicatus*, except for the size. *Xyleborus nitens* has smoother surface of the pronotum; there are other differences which were not recorded.

Previously synonymized species: *Xyleborus fornicatior* Eggers, *Xyleborus tapatapaoensis* Schedl, *Xyleborus schultzei* Schedl, *Xyleborus perbrevis* Schedl, *Xyleborus whitfordiodendrus* Schedl

Biology: Although the native range of the species is SE Asia and Oceania, it is now distributed throughout the world tropics, including Central America and Hawaii (Schedl 1941f). Literature reports unusual habits of *E. fornicatus*. According to several hundreds of my own records from New Guinea and Borneo, *E. fornicatus* (and probably several related species) is rather unique among xyleborines in its preference for *Artocarpus* spp. (Hulcr et al. 2007). However, this species is also often mentioned as a pest in tea plantations (Beaver & Browne 1978). Browne (1961c) remarks on several records of this species from fallen fruit or banana stems. The author also discussed the allegedly distinct morphological form seen in individuals specialized on tea bushes, *E. (X.) fornicatior*, which allegedly causes sudden outbreaks of the species in tree plantations. There seem to be two common morphs of *W. fornicatus* in New Guinea. One is the typical dark variant, the other one is much lighter, yellow to orange to light brown colored, with more rounded elytra. No ecological difference between the two was found, both are found predominantly on Moraceae.

Examined material: India, Dehra Dun, (neotype, NHMW); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Ficus* sp. branches, (Hulcr coll.); New Guinea, Morobe Province, Bulolo, (FICB); New Guinea, Morobe Province, Bulolo, (MSUC); New Guinea, Madang Province, Ohu, *Artocarpus camansii* twigs, (Hulcr coll., 10 indiv.); Thailand, Pong Yaeng N. P., (Hulcr coll., 6 indiv.), R. A. Beaver det.; PNG: Madang Prov. (560), Oro Prov. (75), West Sepik (59), J. Hulcr 2002-2006.

Wallacella funereus **comb. n. (Lea, 1910)**

J.H. database code: Scol 44

Previous genus: *Ambrosiodmus*

Compared to homotype in NHMW

Diagnosis: The species differs from most other *Wallacella* by its greater size and by the presence of enlarged tubercles on the second and third declivital interstriae. The size and pattern of the tubercles varies greatly, but there seem to be no tubercles in the first (sutural) interstriae.

Length: 3.2-3.6 mm.

Discussion

Type specimen of *X. funereus* is currently absent from SAM, a lectotype is present in NHMW. Schedl (1933e) pointed out to the similarity between *A. funereus* (as *Xyleborus*) and the genus *Euwallacea*, specifically *E. interjectus* (as *Xyleborus*). *X. nepos* Eggers has also rather large tubercles on interstriae 2 and 3. Schedl (1933e) distinguished *X. nepos* var. *robustus* Schedl by stouter pronotum. Wood (1989) synonymized *X. nepos-robustus* with this species. We confirm the synonymy of *X. nepos* based on the examination of a lectotype and a "co-type".

Previously synonymized species: *Xyleborus nepos* Eggers, *Xyleborus nepos robustus* Schedl, *Xyleborus signatus* Schedl

Biology: Just as *Wallacella fornicatus* and *Wallacella xanthopus* (in Borneo), this species seems to prefer *Artocarpus* sp. (Moraceae).

Examined material: Malaysia, Sabah, Danum Valley, *Artocarpus camansii* branches, (Hulcr coll., 2 indiv.); New Guinea, New Britain, (BBM), Identified as *X. nepos* by Wood; New Guinea, (FICB); New Guinea, Madang, *Ficus*, (Hulcr coll., 2 indiv.); Philippines, Bolivac, (compared to type, NHMW); Philippines, Bolivac, (compared to type, NHMW); PNG: Madang Prov. (24), Oro Prov. (4), J. Hulcr 2002-2006.

Wallacella piceus **comb. n. (Motschulsky, 1863)**

J.H. database code: Scol 52

Previous genus: *Euwallacea*

Compared to holotype photograph in IZM

Diagnosis: Uniformly dark, black or dark brown. Elytrae broadened and costate posterolaterally, creating an appearance of angulate end. Pronotum distinctly long and quadrate at the frontal margin, with no distinct serration at the edge. No conspicuous structures on the elytral declivity, such as large tubercles or strial ridges. Almost always black. The narrow and broadened elytra can be confused with those in *Planiculus* spp., but the pronotum, color (never bicolored) and other characters place the species in *Wallacella.*

Length: 2.1-2.5 mm.

Discussion

Correctly synonymized with *X. imitans* Eggers. *Xyleborus indicus subcoriaceus* (Eggers, 1927c) was separated from *X. indicus* based only on minor differences in color and body shape. Eggers (1927b) in his description of *X. imitans* mentioned its close similarity to *E. piceus* (as *X. indicus*). Beeson's (1929) illustration of his *Xyleborus samoensis* remarkably resembles *E. piceus*, suggesting that the synonymy is correct. In many collections and publications, this species is mentioned under the once-widespread name *X. indicus* Eichhoff.

Previously synonymized species: *Xyleborus indicus subcoriaceus* Eggers, *Xyleborus indicus* Eichhoff, *Xyleborus imitans* Eggers, *Xyleborus samoensis* Beeson

Biology: Species with broad distribution ranging from Africa throughout tropical Asia to Pacific Islands. It is relatively abundant throughout its range.

Examined material: Malaysia, Sabah, Danum Valley, *Artocarpus camansii* branches, (Hulcr coll., 2 indiv.); New Guinea, (BBM, 7 indiv.); New Guinea, Fiume Purari, (MCG); Sri Lanka, Montagnes de Nura-Ellia, (holotype photograph, IZM), photograph; Thailand, Pong Yaeng N. P., (Hulcr coll.); PNG: Madang Prov. (656), Oro Prov. (51), West Sepik (16), J. Hulcr 2002-2006.

Wallacella similis **comb. n. Ferrari (1867)**

J.H. database code: Scol 124

Previous genus: *Xyleborus*

Compared to holotype of *X. novaguineanus* in NHMW

Diagnosis: Similar in body shape to *Wallacella piceus*, but the pronotum is slightly shorter, elytra less parallel-sided, and the body color is always lighter, reddish brown. All examined specimens have broadened and of the first sutural interstriae on elytral declivity, and a single larger tubercle in each. Browne (1966) notes that the species varies in size between 2.0 and 2.5 mm. even within the Philippines. The color and overall body shape also strongly resemble species of *Xyleborus s. str.*, especially *Xyleborus bispinus* which also has two conspicuous tubercles on the elytral declivity. However, the subquadrate pronotum, rounded protibial edges (not triangular), and broadened and opalescent declivity distinguishes *W. similis* from *Xyleborus* spp.

Length: 2.0-2.9 mm.

Discussion

Wood (1989) included *X. dilatatulus* Schedl 1953 as a synonym. Browne (1961c) remarked that *X. parvulus* is probably just a smaller variety of *X. similis.* One of the synonyms of *W. similis* (Ferr.) is *X. ferrugineus* Boheman (Schedl, 1960h), which has no taxonomic relation to *Xyleborus ferrugineus* (Fab.).

Previously synonymized species: *Xyleborus obscurus* Schedl, *Xyleborus ferrugineus* Boheman, *Xyleborus dilatatus* Eichhoff, *Xyleborus submarginatus* Blandford, *Xyleborus bucco* Schaufuss, *Xyleborus capito* Schaufuss, *Xyleborus novaguineanus* Schedl, *Xyleborus parvulus* Eichhoff, *Xyleborus dilatatulus* Schedl

Biology: Common in both disturbed and pristine areas. Browne (1961c) mentioned that it is commonly attracted to light.

Examined material: Australia, Queensland, (BMNH); Ecuador, Pichincha, Santo Domingo, (FMNH, 2 indiv.); Malaysia, Sabah, Danum Valley, (Hulcr coll., 9 indiv.); Malaysia, Sabah, Danum Valley, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll.); New Guinea, (BBM, 10 indiv.); New Guinea, *Pterocarpus indicus* roots, (BMNH); New Guinea, (BMNH); New Guinea, (holotype of *X. novaeguinensis*, NHMW, 2 indiv.), poor labeling: "Neu. Guinea"; PNG: Madang Prov. (778), Oro Prov. (6), West Sepik (8), J. Hulcr 2002-2006.

***Wallacella striatulus* comb. n. Browne (1980)**

J.H. database code: Scol 128

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Diagnosis: *Wallacella striatulus* can be easily distinguished from other *Wallacella* by its distinctly quadrate pronotum, and by the conspicuous strial furrows and interstrial ridges covering most of declivital surface. Just as *W. similis, W. striatulus* often has the end of interstriae 1 broadened and with one or more of dominant tubercles (not always present), second interstriae with no or minute tubercles, third interstria often again with prominent tubercles.

Length: 2.5-2.6 mm.

Discussion

Browne (1980c) mentioned that the species is similar to *Xyleborus latecarinatus* (Malaysia), except that the strial impressions begin about the basal third of the elytra.

Examined material: New Guinea, East Sepik, Vanimo, (holotype, BMNH), imported to Japan (Nagoya); PNG: Madang Prov. (68), Oro Prov. (5), J. Hulcr 2002-2006.

***Wallacella timidus* comb. n. Schedl (1973)**

J.H. database code: Scol 716

Previous genus: *Xyleborus*

Compared to paratype in NHMW

Diagnosis: Light brown to yellow, middle-sized *Wallacella*. Pronotum conspicuously flat, Dryocoetina-like, quadrate from above. Declivity opaque. No prominent tubercles on top of declivity, but a long posterolateral carina bears sharp tubercles apically.

Length: 2.1-2.6 mm.

Discussion

A paratype deposited at NHMW was examined, which agrees with the photographed holotype (at AMNH). Schedl (1973f) included the species in his "Xylebori sordicaudi" group, likely solely based on the elytral declivity. He distinguished the species by its subquadrate pronotum and the long, very oblique elytral declivity. Schedl included the junior synonym of this species, *Xyleborus granulipes*, in "Xylebori granulosi". Placement of two representatives of the same species in two different groups illustrates the inconsistency of Schedl's grouping of Xyleborina.

New junior synonym(s): *Xyleborus granulipes* Schedl

Examined material: New Guinea, New Britain, Gazelle peninsula, (BBM), 900 m a.s.l.; New Guinea, Mt. Riu, (paratype, NHMW).

Genus *Webbia* Hopkins (1915)

J.H. database code: Scol 780

Type species: *Webbia dipterocarpi* Hopkins.

Redescription: Eyes deeply emarginate, sometimes almost disjunct, upper portion of eyes smaller than lower part, or as large as the lower part. Antennal club appears broader than tall, club type three (with first segment straight or convex). First segment of club straight (may be slightly concave or convex) on anterior face, margin of the first segment mostly costate, may appear softer on posterior side. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only. Third segment of club absent from the posterior side of club, or partly visible on the posterior side of club, or clearly visible on both sides of the club. First segment of antennal funicle shorter than pedicel, funicle composed of 2 or 3 segments, scapus regularly thick. Frons above epistoma mostly smooth, alutaceous, with minor punctures. Submentum deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view long, flat, bulging frontally (type B). From dorsal view prolonged and quadrate or subquadrate (type 8), or long, quadrangular (type A). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous. Tuft on pronotal basis associated with mesonotal mycangium absent, but setae on elytral bases associated with elytral mycangium present. Scutellum not visible. Elytral bases curved, costate due to the presence of elytral mycangium. Elytral disc longer than declivity, flat, punctures on elytral disc in strial lines (which may be difficult to discern). Lateral profile of elytral declivity truncated, sometimes with costa or carina on the edge, or truncated, with teeth or ridges on the edge, dorsal profile of elytral end truncated. Elytral declivity with few setae or scales, not conspicuously pubescent. Circumdeclivital costa reaching beyond 5th interstriae, encircling most or all of declivity. In the only New Guinean species W. pabo, there are tubercles on an elevated costa around declivity, and two large projections on the declivity, one in each elytron. First interstriae are parallel (sometimes slightly broadened towards elytral summit). Protibiae very slender, slightly broader only at the distal end. Posterior side of protibia inflated and granulated. Protibial denticles small, numerous, bases of the denticles not enlarged, protibial margin rounded. Metatibiae of regular size.

Color uniformly dark brown, or pronotum dark but elytra white (semitransparent), or with a whitish patch. Length: 2.1-2.4 mm.

Discussion

Due to its many derived features, the genus *Webbia*, along with *Arixyleborus*, *Schedlia* and *Cryptoxyleborus*, has been commonly treated as a representative of a separate tribe Webbini (e.g., Browne 1961c). Browne (1963) proposed 4-segmented and 3-segmented antennal funicle as the genus-specific character for *Webbia*. Schedl erected genus *Xelyborus* (*sic*) for *X. bicornis* Schedl, based on its 3-segmented funicle, but Browne observed that 3-segmented funicle is common in small species of *Webbia* and synonymized *Xelyborus* with *Webbia* (Browne, 1963). Browne (1960) separated *Prowebbia* from *Webbia* as having 5-segmented antennal funicle. Later on, Browne (1972) found the funicular segmentation to vary widely in *Webbia*, and synonymized *Prowebbia* back with *Webbia*. In *Webbia* the number of teeth on declivity can vary within species and also between two elytra in one individual (Browne, 1963).

Biology: Browne (1958) discusses specificity of representatives of this genus to trees from Dipterocarpaceae.

Figure 58: *Webbia pabo*, a typical representative of the genus. Size: 2.1 mm.

Webbia denticulatus **syn. n. Browne (1983)**

Synonymized with: *Pseudowebbia squamatilis (Schedl)*

J.H. database code: Scol 657

Previous genus: *Webbia*

Compared to holotype in BMNH

Length: 1.8-1.9 mm.

Discussion

The species belongs to *Pseudowebbia* based on the antennal club, pronotum type, body vestiture, etc., and is identical to the holotype of *P. squamatilis* in all details, including antennal club, body vestiture, and the shape and distribution of conical scales on the elytral declivity. According to Browne (1983b), it is related to *Webbia trigintaspinatus* (Sampson) from continental Asia, but is smaller.

Biology: Reported from West Papua by Browne (1983b).

Examined material: Indonesia, West Papua, (holotype, BMNH).

***Webbia pabo* Sampson (1922)**

J.H. database code: Scol 314

Compared to holotype in BMNH

Diagnosis: The characters distinguishing this species (and the locally monotypic genus) from other Xyleborina is the pronotum, elytral mycangia, and the elytral declivity. The pronotum is inflated anterolaterally, which results in a quadrate appearance dorsally, and has extremely extended pronotal disc. The presence in mycangial opening in elytral bases resulted in the absence of scutellum and the elytral bases being costate and rounded, convex. The elytral declivity is abruptly truncated, mostly flat, with a pair of long pointed projections at lateral-lower edges. These projections vary greatly in shape (e.g., they often have a small downward spine in the second third of this projection, such as in the type specimen, or are long, slender and simple, or short and robust). The very tip of elytra bear additional pair of small pointed projections/spines.

Length: 2.1-2.4 mm.

Discussion

The only *Webbia* species confirmed from New Guinea. The elytral declivity of *W. pabo* varies greatly across collections and localities, from a form with simple and long processes, to one with thick, branching spines (USNM specimens identified by S. L. Wood). Coloration of the species varies perhaps even more, from bicolored specimens with whitish semitransparent elytra, to almost completely black ones. Several authors described large numbers of dubious species based solely on deviations of the posterolateral elytral processes. Since the spines are a greatly plastic feature which varies from locality to locality (often bifurcating more laterally, more curved, flat, the bottom spines further apart, etc.), it cannot be used as a sole indication of species boundaries. These species are considered junior synonyms of *W. pabo* Sampson, but could not be officially synonymized here, as we did not have access to the holotypes or series. Specimens with more pronounced secondary spines on the main spines are often identified as *W. picicauda* Schedl. In NHMW, the following species are deposited which may be synonymized in the future: *W. platypoides* Eggers, *W. obtusispinosus* Schedl, *W. biformis* Browne, *W. piscecauda* Browne, *W. diversicauda*. Browne (1960) treated the few species similar to *W. pabo* as the "pabo group", in which he included *W. piscecauda*, *W. pabo*, *W. platypoides*, *W. biformis*, *W. obtusispinosus*. The only differences among the species were the size, shape and extent of bifurcation of the declivital processes. *W. pabo* was said to have the simplest, non-bifurcate, subparallel processes (Browne, 1960).

New junior synonym(s): *Webbia quadricinctus* Schedl

Biology: Unlike other *Webbia* species which are almost uniformly specialized on Dipterocarpaceae, species of the *Webbia* pabo group are known to colonize Fagaceae (Browne 1960, Hulcr, unpubl.).

Examined material: India, Kheri Lakhimpur, (holotype, BMNH); New Guinea, Morobe Province, Bulolo, (B. H. Jordal, 2 indiv.); New Guinea, Morobe, (FICB, 4 indiv.); New Guinea, Morobe Province, Bulolo, (MSUC, 2 indiv.); New Guinea, Morobe Province, Bulolo, (compared to holotype, MSUC); PNG: Oro Prov. (4), J. Hulcr 2002-2006.

***Webbia quadricinctus* syn. n. Schedl (1972)**

Synonymized with: *Webbia pabo Sampson*

J.H. database code: Scol 660

Compared to paratype in FICB and BBM

Discussion

Wood & Bright (1992) indicated that the holotype is deposited in ANIC however this could not be confirmed by the museum staff. *Webbia pabo* displays a large variation of posterolateral elytral processes and body coloration. The putative *W. quadricinctus* fits comfortably within this variation with the spines branching at the end by a small denticle, but this character is variable even within the several *W. quadricinctus* examined here.

Examined material: New Guinea, Morobe, (FICB); New Guinea, Morobe, Wau, (paratype, NHMW).

Genus *Xyleborinus* Reitter (1913)

J.H. database code: Scol 782

Type species: *Xyleborinus* (*Bostrichus*) *saxeseni* (Ratzeburg).

Redescription: Eyes deeply emarginate, upper portion of eyes smaller than lower part. Antennal club taller than wide, club type one (truncated, first segment covering posterior side), or two (obliquely truncated, second segment visible on posterior side). First segment of club circular around the club, covering most of the posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club narrow, pubescent, visible on the anterior side only, or visible on both sides of the club, but soft, or the corneous part on the anterior side only. Third segment of club absent from the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view prolonged, with low summit (type 7). From dorsal view it has prolonged basic shape with rounded frontal margin (type 7). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process short, conical or flat, inconspicuous, or tall and pointed, or conical and slightly inflated. Tuft on pronotal basis associated with mesonotal mycangium absent, but elytral bases bear dense tuft of setae around the small conical scutellum, associated with elytral mycangium present. Elytral bases mostly straight, curved around the scutellum due to the presence of elytral mycangium. Elytral disc longer than declivity, flat, punctures on elytral disc in strial lines. Boundary between elytral disc and declivity distinct, or sometimes indistinct when the disc is rounded and smoothly transitioning into declivity. Lateral profile of elytral declivity mildly flat or rounded, or steep, especially towards the apex, or slowly descending, often flat. dorsal profile of elytral end rounded, or prolonged apically, attenuated or angulate. Elytral declivity covered with few sparse setae. Circumdeclivital costa absent or indefinable, or very short. The inner part of declivity has no tubercles in interstria 2, and several tubercles in interstriae 1, 3 and beyond; there may be exceptions. Tubercles in interstriae 1 sometimes absent, or present as minor granules. First interstriae are parallel on disc but broadened towards the apex of elytra, where they sometime bear tubercles. Protibiae obliquely triangular, broadest in 2/3 of the length. Posterior side of protibia flat, with setae only. Protibial denticles small, or large, distinctly longer than wide, bases of the denticles not enlarged, protibial margin rounded, fewer than 6 protibial denticles present. Metatibiae of regular size. Color uniformly light brown, or uniformly dark brown, or uniformly black; pronotum sometimes slightly lighter. Usually minute species, length: 1.4-2 mm., length beyond 2 mm. is rare.

Discussion

Reitter (1913a) did not provide description of the genus *per se*, but defined the genus by re-describing two species, *X. saxeseni* and *X. angustatus*. No generic characters were provided. The classification of species of *Xyleborinus* is an epitome of the difficulties encountered in Xyleborina classification. Most oriental *Xyleborinus* share identical morphology. The morphological differences are all continuous, and in characters that are known to be extremely variable in Xyleborina. At this time however, extensive synonymizing would be unwarranted, since some of the morphological differences, which may be considered minute, are accompanied by major ecological differences. For example, *Xyleborinus artestriatus* and *X. saxeseni* do not have any clear distinguishing differences beyond vague dissimilarity in body shape and elytral tubercles, and their identification requires direct comparison of specimens. Ecologically however, the species are very different. *X. artestriatus* is a rather rare species confined to the tropics of SE Asia and the highlands of New Guinea, while *X. saxeseni* is a temperate species (i.e., adapted to freezing) and is one of the most widespread invasive beetles worldwide. On the other hand, there is a significant intraspecific variation in the common *X. andrewesi* and *X. exiguus* throughout the Paleotropics. This includes differences in size (nearly double), coloration, elytral shape, and so on. There are no known ecological or molecular features corresponding to these dissimilarities, and many forms seem to occur sympatrically. The species definitions and the key given in this work should be considered preliminary, pending a study that includes more molecular and biogeographical data to delimit natural groups. In this work we decided for the most conservative solution - to synonymize species in which intraspecific morphological variability does not allow reliable identification, and retain species which are identifiable.

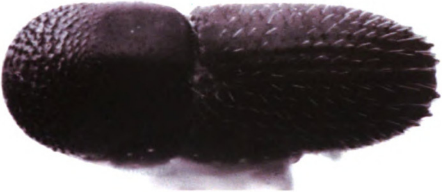

Figure 59: *Xyleborinus exiguus*, a typical representative of the genus. Size: 1.5 mm.

***Xyleborinus andrewesi* (Blandford, 1896)**

J.H. database code: Scol 35

Compared to holotype in BMNH

Diagnosis: The most conspicuous character of the species is the long, tapering elytral end with straight sides. The length and shape of the attenuated abdomen is greatly variable in this species, with large differences between populations even within New Guinea, and with many intermediates between *X. andrewesi* and *X. exiguus*. Declivity shagreen, the extent of shagreen is variable - from confined to the apical portion of declivity in PNG highlands representatives, to spanning almost all upper surface of elytra from the apex almost to the base in some lowland or SE Asian specimens. Body usually black, sometimes with lighter colored pronotum, to yellow pronotal sides in specimens from Borneo.

Length: 1.7-2.2 mm.

Discussion

The type specimen is not very representative of the species; rather, it resembles *X. exiguus*. It has few and small teeth on declivity, which is rounded rather than tapering. The body length and especially the length of the tapering part of elytra is an extraordinarily plastic character in this species. Much of the variation seems to be attributable to altitude. Increase in size with altitude is a very common phenomenon in Xyleborina. We confirmed the synonymies of *Cryptoxyleborus gracilior* Browne and *Xyleborus persphenos* Schedl (Wood 1989, Beaver 1995). Blandford (1896) related the species to *Xyleborinus exiguus*, and noted the differences in the elytral declivity.

Previously synonymized species: *Cryptoxyleborus gracilior* Browne, *Xyleborus insolitus* Bright, *Xyleborus persphenos* Schedl

Biology: Uncommon, but with large area of occurrence throughout the Paleotropics.

Examined material: India, Belgaum, (holotype, BMNH); India, Kerala, Munnar, (FMNH, 3 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 3 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 7 indiv.); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll.); New Guinea, Morobe Province, Bulolo, Antiaris, (FICB); New Guinea, Morobe Province, Bulolo, Cryptocaria trunk, (FICB); Thailand, Pong Yaeng N. P., (Hulcr coll.), R. A. Beaver det.; Thailand, Pong Yaeng N. P., (Hulcr coll., 4 indiv.), R. A. Beaver det.; PNG: Chimbu Prov. (1), Madang Prov. (229), Oro Prov. (9), West Sepik (2), J. Hulcr 2002-2006.

Xyleborinus ankius **syn. n. (Schedl, 1975)**

Synonymized with: *Xyleborinus exiguus (Walker)*

J.H. database code: Scol 664

Compared to holotype in NHMW

Length: 2.0 mm.

Discussion

Schedl (1971c) separated *X. perexiguus* from *X. exiguus* based primarily on its smaller size, and he indicated that the smaller form is distributed East of the continental SE Asia. Later, Schedl (1975f) separated New Guinean *X. ankius* from *X. exiguus* based on its larger size, among other characters. As far as it is known, only one specimen has ever been identified as *X. ankius*. *X. exiguus* displays characteristic size variation in all areas, including those east of the Orient, but Schedl, did not recognize thisintraspecific variability.The larger size of the specimen from higher elevation (*X. ankius*) as compared to specimens from lowlands (*X. exiguus s. str.*) is in fact congruent with the same pattern of altitudinal size increase seen in other Xyleborina, and yields support to the hypothesis that the phenomenon occurs throughout the whole subtribe. The other two characters that

Schedl (1975f) mentioned as different between *Xyleborinus exiguus* and *X. ankius* was the less cuneiform elytral apex and the slightly longer slender spines on the apical margin of elytra of the latter species. Examination of the two characters in individuals of *X. exiguus* from multiple regions revealed that the two characters are some of the most variable in this taxonomic entity, and thus are not considered decisive. Interestingly, the holotype of *X. ankius* being larger and slightly stouter than most *X. exiguus*, almost resembles some specimens identified as *Xyleborinus artestriatus.* The only difference between these two species is the slightly smaller size of *X. ankius*, and its more pronounced and pointed declivital tubercles.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

***Xyleborinus artestriatus* (Eichhoff, 1878)**

J.H. database code: Scol 665

Compared to neotype in NHMW

Diagnosis: Species of unclear validity. According to our analysis it cannot be reliably distinguished from other New Guinean *Xyleborinus* by any other characters except for body proportions, and sometimes by pronotal disc surface and the approximate elytral end shape. The species lies on the gradient of morphological variation between *X. saxeseni* and *X. exiguus* (especially the larger montane form of *X. exiguus* originally described as *X. ankius*). It is larger than *X. exiguus* (2.35-2.58 mm. compared to 1.45-2.01 mm.), and bulkier than *X. saxeseni* (elytral l/w ratio 1.44-1.53 compared to 1.68-1.81). Furthermore, many specimens have less pronounced tubercles on declivity and less acuminate elytral end than *X. exiguus*, and more rounded, rather than parallel elytral sides at the posterior half, but these characters are subject to much variation. It is possible that many similar *Xyleborinus* spp. are a single polyphyletic clade with variable body proportions. Individuals of *X. saxeseni* seen by the authors also have minutely alutaceous surface of pronotal disc, while the disc in *X. artestriatus* seems to always shine, but the universality of this character is unclear.

Length: 2.35-2.58 mm.

Previously synonymized species: *Xyleborus rugipennis* Schedl, *Xyleborus laticollis* Blandford

Examined material: Indonesia, Java, (neotype, NHMW); New Guinea, Umboi, (BBM); New Guinea, Hula River, (BBM); New Guinea, Oriomo, (BBM, 2 indiv.); New Guinea, Umboi-Awelkom, (BBM); New Guinea, Morobe, Wau, (BBM, 4 indiv.); New Guinea, (FICB); Thailand, Pong Yaeng N. P., (Hulcr coll., 3 indiv.), R. A. Beaver det.

***Xyleborinus exiguus* (Walker, 1859)**

J.H. database code: Scol 436

Compared to holotype in BMNH

Diagnosis: *X. exiguus* can be distinguished from the similarly shaped *X. artestriatus* by smaller body length (no more than 2.01 mm.), by the alutaceous surface of pronotal disc, and occasionally by flattened and semi-translucent tubercles at the apex of the circumdeclivital costa on each elytron, but this character varies. From the smaller *X. perpusillus* it can be distinguished by body length mostly exceeding 1.5 mm., and by bulkier body shape (elytral l/w ratio at most 1.68, versus 1.80 in *X. perpusillus*). From all other species it can be distinguished by the less rounded, more acuminate elytral apex (but it is evenly rounded in some individuals), however it is not as extended as in *X. andrewesi*. The narrowness of elytral apex is a continuous gradient from rounded elytra (*X. saxeseni*, *X. artestriatus*, *X. perpusillus*) through slightly acuminate (*X. exiguus*) to conspicuously acuminate, almost pointed in *X. andrewesi*; many intermediates can be found between all forms.

Length: 1.45-2.01 mm.

Previously synonymized species: *Xyleborus muriceus* Eichhoff

New junior synonym(s): *Xyleborinus perexiguus* (Schedl), *Xyleborinus ankius* (Schedl)

Biology: Probably the most common species of *Xyleborinus* in the Paleotropics, certainly so in New Guinea.

Examined material: Malaysia, Sabah, Danum Valley, *Ficus* sp. trunk, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll.); New Guinea, Morobe, Wau, (BBM), identified as *X. exiguus* by Schedl; New Guinea, Madang, Karkar Island, Muluk, (FICB); New Guinea, (FICB); Sri Lanka, (holotype, BMNH); Thailand, Pong Yaeng N. P., (Hulcr coll., 2 indiv.), R. A. Beaver det.

Xyleborinus perexiguus syn. n. (Schedl, 1971)

Synonymized with: _Xyleborinus exiguus_ (Walker)

J.H. database code: Scol 31

Compared to holotype in NHMW

Length: 1.6 mm.

Discussion

Schedl (1971c) mentioned that the species was separated from *X. exiguus* by Eggers, but the species designation had not been published. Schedl (1971c) officially described the new species. From the description, two putative differences can be inferred: *X. perexiguus* has elytra as long as pronotum, and the overall length is between 1.5 - 1.6 mm. (Holotype: 1.6 mm long, 0.55 mm. wide.) Schedl mentioned that *X. perexiguus* occurs in New Guinea, Australia, Philippines and Pacific Islands, while *X. exiguus* occupies regions to the West. However, he also points out that *X. perexiguus* occurs in Java and Timor Islands. We uncovered significant size variation with closer examination of *X. exiguus s. l.* (with specimens identified as *X. perexiguus*, including the holotype) across the Paleotropics (Figure 60). Body length of *X. exiguus* varies between 1.41 mm. to 2.01 mm. (over 2,600 individuals from PNG seen, plus 9 individuals from elsewhere). Most of the smaller specimens originated in PNG lowlands, while those in PNG Highlands tend to be the longest. Representatives from other areas are very variable. Because most of the variation can occur within a single locality, while there is no East-West gradient, and because the variation is entirely continuous, *X. exiguus* and *X. perexiguus* cannot be distinguished based on body size.

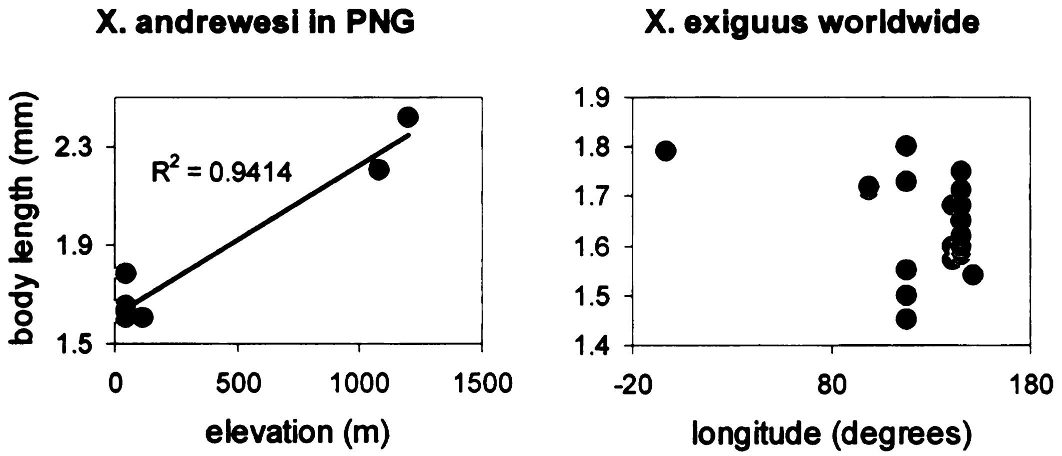

Figure 60: Size variation in *Xyleborinus* spp. In *Xyleborinus andrewesi*, where individuals from multiple elevations within PNG were available, it is clear that body length increases dramatically with altitude (*n* = 7, R2 = 0.94). On the other hand, there is no East-West gradient of body length in *Xyleborinus exiguus s. l.* (including *X. perexiguus*), the entire span of length variation can occur within a single locality (n = 23, no correlation).

The increase in size with altitude is almost uniform across most Xyleborina, and the same could have been expected in *Xyleborinus exiguus*. Indeed, one larger form of *X. exiguus* from PNG Highlands (Bulolo, Morobe province) has been found and confirmed the hypothesis (see, *X. ankius*). The variability of individual features of declivity of *X. exiguus* is equally broad, although apparent only upon detailed examination. The biogeographical significance of these characters, or their correlation with genetic distances, is unknown, but does not support the division between *X. perexiguus* and *X. exiguus s. str.* according to Schedl (1971c). In fact, the intraspecific variation in *X.*

exiguus is so great that there may be more differences among specimens currently identified as *X. exiguus* from different regions, than between similar specimens identified either as *X. exiguus* and *X. andrewesi*. Although the holotypes and average specimens are clearly different, there is an intergradation in the main difference - the acuminate elytral apex in *X. andrewesi*. On the other hand, many representatives identifiable as *X. exiguus* from Africa, SE Asia and New Guinea differ in the absence, presence, and extent of the shagreened surface of declivity, in the shape and sharpness of tubercles, in whether or not tubercles are present in the 2nd interstria, and so on.

Examined material: Malaysia, Sabah, Danum Valley, *Artocarpus camansii* branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Mallotus sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll., 3 indiv.); Malaysia, Sabah, Danum Valley, *Ficus* sp. trunk, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* trunk, (Hulcr coll.); New Guinea, Madang Province, Ohu, *Gymnacranthera paniculata* trunk, (Hulcr coll.); Philippines, Luzon, Tayabas, (holotype, NHMW); PNG: Madang Prov. (2608), Oro Prov. (62), West Sepik (20), J. Hulcr 2002-2006.

Xyleborinus perpusillus **(Eggers, 1927)**

J.H. database code: Scol 376

Compared to holotype in USNM

Diagnosis: Similar to *Xyleborinus exiguus*, but the teeth around declivital apex are further apart. Declivity steeper. From Popondetta - 1.5 mm. Unlike *Microperus recidens*, *X.*

perpusillus does not have a costa below elytral declivity, but does have a miniature knob-like scutellum.

Length: 1.5 mm.

Discussion

Many representatives of *X. perpusillus* resemble *X. exiguus*. Given the large but not fully explored intraspecific variability in *X. exiguus*, it is as yet impossible to decide if *X. perpusillus* is a unique entity, or a collection of smaller representatives of *X. exiguus*.

Previously synonymized species: *Xyleborus angustatulus* Schedl

Biology: Borneo. Complex flat chamber. The species is widely distributed - the type specimen was collected on Java (by L. G. E. Kalshoven), while I have specimens from Borneo and Papua New Guinea.

Examined material: Indonesia, Sumatra, (holotype); Malaysia, Sarawak, Gunung Buda, (R. A. Beaver det., UCD); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 10 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, Artocarpus camansii branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll., 3 indiv.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 12 indiv.); PNG: Oro Prov. (5), J. Hulcr 2002-2006.

***Xyleborinus saxeseni* (Ratzeburg, 1837)**

J.H. database code: Scol 589

Diagnosis: Shagreen declivity, interstriae 2 impressed. It is difficult to distinguish from *Xyleborinus artestriatus*. Individuals of *X. saxeseni* seen by the author also have minutely alutaceous surface of pronotal disc, while the disc in *X. artestriatus* seems to be mostly shining, but the universality of this character is unclear.

Length: 2.2 mm.

Previously synonymized species: *Xyleborus sobrinus* Eichhoff, *Xyleborus pseudogracilis* Schedl, *Xyleborus librocedri* Swaine, *Xyleborus tsugae* Swaine, *Xyleborus subspinosus* Eggers, *Xyleborus arbuti* Hopkins, *Xyleborus quercus* Hopkins, *Xyleborus pecanus* Hopkins, *Xyleborus floridensis* Hopkins, *Xyleborus subdepressus* Rey, *Xyleborus pseudoangustatus* Schedl, *Xyleborus aesculi* Ferrari, *Xyleborus angustatus* Eichhoff, *Xyleborus decolor* Boieldieu, *Xyleborus dohrni* Wollaston, *Xyleborus frigidus* Blackburn, *Xyleborus retrusus* Schedl, *Xyleborus peregrinus* Eggers, *Xyleborus cinctipennis* Schedl, *Xyleborus paraguayensis* Schedl

Biology: The species is found in neighboring temperate regions, such as Australia (Schedl 1964i, 1968g) or New Caledonia (Hulcr & Mille, unpubl.). Wood & Bright (1992) indicate that the species has been recorded from New Guinea, but the we could not confirm the original record. Given the typical temperate distribution of this species, and given the fact that it is extremely similar to other species from New Guinea, it is possible that the record resulted from a misidentification.

Examined material: USA, MI, Cassopolis, light trap, (Hulcr coll. 2007); USA, Michigan, Lansing, (Hulcr coll. 2007); USA, MI, Minden City State Game Area, Hulcr coll. 2007); USA, MD, Patuxent, *Acer rubrum*, (Hulcr coll. 2007); USA, MD, Patuxent Park, *Liquidambar*, (Hulcr coll. 2007, 32 indiv.).

Genus *Xyleborus* Eichhoff (1864)

J.H. database code: Scol 781

Type species: *Xyleborus* (*Bostrichus*) *monographus* (Fabricius).

Redescription: Eyes shallowly or deeply emarginate, upper portion of eyes smaller than lower part. Antennal club more-less circular shape, club type two (obliquely truncated, the pubescent second segment slightly visible on posterior side). First segment of club circular around the club, covering most of the posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club visible on both sides of the club, but soft, or the corneous part on the anterior side only. Third segment of club absent or partly visible on the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick. Frons above epistoma rugged, coarsely punctate. Submentum deeply impressed, shaped as a narrow slit, or a narrow triangle. Anterior edge of pronotum with no conspicuous row of serrations (serrations don't differ from those on the pronotal slope). Pronotum from lateral view of basic shape (type 0), or prolonged, with low summit (type 7). From dorsal view it is basic, short, parallel-sided, rounded frontally (type 2). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum obliquely costate. Procoxae contiguous, prosternal posterocoxal process bulging, rounded, not pointed. *Xyleborus* s. str. have mandibular mycangia; there is no tuft on the pronotal basis associated with mesonotal mycangium absent, and there are no setae on elytral bases associated with elytral mycangium. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity, flat; elytral disc has distinct lines of strial punctures. Lateral profile of elytral declivity mildly flat or rounded, or steep, especially towards the apex, dorsal profile of elytral end rounded, not broadened posterolateraly. Elytral declivity with few setae, not conspicuously pubescent. Circumdeclivital costa absent or indefinable, or very short. The inner part of declivity has no tubercles in interstria 2, and several tubercles in interstriae 1, 3 and beyond. Sometimes tubercles in interstriae 1 are absent, or present as minor granules, tubercles in interstriae 3 are almost always distinct. First interstriae are parallel (sometimes slightly broadened towards elytral summit), or parallel on disc but broadened towards the apex of elytra, where they sometime bear tubercles. Protibiae obliquely triangular, broadest in 2/3 of the length, or distinctly triangular, slender on the upper part, broad and denticulate on the lower part. Posterior side of protibia flat, with setae only. Protibial denticles large, distinctly longer than wide, bases of the denticles slightly elevated, or distinctly enlarged, conical; fewer than 6 protibial denticles present. Metatibiae of regular size. Color uniformly light brown or reddish (pronotum sometimes slightly lighter), or uniformly dark brown, never black. Length: 2.1-3 mm.

Discussion

Xyleborus is the most speciose Xyleborina genus. This is a polyphyletic genus but cladistic analysis identified synapomorphies and a unique combination of homoplastic characters, that suggests monophyly for a subset of species, *Xyleborus* s. str (Figure 21). However, many species whose placement remain uncertain or unstudied are currently placed in *Xyleborus* (i. e., *Xyleborus* s. l., below). Admittedly, there are few synapomorphies of *Xyleborus s. str.*, among them is for example the bulging, globular or almost cubical prosternal posterocoxal process.

Previously synonymized genera: *Phloeotrogus* Motschulski, *Anaeretus* Duges, *Progenius* Blandford, *Mesoscolytus* Broun, *Eurydactylus* Hagedorn, *Heteroborips* Reitter, *Notoxyleborus* Schedl, *Xyleborips* Reitter, *Xelyborus* Schedl, *Terminalinus* Hopkins, *Boroxylon* Hopkins.

Figure 61: *Xyleborus perforans*, a typical representative of the genus and the most common ambrosia beetle in New Guinea. Size: 2.6 mm.

Xyleborus s. str. affinis **Eichhoff (1868)**

J.H. database code: Scol 127

Compared to cotype in USNM

Diagnosis: Very similar to *Xyleborus perforans*, the most decisive identification character being the dull (shagreen) elytral declivity. *X. affinis* is also often slightly smaller, and has much smaller tubercles on the declivity. If specimens are submerged in ethanol, the dull surface of the declivity is not apparent and the two species are indistinguishable.

Misidentifications are frequent in collections worldwide, especially when made by early taxonomists (Beeson 1929).

Length: 2.4 mm.

Discussion

Although in other genera or species complexes, a character such as declivity surface dullness would be considered a matter of intraspecific variation, in *X. affinis* this character may indeed delimit consistent genetic lineage (Jordal, pers. comm.). On the other hand, our molecular analysis (Cognato et al., 2009) does not support *X. affinis* and *X. perforans* as independent clades.

Previously synonymized species: *Xyleborus proximus* Eggers, *Xyleborus societatis* Beeson, *Xyleborus subaffinis* Eggers, *Xyleborus sacchari* Hopkins, *Xyleborus affinis fuscobrunneus* Eichhoff, *Xyleborus affinis mascarensis* Eichhoff, *Xyleborus affinis parvus* Eichhoff, *Xyleborus mascarensis* Eggers, *Xyleborus beta-mascarensis*, *Xyleborus alpha-parvus*, *Xyleborus gamma-fusco-brunneus* Eichhoff

Examined material: Ecuador, Pichincha, Santo Domingo, (FMNH, 3 indiv.); Ghana, Bia NP, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Ficus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll., 9 indiv.); Malaysia, Sabah, Danum Valley, *Ficus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Ficus* sp. trunk, (Hulcr coll., 14 indiv.); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* trunk, (Hulcr coll., 3 indiv.); Nearctic, (co-type, USNM); New Guinea, (Zhu Hongbin, Chinese

Port Quarantine, 2 indiv.); New Guinea, (Zhu Hongbin, Chinese Port Quarantine, 2 indiv.); New Guinea, (Zhu Hongbin, Chinese Port Quarantine, 2 indiv.); PNG: Madang Prov. (1405), Oro Prov. (174), West Sepik (210), J. Hulcr 2002-2006.

Xyleborus s. str. bispinatus **Eichhoff (1868)**

J.H. database code: Scol 81

Compared to paralectotype in UZMC

Diagnosis: Declivity flat, shining, with a conspicuous tubercle in each interstria 3, near the middle of the declivital slope. Usually larger than most *X. perforans*, but the ranges of body size overlap in the two species. Red to red-brown color, unlike yellow to light brown in most *Xyleborus s. str*.

Length: 2.2-3.0 mm.

Discussion

Until recently, this very common circumtropical species has been almost universally identified as *X. ferrugineus* Fabricius by most taxonomists. Recently however, Kirkendall and Jordal (2006) reanalyzed the lectotype of *X. bispinatus* and *X. ferrugineus*. So far as it is known, the pantropical species usually mistakenly identified as *X. ferrugineus*, which is also very common in Papua New Guinea, is *X. bispinatus*, while *X. ferrugineus* is likely confined to the Neotropics. Distinguishing characters of the two species are given in Kirkendall and Jordal (2006). *X. bispinatus* was not described by Eichhoff in 1968, as reported by Wood & Bright (1992), but in 1987. Kirkendall and Jordal (2006) designated a lectotype of *X. bispinatus* from the original Eichhoff series of syntypes.The Neotropical species, *X. impressus* Eichhoff, may be confused with *X. bispinatus* and *X. ferrugineus*. Rabaglia et al. (2006) provided distinguishing characters for this species.

Many species have been synonymized with *X. ferrugineus*, however several of these species should have been synonymized with *X. bispinatus*. We could only confirm the synonymy of *X. notatus* Eggers with comparison of the lectotype. Beaver (1991) included *X. nesianus* Beeson. The rest await confirmation.

Eichhoff (1867) described *X. confusus*, which was later synonymized with *X. ferrugineus* (Schedl 1957d). The series of syntypes of *X. confusus* Eichhoff was examined. It is a series of slightly variable individuals without doubt belonging to *X. bispinatus*, rather than to *X. ferrugineus*.

Schedl (1960h) described appreciable variation of body size (2.1 - 3.0 mm.) and declivital sculpturing in what he called *X. ferrugineus* from Africa. *Xyleborus* (as *Bostrichus*) *ferrugineus* (Boheman) is a synonym of *Wallacella similis* Ferr. (orig. *Xyleborus*; Schedl, 1960h).

Biology: Widespread, common even on isolated islands such as Madagascar or Hawaii (Schedl 1942b).

Examined material: Congo Belge, (syntype, IRSNB); Ecuador, Pichincha, Santo Domingo, (FMNH, 5 indiv.); Guyana, Essequibo, (paralectotypes of *X. ferrugineus* Eggers, 6 indiv.); Panama, Barro Colorado, (UCD), confirmed *X. bispinatus*; Taiti (Haiti?), (syntype, IRSNB); Venezuela, Caracas, (syntype, IRSNB, 4 indiv.); Venezuela, Cumana(?), (syntype, IRSNB, 2 indiv.); PNG: Madang Prov. (117), West Sepik (7), J. Hulcr 2002-2006.

***Xyleborus s. str. devexipennis* sp. n. Hulcr & Cognato**

J.H. database code: Scol 280

Compared to holotype in USNM

Diagnosis: Superficially, the species resembles *X. perforans*. The main distinguishing characters from this and other *Xyleborus s. str.* are the antennae type 2 with straight or convex 1st segment and a narrow stripe of corneous surface of segment 2; slightly prolonged pronotal disc, markedly steep elytral declivity, broadened interstria 1 towards the abdominal apex, and the very short declivital costa, substituted laterally by blunt edge with granules.

Description: Antennal scapus short and robust, first segment of funicle short, conical; antennal club type 2 (first segment dominant, straight or slightly convex, second and third segments soft, pubescent, second segment sometimes with narrow corneous carina).Eyes medium to large compared to other Xyleborina, emarginate. Submentum impressed, submental sutures forming a narrow strip around hypostomal ridge. Pronotum rounded frontally when viewed from top; no bulging sides, pronotal summit low and pronotal disc slightly longer than the frontal slope. Pronotal anterior edge without any conspicuous serrations, pronotal disc shining, sparsely punctate. Protibiae flat, triangular, with 6 robust socketed denticles with slightly enlarged sockets. Procoxae contiguous, posterocoxal prosternal process bulging. No mycangial opening between pronotum and mesonotum, neither in the elytral edges. Scutellum or regular size, triangular shape, flush with surface. Elytra with regular rows of shallow punctures. No hair on elytral disc, sparse erect setae on elytral declivity. Declivity steep, interstriae 1 broadened towards the and of declivity, with two pairs of prominent tubercles. A small tubercle in the 2nd interstria on the top of declivity, more tubercles in interstria 3 and beyond. End of declivity rounded. Posterolateral costa short, largely supplanted by several unorganized tubercles.

Length: 2.5 mm.

Etymology: the name refers to the steep elytral declivity.

Discussion

The antennae of type 2, prolonged pronotal disc, and the enlarged interstria 1 on elytral declivity suggest alternative placement of this species in *Emarginatus* gen. n. However, the elytral apex is not emarginate. *Emarginatus dolosus*, is a similar species which is smaller, has broader and longer posterolateral sides of declivity, and thus appears slightly emarginate.

Holotype deposited in USNM, paratype in MSUC.

Examined material: New Guinea, Oro Province, Popondetta, (BBM); PNG: West Sepik (2), J. Hulcr 2002-2006.

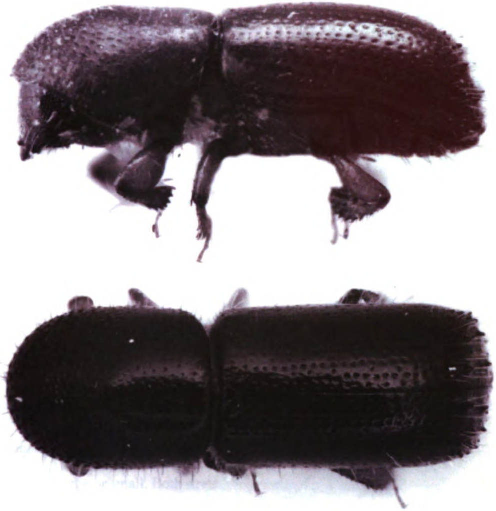

Figure 62: *Xyleborus devexipennis sp. n.* Size: 2.5 mm.

Figure 63: *Xyleborus devexipennis sp. n.*, steep elytral declivity with broadened interstriae 1 apically.

***Xyleborus s. str. perforans* Wollaston (1857)**

J.H. database code: Scol 23

Compared to syntypes in BMNH

Diagnosis: Declivity convex, not flattened. Tubercles on declivity varied, from uniform to unevenly large or small. Both striae 1 and 3 (not 2) have several tubercles each. Pale color, dark yellow to light brown. Declivital surface shining, not dull (visible when dry).

Length: 2.1-2.8 mm.

Discussion

Differences between *X. perforans, X. cognatus, X. volvulus, X. pfeili* and many other species are unclear. Due to the extreme circumtropical abundance of *X. perforans s. l.*, and the paucity and variability of morphological characters, a comprehensive molecular phylogenetic analysis is needed to resolve the uncertainties in the *X. perforans* group. We confirmed the synonymiesof *X. minimus* Schedl and *X. testaceus* Walker with *X.*

perforans. The case of *X. testaceus* is another example of the confusion between *X. perforans* and *X. cognatus*. Two individuals on the same point represent the holotype of *X. testaceus:* one is of the typical *X. perforans* morphology, and the other is larger, similar to the holotype of *X. cognatus*. *X. parvipunctatus* Eggers from South America also appears to be a synonym of *X. perforans*. Beeson (1929) mentioned that *X. buxtoni* Beeson differs from *X. perforans* in size and the tubercles on declivity, but he also mentions considerable variation in the relative position of the declivital tubercles. According to Beeson's illustration, it certainly falls within the variation in the *X. cognatus-X. perforans* complex (holotype not examined). Eggers' collection in USNM includes a few species not listed by Wood & Bright (1992), which should be synonymized with *X. perforans*: X. *zahntneri* Eggers, *X. brunneus* Eggers, *X. indonesus* Eggers. However, official descriptions of these species have not been located, and the names may be invalid.

Previously synonymized species: *Xyleborus minimus* Schedl, *Xyleborus cylindrus* Schedl, *Xyleborus apertus* Schedl, *Xyleborus testaceus* Walker, *Xyleborus duponti* Montrouzier, *Anodius tuberculatus* Motschulsky, *Xyleborus kraatzi philippinensis* Eichhoff, *Xylopertha hirsutus* Lea, *Xyleborus whitteni* Beeson, *Xyleborus criticus* Schedl, *Xyleborus kraatzi* Eichhoff, *Anodius denticulus* Motschulsky, *Xyleborus immaturus* Blackburn

New junior synonym(s): *Xyleborus cognatus* Blandford

Examined material: Malaysia, Sabah, Mt. Kinabalu, (unspecified "type", BMNH); Malaysia, Sabah, Mt. Kinabalu, (lectotype of *X. apertus* Schedl); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll., 5 indiv.); Malaysia, Sabah, Danum Valley, *Ficus* sp. trunk, (Hulcr coll., 13 indiv.); Malaysia, Sabah, Danum Valley, Parashorea malaanonan trunk, (Hulcr coll.); New Guinea, Madang Province, Baiteta, (IRSNB); New Guinea, Madang Province, Baiteta, (IRSNB); Sri Lanka, (holotype of *X. testaceus* Walker,, BMNH), both *X. perforans* and *X. cognatus* morphotypes on a pin.; PNG: Madang Prov. (25156), Oro Prov. (843), West Sepik (195), J. Hulcr 2002-2006.

***Xyleborus s. str. volvulus* Fabricius (1775)**

J.H. database code: Scol 116

Compared to lectotype in UZMC

Discussion

A species whose identity caused much confusion until recently. Given the large variation of individuals ascribed to *X. volvulus* by many taxonomists, and given the large overlap in morphological features with *X. perforans* and *X. cognatus*, it is unclear whether it is a valid species. The principal characters usually used to distinguish *X. volvulus* from similar species, namely *X. perforans*, were those that distinguish the lectotype of *X. volvulus* from the average morphology of *X. perforans*. The lectotype and three paralectotypes from Cuba have distinctly rounded, steep elytra, slightly more prominent tubercles, the apical edge of declivity almost costate. However, any series of representatives of the *X. perforans* complex from multiple localities and elevations always reveals great variation in exactly these characters (Figure 64). Beeson (1939b) remarked on large color and shape variation in what were considered subspecies or morphs of *X. volvulus*. Wood & Bright (1992) indicate that: "[*X. volvulus*] is doubtfully distinct from *X. perforans* and may intergrade with that species; reports of it from S-E

Asia to the S-W Pacific region probably refer to *X. perforans* as do many records from Africa." Without any further analysis we are unable to distinguish *X. volvulus* from *X. perforans s. str.* in samples from New Guinea. On the other hand, a combination of declivital characters congruent with molecular phylogeny of the species complex may in the future support the species concept of *X. volvulus*. Thus we do not suggest synonymizing the species without future analyses (B. Jordal, pers. comm.), but we are not recognizing the species as a distinguishable entity in New Guinea.

Previously synonymized species: *Xyleborus alternans* Eichhoff, *Xyleborus badius* Eichhoff, *Xyleborus granularis* Schedl, *Xyleborus grenadensis* Hopkins, *Xyleborus guanaguatensis* Duges, *Xyleborus hubbardi* Hopkins, *Xyleborus interstitialis* Eichhoff, *Xyleborus kraatzii* var. *philippinensis* Eichhoff, *Xyleborus rileyi* Hopkins, *Xyleborus Hopkins*, *Xyleborus silvestris* Beeson, *Xyleborus torquatus* Eichhoff, *Xyleborus vagabundus* Schedl,

Examined material: Cuba, (lectotype, UZMC, 4 indiv.); Ecuador, Pichincha, Santo Domingo, (FMNH, 3 indiv.); Ecuador, Oncon Gare, (S. Dole, 6 indiv.); PNG: Madang Prov. (275), J. Hulcr 2002-2006.

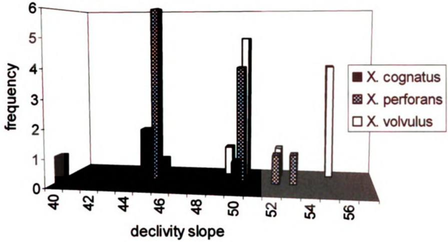

Figure 64: Histogram of morphological overlap between *Xyleborus perforans* and the putative species *Xyleborus cognatus* and *Xyleborus volvulus*. Some taxonomists distinguished *X. volvulus* and *X. perforans* by the slope of elytral declivity (measured here as the angle between the abdominal surface and the tangent in lower half of the elytral declivity, where declivity is approximately flat). This metric appears to be continually distributed, not usable for distinguishing the three species.

Genus *Xyleborus s. l.*

J.H. database code: Scol 838

Discussion

This is an unnatural group containing species with unclear placement, which were originally described as *Xyleborus*.

***Xyleborus s. l. bidentatus* (Motschulsky, 1863)**

J.H. database code: Scol 493

Compared to holotype photo in IZM

Diagnosis: Dark species, greatly variable in size, appearing rugose over most of the body. Antennae of type 2, with concave segment 1, and soft, pubescent and inconspicuous segments 2 and 3. Antennal club in some specimens conspicuously small. Eyes only shallowly emarginate, bean-shaped. Pronotal frontal edge greatly prolonged into a "hood" with prominent serrations. Pronotal disc with sparse asperities, similar as in *Ambrosiodmus* spp., disc surface varies from uniformly shagreen, to partly shining, to mostly shining. Procoxae contiguous, posterocoxal prosternal process flat to slightly inflated. Protibiae slender, abruptly broadened and triangular at the distal ends, with 6-7 small denticles. No signs of mycangial opening in mesonotum. Elytral bases with an unusual overhanging curved costa, but the no mycangial opening associated with it was be found. Scutellum of regular size. Elytral surface rugged, mostly due to broadened and somewhat irregular strial punctures. Elytrae broadest around declivity, declivity gently sloped, almost concave at the end. Interstriae 2 and 3 each with at least one large tubercle. The end of elytra characteristically protruding backwards, angulate.

Length: 3.0-4.5 mm.

Discussion

Synonymy with *Boroxylon webbi* Hopkins, *Boroxylon stephegynis* Hopkins, *Xyleborus riehli* Eggers and *X. brevidentatus* Eggers weres confirmed.

Previously synonymized species: *Boroxylon webbi* Hopkins, *Boroxylon stephegynis* Hopkins, *X. brevidentatus* Eggers, *Xyleborus riehli* Eichhoff, *Xyleborus quadridens* Eggers

New junior synonym: *Xyleborus subcostatus* Eichhoff

Biology: Widespread throughout Asia and Africa (Gray 1968), uncommon in New Guinea. Browne (1966) claims that the species inhabits primarily seashore habitats, occurring on tropical coasts throughout the Indian and South Pacific oceans.

Examined material: New Guinea, Oro, Anisoptera, (FICB), Coppock coll. 1960; New Guinea, (FICB, 2 indiv.); New Guinea, (FICB); New Guinea, Madang (IRSNB).

Xyleborus s. l. cinctipes Schedl (1979)

J.H. database code: Scol 578

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: Antennae type 3, broad, with first corneous segment straight or convex, second partly corneous, pronotum with a row of serrations on the frontal edge, slightly prolonged posteriad. No sign of mesonotal or elytral mycangia. The elytra are rounded, slowly descending, attenuated at the end. Interstriae on elytral declivity each with a dense row of sharp recurved spines, all interstriae except the first, sutural.

Two other Xyleborina in New Guinea have acuminate elytra and somewhat similar body shape - *Xyleborus metacuneolus* and *Xyleborus pileatulus* - but they do not have the distinct pointed tubercles on declivity. The three species are probably related, but may not form a strictly monophyletic group. Their placement on a phylogram (Figure 21) is not supported by all parsimonious trees. Material for molecular analysis is not available.

Length: 2.8 mm.

Discussion

Unclear generic placement. The species is missing sufficient number of synapomorphies with any other genus, its only conspicuous feature is the attenuated declivity with spines, which is largely autapomorphic. Schedl (1979g) tentatively placed the species in groups Xylebori angustati or Xylebori solitari.

Examined material: New Guinea, Morobe, Mt. Amingwiva, (FICB); New Guinea, Gulf Province, Ivimka, (compared to type, UCD).

***Xyleborus s. l. declivispinatus* comb. n. (Schedl, 1969)**

J.H. database code: Scol 254

Previous genus: *Ambrosiodmus*

Compared to paratype in FICB

Diagnosis: Unmistakable combination of large spines on declivity and the quadrate pronotum. Antenna 1 club type 2 or 3, unusually tall, the margin of the first segment is convex, second segment is also corneous on both sides of the club, third segment is soft, reduced. The upper part of eye is very small. The pronotum is rectangular in outline, bulging in its anterolateral sides to the point that its frontal edge is slightly concave. The pronotal anterior margin has a faint row of serrations (slightly removed from the edge). Protibiae are flat, their edges very broadly curved, with numerous minute denticles (13-16 in protibia). Procoxae are contiguous, posterocoxal prosternal process is inflated to bulging. No sign of mycangia in mesonotum or in elytral bases, scutellum normal, large. The elytral disc is shining, with parallel rows of conspicuous punctures. The declivity is greatly modified: strial punctures are enlarged, broadened, densely packed in the strial rows, with dense chagrenation inside. All interstriae bear sharp tubercles on the edge of declivity, Interstriae 2, 5 and 6 have other pointed tubercles in the middle of declivity, and each interstria 3 bears one large, curved spine and several smaller ones.

Length: 4.4 mm.

Discussion

The generic placement of the species is unclear. Wood (1989, 6761) synonymized *X. tectus* Schedl with this species. Schedl (1972h) described *X. tectus* without any reference to its similarity to *X. declivispinatus*. Instead, he relates it to *Coptodryas quadricostatus* (as *Xyleborus*), an unrelated species from Borneo.

Previously synonymized species: *Xyleborus tectus* Schedl

Biology: Tends to breed in extremely wet wood partly submerged in water, along streams. Found in middle elevations in Eastern New Guinea.

Examined material: New Guinea, (paratype, FICB); PNG: Oro Prov. (30), J. Hulcr 2002-2006.

Xyleborus s. l. granulosus **Schedl (1975)**

J.H. database code: Scol 303

Compared to holotype in NHMW

Diagnosis: Unmistakable quadrate pronotum, wider than long, a shape otherwise present only in males of Xyleborina. The surface of elytral declivity is sharply different from the surface of the elytral disc. Disc is shining, with small aligned strial punctures, while the declivity lack striae, is densely conspicuously dull, coriaceous and densely covered with small granules. The elytra closely resemble those of *Xylosandrus crassiusculus*.

Length: 2.9-3.2 mm.

Discussion

The species was unnecessarily synonymized with *X. partitus* Browne (Schedl 1980d). Beaver (1991) reinstated the species *X. granulosus*. *X. partitus* from Fiji is very similar (holotype examined), but in this species, the granules on elytral declivity are much larger and aligned in interstriae. The large tubercles at the apical area of elytra are larger than in *X. granulosus*. *X. granulosus* is smaller (3.2 mm.) than *X. partitus* (3.6-3.8 mm.) (Beaver 1991). The difference is confirmed here and the resurrection of the species supported. Another similar species is *X. deformatus* Browne from Fiji, with deep, saddle-like concavity at the upper chagrenated area on declivital disc.

Examined material: New Guinea, Western Highlands, Giuwe, (FICB); New Guinea, Morobe Province, Bulolo, (FICB); New Guinea, Morobe Province, Bulolo, (holotype, NHMW); PNG: Madang Prov. (6), J. Hulcr 2002-2006.

***Xyleborus* s. l. *judenkoi* comb. n. (Schedl, 1959)**

J.H. database code: Scol 249

Previous genus: *Coptodryas*

Compared to holotype in NHMW

Diagnosis: Very small species, tentatively placed in *Xyleborus* s. l. Although superficially the species resembles *Xyleborus* s. str, it has a number of decisively distinct characters: antennal club type 3, submentum nearly flat, mesosternal posterocoxal process flat, tubercles on declivity very evenly small, evenly distributed in all interstriae except 1.

Length: 1.5-1.8 mm.

Discussion

The holotype, paratypes, and other individuals compared to the holotype do not correspond to the description (Schedl 1959a), which indicated that the declivity commences in the middle of the elytral length. Wood & Bright (1992) included the species in *Coptodryas*. However, the species lacks elytral mycangia and have visible flat scutellum, albeit small thus the transfer to *Coptodryas* is not supported. Superficially, *X. judenkoi* resembles species of *Xyleborus* s. str., but its placement into the group is not supported by a number of characters (Figure 21), notably the antennal club of type 3, and the small, pointed prosternal posterocoxal process. The species is tentatively placed in *Xyleborus* s. l.

Schedl mistakenly relates the species to two species with similar declivity, which however belong to different genera: *X. nutans* (now synonymized with *Truncaudum agnatum* comb. nov.) and *X. pullus* (now *Coptodryas*). Vaguely similar is *X. minutus* from Fiji (type seen), but that has shorter and more flat pronotum, declivity slightly concave, feeble bulges on the elytral declivity, granules scattered on the upper part of declivity.

New junior synonym(s): *Xyleborus immitatrix* Schedl

Examined material: Sri Lanka, Sabargamuva, (holotype, NHMW); Sri Lanka, Sabargamuva, (paratype, NHMW, 2 indiv.); PNG: Madang Prov. (2), J. Hulcr 2002-2006.

***Xyleborus s. l. metacuneolus* Schedl (1940)**

J.H. database code: Scol 39

Previous genus: *Xyleborus*

Compared to non-type in BMNH

Redescription: Gradually tapering elytra, no tubercles or granules on elytral surface. Pronotum mildly prolonged posteriad, parallel-sided, appearing broader than the elytra. Miniature scutellum. Most specimens very lightly colored, yellow to reddish brown. The whole body densely but softly pubescent, especially the elytral declivity

Length: 2.2 mm.

Discussion

Type not in ZMA or RMNH; possibly in Kalshoven's collection in MZB.. Similar, but smaller, narrower and dark brown is *Xyleborus cuneiformis* Schedl from Malaysia.

Two other Xyleborina in New Guinea have acuminate elytra and similar body shape: *Xyleborus cinctipes* (asperate elytral surface) and *Xyleborus pileatulus* (antennal club nearly type 1, no serrations on the anterior edge of pronotum). Most characters in the three similar species are also similar to those of *Xyleborus* s. str., cladistic analysis placed them in various positions in respect to *Xyleborus* s. str, and to each other (Figure 21).

Biology: This species has a large range (across most of SE Asia and Melanesia) and little morphological diversity; it's rare wherever it occurs (Browne 1961c).

Examined material: Indonesia, Java, Semarang, (RMNH, 4 indiv.); Indonesia, Java, Buitenzorg, (RMNH, 2 indiv.); New Guinea, Toricelli Mts, (BBM); Taiwan, Taihoku, (NHMW); PNG: Madang Prov. (4), Oro Prov. (1), J. Hulcr 2002-2006.

***Xyleborus s. l. papuanus* Blandford (1896)**

J.H. database code: Scol 700

Compared to lectotype in BMNH

Length: 3.0 mm.

Discussion

Poor condition and mounting of specimen prevents generic placement. The truncated antennal club type 1, dark color, bulky body, dense punctures on elytra suggesting rich vestiture (most setae brushed off), and the large sockets of tibial denticles suggest affinity with *Anisandrus*. However, there is no sign of mycangium or mycangium-associated setae on the basis of pronotum, and the frontal edge of pronotum lacks the pair of serrations characteristic for *Anisandrus*. The antennae and general body shape also suggest placement in *Xylosandrus*, but prosternum is not accessible for examination of the prosternal process and procoxal separation.

Examined material: New Guinea, (unspecified "type", BMNH).

Xyleborus s. l. pileatulus **Schedl (1975)**

J.H. database code: Scol 702

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: The species is nearly identical to *X. metacuneolus*, except for the lack of a row of serrations on the pronotal apical margin, more prolonged pronotal disc, and antennal club nearly obliquely truncated, with the first segment dominant. The surface of elytral declivity does not have tubercles or spines.

Length: 2.1 mm.

Discussion

Schedl (1975f) mentioned similarity of this species to *Cryptoxyleborus* (*Xyleborus*) *vestigator*, and distinguished it by several characters, however without mentioning the decisive antennae and elytral mycangia. Schedl mentioned small, knob-like scutellum. The scutellum of *X. pileatulus* is smaller than what is usual in Xyleborina, but it is flush with elytral surface, not knob-like as in *Xyleborinus*, and the species does not have elytral mycangia.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

Xyleborus spp. synonymized with species in other genera

***Xyleborus abbreviatipennis* syn. n. Schedl (1973)**

Synonymized with: *Cyclorhipidion bituberculatum* (Eggers)

J.H. database code: Scol 670

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Discussion

According to Schedl (1973e), the species is similar to *X. flavopilosus* Schedl, and differs in its larger size, less cylindrical pronotum, the elytral disc with more numerous punctures and perforated appearance. The holotype of *X. abbreviatipennis* is nearly identical to that of *Cyclorhipidion bituberculatum*. Both *X. abbreviatipennis* and *X. flavopilosus* are synonymized with *C. bituberculatum*.

Examined material: New Guinea, Bismarck Geb., (holotype, NHMW).

Xyleborus annexus syn. n. Schedl (1973)

Synonymized with: _Beaverium insulindicus_ (Eggers)

J.H. database code: Scol 672

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Discussion

Schedl (1973) mentioned the similarity of this species to *Beaverium* (as *Xyleborus*) *insulindicus*, and the difference in smaller size, in more densely punctured elytral intrestriae, the apical margin of elytral declivity being carinate only at the suture, and in the declivital face being slightly convex. All these characters however vary greatly within individual lineages of *Beaverium*, while the decisive characters are identical between *Xyleborus annexus* and *Beaverium insulindicus* (pronotal margin, lateral profile of elytra, overall pattern of elytral punctures, breadth of the declivital plane, etc.)

Examined material: New Guinea, Eastern Highlands, (holotype).

Xyleborus apiculatus syn. n. Schedl (1942)

Synonymized with: _Biuncus justus_ (Schedl)

J.H. database code: Scol 747

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Discussion

The holotype of *Xyleborus apiculatus* is relatively slender compared to the holotype of *Biuncus justus*, nevertheless easily fitting the concept of the species. It is nearly identical to the holotype of *Xyleborus ciliatoformis* in all important characters, including the body shape, end of elytra, and the elytral declivity are the same, including the characteristic impression on declivity traversing from 1st interstria on the declivital summit to 3rd interstria towards the apex. Both are synonymized here with *Biuncus justus*.

Examined material: Philippines, Kepong, (holotype).

***Xyleborus aplanatideclivis* syn. n. Schedl (1942)**

Synonymized with: *Beaverium sundaensis* (Eggers)

J.H. database code: Scol 286

Previous genus: *Xyleborus*

Compared to lectotype in NHMW

Discussion

Schedl (1942c) included the species in the "insulindicus" group, noting its similarity with *X. sundaensis*. The holotype of *X. aplanatideclivis* is smaller than the holotype of *Beaverium sundaensis*, its elytral disc is more finely punctated, are more interstriae more densely punctuated, however these characters vary and are not correlated within lineages of *Beaverium*.

Examined material: Fiji, (lectotype); Fiji, (paratype, NHMW); PNG: Madang Prov. (3), Oro Prov. (7), J. Hulcr 2002-2006.

***Xyleborus approximatus* syn. n. Schedl (1951)**

Synonymized with: *Biuncus haberkorni* (Eggers)

J.H. database code: Scol 27

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Discussion

The holotype of *Xyleborus approximatus* is almost identical to the lectotype of *X. haberkorni*, mainly due to the same two pairs of declivital teeth which are nearly the same size, on conical bases rather than sharp spines, and the pair in 3rd striae is positioned further in the declivity rather than on declivital summit. The shared features also include the small asperities on the disc-declivity boundary in interstriae 4,5 and 6. Wood (1989) included *X. potens* as a synonym of *X. approximatus*. Schedl (1964c) mentioned smaller declivital teeth as the only difference between the newly described *X. potens* and *X. approximatus*.

Previously synonymized species: *Xyleborus potens* Schedl

Examined material: Australia, Queensland, Kurande, (B. H. Jordal); Malaysia, Selangor, Kepong, (holotype, NHMW); New Guinea, (FICB); unknown locality, (BMNH); unknown locality, (BMNH); PNG: Madang Prov. (5), Oro Prov. (13), J. Hulcr 2002-2006.

***Xyleborus australis* syn. n. Schedl (1980)**

Synonymized with: *Ambrosiophilus restrictus (Schedl)*

J.H. database code: Scol 132

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Discussion

Identical to *Ambrosiophilus restrictus* in all important features including the antennal structure, shagreen declivital surface, impressed interstria 1, one tubercle in interstria 2, two in interstria 3.

Biology: Mycocleptic associate of *Beaverium* spp., mostly *B. sundaensis.*

Examined material: PNG: Madang Prov. (2), Oro Prov. (14), J. Hulcr 2002-2006.

***Xyleborus biuncus* syn. n. Browne (1984)**

Synonymized with: *Biuncus papatrae (Schedl)*

J.H. database code: Scol 19

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Discussion

The holotypes of *Xyleborus mucronatoides*, *Xyleborus papatrae* and *Xyleborus biuncus* are virtually identical and are synonymized with the senior name *Biuncus papatrae*. Browne (1984d) mentioned similarity of this species to *Biuncus* (as *Xyleborus*) *dossuarius*, and distinguished it by the smooth elytra with sparse punctuation. He did not, however, mention the similarity of his new species to *X. mucronatoides* or *Biuncus*

(*Xyleborus*) *papatrae*. The holotypes of the two species are nearly identical, except that the more recently collected holotype of *X. biuncus* has retained the naturally darker elytra.

Examined material: New Guinea, (holotype); PNG: Madang Prov. (77), Oro Prov. (13), J. Hulcr 2002-2006.

***Xyleborus brevicollis* syn. n. Browne (1984)**

Synonymized with: *Biuncus mesoleiulus* (Schedl)

J.H. database code: Scol 356

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Length: 2.5 mm.

Discussion

Browne (1984d) mistakenly related the species to *X. metacuneolus*. The holotype is identical to *Biuncus mesoleiulus*, including size, declivity morphology, color, etc.

Examined material: New Guinea, Morobe Province, Gumi, (holotype); New Guinea, Morobe Province, Gumi, (paratype, FICB).

***Xyleborus canarivorus* syn. n. Browne (1986)**

Synonymized with: *Truncaudum longior* (Eggers)

J.H. database code: Scol 675

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Length: 2.0 mm.

Discussion

The holotype of *X. canarivorus* Browne is identical to the holotype and a large series of *Truncaudum longior*. Antennae, pronotal shape, protibiae, body coloration, even details of elytral declivity are the same in both species (the declivity has oblique angulate margin, not costate or serrate, several pairs of small tubercles in interstriae 1 and 3, several recurved tubercles on the apical margin of declivity). Browne (1986a) indicated that the species is similar to *X. mukunyae* Schedl, a species not studied by us.

Biology: Reported by Browne (1986a) as imported from PNG to Japan.

Examined material: New Guinea, (holotype).

***Xyleborus ciliatoformis* syn. n. Schedl (1953)**

Synonymized with: *Biuncus justus (Schedl)*

J.H. database code: Scol 439

Previous genus: *Xyleborus*

Compared to "type" in BMNH

Length: 1.6-2.4 mm.

Discussion

Schedl (1953f) remarked on the similarity between this species, *Xyleborus ciliatoformis*, *Xyleborus ciliatus*, and *Biuncus* (*Xyleborus*) *justus*, and distinguished it by the comparatively longer abdomen. All three species only vary in the relative proportions and shape of elytral declivity, which is extremely variable in *Biuncus* and is not a species-delimiting character. Biology: Found in trunk, unclear whether associated with anything.

Examined material: Indonesia, Borneo, (unspecified "type", BMNH); Indonesia/Australia, Borneo, (lectotype, NHMW); Malaysia, Sarawak, Kuching, (BMNH), Browne det. as *X. ciliatoformis*; Malaysia, Sabah, Danum Valley, *Ficus* sp. trunk, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* trunk, (Hulcr coll., 2 indiv.).

Xyleborus ciliatus syn. n. Eggers (1940)

Synonymized with: _Biuncus justus_ (Schedl)

J.H. database code: Scol 543

Previous genus: *Xyleborus*

Compared to cotype in USNM

Discussion

The type of *Biuncus justus* and the cotypes of *Xyleborus ciliatus* (two specimens on a single point) don not differ in any important character. Even the direction and size of declivital setae is identical. Wood & Bright (1992) indicated that the holotype is in an unspecified Kalshoven collection. The type specimen is absent from both RMNH and ZMA, may be deposited in LIPI. Cotype of unclear validity was available from USNM.

Examined material: Indonesia, Java, Gn. Gedeh, (co-type, USNM, 2 indiv.); New Guinea, New Ireland, (BBM), 250-750 m as.

Xyleborus circumspinosus syn. n. Schedl (1972)

Synonymized with: *Truncaudum impexus* (Schedl)

J.H. database code: Scol 677

Previous genus: *Xyleborus*

Compared to paratype in NHMW

Discussion

Schedl (1972i) provided characters distinguishing the species from *Truncaudum* (as *Xyleborus*) *impexus*: it is a little larger, the truncated declivity aplanate, with a pair of conical tubercles on the first interstriae in the lower third. A paratype of this species was examined, and found and fits within the variation found in *T. impexus*. The above mentione conical tubercles in the first declivital interstriae are especially prone to variation.

Examined material: New Guinea, Morobe Province, Bulolo, (Schedl det., MSUC); New Guinea, Morobe, Umboi, (paratype, NHMW).

***Xyleborus cognatus* syn. n. Blandford (1896)**

Synonymized with: *Xyleborus s. str. perforans Wollaston*

J.H. database code: Scol 284

Compared to holotype in BMNH

Discussion

The species concept of *X. cognatus* has been used in many collections to group large specimens of *X. perforans*. Browne (1961c) mentioned that it differs form *X. perforans* by larger size and darker color. The holotype of *X. cognatus* is indeed larger than most *X.*

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perforans, however there is an expectable continuum of body size present in the *X. cognatus* - *X. perforans* complex. Individuals identified as *X. cognatus* in multiple collections range in size from 2.3 to 2.9 mm., while those identified as *X. perforans* range from 2.1 to 2.6, and therefore overlap significantly. No other character seems to be consistently associated with the larger specimens. The declivital armature is as variable as in typical *X. perforans* and ranges from large and sparse tubercles, to rows of uniform smaller tubercles in interstriae 1 and 3. Many larger specimens also appear different from typical *X. perforans* due to their larger punctures on elytral disc, but the significance of this character is unclear. The slope of declivity is variable, fully within the variation of *X. perforans* (Figure 65). An example of the ambiguity associated with this species concept is the fact that, both the holotype and the lectotype of the now invalid *X. apertus* (Schedl) resemble the type of *X. cognatus* more than that of *X. perforans*, but it has been synonymized with *X. perforans* (Bright & Skidmore 1979).

Examined material: Bangladesh, (B. H. Jordal, 2 indiv.); China, (syntype, BMNH); Malaysia, Borneo, (BMNH); Malaysia, Sabah, Danum Valley, *Ficus* sp. trunk, (Hulcr coll., 4 indiv.); New Guinea, (BBM, 2 indiv.); New Guinea, (FICB, 2 indiv.); New Guinea, Havezi, (MCG, 8 indiv.); locality not recorded, (BMNH); PNG: Madang Prov. (2), West Sepik (5), J. Hulcr 2002-2006.

Xyleborus cruciatus syn. n. Schedl (1973)

Synonymized with: *Stictodex dimidiatus (Eggers)*

J.H. database code: Scol 678

Previous genus: *Xyleborus*

Compared to holotype in FICB

Length: 3.2 mm.

Discussion

A slightly larger representative of *Stictodex dimidiatus*. The elytral declivity, despite being very variable in this genus, is nearly identical in holotypes of *X. cruciatus* and *X. tunggali* (both synonymized here with *S. dimidiatus*). Both have a single tubercle in the first interstria on the summit of declivity, and rows of tubercles in all other interstriae on the declivity. The type specimen was reported as deposited in ANIC, however, it resides in the FICB. Schedl (1973e) errorously related the species to *Xyleborinus undatus* Schedl.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype); New Guinea, Central, Vanapa R., (paratype, NHMW).

Xyleborus cylindricus syn. n. Eggers (1927)

Synonymized with: _Emarginatus pumilus (Eggers)_

J.H. database code: Scol 679

Previous genus: *Xyleborus*

Compared to lectotype in USNM

Length: 1.8-2.0 mm.

Discussion

Eggers (1927c) placed the specie in the "fallax group", while Browne (1961c) placed it in his "*Coptoborus* group" (with other *Emarginatus* spp.).The holotype of *Xyleborus cylindricus* is in most aspect identical to that of *Emarginatus pumilus*. Also the declivity features are similar, except that the major pair of denticles in the middle of the declivital slope is not on the flat part of the declivity, but closer to the edge. This makes the denticles and their bases appear larger, and gives the impression that the declivity is slightly excavated. As discussed above, such a small difference in a very plastic character is not considered a species-delimiting feature. Thus *X. cylindricus* is synonymized here with *E. pumilus*.

Previously synonymized species: *Ips kelantanensis* Browne

Examined material: Philippines, Luzon, Balbalan, (lectotype, USNM).

Xyleborus decumans **syn. n. Schedl (1953)**

Synonymized with: *Stictodex dimidiatus (Eggers)*

J.H. database code: Scol 375

Previous genus: *Xyleborus*

Compared to lectotype in NHMW

Length: 3.2 mm.

Discussion

The declivity of *X. decumans* represents one end of the broad continuum of variation of the *Stictodex* declivity, easily fitting in the variation of *S. dimidiatus*. The first interstria is slightly broadened around the declivital summit, and all declivital interstriae including interstria 2 bear rows of pointed tubercles. The second stria is slightly impressed. The declivity itself is flat, coarsely punctured. A junior synonym of *S. dimidiatus* and the holotypes of the two species are nearly identical. Schedl (1953c) proposed a placement of this species in his Xylebori adjuncti, near *X. pseudopilifer*. This was based on a very vague similarity, not supported by his discussion of characters. *X. pseudopilifer* is not similar to *X. decumans*, and both clearly belong to different genera. Similarity to *X. tunggali* or *X. dimidiatus* is not mentioned in the species description.

Biology: Borneo.

Examined material: Malaysia, Kelantan, (lectotype); Malaysia, Sabah, Danum Valley, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Rhino Ridge, Danum Valley, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, (Hulcr coll., 2 indiv.); Malaysia, Sabah, Danum Valley, Mallotus sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll., 5 indiv.); New Guinea, Umboi, (BBM); Sri Lanka, Sabargamuva, (NHMW); PNG: Madang Prov. (4), J. Hulcr 2002-2006.

Xyleborus dentatulus **syn. n. Browne (1981)**

Synonymized with: *Truncaudum impexus* (Schedl)

J.H. database code: Scol 62

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Discussion

The holotype of *X. dentatulus* Browne is virtually identical to that of *Truncaudum impexus*. The serration on the upper edge of declivity in the *X. dentatulus* holotype is smaller that in the usual *T. impexus*, but this particular character is extremely variable in this species. Browne (1981a) mentioned the similarity of this species to the African

Cyclorhipidion (as *Xyleborus*) *agnaticeps*. He mentioned that the circumdeclivital teeth are closely spaced, and larger in the bottom half.

Biology: First recorded by Browne (1981a) from a log imported to Japan from New Ireland.

Examined material: New Guinea, New Ireland, Kamdaru (holotype); Takehara coll. 1975.; New Guinea, Morobe Province, Bulolo, (FICB, 3 indiv.); PNG: Madang Prov. (225), West Sepik (3), J. Hulcr 2002-2006.

Xyleborus depressurus **syn. n. Browne (1985)**

Synonymized with: *Beaverium insulindicus (Eggers)*

J.H. database code: Scol 845

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Discussion

X. depressurus from New Britain is a junior synonym of *Beaverium insulindicus*. It has the same elevated carina on pronotal anterior edge, asperities behind the pronotal summit, elytral disc strongly convex, declivity flat, broad, strial punctures arrayed on the upper part of declivity, confused on the bottom part, elytral apex appears shallowly emarginated.

Examined material: New Guinea, New Britain, Pomio, (holotype), imported to Japan.

Xyleborus devius **syn. n. Schedl (1979)**

Synonymized with: *Ambrosiophilus restrictus* (Schedl)

J.H. database code: Scol 681

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Discussion

The holotype is very similar to many specimens of *Ambrosiophilus restrictus* from NG as well as SE Asia, with the exception that it is smaller than most and has very feebly punctuation on pronotal disc. According to Schedl (1979g), it is similar to *Xyleborus australis* (here synonymized with *Ambrosiophilus restrictus*), but is smaller, the elytral disc is more coarsely punctured, the declivity evenly convex, striate-punctate, and the third interstriae bear very small pointed granules.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype).

Xyleborus falcarius syn. n. Schedl (1942)

Synonymized with: _Truncaudum impexus_ (Schedl)

J.H. database code: Scol 682

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: Fully consistent with the species definition of *Truncaudum impexus*.

Length: 2.5 mm.

Discussion

Schedl (1942c) states that the species (along with *X. impexus*) is related to *X. trepanicauda* based on characters on elytral declivity. However, all other characters, including the absence of elytral mycangium, which is a generic character of *Pseudowebbia,* point clearly to its relatedness to the *Truncaudum* group. According to Schedl (1942c), it differs from *T. impexus*by the presence of the prominent tooth in the first interstria on the edge of declivity. This tooth however has been observed to vary substantially among multiple specimens from New Guinea (intermediates can be seen among non-types identified as *X. circumspinosus* in NHMW). This single and variable difference between the putative species, it is not considered a decisive character here and the two species are synonymized. Interestingly, Schedl identified a specimen in the ANIC with larger teeth in the first interstriae on the declivital summit as *X. circumspinosus* (described by himself without mentioning this tooth pair), rather than as *X. falcarius,* suggesting that he did not always consider this character decisive. The species of *X. falcarius* and *X. impexus* were described simultaneously (Schedl 1942). Since the principle of priority is not applicable here, *T. impexus* is chosen to be the valid name for the species, as its shorter teeth in the first interstriae on the declivital summit are more typical for the species as compared to the slightly longer teeth present in the holotype of *X. falcarius.*

Examined material: New Guinea, (holotype, NHMW).

Xyleborus fastigatus **syn. n. Schedl (1935)**

Synonymized with: *Emarginatus fallax* (Eichhoff)

J.H. database code: Scol 683

Previous genus: *Xyleborus*

Compared to lectotype in NHMW

Discussion

The lectotype of *X. fastigatus* falls within the variation of *X. fallax*. The label of the *X. fastigatus* lectotype does not indicate the locality of the specimen's origin. Neither it is mentioned in the published description (Schedl, 1935b), however, the paper describes new species from Philippines, which is thus assumed to be the country of origin.

Examined material: Philippines, label: Sch. of For., Univ. P.I., (lectotype).

Xyleborus flavipennis **syn. n. Schedl (1979)**

Synonymized with: *Cyclorhipidion bituberculatum* (Eggers)

J.H. database code: Scol 684

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Discussion

According to Schedl (1979g), the species is similar to *Xyleborus flavipilosus* Schedl, but is more slender, with the elytral apex more angulately rounded and the pubescence at the declivity less prominent. Schedl (1979) puts the species in his Xylebori obtusi. The pair of tubercles characteristic for *C. bituberculatum* is very small in the holotype of *X. flavipennis*, pointing forward. The specimen is slightly smaller than majority of *C. bituberculatum* representatives, but easily fits within the intraspecific variation.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype).

Xyleborus flavopilosus **syn. n. Schedl (1936)**

Synonymized with: *Cyclorhipidion bituberculatum* (Eggers)

J.H. database code: Scol 685

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Discussion

According to Schedl (1979c), the species resembles *Xyleborus flavipennis. X. flavopilosus* has slightly more prominent declivital forward-pointing tubercles than *X. flavipennis*, otherwise the two specimens are virtually identical. Both forms are slightly smaller than *Cyclorhipidion bituberculatum*, but both fit within the range of its intraspecific variation.

Examined material: New Guinea, (holotype).

Xyleborus glabratulus syn. n. Browne (1983)

Synonymized with: _Planiculus bicolor_ (Blandford)

J.H. database code: Scol 313

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Discussion

This species is nearly identical to *Planiculus bicolor*. The only observed differences are the slightly more rugged surface of elytral declivity, which is a combination of greater number of granules associated with setae, and more abundant setae. Specimens of *P. bicolor* with slightly rugged declivity (=*Xyleborus glabratulus*) were previously reported from the Solomon Islands. However, the first author collected specimens of a slightly different appearance but with a similar declivital phenotype in the New Guinea mainland. This suggests that more conspicuous granules on declivity may frequently arise as a local deviation in *P. bicolor*. The morph also represents some variability in the circumdeclivital costa. This is slightly more prominent in the holotype, while the lateral costal margin may be replaced by granules in other specimens of *P. bicolor*. Similar is *E. subparallelus* - tubercles in interstria 1 larger, declivity equally shallowly emarginate, about 1.3x larger, more robust, shorter pronotum and less concave laterally, elytra tapering towards the end laterally, with similar color.

Examined material: New Guinea, Solomon Islands, Visu Harbour, (holotype), imported to Japan (Nagoya); PNG: Oro Prov. (2), J. Hulcr 2002-2006.

Xyleborus granulipes **syn. n. Schedl (1973)**

Synonymized with: *Wallacella timidus* (Schedl)

J.H. database code: Scol 584

Previous genus: *Xyleborus*

Compared to paratype in FICB

Discussion

The type specimen is currently absent from ANIC, but paratypes are located in NHMW and FICB. Schedl (1973e) puts the species in his "Xylebori granulosi", and notes that it can be distinguished by its subquadrate pronotum, very oblique elytral declivity, and the declivital surface. *Xyleborus granulipes* and *Wallacella* (as *Xyleborus*) *timidus* arevirtually identical, and no doubt representing the same species. Both have subquadrate pronotum with the summit located close to the pronotal base, slowly descending declivity with opaque surface, a distinct posterolateral carina, and a few pointed granules on the edge of declivity. *E. (X.) timidus* was described in issue 2, while *X. granulipes* was described in issue 3 of the same journal, and is thus considered a junior synonym of *E. timidus* (Schedl 1973e, 1973f). *E. granulipennis* (now *Wallacella andamanensis*) has similar elytra, but longer, different pronotum.

Examined material: New Guinea, Milne Bay, Naura, (paratype).

Xyleborus gratiosus syn. n. Schedl (1975)

Synonymized with: _Truncaudum agnatum_ (Eggers)

J.H. database code: Scol 689

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Discussion

The "species" is no doubt a derived form of *T. agnatum*, even though its superficial appearance seems substantially different. The regular strial punctures on the declivity of the holotype of *X. gratiosus* (the only specimen known to us) are substantially extended. Their inner surface is shagreen. The large area covered by these shagreen punctures gives the beetle an appearance of a much more rugged declivity. However, no other character separates *X. gratiosus* form the hypervariable *T. agnatum* According to Schedl (1975f), the species is similar to *Xyleborinus artestriatus* (as *Xyleborus artestriatus*). Schedl lists several distinguishing characters, however, did not discuss the characters, which define the two species as two different genera, most importantly the regular, triangular scutellum and the absence of elytral mycangia.

Examined material: New Guinea (holotype).

***Xyleborus hashimotoi* syn. n. Browne (1986)**

Synonymized with: *Planiculus immersus* (Schedl)

J.H. database code: Scol 125

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Discussion

This species is nearly identical to that of *X. immersus*. The holotype of *X. hashimotoi* has slightly greater declivital tubercles, otherwise all important characters are the same in both species: antennae, pronotum shape, protibiae, elytral declivity and the pattern of tubercles. Browne (1986a) does not mention similarity to any other Xyleborine except the African *X. nitidulus* Egg.

Examined material: New Guinea, West Papua, Fakfak, (holotype), imported to Japan (Nagoya).

***Xyleborus hopeae* syn. n. Browne (1986)**

Synonymized with: *Truncaudum tuberculifer* (Eggers)

J.H. database code: Scol 490

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Discussion

Several specimens compared to holotype of Eggers (1923). Representatives of *X. hopeae* and *Truncaudum tuberculifer* are very similar, all major characters are shared: the large eyes, antennal club, armed pronotal edge, narrow protibiae, and the elytral declivity. Browne (1986a) mentioned its similarity to *Xyleborus subagantum* (synonymized here with *Truncaudum agnatum*), and pointed out the different truncated declivity.

Examined material: New Guinea, Western Province, Wavoi, (FICB, 3 indiv.).

Xyleborus immitatrix syn. n. Schedl (1975)

Synonymized with: _Xyleborus s. l. judenkoi_ Schedl

J.H. database code: Scol 691

Compared to holotype in NHMW

Diagnosis: According to Schedl (1975f), the species is similar to *X. pullus* (now *Coptodryas*) from the Philippines.

Discussion

The species has been omitted from Wood & Bright (1992) and the subsequent supplements. The holotype (the only known specimen) is almost identical to the holotype of *X. judenkoi*. All important characters are identical:antennae, elytral declivity with uniform evenly spaced tubercles in interstriae 1-3 and on the bottom margin of declivity, and a minute scutellum. Except, *X. imitatrix* has more shagreen pronotal disc. However, this character is mildly variable even within the type series (the holotype and two paratypes) and is not considered decisive. The type specimen of *X. imitatrix* is also black, not yellowish brown, but likely because it was recovered from a sticky trap.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

Xyleborus ipidia syn. n. Schedl (1972)

Synonymized with: _Emarginatus pumilus_ (Eggers)

J.H. database code: Scol 770

Previous genus: *Xyleborus*

Compared to paratype in FICB

Diagnosis: The examined paratypes of *X. ipidia* and the holotype of *E. pumilus* are essentially identical, except that the declivital spines are slightly less produced in the *E. pumilus* holotype. There may be other variants of the ipidia-pumilus form in other Pacific Ocean islands, which differ in the exact configuration of declivital armature and punctuation (R. A. Beaver, pers, comm.). These have not been examined; they may be sufficiently distinct to deserve a species rank, but are most likely only insular deviations of the variable *E. pumilus* declivity.

Discussion

Holotype is probably lost. Paratypes are located in FRI Lae and NHMW. Designation of a lectotype is not necessary since the species is a junior synonym of *Emarginatus pumilus*. Browne (1974) described *X. planodeclivis* from Fiji, which was later synonymized with *X. ipidia*, now synonymized with *E. pumilus*. The description of *X. planodeclivis* does not conflict with that of *E. pumilus*, the holotype easily fits the variation in *X. planodeclivis* (examined in BMNH).

Previously synonymized species: *Xyleborus planodeclivis* Browne

Examined material: New Guinea, New Ireland, (paratype, FICB).

Xyleborus mucronatoides syn. n. Schedl (1975)

Synonymized with: *Biuncus papatrae* (Schedl)

J.H. database code: Scol 695

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Length: 2.1-2.5 mm.

Discussion

The holotypes of *Xyleborus mucronatoides*, *Xyleborus papatrae* and *Xyleborus biuncus* are virtually identical, all are synonymized here with the senior specific epithet *Biuncus papatrae*. Wood & Bright (1992) suggested this synonymy. According to Schedl (1975f), the species is similar to *Biuncus* (as *Xyleborus*) *papatrae*, but it is larger, stouter, and the elytral apex less angulate, and the elytral disc shorter. These details of elytral declivity vary substantially within lineages of *Biuncus*, and do not justify species split. Schedl (1975f) designated a holotype in Bernice P. Bishop Museum in Honolulu, Hawaii, but the type resides in NHMW. Despite its name, *Xyleborus mucronatoides*, is not very similar to X. *mucronatus* Eggers or *X. mucronatulus* Eggers. The latter two have more prolonged body and two pairs of blunt tubercle-like declivital teeth on elytral declivity, among other differences.

Examined material: New Guinea, Vogelkopf, Bomberai, (holotype), from West Papua.

***Xyleborus multipunctulus* syn. n. Browne (1984)**

Synonymized with: *Cyclorhipidion multipunctatus* (Browne)

J.H. database code: Scol 696

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Discussion

This is clearly a synonymy of *Cyclorhipidion* (as *Xyleborus*) *multipunctatus*. Both the species description and the type specimen fully correspond to *C. multipunctatus*. In his original description, Browne (1984d) does not mention any similarity of *C. multipunctulus* to *C. multipunctatus*. He indicated that the species is similar to *Cyclorhipidion perpilloselum* (as *Xyleborus pruinosus*) (Blandford), but distinctively more slender, and that there is an abrupt change of elytral surface in the middle of elytral disc. This abrupt change of elytral surface is characteristic for *C. multipunctatum*.

Examined material: New Guinea, Morobe Province, Gumi, (holotype).

***Xyleborus nitens* syn. n. Browne (1984)**

Synonymized with: *Ambrosiophilus semicarinatus (Schedl)*

J.H. database code: Scol 697

Previous genus: *Xyleborus*

Compared to paratype in FICB

Discussion

Browne (1984d) mentioned the similarity of this species to *Xyleborus restrictus*, and noted that it differs in the more closely and finely punctate elytra, and in small granules, instead of moderately large tubercles on the declivital interstriae. Similarity to *X. semicarinatus* was not discussed. The paratype and a series of non-types of *X. nitens* was compared to the holotype of *Ambrosiophilus semicarinatus* and was found identical in all aspects, such as the body shape, declivital tubercles, color, or antennal structure.

Examined material: New Guinea, Oro Province, Popondetta, (paratype, FICB).

***Xyleborus opulentus* syn. n. Schedl (1975)**

Synonymized with: *Emarginatus latecornis* (Schedl)

J.H. database code: Scol 478

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Discussion

Schedl (1975f) distinguished *X. opulentus* from other 'Xylebori emarginati' by the blunt triangular postero-lateral process of the elytra. The exact shape of this process is one of the most plastic body parts of *Emarginatus*. The holotype of *X. opulentus* is virtually identical to its senior synonym *X. latecornis* Schedl, including such details as opalescent shagreen declivity. *X. aff. subdentatus* (B. H. Jordal's coll.) is similar (slightly bigger) but it has remnants of a stria in declivity. *X. cavulus* Browne (type seen) from Malaysia is similar , but it is slightly more slender, parallel-sided, and tubercle in 1st stria in upper part of declivity is missing. However, the tubercule in 2nd stria is elevated, making the upper part of declivity more emarginate and abrupt. Bottom corners of emargination are not bulging, without the presence of a small tooth.

Examined material: New Guinea, Milne Bay, Mt. Dayman, (holotype, NHMW); New Guinea, Morobe Province, Bulolo, (NHMW).

***Xyleborus platyurus* syn. n. Browne (1984)**

Synonymized with: *Beaverium perplexus* (Schedl)

J.H. database code: Scol 703

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Discussion

The holotypes of *X. platyurus* and *Beaverium perplexus* are identical (elytral punctuation, broad elytral costa, identical asperities on pronotal disc, body size, etc.).

Examined material: New Guinea, Morobe, Wau, (B. H. Jordal), 2000m a.s.l.; New Guinea, Morobe Province, Mt. Kaindi, (holotype), 2350 a.s.l.; New Guinea, Morobe, (2350 m a.s.l., BMNH), male, 2350 m a.s.l.

***Xyleborus protii* syn. n. Browne (1984)**

Synonymized with: *Truncaudum longior* (Eggers)

J.H. database code: Scol 705

Previous genus: *Xyleborus*

Compared to paratype in BMNH

Discussion

A Browne's paratype and a non-type specimen (apparently from the same collection event) are nearly identical to the holotype of *T. longior*. Also the original description agrees with the characters of *T. longior* (Browne 1984d). Browne (1984d) related the species to *T. truncaticauda*, noting that it differed in the shining elytral disc.

Examined material: New Guinea, Stony L. A, (paratype); New Guinea, Stony L. A., *Protium*, (FICB).

Xyleborus pseudopilifer syn. n. Schedl (1936)

Synonymized with: _Fortiborus pilifer_ (Eggers)

J.H. database code: Scol 738

Previous genus: *Xyleborus*

Compared to lectotype in NHMW

Discussion

Browne (1961c) included the species among "major group". The only difference between representatives of *Xyleborus pseudopilifer* from Malaysia and the holotype of *X. pilifer* (possibly the only specimen known) is that the Malaysian specimens have larger tubercles on the disc/declivity boundary. Thus *X. pseudopilifer* is considered a junior synonym of *Fortiborus pilifer*.

Biology: Relatively common throughout SE Asia. Browne (1986b) reported the species from logs imported from New Guinea to Japan. Browne (1958) indicated that the species is specialized to Dipterocarpaceae.

Examined material: Malaysia, Kepong, Selangor Kepong, (lectotype, NHMW); Malaysia, Sarawak, Kuching, (BMNH).

Xyleborus putputensis syn. n. Browne (1986)

Synonymized with: _Truncaudum impexus_ (Schedl)

J.H. database code: Scol 815

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Discussion

Invalid species designation. The holotype of *X. putputensis* is a male of *Truncaudum impexus*. Males of Xyleborina are nondescript, variable even within families, and unknown for majority of species, thus they shouldn't be used for species designation. Browne (1986a) mentioned similarity of the species to *X. canarivorus* (now synonymized with *Truncaudum longior*), but did not indicate sex of the holotype.

Examined material: New Guinea, New Britain, (holotype).

Xyleborus siclus **syn. n. Schedl (1936)**

Synonymized with: *Fortiborus major* (Stebbing)

J.H. database code: Scol 818

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: Declivity slightly resembles *Beaverium*, but the pronotum is subquadrate, elytral punctuation seriate from the elytral base to apex, very large eyes. Holotype length: 5.8 mm.

Discussion

Two holotypes of unclear validity seem to exist, one in BMNH and one in NHMW. In Browne's BMNH collection there is a series of identical individuals identified as *X. siclus*, one of them is designated and labeled as holotype by Schedl. Some of these specimens are also labeled *X. major*, the identifier is unknown. Another such "holotype" is deposited in NHMW. Holotypes of *X. siclus* and *Fortiborus major* were compared and found indistinguishable in all important characters, thus *X. siclus* is considered a junior synonym. Due to the synonymy, we do not recify the ambiguous types.

Biology: Browne (1983) reported one specimen imported from West Irian into Japan, but the identification could not be verified.

Examined material: Malaysia, Selangor, (compared to holotype, BMNH); Malaysia, Kelantan, (compared to holotype, BMNH); Malaysia, Penang, (compared to holotype, BMNH); Malaysia, Selangor, (holotype, BMNH); Malaysia, (BMNH, 3 indiv.); Malaysia, Selangor, (holotype, NHMW).

***Xyleborus subcostatus* syn. n. Eichhoff (1869)**

Synonymized with: *Xyleborus s. l. bidentatus* (Motschulsky)

J.H. database code: Scol 711

Compared to holotype in IRSNB

Discussion

The holotype is nearly identical to many representatives of *Xyleborus bidentatus*, and fits within the range of variation of this species.

Previously synonymized species: *Xyleborus subcostatus dearmatus* Eggers, *Xyleborus fleutiauxi* Blandford, *Xyleborus webbi* Hopkins

Biology: According to Browne (1961c), the species is specialized to mangroves and swampy habitats.

Examined material: New Guinea, (BMNH), Identified as *X. flieutiauxi* by D. J. Atkinson; Thailand, (holotype).

Xyleborus subdentatulus **syn. n. Browne (1986)**

Synonymized with: *Truncaudum impexus* (Schedl)

J.H. database code: Scol 712

Previous genus: *Xyleborus*

Compared to holotype in BMNH

Length: 2.1 mm.

Discussion

Browne (1986a) related this species to *X. dentatulus*, and distinguished the two by unspecified differences on elytral declivity sculpturing. The holotype has four pairs of tubercles in the first elevated interstria in the elytral declivity, a feature common in *T. impexus*. The tubercles are clearly larger than in most representatives of *T. impexus*, but not exceedingly large, and are in the same positions. No other significant difference between the holotype of *X. subdentatulus* and a series of *T. impexus* was found.

Examined material: New Guinea, (holotype, BMNH).

Xyleborus tunggali **syn. n. Schedl (1936)**

Synonymized with: *Stictodex dimidiatus* (Eggers)

J.H. database code: Scol 293

Previous genus: *Xyleborus*

Compared to lectotype in NHMW

Length: 2.5-3.1 mm.

Discussion

Based on superficial similarity, Browne (1961c) placed the species in an unnatural group "*Xyleborus artestriatus* group", composed mostly of *Xyleborinus* and *Coptodryas* spp.

Examined material: Malaysia, Botan Tunggal, (lectotype); New Guinea, Western Highlands, Jimi Valley, (FICB); Sri Lanka, Sabargamuva, (NHMW), Schedl det.

***Xyleborus vernaculus* syn. n. Schedl (1975)**

Synonymized with: *Truncaudum impexus (Schedl)*

J.H. database code: Scol 719

Previous genus: *Xyleborus*

Compared to holotype in NHMW

Diagnosis: Schedl (1975f) distinguished the species from *Truncaudum falcarius* by the gradually decreasing size of the teeth in the alternate interstriae 1, 3, 5 and 7 on the upper declivital margin . The teeth at the bottom side of declivity are all equally small.

Discussion

This difference in teeth size between the holotype of *X. vernaculus* and many representatives of *Truncaudum impexus* is minor, fully expectable given the observed variation in elytral declivity in this group. Schedl (1975f) correctly related the species to *Xyleborus falcarius* (synonymized here with *Truncaudum impexus*), but also incorrectly to *Pseudowebbia* (as *Xyleborus*) *spinachius*.

Examined material: New Guinea, Manus island, Nuvok, (holotype, NHMW).

Xyleborus viaticus **syn. n. Schedl (1974)**

Synonymized with: *Truncaudum longior* (Eggers)

J.H. database code: Scol 720

Previous genus: *Xyleborus*

Compared to holotype in FICB

Discussion

The holotype is virtually identical to the holotype of *Truncaudum* (as *Xyleborus*) *longior* in all important aspects, notably the oblique circumdeclivital costa, flat declivity with a few tubercles at the apex, and the occurrence of several tubercles in the 1st and 3rd interstriae on the declivity. Schedl indicated similarity of this species to *Amasa* (as *Xyleborus*) *tereticollis* (Schedl) from PNG and to *Amasa* (as *Xyleborus*) *circumcisulus* (Schedl) from Java. He noted the differences of the upper margin of declivity which is angulate, not carinate, and of declivital interstriae one and three which have pointed tubercles.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype).

Genus *Xylosandrus* Reitter (1913)

J.H. database code: Scol 792

Type species: *Xyleborus morigerus* Blandford.

Redescription: Eyes shallowly or deeply emarginate, upper portion of eyes smaller than lower part. Antennal club more-less circular shape, or taller than wide, flat. Club type one (truncated, first segment covering posterior side), with one rare exception - type 4 in *X. mixtus*. First segment of club circular around the club, covering the entire posterior face, margin of the first segment clearly costate all around the antenna. Second segment of club narrow, pubescent, visible on the anterior side only. Third segment of club absent from the posterior side of club. First segment of antennal funicle shorter than pedicel, funicle composed of 4 segments, scapus regularly thick, or appear long and slender. Frons above epistoma mostly smooth, alutaceous, with minor punctures, or rugged, coarsely punctate. Submentum slightly impressed, or deeply impressed, shaped as a narrow slit, or a narrow triangle, the impression sometimes surrounded with costate edge or even carina. Anterior edge of pronotum with a distinct row of serrations. Pronotum from lateral view low and rounded (type 1), or tall (type 2), or rounded and robust (type 5). From dorsal view it is rounded (type 1). Pronotal disc shining or smoothly alutaceous, with small punctures, lateral edge of pronotum obliquely costate. Procoxae narrowly to widely separated, anterocoxal and posterocoxal prosternal processes merged into a process of very variable shape, from short, conical or flat, inconspicuous, or tall and pointed. Base of pronotum with small tuft of setae associated with mesonotal mycangium (sometimes very faint). No elytral mycangium and no setae associated with it on elytral bases. Scutellum flat, flush with elytra. Elytral bases straight, with oblique edge, elytral disc longer than declivity and slightly convex or bulging, or short compared to the declivity and often convex to bulging, punctures on elytral disc in strial lines (which may be difficult to discern in some montane species). Lateral profile of elytral declivity variable, rangin from mildly flat or rounded, to steep, especially towards the apex, to obliquely truncated; dorsal profile of elytral end rounded, or truncated, or rounded and broadened laterally. Circumdeclivital costa ending in 7th interstriae. Elytral declivity without armature, usually smooth or granulate-punctate, sometimes abruptly truncated. Striae and interstriae on the upper part of declivity are flat, in some SE Asian species ridges and furrows are present. First interstriae are parallel (sometimes slightly broadened towards elytral summit). Protibiae very slender, slightly broader only at the distal end. Posterior side of protibia flat, with setae only. Protibial denticles mostly large, distinctly longer than wide, bases of the denticles usually distinctly enlarged and almost conical, in most species fewer than 6 protibial denticles present. Metatibiae of regular size. Body length varies greatly, from minute and very short, almost globular species to rather large montane species (1.3-4.2 mm.). Moderately to densely hairy over most of the body surface. Color variable, from uniformly light brown to uniformly black, or pronotum dark, but elytra white (semitransparent) with a whitish patch.

Discussion

Biology: All known *Xylosandrus* excavate very short entrance tunnel, which quickly expands into a cavity of variable shape. This habit seems to be shared with *Cnestus*, but not with *Hadrodemius* or *Anisandrus*, both of which create tunnels only.

Figure 65: *Xylosandrus morigerus*, a typical representative of the genus. Size: 1.6 mm.

Xylosandrus compactus (Eichhoff, 1875)

J.H. database code: Scol 131

Compared to cotype in BMNH

Diagnosis: One of the smallest *Xylosandrus*. Color usually brown, vestiture abundant all over body but not dense. Antenna type 1 (truncated club). Protibia extremely is narrow, stick-like, usually with only 4 socketed denticles. Prosternal intercoxal process is very broad andlow. The main difference from the very similar *Xylosandrus morigerus* is the elytral disc which is as long or longer than elytral declivity. In *X. morigerus*, the elytra are conspicuously short, obliquely truncated, elytral disc significantly reduced. *X.*

compactus is almost always brown, while *X. morigerus* is mostly black. Patterns of elytral punctuation are very variable especially in *X. morigerus*.

Length: 1.6-1.7 mm.

Discussion

Transferred to *Xylosandrus* from *Xyleborus* by Browne (1963). This was the first record from New Guinea, unfortunately the specimens were lost.

Previously synonymized species: *Xyleborus morstatti* Hagedorn

Biology: A twig borer of occasional economic importance, especially in coffee and cocoa plantations (Beaver & Browne 1978). The species seems to be extremely rare in New Guinea. Wood & Bright (1992) and Bright & Skidmore (1997, 2002) do not list the species from New Guinea, and our two specimens are thus probably the first record from NG. The overwhelming majority of small *Xylosandrus* from NG are *X. morigerus*.

Examined material: Africa, (co-type of *Xylosandrus morstadti* (Eichhoff), nomen nudum, BMNH); Brazilia, (SLW, 12 indiv.), many larvae, multiple families, loan to A. Cognato from an anonymous in Brazil, beetles were attacking orchard trees; New Caledonia, Laguerre, *Swetenia mahogani*, (Christian Mille, 2 indiv.); PNG: Madang Prov. (2), J. Hulcr 2002-2006.

***Xylosandrus crassiusculus* (Motschulsky, 1866)**

J.H. database code: Scol 32

Compared to lectotype photograph in IZM

Diagnosis: Medium-sized, robust species. It differs from other *Xylosandrus* mainly by small and pointed intercoxal prosternal process, the rugose, densely granulated and coriaceous surface of elytral declivity, and by the slightly elevated suture at the end of interstria which results in the end of abdomen appearing angulate, rather than rounded. Body is always brown to red-brown.

Length: 2.7 mm.

Discussion

The species was historically named *X. semiopacus* Eichhoff, because the older Motschulsky's species was rediscovered only recently (Anderson 1975). The species is somewhat variable, which led to the description of several subspecies or forms (currently all synonymized), which could be commonly found at the same localities (Beaver & Browne 1978).

Previously synonymized species: *Xyleborus semiopacus* Eichhoff, *Xyleborus okoumeensis* Schedl, *Dryocoetes bengalensis* Stebbing, *Xyleborus mascarenus* Hagedorn, *Xyleborus semigranosus* Blandford, *Xyleborus declivigranulatus* Schedl, *Xyleborus ebriosus* Niisima

Biology: The pattern of occurrence of this species in New Guinea is unusual, and suggests the hypothesis that the species is not native to the island. The authors collected approximately 1250 individuals around Madang, which indicates that *X. crassiusculus* is one of the most abundant xyleborine species locally. However, despite extensive collecting by these and other authors, only three other records exits: one from a logging are in Wau, Morobe province, 3 specimens in 1981 (deposited in BBM), another two, in

Eggers's collection in USNM from West Papua: one undated specimen from Dutch New Guinea, and another specimen from 1894, Fiume Purari (?). No other ambrosia beetle species displayed such patchy distribution (Hulcr et al. 2007). It is possible that the Madang population is a recent introduction.

Examined material: Malaysia, Sabah, Danum Valley, (Hulcr coll., 5 indiv.); Malaysia, Sabah, Danum Valley, *Artocarpus camansii* trunk, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Mallotus* sp. branches, (Hulcr coll.); Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll.); New Guinea, Morobe, Wau, (BBM, 2 indiv.), 1200m; New Guinea, Morobe, Wau, (BBM), 1350m; New Guinea, Morobe, Wau, (BBM, 3 indiv.); New Guinea, Fiume Purari, (MCG); New Guinea, Madang Province, Ohu, *Gymnacranthera paniculata* trunk, (Hulcr coll.); Sri Lanka, Montagnes de Nura-Ellia, (lectotype photograph, IZM); Thailand, Pong Yaeng N. P., (Hulcr coll., 6 indiv.), R. A. Beaver det.; USA, MD, Patuxent, *Acer rubrum*, (Hulcr coll. 2007); USA, MD, Patuxent Park, *Liquidambar*, (Hulcr coll. 2007, 15 indiv.); PNG: Madang Prov. (1226), J. Hulcr 2002-2006.

***Xylosandrus discolor* (Blandford, 1898)**

J.H. database code: Scol 118

Compared to non-type in NHMW

Diagnosis: One of the smallest *Xylosandrus*. The main difference between this species and other *Xylosandrus* spp. is its sharply truncated elytra surrounded by costate margin on the top and by elevated carina on the declivital bottom. The short and sharply truncated elytra give the species an unusually short, stout appearance. The protibia of this species is very slender as in other *Xylosandrus*, but it is slightly triangular at the distal end, and its socketed denticles are small, and concentrated towards the apex. Procoxae are widely separated, but the intercoxal prosternal process itself is reduced, making the area between coxae flat.

Length: 1.3-2.0 mm.

Discussion

Transferred to *Xylosandrus* from *Xyleborus* by Browne (1963). *Xylosandrus posticestriatus* (Eggers) from SE Asia is probably a junior synonym (R. A. Beaver, pers. comm.). Blandford (1898a) suggested that the species can be distinguished from other *Xyleborus* based on color. Schedl (1959a) mentioned large variation of this species in size, from 1.5 mm. to 2.0 mm.

Biology: Twig borer, rare in New Guinea.

Examined material: PNG: Madang Prov. (4), J. Hulcr 2002-2006.

Xylosandrus hulcri **Dole & Cognato (2009)**

J.H. database code: Scol 342

Compared to holotype in MSUC

Diagnosis: Mid size *Xylosandrus* with black pronotum and the end of abdomen, but yellow to light brown elytra. Its morphological characters are largely shared with *X. rotundicollis* (another montane species), with the exception of carinate end of declivity, blunt intercoxal prosternal process with transversal carina, and the distinctly bicolored elytra. Another similar species is *X. crassiusculus*, except for the anterior edge pronotum bearing short but conspicuous row of serrations, broader prosternal intercoxal process with transversal costa, hairy and shiny surface of elytral declivity with abundant setae-bearing granules, not rugose, dull.

Length: 2.4 mm.

Biology: The ecology of this species is unique among *Xylosandrus* in that it seems to be an obligate mycocleptes. All four known individuals we found creating galleries which closely followed galleries of *Xylosandrus russulus*.

Examined material: PNG: Chimbu Prov. (4), J. Hulcr coll. 2006.

***Xylosandrus mixtus* (Schedl, 1979)**

J.H. database code: Scol 593

Compared to holotype in NHMW

Diagnosis: The species closely resembles *Xylosandrus crassiusculus* and *Xylosandrus hulcri*, but is unusual among *Xylosandrus* spp. because it has antennal club No. 4 (first segment small, convex, second and third segments both corneous and prominent on both faces of the club). The whole body is softly pubescent with long setae, declivital interstriae are a mixture of shining and shagreen surfaces, and minute dense granules.

Length: 2.7 mm.

Discussion

Schedl (1979g) indicated that the species is similar to *Xyleborus setulosus* Eggers from Java. Transferred to *Xylosandrus* by Dole & Cognato (2009) based on the presence of pronotal mycangium and separate procoxae.

Biology: Only one specimen known.

Examined material: New Guinea, Morobe Province, Bulolo, (holotype, NHMW).

***Xylosandrus morigerus* (Blandford, 1894)**

J.H. database code: Scol 63

Compared to holotype in BMNH

Diagnosis: One of the smallest *Xylosandrus*, with greatly reduced length of elytral disc and enlarged surface area of elytral declivity, which gives the specimen almost a globular appearance. Usually black, with sparse vestiture, both pronotum and elytra mostly shining. Elytral declivity greatly varied, ranging from evenly rounded (holotype, many PNG specimens) to a truncated appearance with an additional "hump" in the middle of the slope (many PNG individuals). It has a pronounced elevated costa. Minute setae-bearing granules in interstriae, shallow arrayed strial punctures. Length: 1.4-1.9 mm.

Discussion

Transferred to *Xylosandrus* from *Xyleborus* by Browne (1963) (or possibly by Reitter 1913). The type specimen was collected from an orchid from New Guinea. Holotype locality label almost illegible: "from Orchids, Bal...(?)". Only one of three original specimens remains on the mounting board, and is missing an elytron. In Schedl's collection in NHMW some specimens identified as *X. morigerus* appear to be misidentified, or are examples of great intraspecific variation. Synonymy with *X. difficilis* by Bright & Skidmore (1997: 169) most likely correct, despite some variation in the declivital slope and elytral surface and the poor condition of the lectotype of *X. difficilis*.

Previously synonymized species: *Xyleborus luzonicus* Eggers, *Xyleborus coffeae* Wurth, *Xyleborus difficilis* Eggers

Biology: The most common twig-borer in New Guinea. It is of occasional economic importance in SE Asian plantations, though less common than its relative *Xylosandrus compactus* (Beaver & Browne 1978, Browne 1961c). It often breeds in large tree leafstalks. Kalshoven (1960b) and references therein reported rather heavy infestation of the galleries of *X. morigerus* with at least two species of hymenopteroid parasites (?) in Java, up to 43% galleries affected.

Examined material: New Guinea, (holotype), labeled: "form (*sic*) Orchids, Bal...(?)"; Malaysia, Sabah, Danum Valley, *Parashorea malaanonan* branches, (Hulcr coll.); Malaysia, Sabah, Rhino Ridge, Danum Valley, Burseraceae sp. twigs, (Hulcr coll.); New Guinea, (holotype, BMNH), of *Xyleborus moreqeius* (sic!) Blandf.; New Guinea, (FICB, 2 indiv.); New Guinea, Madang Province, Ohu, *Pterocymbium becarii* twigs, (Hulcr coll.); no label, (allotype of male, BMNH); Thailand, Pong Yaeng N. P., (Hulcr coll.), R. A. Beaver det.; unknown locality, (BMNH, 3 indiv.); locality not recorded, (BMNH); PNG: Madang Prov. (80), Oro Prov. (14), West Sepik (2), J. Hulcr 2002-2006.

***Xylosandrus rotundicollis* (Browne, 1984)**

J.H. database code: Scol 347

Compared to holotype in BMNH

Diagnosis: Rounded and attenuated elytra. Oblique and short declivital costa, not carinate. Intrestrial dots abundant, in some specimens confused. Very abundant long setae on the whole body surface. Pronotal asperities dense and variable in size, anterior edge of pronotum with a short conspicuous row of serrations. Protibia slender, with 6 socketed teeth. Intercoxal prosternal process narrow, pointed, but not as tall as in *X. russulus*.

Surface of declivity the same as that of elytral disc, with abundant strial and interstrial punctures and setae. Size greatly variable, ranging from 2.5 to 4.2 mm. The most similar species is *Xylosandrus hulcri*, from which it can be distinguished by non-carinate end of elytral declivity, pointed intercoxal prosternal process, and uniformly brown elytra (the elytra can be slightly paler at their bases).

Length: 2.5 mm.

Discussion

Almost identical to the holotype from New Zealand, except slightly smaller, and the pronotum a little more angulate frontally. Browne (1984f) suggested that the species may be related to *Anisandrus dispar* (as *Xyleborus*). In the species description, the author indicated a range of sizes between 3.0 to 3.2 mm. Very similar to *Xylosandrus russulus*, only smaller, with more conspicuous interstrial punctuation on elytra, and less pointed prosternal posterocoxal process. Similar to *Xyleborus hulcri*, but lacking the white area of elytral disc, with prosternal intercoxal process pointed, instead of stout and oblique, and free-living, instead of mycocleptous.

Biology: *X. rotundicollis* builds its own independent galleries, unlike the apparently close relative *Xylosandrus hulcri*, which seems to be strictly mycocleptous.

Examined material: New Guinea, Morobe Province, Mount Kaindi, (holotype), 2350 m; PNG: Chimbu Prov. (4), J. Hulcr 2002-2006.

***Xylosandrus russulus* (Schedl, 1942)**

J.H. database code: Scol 325

Compared to holotype in NHMW

Diagnosis: One of the largest *Xylosandrus*. Very similar to *Xylosandrus rotundicollis*, except for its size, elytra surface (declivity shining, bluish opalescent even on old specimens, with almost no interstrial punctures), the shape of prosternal intercoxal process (much taller, pointed), and the protibial shape, which is broadened from about the midlength in *X. russulus* with 7 socketed teeth, and narrow in *X. rotundicollis* with 6 denticles in enlarged sockets.

Length: 3.5-4.2 mm.

Discussion

Xylosandrus russulus is a sister taxon to *X. rotundicollis* in a molecular phylogeny containing many *Xylosandrus* spp. (Dole et al., in review), nevertheless the two taxa are divided by appreciable molecular distance. Shared morphological characters included the pronotal asperities (dense and variable in size), a short row of serrations on the pronotal edge, blunt costa at the posterolateral sides of declivity, abundant erect setae over most of the body. The species was included in *Euwallacea* by Wood & Bright (1992), and transferred to *Xylosandrus* by Dole & Cognato (2009). Schedl (1942c) mentions that *Xylosandrus* (as *Xyleborus*) *russulus* is similar to *Xyleborus lativentris* Schedl from Malaysia, which lacks an impression on elytral declivity. This impression on declivity does not occur in *X. russulus* specimens, including the holotype.)

Examined material: New Guinea, Kupa Range, (FICB), 2000 m a.s.l.; New Guinea, (holotype); PNG: Chimbu Prov. (50), J. Hulcr 2002-2006.

Species reported from New Guinea for which material was not available

***Amasa aglaiae* (Browne, 1984)**

J.H. database code: Scol 827

Length: 3.3 mm.

Discussion

Specimens were unavailable for examination. Browne (1984) relates the species to *A.* (as *Xyleborus*) *amputatus* Blandford, but mentions its larger size and different (not specified) arrangements of elytral punctures. Transferred to *Amasa* by Beaver (1995).

Biology: Reported by Browne (1984) from a log imported from New Britain to Japan.

***Arixyleborus deceptus* (Schedl, 1979)**

J.H. database code: Scol 604

Discussion

Specimens were unavailable for examination. Schedl (1979g) relates the species to *A. granulicauda*, but notes that it is much larger, stouter, elytral disc more strongly striate-punctate, and the apical margin of the declivity without pointed granules.

***Arixyleborus granulicauda* Schedl (1975)**

J.H. database code: Scol 605

Discussion

Type not available. The only specimen available for examination was an individual of *Microperus popondettae* misidentified by Schedl as *Arixyleborus granulicauda*. The status and classification of the species remains unknown. According to Schedl (1975f), the species is similar to *A. abruptus*, but it is easily distinguishable by much slender body shape and by less abrupt slope of the elytral declivity.

Cnestus rotundatus Schedl (1975)

J.H. database code: Scol 611

Length: 2.7 mm.

Discussion

Specimens were unavailable for examination. According to (Schedl, 1975f), the species is allied to *C. pseudosuturalis* Schedl, from which it differs mainly by its uniform black color, bulkier body and much steeper declivity.

Coptodryas amphicauda (Browne, 1986)

J.H. database code: Scol 616

Compared to male paratype in BMNH

Discussion

Female type not available. Transferred to *Coptodryas* by Beaver (1995). Browne (1986c) described the species as related to *Micorperus perparva* (Schedl) (as *X. perparvus*), with the distinction that the apex of each elytron is weakly produced.

Biology: Recorded by Browne (1986c) from a log imported from New Guinea to Japan.

Examined material: New Guinea, (BMNH), male.

Coptodryas rosseli (Schedl, 1975)

J.H. database code: Scol 623

Compared to holotype in AMNH

Discussion

The identity of this species is unclear. Schedl (1975m) described a species *Taphroterus rosseli* Schedl. The holotype is deposited in AMNH under cat. No. 1379, and a photograph is available on the museum's website. It agrees with the paratype in NHMW. The genus *Taphroterus* is now considered a synonymy of *Taphrorychus*, and a member of Dryocoetina. Wood and Bright (1992) indicated the existence of *Coptodryas roselli* Schedl, and synonymized the species *Coptodryas chimbui* (Schedl, 1973b: 74) with it. However, there is no evidence that the xyleborine species exists, further, the holotype of the alleged *Coptodryas rosseli* has the same collection data in Wood & Bright (1992) as the real holotype of *Taphrorychus* (as *Taphroteres*) *rosseli* Schedl. Thus, *Coptodryas rosseli* Schedl is considered an invalid combination.

Previously synonymized species: *Xyleborus chimbui* Schedl

Examined material: New Guinea, Rossel Island, Abaleti, (paratype of *Taphrorychus* (as *Taphroterus*) *rosseli* Schedl, NHMW).

Cyclorhipidion brevius (Eggers, 1923)

J.H. database code: Scol 627

Discussion

Specimens were unavailable for examination. Type locality (Wood & Bright, 1992): Deutsch New-Guinea (=West Papua), Kaiserin Augustafluss. Comment by Wood & Bright (1992): "Type in MNB, apparently still in Eggers Collection when Schedl borrowed it, now in NHMW." Comment from J. Willers at the Berlin museum: "*X. brevior* (*brevius*?) seems to be have been lost during the WWII."

Cyclorhipidion hastatum **(Schedl, 1942)**

J.H. database code: Scol 630

Compared to male holotype in NHMW

Discussion

Female holotype not available for examination. One female specimen identified as *X. hastatus* by S. L. Wood in the BBM was a misidentified *Cyclorhipidion perpilosellum*. A male labeled "Type *Xyleborus hastatus* Schedl; female; Kalshoven lgt. Mount Gede, Java, Pasang". The specimen is clearly a male.

Examined material: Indonesia, Java, Mt. Gede, (holotype), label: "female", but the specimen is a male; New Guinea, Star Mts, (BBM).

Euwallacea kersianus **(Browne, 1981)**

J.H. database code: Scol 816

Discussion

Specimens were unavailable for examination. Browne (1981a) mentioned its similarity to *Anisandrus dispar* (as *Xyleborus*), and noted that it is smaller, with different elytra sculpturing. Beaver (1995) moved the species to *Euwallacea*. It remains unverified whether the species belongs to *Euwallacea*, *Wallacella*, or *Anisandrus*. The species is not treated here any further.

Biology: Reported by Browne (1981a) from a log imported from New Britain to Japan.

Webbia circumcisus **Schedl (1975)**

J.H. database code: Scol 656

Diagnosis: Schedl distinguishes it from other *Webbia* by the pronotum having the antero-lateral angles more pronounced, bearing a few small asperities, the declivital face is opaque, densely punctured, the lower margin finely carinate.

Length: 1.9 mm.

Discussion

Holotype allegedly from New Guinea (Wood & Bright, 1992), unfortunately no specimen of this species was available for examination. Wood & Bright (1992) indicated that the holotype is deposited in AMNH; this was not confirmed by the museum staff. Schedl (1975f) relates the species to *Webbia talauticus*(sic) group (changed to *W. talauricus*). The species is not treated here.

Webbia picicauda **Schedl (1979)**

J.H. database code: Scol 659

Discussion

Species of unknown status. Described from New Guinea, but no specimen of this species was available for examination. The holotype was allegedly deposited in NHMW, but

Wood and Bright (1992) indicated that the holotype was not located. The present authors also did not find the specimen. The species is not treated here.

Xyleborus cavatus **Browne (1980)**

J.H. database code: Scol 817

Discussion

Specimens were unavailable for examination. Holotype not located in BMNH.

Biology: Browne (1983) reported one specimen imported from West Irian into Japan.

Xyleborus fuyugei **Schedl (1973)**

J.H. database code: Scol 686

Discussion

Specimens were unavailable for examination.Schedl (1973f) relates the species to *Xyleborus subagnatus* Schedl, and notes that it differs in the larger size, a little more oblique elytral declivity, and much smaller granules on the declivital face.

Xyleborus graniger **Schedl (1955)**

J.H. database code: Scol 688

Discussion

No specimen available for examination. Schedl (1955b) classified the species in his Xylebori granulosi group.

Xyleborus lineatopunctatus **Eggers (1927)**

J.H. database code: Scol 820

Length: 1.8 mm.

Discussion

Eggers (1927b) in his description of the species mentioned that it is related to both the tropical *Xyleborus* s. str. (*X. perforans*, *X. affinis*) but even more to the Palearctic *X. cryptographus*. According to the original description it should reside in "sammlung Eggers". According to Anderson and Anderson (1971), the holotype resides in USNM, but was not available for examination. One specimen from NHMW was available, labeled "compared to holotype in USNM" by Schedl. However, the specimen belongs to the genus *Cyrtogenius* sp. (Dryocoetina). Thus the identity of *X. lineatopunctatus* is unknown.

Examined material: New Guinea, Oro Province, Popondetta, (NHMW), *Cyrtogenius* sp. labeled: "Mit *X. lineatopunctatus* Eggers Mus. USNM verglichen Schedl 1970".

Xyleborus operosus **Schedl (1973)**

J.H. database code: Scol 699

Compared to holotype in NHMW

Discussion

Female type not available. The holotype (the only known representative) is a male of another unidentified species, probably *Euwallacea* sp. The pronotum has the typical concave oblique anterior margin, miniaturized antennal clubs and eyes, and fused elytra. Type never sent to BPBM, its published destination.

Examined material: New Guinea, Morobe, Wau, (holotype).

***Xyleborus scabricollis* Schedl (1975)**

J.H. database code: Scol 708

Discussion

Described by Schedl (1975g) as *Ozopemon scabricollis*. The species was included in Xyleborina by Wood & Bright (1992) without justification. Material was not available for examination, the species is not treated here.

***Xyleborus suaui* Schedl (1973)**

J.H. database code: Scol 710

Discussion

Schedl (1973f) (change of citation compared to Wood & Bright (1992)) related the species to *Xyleborus judenkoi* Schedl, and noted that it differs by a slightly larger size, it is more slender, and has a shorter, more oblique declivity without larger granules. The identity of the species is unclear. The AMNH collection houses a holotype of *Coccotrypes* (as *Poecilips*) *suaui* Schedl (Dryocoetina), and the NHMW hosts two paratypes of the same dryocoetine species. The authors could not locate a representative of *Xyleborus suaui*.

***Xyleborus takeharai* Browne (1983)**

J.H. database code: Scol 714

Length: 4.0 mm.

Discussion

According to Browne (1983b), the species resembles *X. siclus*, but is smaller, and the elytral declivity is strongly flattened. Holotype not found in BMNH, the species is not treated here.

***Xyleborus teminabani* Browne (1986)**

J.H. database code: Scol 715

Discussion

Browne (1986c) described the species as related to *X. siclus*, but noted that it differed in the elytra which were granulate well before the declivity. Holotype not found in BMNH, the species is not treated here.

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