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PHYLOGENETIC ANALYSIS OF THE LOPHOSPIRIDAE
(GASTROPODA : PLEUROTOMARIINA)
OF THE ORDOVICIAN AND SILURIAN

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PHYLOGENETIC ANALYSIS OF THE LOPHOSPIRIDAE (GASTROPODA: PLEUROTOMARIINA) OF THE ORDOVICIAN AND SILURIAN

By

Peter J. Wagner III

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ABSTRACT

PHYLOGENETIC ANALYSIS OF THE LOPHOSPIRIDAE (GASTROPODA: PLEUROTOMARIINA) OF THE ORDOVICIAN AND SILURIAN

By

Peter J. Wagner III

The Ordovician-Silurian Lophospiridae are one of the earliest diverse gastropod clades within the suborder Pleurotomariina. A phylogenetic analysis was conducted using 92 meristic characters for 47 lophospirid species in the genera *Lophospira*, *Donaldiella*, *Trochonemella*, *Schizolopha*, *Ruedemannia*, *Arjamannia*, and *Longstaffia*. Additional Ordovician-Silurian species from non-lophospirid genera such as *Trochonema* and *Eunema* that have been linked with the Lophospiridae were included also. To recognize patterns of parallel evolution, the phylogenetic analysis nested species by time of first appearance. Three sub-families are recognized, the Lophospirinae (*Ambilophospira* n. gen., *Lophospira*, *Paralophospira* n. gen., *Donaldiella*, *Loxoplocus* and *Eunema*), the Ruedemanniinae (*Hellermannia* n. gen., *Schizolopha*, *Ruedemannia*, *Arjamannia*, ?*Longstaffia*, and the later *Worthenia*) and the Trochonemanninae (*Trochonemella* and *Trochonema*). Four conclusions were drawn from the analysis: 1) the major subclades within the family were derived from a very few species of the metagenera *Ambilophospira* and *Lophospira*; 2) Ordovician genera classified in the superfamily Trochonematiina evolved independently from different lophospirid clades, hence this superfamily is polyphyletic; 3) the revised taxonomies suggest that previous taxic diversity studies at higher levels do not represent the evolutionary patterns of clades but of historically recognized morphotypes; and, 4) long-recognized genera such as *Lophospira* are more likely to be over-split at the species level than more recently recognized genera, and re-appraisals of previous species descriptions are necessary before conclusions about species-level diversity patterns can be made.

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INTRODUCTION

The Lophospiridae of the Ordovician and Silurian represent one of the earliest groups of pleurotomariine gastropods to achieve significant levels of diversity. Many species and several genera have been described, but no rigorous phylogenetic analyses have ever been attempted. The lophospirids diversified early in the history of the Pleurotomariacea and a phylogenetic reconstruction of the group would be interesting for a number of reasons. First, these early species represent the stem members of a family that lasted until the Triassic (Knight *et al.* 1961) and reconstructing the early phylogenetic relationships can produce information about the relationships of later members (e.g Smith 1988, Massare & Callaway 1990). Second, the lophospirids have been suggested as the ancestors of such higher taxa as the pleurotomariine family Phanerotrematidae (Ulrich & Scofield 1897) and the superfamily Trochonematacea (Knight *et al.* 1961). Early pleurotomariines in general have been suggested as the possible ancestors for the suborder Murchisoniina (Donald 1902; Knight *et al.* 1961) and some members of the Lophospiridae may represent valid potential ancestors. Thus, a phylogenetic analysis of the early Lophospiridae could offer information not only about the family, but also about the early evolution of the pleurotomariines.

Another purpose of this study is to examine the validity of the current taxonomy and better estimate early lophospirid diversity at lower taxonomic levels. Early Paleozoic Lophospiridae are divided into two subfamilies, six genera and three sub-genera. Most of these taxonomic units were used specifically as morphologic grades. For example, Knight (1944) used the concepts of *Lophospira*, *Donaldiella* and *Loxoplocus* explicitly to represent morphotypes, considering them "artificial and intergrading" (Shimer & Shrock 1944 : 449). Others erected genera that were polyphyletic in their original descriptions (e.g. *Schizolopha* in Ulrich & Scofield 1897, p. 962). Therefore, the number of higher monophyletic lophospirid clades is unclear. It also is unclear how many early Paleozoic lophospirid species exist

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existed. Over 100 species have been described from the genus *Lophospira* alone, but early workers emphasized any morphologic, temporal and/or biogeographic differences and may have oversplit species. For example, Ulrich & Scofield (1897) described 38 species from Middle and Upper Ordovician of the midwestern and eastern North America; Longstaff *née* Donald (1902, 1906, 1924) described 21 from the Ordovician and Silurian of Britain, and Grabau (1922) and Kobayashi (1930) described 14 from the Middle Ordovician of northeastern Asia. Endo (1932) described eight species from the same Early Ordovician limestone unit. While *Lophospira* does represent one of the oldest molluscans with congeneric species in the same assemblage (Tofel & Bretsky 1987), more species have been named than can be justified. Questions about lophospirid species longevities, biogeographic ranges, speciation rates and patterns of species diversity can not be asked without significant taxonomic revision.

MATERIALS

Several hundred silicified specimens collected in Kentucky by the U.S.G.S. in the 1960's and early 1970's and representing several species from the Caradoc and the Ashgill were examined. The depositional environments have been analyzed for most of the formations (Weir & Peck 1968; Anstey & Fowler 1969; Cressman 1973). Faunal descriptions have been given for brachiopods (Howe 1979), bryozoans (Karklins 1984), rugosan corals (Elias 1983), echinoderms (Parsley 1981) and trilobites (Ross 1979), although not for molluscs. Few paleoecological studies have been conducted (Ettensohn *et al.* 1986) to date.

In addition, specimens housed at the United States National Museum were examined. These included all Lower Ordovician species described from southeastern North America by Butts (1926) and southern Manchuria by Endo (1932), all of the Middle and Upper Ordovician lophospirids from North America previously described by Ulrich & Scofield

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(1897), Rohr (1980, 1988) and Rohr & Boucot (1985), all of the Upper Ordovician and Silurian species described by Peel (1975) from northeastern North America and Britain and one of the several Silurian lophospirid species from northern Europe described by Lindström (1884). Additional Ordovician and Silurian material still listed as *Pleurotomaria* or *Murchisonia* was not examined due to time constraints, and was therefore excluded from this study. Descriptions of some of the species examined are found in Appendix A.

Previous descriptions were consulted in order to determine the extent of temporal and geographic distributions of the different lophospirid species and sub-groups. In addition to the works cited above, these include Hall (1847, 1852), Salter (1859), Meek & Worthen (1873), Whiteaves (1884, 1895, 1897, 1906), Longstaff *née* Donald (1902, 1906, 1924), Raymond (1908), Grabau & Sherzer (1910), Foerste (1914, 1922, 1924), Grabau (1922), Twenhofel (1928), Kobayashi (1930, 1958), Okulitch (1935), Shrock & Raasch (1937), Cullison (1938), Wilson (1951), Yü (1961a, 1961b), Saladzhias (1966), Steele & Sinclair (1971), Kurushin (1986) and Tofel & Bretsky (1987). Relevant paleoenvironmental and paleoecological studies include Schrock (1937), Bretsky (1970), Bretsky & Bretsky (1975), Harrison & Harrison (1975), Stanley (1977), Peel (1978), Copper & Grawbarger (1978), and McNamara (1978).

METHODS

Determination of Traits and Character States

Temporal information was the most important criteria used in determining character polarities. Outgroup comparisons were also commonly used with ontogenetic information used infrequently. Transformation series analysis as described by Mickevich (1982) was used to determine the existence and relative polarities of morphoclines. Temporal information was used as described by Harper (1976) and Szalay (1977) with states appearing earlier in the fossil re

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fossil record considered more primitive than homologous states appearing later. There are obvious limits to this approach - character states first appearing lower in the same rock unit may be older than those appearing higher, but this may reflect either regional depositional patterns or environmental shifts (Schindel 1980, 1982). Confidence intervals were calculated to determine the likelihood of character states first known from younger strata actually being older than states first known from older strata (Table I). Table I lists the first known appearances of the older state (with the earliest ages of states also apparent in Upper Cambrian pleurotomariines marked

Table I 95% Confidence Intervals for Lophospirid Character States

Character	First Known Appearance of Older State	First Known Appearance of Younger State	Total Horizons for Species with Younger State (H)	C_1 = 99% Extension of Younger State's First Appearance[1]
1(0 -> 1)	495 ma*	485 ma	257	486.1 ma
2(0 -> 1)	495 ma*	466 ma	12	487.8 ma
3(0 -> 1)	495 ma*	485 ma	232	486.2 ma
3(1) -> 4(1)	485 ma	471 ma	113	472.3 ma
5(0 -> 1)	495 ma	471 ma	102	472.4 ma
6(0 -> 1)	495 ma	468 ma	16	477.3 ma
6(1 -> 2)	468 ma	466 ma	14	476.2 ma
7(0 -> 1)	495 ma	471 ma	159	472.4 ma
8(0 -> 1)	495 ma	471 ma	100	472.1 ma
9(0 -> 1)	495 ma	471 ma	100	473.0 ma
10(0 -> 1)	495 ma	480 ma	85	468.5 ma
10(0 -> 2)	495 ma	427 ma	6	459.0 ma
11(0 -> 1)	495 ma	463 ma	59	464.3 ma
12(0 -> 1)	495 ma	471 ma	38	478.4 ma
13(0 -> 1)	495 ma	471 ma	21	482.2 ma
14(0 -> 1)	495 ma	471 ma	88	472.8 ma
15(0 -> 1)	495 ma	467 ma	19	476.2 ma
16(0 -> 1)	495 ma	471 ma	87	472.8 ma
17(0 -> 1)	495 ma	485 ma	273	486.0 ma
17(0 -> 2)	495 ma	471 ma	41	476.7 ma
17(0 -> 3)	495 ma	468 ma	11	492.6 ma
17(1 -> 2)	485 ma	471 ma	41	476.7 ma
18(0 -> 1)	495 ma	471 ma	41	475.4 ma
19(0 -> 1)	495 ma	450 ma	16	443.0 ma
19(0 -> 2)	495 ma	427 ma	4	444.6 ma
19(1 -> 2)	450 ma	427 ma	4	444.6 ma
20(0 -> 1)	495 ma	427 ma	5	436.1 ma
21(0 -> 1)	495 ma	455 ma	3	477.5 ma
22(0 -> 1)	495 ma*	485 ma	235	486.2 ma
22(1) -> 23(1)	485 ma	467 ma	85	469.4 ma
24(0 -> 1)	495 ma*	471 ma	62	473.8 ma
25(0 -> 1)	495 ma*	462 ma	42	463.1 ma
26(0 -> 1)	495 ma	471 ma	49	475.7 ma
27(0 -> 1)	485 ma	468 ma	16	479.9 ma
28(0 -> 1)	485 ma	450 ma	11	439.8 ma
29(0 -> 1)	495 ma	471 ma	65	468.9 ma
29(0 -> 2)	495 ma	455 ma	2	753.0 ma
30(0 -> 1)	495 ma	485 ma	250	486.1 ma
30(1) -> 31(1)	485 ma	471 ma	87	469.7 ma
32(0 -> 1)	485 ma	471 ma	23	462.2 ma
33(0 -> 1)	495 ma	454 ma	71	473.7 ma
34(0 -> 1)	485 ma	450 ma	7	467.2 ma
35(0 -> 1)	485 ma	444 ma	7	467.0 ma
35(1) -> 36(1)	444 ma	427 ma	4	448.8 ma
36(0 -> 1)	495 ma	480 ma	107	482.0 ma
38(0 -> 1)	495 ma*	463 ma	24	470.4 ma
38(1) -> 39(1)	463 ma	451 ma	15	460.1 ma
40(0 -> 1)	495 ma*	463 ma	3	532.0 ma
41(0 -> 1)	495 ma*	450 ma	15	460.1 ma
41(1) -> 42(1)	450 ma	435 ma	13	440.1 ma
42(1) -> 43(1)	435 ma	431 ma	3	471.5 ma
42(1) -> 44(1)	435 ma	435 ma	10	440.7 ma
44(1 -> 2)	435 ma	435 ma	4	449.6 ma
45(0 -> 1)	495 ma*	427 ma	3	481.0 ma
46(0 -> 1)	495 ma*	460 ma	62	489.8 ma
46(1 -> 2)	485 ma	435 ma	12	440.7 ma
47(0 -> 1)	495 ma*	450 ma	22	456.4 ma
47(0 -> 2)	495 ma*	471 ma	91	472.1 ma
48(0 -> 1)	495 ma*	471 ma	44	476.1 ma
48(0 -> 2)	495 ma*	455 ma	63	468.3 ma
49(0 -> 1)	495 ma	485 ma	219	486.3 ma
49(1) -> 50(1)	495 ma	450 ma	24	455.8 ma
51(0 -> 1)	495 ma*	480 ma	40	485.6 ma
52(0 -> 1)	495 ma*	444 ma	18	458.1 ma
52(1) -> 53(1)	444 ma	444 ma	13	462.2 ma
54(0 -> 1)	495 ma	483 ma	36	493.6 ma
55(0 -> 1)	495 ma	485 ma	299	485.9 ma
55(1) -> 56(1)	485 ma	480 ma	20	492.3 ma
56(1) -> 57(1)	480 ma	471 ma	10	476.3 ma
58(0 -> 1)	495 ma	468 ma	16	483.9 ma
59(0 -> 1)	495 ma	457 ma	23	456.1 ma
60(0 -> 1)	495 ma	485 ma	218	486.3 ma
60(1) -> 61(1)	485 ma	480 ma	84	482.6 ma
61(1 -> 2)	480 ma	471 ma	16	483.9 ma
62(0 -> 1)	495 ma	463 ma	90	463.7 ma
62(1) -> 63(1)	463 ma	460 ma	36	463.5 ma
64(0 -> 1)	495 ma*	467 ma	79	467.8 ma
64(0 -> 2)	495 ma*	480 ma	20	492.3 ma
64(0 -> 3)	495 ma*	450 ma	8	464.0 ma
65(0 -> 1)	495 ma*	457 ma	6	466.9 ma
66(0 -> 1)	495 ma	450 ma	8	464.0 ma
67(0 -> 1)	495 ma	463 ma	49	464.7 ma
67(1) -> 68(1)	463 ma	460 ma	36	463.5 ma
69(0 -> 1)	495 ma	471 ma	24	479.0 ma
69(1) -> 70(1)	471 ma	450 ma	8	464.0 ma
71(0 -> 1)	495 ma*	483 ma	36	493.6 ma
71(0 -> 2)	495 ma*	450 ma	18	458.1 ma
72(0 -> 1)	495 ma*	480 ma	20	495.4 ma
73(0 -> 1)	495 ma	483 ma	325	487.8 ma
73(0 -> 1)	495 ma	485 ma	37	486.1 ma
74(0 -> 1)	495 ma*	485 ma	199	486.4 ma
75(0 -> 1)	495 ma*	483 ma	37	486.1 ma

[1] extension = earliest appearance of state + ½α(time span of all species displaying state) with $\alpha = (1 - C_1)^{-1/(H - 1)}$ (From Marshall 1990).

*: state already present on Upper Cambrian pleurotomariines.

with an asterisk), the earliest possible appearances of the younger states and a 99% level extension of the temporal range for the younger state. The table has been amended to include comparisons between intermediate and most highly derived states of morphoclines (see Appendix B and discussions below), and the intermediate steps are used as older in these cases. In 78 of the 92 cases, the apparently younger state (or states) were found to be significantly younger than the older states at a confidence level of 99%. The older states in these cases were considered primitive to the younger ones.

The number of horizons per state is the total number of formations from each site that the species sharing the derivation are known from. These were based upon a survey of the literature. The number of horizons species were found at is vague in many descriptions and minimum numbers were used (e.g. horizons for a "few" localities). Therefore the given horizons represent underestimates for most states.

The origins of fossil species (and their character states) known from relatively few horizons and/or over a significant temporal range can not be described with as much confidence as can those known from many horizons and/or restricted time spans (see Marshall 1990 Table 1). When calculating confidence intervals the known temporal range of a group is multiplied by a coefficient α (see bottom of Table I). This coefficient α is calculated in part using the negative reciprocal of the number of fossiliferous horizons known for the group as an exponential. Thus fewer horizons produce greater α's and therefore greater and less certain confidence intervals. Herein lies the major weakness of using confidence intervals, for this procedure presumes that strata throughout the temporal range of a group have been relatively equally well studied. Character states with under 10 horizons are usually associated with Silurian lophospirids which have been much less thoroughly described and studied than most Ordovician species. Silurian lophospirids are therefore known from far fewer horizons than their Ordovician relatives and states first appearing in the Silurian are thus often

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statistically less likely to be younger than are states first known from the Middle or Upper Ordovician. However, while the absence of these character states among the well known Ordovician species can not be taken into account when calculating confidence intervals, it was considered when determining the polarities of character states. Therefore, for most lophospirid character states, if a state is known to have existed before the earliest appearance of a homologous state, it can usually be assumed with some confidence that the former state was in fact older than and therefore potentially primitive to the younger homologous state.

Homoplasy affects confidence intervals in two ways. When similar species were contemporaneous, the convergent character states have additional horizons within the same temporal range and the apparent temporal ranges for the states are made more robust. However, when similar species are widely spaced in time and known from few horizons each, the origin of the convergent states is much less clear. The latter circumstance appears to be far more common than the former. In these cases, methods other than temporal analysis had to be used to determine character state polarities.

Outgroup analysis is preferred by many workers (e.g. Farris 1982), but proved to be of limited use here. The Lophospiridae represent one of the oldest and most primitive well-known groups of pleurotomariines and other Ordovician pleurotomariines do not represent good outgroups. Further, as pleurotomariines represent a very primitive group within the Gastropoda (Yochelson 1968) non-pleurotomariine taxa could not be reliably used. When possible the Upper Cambrian - Lower Ordovician pleurotomariine genera *Sinuopea* and *Taeniospira* were used as outgroups. While these genera represent the only two pleurotomariines species older and more primitive than the Lophospiridae, they are not as well known as genera such as *Lophospira* and outgroup comparisons could not be made for many character states. When they could be done, outgroup comparisons agreed with temporal information for establishing the polarities of characters such as prosocline growth

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lines, the presence of a small umbilicus, the absence of an upper carina, general whorl number and the alignment of the whorls. Polarities suggested by outgroup analysis differed with those suggested by temporal comparisons for only one trait, the convexity of the whorls. While earlier pleurotomariines possessed convex upper slopes, the earliest lophospirids possessed concave ones with the whorls of later species being more ventricose. However, the upper whorl slope of *Taeniospira* was flatter than that of *Sinuopea*. As the former genus is in other ways intermediate between *Sinuopea* and early *Lophospira*, it appears that the polarity of this trait within the Lophospiridae is opposite of its polarity within early pleurotomariines in general.

Ontogenetic comparison is another favored method of determining character polarity (e.g. Nelson 1978; de Queiroz 1985). Assuming less general morphologies to be more derived than more general morphologies agreed with temporal information for traits such as spiral ornamentation. However, most lophospirids are morphologically simple and character states are difficult to describe in terms of relative complexity. Another line of ontogenetic evidence involves the assumption that more primitive traits and character states generally appear earlier in ontogeny than more derived ones (e.g. Hennig 1966). This agreed with temporal evidence regarding the primitive suture point, and also for some more specific traits such as the development of selenizone imbrications on *Trochonemella* species and the re-emergence of the upper carina on some Silurian *Arjamannia* species. In general, ontogenetic methods were of limited use in determining character polarity.

Where ambiguity existed on the magnitude of traits (e.g. "strong" versus "very strong"), only a single derived state was used. Traits based upon growth parameters such as whorl expansion rates were always considered unordered owing to the easy mutability of growth parameters (Bookstein *et al.* 1985 Chap 5). For more qualitative traits clearly showing multiple states, potential morphoclines were determined using transformation series analysis

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as described by Mickevich (1982). If different states were consistently shown to be independently derived from the primitive condition, they were re-coded as separate traits. If states appeared to have multiple possible ancestral states, they were considered independent states of the same trait and kept unordered. For character states shown to represent morphoclines, either additive binary coding or nonredundant linear coding as described by O'Grady & Deets (1987) were used. There is no difference in the way PAUP perceives either style. For the sake of easier data entry and legibility, additive binary coding was generally used for features concerning many taxa while the nonredundant linear coding was used for traits applying to few taxa.

Distinguishing between separately derived states and continuous morphoclines is crucial because of the differences in importance attached to the sharing of the different types of states. If two species exhibit different states for a trait with unordered states, they are considered to differ by only one step by PAUP (assuming no weighting). However, if the states are presumed to be independent and are coded as separate traits, the difference between the two is effectively doubled. Finally, if a series of traits was determined to represent a continuous morphocline, the effective significance of the most derived states can be very high.

Traits and Character States Used

While belonging to a primitive group and generally possessing relatively simple morphologies, lophospirids display a surprising number of different traits and character states. The traits and character states used in this analysis are described below, with the resulting data matrix in Appendix C. States described as appearing significantly later or earlier than others are considered significantly so at a 99% level of confidence (see Table I).

Character 1. Growth line strength. Fine growth lines occur on outgroup taxa, appear significantly earlier within the Lophospiridae than sharper growth lines and are therefore

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presumed to represent the primitive state. As the growth lines of later, derived species are observable even on more poorly preserved specimens this is not thought to be a preservational artefact. Different degrees of coarseness of growth lines may exist, but no attempt was made to code these because of the possibilities of ecophenotypic or preservational differences. Very coarse growth lines are often described, but these are always on species such as *Lophospira helicteres* or *Trochonemella notablis* (e.g. Wilson 1951; Tofel & Bretsky 1987) displaying gerontic phases. Gerontic whorls were disregarded here as their growth lines are usually strongly exaggerated.

Character 2. Lamellose Growth Lines. Some *Trochonemella* and *Longstaffia* species exhibit cyclical changes in growth line strength. This is not observed on older *Lophospira* or outgroup species and is therefore presumed to represent a derived condition. As other lophospirids from the same localities display evenly strong growth lines, lamellose growth lines are not thought to be a solely ecophenotypic feature. While lamellose growth lines are sometimes described as a variable feature on some early *Lophospira*, these are haphazard rather than cyclical on such species and generally observed only on gerontic whorls.

Characters 3 - 4. Growth Line Sweep. Strongly prosoclinal growth lines are displayed on outgroup taxa and appear significantly earlier among lophospirids than more orthoclinal growth lines. Prosocline growth lines are therefore presumed to represent the more primitive condition. Among orthoclinal lophospirids, a major group of lophospirids (e.g. *Lophospira milleri* or *Ruedemannia* species) are orthocline, with growth lines straight over the suture point but abaperturally swept to the selenizone. Other lophospirid species (e.g. *L. centralis* or *L. helicteres*) display almost no growth line curvature. The latter state appears significantly later than the former and transformation series analysis indicates that the latter is derived from the former. Thus for characters 3 and 4 species such as *L. milleri* are coded {10} while those with growth lines like *L. helicteres* are coded {11}. Species with the upper carinae clos

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closer to the selenizone exhibit intermediate growth line sweep. However, as this is directly correlated with the upper carina location, coding this reduction in growth line sweep would be redundant with the coding of Character 26.

Character 5. Lunulae Shape. The lunulae of the earliest lophospirids have a sharp "V" -or "U"-shape. Some of the later, more orthoclinal species (e.g. *Lophospira helicteres* or *L. centralis*) display much straighter lunulae. As this appears significantly later than more acute lunulae, straighter lunulae are presumed to be derived. Straightened lunulae are not strictly correlated with characters 3 and 4 and therefore considered to represent an independently derived state.

Character 6 (States 1 & 2). Imbricated Lunulae. The lunulae of most lophospirids are approximately as strong as the growth lines, which is assumed to represent the primitive condition. *Trochonemella penguini* n. sp. displays imbricated lunulae on juvenile whorls, with the adult whorls exhibiting fine lunulae as seen on other lophospirids (State 1). These imbrications are fixed throughout life on the slightly younger *T. notablis*, and similarly displayed on all later *Trochonemella* (State 2). Transformation series analysis suggests that this represents a morphocline with State 2 derived from State 1.

Character 7. Selenizone Width. Most species, including early ones such as *Lophospira perangulata*, have a selenizone width of approximately 0.75 mm wide at a whorl height of approximately ten millimeters. Some later species (e.g. *L. helicteres* or *Ruedemannia lirata*) show substantially wider selenizones at the same whorl heights, usually from 1 - 1.5 mm. Wider selenizones are thought to be derived as they appear significantly later than thinner selenizones.

Character 8. Selenizone Loss. See *Trochonemella/Trochonema* discussion below.

Character 9. Selenizone Protrusion. The selenizone does not protrude significantly on most lophospirid species, with little change in the angle between the upper and lower ramps. The selenizone of some later species juts out strongly, usually with a noticeably square shape. This state appears significantly later than the non-protruding state and is therefore thought to be derived. (In some later species increased base width reduces the selenizone protrusion relative to the lower whorl, although it is still observable relative to the upper whorl).

Character 10 - 12. Selenizone Middle Thread Strength. The selenizones of most pre-Caradoc lophospirids exhibit three fine lirae of equal strength. This state appears significantly earlier than any other and is therefore considered to represent the primitive condition. A noticeably thicker middle lirae is present on some later species such as *Lophospira helicteres* or *L. quadrisulcata* (Character 10 State 1). *Longstaffia* species show an extremely thick middle thread (Character 10 State 2). It is not clear if there is a relationship between the two states so Character 10 was run as an unordered series. Species such as *L. oweni* possess middle threads wider but duller than bordering lirae and that often becomes indistinguishable with age (Character 11). Finally, the middle thread is noticeably weaker than the bordering lirae on some *Donaldiella* species (Character 12). There is no indication that any of the three derived states are connected to another.

Character 13 - 14. Trilineate Selenizone. A trilineate selenizone is one of the most diagnostic lophospirid traits and appears significantly earlier within the Lophospiridae than either the absence of the middle thread (Character 13) or of the bordering lirae (Character 14). The former character state is observed on post-Llandeilo *Trochonemella* species and as older *Trochonemella* retain three equally strong selenizone lirae, Character 13 is not considered a derivation of either Characters 11 or 12.

Character 15. Serrated Middle Lirae. Serrated carinae were originally described as a diagnostic trait of the genus *Lophospira* (Whitfield 1886), but they appear on only two known species, *L. serrulata* and *L. pteronoides*. This condition appears significantly later than

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simple thread-like lirae and is therefore considered derived. While it is not clear that feature is homologous between the two, given its uniqueness the two are coded as having the same trait. The imbricated lunulae on at least one species of *Trochonemella* can resemble this trait. However, the lunulae on those *Trochonemella* can easily be distinguished from the serrations of *L. serrulata* by their scoop-like nature (see Appendix A).

Character 16. Mid-Whorl Internal Channel. An internal channel beneath the mid-whorl carina is cited as a diagnostic trait of the Trochonematiina (Knight *et al.* 1961 p. I224). However, this trait is weakly present in primitive lophospirids such as *Lophospira perangulata*. A much stronger internal channel approaching the state found on *Trochonema* appears in *Trochonemella trochonemoides*. As this appears significantly later than the weaker internal channels of *Lophospira* it is considered derived.

Character 17 (States 1 - 3). Upper Ramp Shape. On early lophospirids the upper ramp is very concave. This state appears significantly earlier than any of other states displayed by lophospirids and is thought to be the primitive condition (although outgroup taxa display convex upper ramps). Upper ramps of some later species are significantly less concave (State 1), flat (State 2) to convex (State 3). Somewhat concave ramps appear significantly earlier than flat ones and transformation series analyses suggest the former condition is primitive to the latter. However, convex upper ramps appear significantly later than the primitive condition only and character analyses suggest that this condition was derived from both somewhat convex and flat ramps. Thus, although a morphocline appears to exist, the third state could not be accurately placed relative to the first and second states and had to be considered unordered. Also, this is a trait not easily quantified for some specimens and it may be complicated by strong upper whorl carinae or protruding selenizones making the whorl (as opposed to the upper ramp) appear more concave.

Character 18. Elongated Upper Ramp. Outgroup taxa display nearly symmetrical

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upper and lower whorls. Many *Donaldiella* species have a noticeably longer upper ramp. As this appears significantly later within the Lophospiridae than symmetrical whorls and because of the outgroup species, elongated upper ramps are thought to represent the derived condition. While this feature could be simulated by a warping of the whorl placing part of the lower ramp length under the selenizone (fig. 1d), the expected accompanying change in the angle between *Donaldiella* upper ramps and selenizones does not occur (fig. 1b).

Character 19 (States 1 & 2). Lower Ramp Shape. Flat lower ramps appear on early species such as *Lophospira perangulata* and appear significantly earlier than more convex ones (lower ramps are often described as concave, but this is due to the protruding of both the selenizone and lower carina). Some later species display slightly convex lower ramps (State 1) or even extremely convex ones (State 2). Neither appears significantly earlier than the other and character analysis does not suggest this to be a continuous morphocline.

Character 20 - 21. Lower Ramp Lengths. As stated above, outgroup taxa and early *Lophospira* species exhibit nearly equal sized upper and lower ramps. Species such as *Donaldiella decursa* and *D. conoidea* exhibit lower ramps so strongly reduced that the lower carina appears almost as an umbilical carina (Character 20 - see Fig. 1c). Lower ramps noticeably longer than upper ramps occur in *Longstaffia* species (Character 21). While

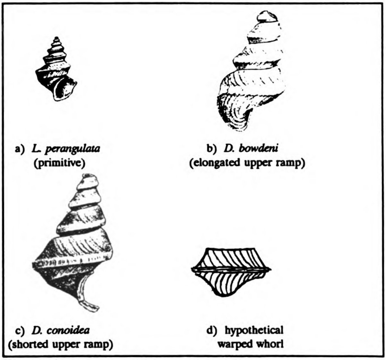
a) *L. perangulata* (primitive)
b) *D. bowdeni* (elongated upper ramp)
c) *D. conoidea* (shorted upper ramp)
d) hypothetical warped whorl

Figure 1 Comparison of Upper and Lower Ramps
(Figures from Ulrich & Scofield 1897)

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neither appears considered significantly later than the condition displayed by *L. perangulata*, both states are considered derived because of the outgroup condition.

Characters 22 - 23. Sharp Upper Whorl Carina. Upper whorl carinae are absent on outgroup taxa and the carina-less condition appears significantly earlier within the Lophospiridae than the presence of a carina (although weak sutural carinae are sometimes visible next to the suture on species such as *Lophospira perangulata*). A sharp upper carina is displayed by species such as *L. milleri* and while the strength of the feature varies on different specimens (see Steele & Sinclair 1971 or Tofel & Bretsky 1987), it is always stronger than seen on *L. perangulata*. On some later species (e.g. *L. helicteres* or some *Trochonemella* species) the upper carina is stronger and wider, more consistent between specimens and less prone to disruption. This state appears significantly later than that of *L. milleri* and transformation series analysis indicates that the younger state is derived from the older one. Thus for Characters 22 - 23 species such as *L. milleri* are coded {10} while species such as *L. helicteres* are coded {11}. Silurian species of *Arjamannia* have upper carinae reduced to a fine lirae. However, this is correlated with Characters 42 - 44), and coding this state here would be redundant.

Character 24. Fine Upper Carina. Species such as *Donaldiella bowdeni* display an upper whorl carina much finer and fainter than that found on *L. milleri*. Transformations series analysis indicates that these upper carinae are not homologous, so this is coded as an independently derived trait.

Character 25. Ontogenetic Weakening of Upper Carina. A third type of upper carina is found on species such as *Lophospira medialis* and *L. oweni* which weakens and may disappear during ontogeny. While the upper carina of species such as *L. milleri* sometimes weakens, this appears to be associated with disruptions in shell growth and is not continuous as on *L. oweni*. The upper carina of *L. medialis* and *L. oweni* is thinner and duller than that of *L. milleri*, although it is much stronger than the upper carinae of *Donaldiella* species. Character analyses suggest that all three upper carinae types were separately derived.

Characters 26. Upper Carina Position. The upper whorl carinae of the earliest carinate species (e.g. *Lophospira milleri*) are approximately one-fifth to one-quarter of the distance from the suture to the selenizone. Species of *Trochonemella* and *Ruedemannia* display upper carina halfway between the suture and selenizone. The state shown by these species appears significantly later than the state shown by *L. milleri* and transformation analyses indicate this state was derived from the previous one. Therefore, species such as *L. milleri* were coded {10} for characters 26 & 27 while appropriate *Trochonemella* and *Ruedemannia* species were coded {11}.

Character 27. Attitude of the Upper Carina. While the upper carina of *Lophospira milleri* projects perpendicularly to the plane of the upper whorl, some *Trochonemella* species have upper carinae projecting abapically. The latter condition appears significantly later than the former and character analysis suggests that abapically projecting carinae were derived from the older state.

Character 28. Serrated Upper Carina. Some *Trochonemella* species display a serrated upper carina. These appear significantly later than thread-like upper carinae and are therefore considered derived.

Character 29 (State 1 & 2). Secondary Sutural Carina. Early species with an upper whorl carina do not have sutural carinae. Later species such as *Lophospira helicteres* and *L. quadrisulcata* display a strong sutural carina as well as upper whorl carinae. Based upon transformation series analysis and the significantly later appearance of species with both upper ramp and sutural carinae, the sutural carinae of species such as *L. helicteres* are considered derived. A much stronger, more rounded sutural carina is found on species such as *L. banksi* (State 2). Character analyses do not indicate a connection between the two states so this was run as

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Character 30 - 32. Lower Whorl Carina. A weak carina marking the boundary between the lower ramp and base is present on the oldest *Lophospira* species. This carina is essentially a slight protrusion of the angle between the ramp and the base. Species such as *L. milleri* display a sharp thread similar to the one exhibited on the upper ramp, although it often disappears on the final whorl. This state appears significantly later than the weaker carina and is considered derived. In species such as *L. helicteres* this carina is much stronger and more consistent through ontogeny. This appears significantly later than the state shown by *L. milleri* and transformation series analysis indicates that the second derived state is derived from the first. Other species (e.g. *Ruedemannia humilis*) have lower carinae reduced to a fine lirae. This state also appears significantly later than and apparently derived from the first derived state. Therefore for Characters 30 - 32, species such as *L. milleri* are coded {100}, ones such as *L. helicteres* {110} and those like *R. humilis* {101}.

Character 33. Lower Whorl Carina Loss. Species such as *Lophospira sumnerensis* or *L. tropidophora* display no lower carina. This state appears significantly later than the weak carinate condition of early lophospirids and is considered derived.

Character 34. Serrated Lower Whorl Carinae. As with upper ramp and selenizone carinae, the earliest lower whorl carina are thread-like. Serrated lower carinae occur on at least two Ashgill species from Alaska that are similar to the serrated upper carinae shown on the same species. (A third species displays a serrated upper carina without a serrated lower one, demonstrating the independence of the two traits.

Character 35. Second Lower Whorl Carina. The earliest lophospirids display one lower whorl carina. A second lower whorl carina is exhibited by only a few lophospirid species (e.g. *Lophospira quadrisulcata* and *Longstaffia* species) and is considered derived. Based upon suture sites, these additional carina occur beneath the initial lower carina.

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Character 36. Third Lower Whorl Carina. A third lower carina is exhibited by *Longstaffia* species (but see discussion of *Longstaffia* relationships below) and is considered derived for the same reason as Character 35.

Character 37. Umbilical Carina. An umbilical carina is exhibited by a number of species (e.g. *Lophospira helicteres* and most *Trochonemella* species). As early lophospirids lack this trait, it is considered derived.

Characters 38 - 39. Lower Whorl Spiral Lirae. Outgroup taxa and early lophospirids do not display any ornamentation. Very fine spiral lirae are found on some later species (e.g. *Lophospira spironema* or *Ruedemannia lirata*). *Arjamannia* species display much stronger spiral lirae. Transformation series analysis indicates that the latter state is derived from the former. Therefore species such as *R. lirata* are coded {10} while *Arjamannia* species are coded {11} for Characters 38 & 39.

Character 40. Fine Spiral Lirae on Upper Whorl. Some species exhibiting fine lower whorl lirae also display similar lirae on the upper whorl. These are considered derived for the same reasons as Character 39. Unlike the upper whorl lirae described below, these lirae do not accompany a reduction in the strength of the upper whorl carina.

Characters 41 - 43. Coarse "Subsuming" Spiral Lirae on Upper Whorl. The spiral lirae of later *Arjamannia* species incorporate the upper whorl carinae. These different characters are coded as a three-step morphocline. The oldest known specimens showing this, *R.* aff. *R. lirata* (in Rohr 1988), have sparse lirae between the upper whorl carinae and is coded {100}. Silurian species show a greater number of spiral lirae accompanied by greater weakening of the upper carinae. This is presumed derived from the previous state and coded {110}. Finally, some Silurian species show an increased number of spiral lirae. As this appears to be morphologically more complex, it is considered the final step of the morphocline {111}.

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Character 44 (States 1 & 2). Return of Upper Carina. While the upper carinae of most Silurian *Arjamannia* are reduced to fine lirae, one of the carina regains some prominence of the juvenile whorls of *A. cancellatula* (State 1) while *A. woodlandi* displays a more prominent upper carina throughout ontogeny (State 2). As the two species are otherwise very similar and as the first state is intermediate between the state shown by *A. woodlandi* and other Silurian *Arjamannia*, this is run as an ordered series with State 1 thought primitive to State 2.

Character 45. Low Juvenile Suture Point. The point on preceding whorls that additional whorls attach to is located on the site of the lower carina for outgroup taxa and early lophospirids. Some *Trochonemella* species display an initial suture point beneath the lower carina. This state appears significantly later and is considered derived.

Character 46 (States 1 & 2). High Juvenile Suture Point. Some *Lophospira* species and early ruedemannids have suture points between the lower carina and selenizone (State 1). Some later ruedemannids have an even higher suture point, with the preceding selenizones covered (State 2) suggesting that the second state is derived from the first and the trait is therefore run as an ordered series.

Character 47 (States 1 & 2). Ontogenetic Change in Suture Point. Suture points lower on adult whorls than juvenile ones are seen on species such as *Lophospira ehlersi* and *Arjamannia woodlandi* (State 1). Species such as *Lophospira helicteres* or *L. serrulata* display open coiling of adult whorls (State 2). Character analyses indicate the second state to be derived from both the primitive and first states so the trait was considered unordered.

Character 48 (States 1 & 2). Onset of Suture Point Change. The change in suture point most often affects only the final whorl (State 1). For some species, multiple whorls are effected (State 2). As with Character 47, this was run as an unordered series.

Character 49. Base Width. The base of outgroup taxa is narrow and creates an

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obtuse angle between the base and lower ramp, causing the lower ramp to descend from the selenizone at a sharp angle. Within the Lophospiridae this condition appears significantly earlier than the wider ramp found on species such as *Lophospira milleri*. The wider base produces a much sharper angle with the lower ramp and causes the lower ramp to descend more vertically from the selenizone.

Character 50 (States 1 & 2). Increased Base Width. Some later species of *Arjamannia* and *Longstaffia* show even further expansion of the base, resulting in the lower ramp descending vertically from the selenizone (State 1) to initially projecting away from the axis of coiling (State 2). It is not clear that these states are continuous, so this was run as an unordered series. However, transformation series analysis indicated that both were ultimately derived from Character 49. Appropriate species are therefore coded either {11} or {12} for Characters 49 and 50.

Character 51 - 52. Umbilicus. Outgroup taxa display small umbilici, generally one millimeter or less. This state appears significantly earlier within the Lophospiridae than any other involving the umbilicus and is therefore presumed primitive. On some later species, especially some *Trochonemella*, the umbilicus is over two millimeters. As intermediate sized umbilici are not known, umbilici over 2 mm are considered derived (Character 51). Meanwhile species such as *Lophospira quadrisulcata* and some ruedemannids are anomphalous (Character 52).

Character 53. Pseudo-Umbilicus. A feature termed a "pseudo-umbilicus" (Peel 1975) found on some anomphalous *Arjamannia* species describes a dimple created by increased convexity of the base. As this feature is not found on all anomphalous species, it is considered a derived trait.

Character 54. Perpendicular Whorl Stacking. On outgroup taxa the whorls are stacked so that the mid-whorls create a high angle with the right line of the apical angle (Fig.

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2a). Within the Lophospiridae this condition appears significantly earlier than any other and is thought to be primitive. *Donaldiella* and *Pagodospira* species display a "right-angle" whorl stacking with the selenizones perpendicular to the right line of the apical angle (Fig. 2b).

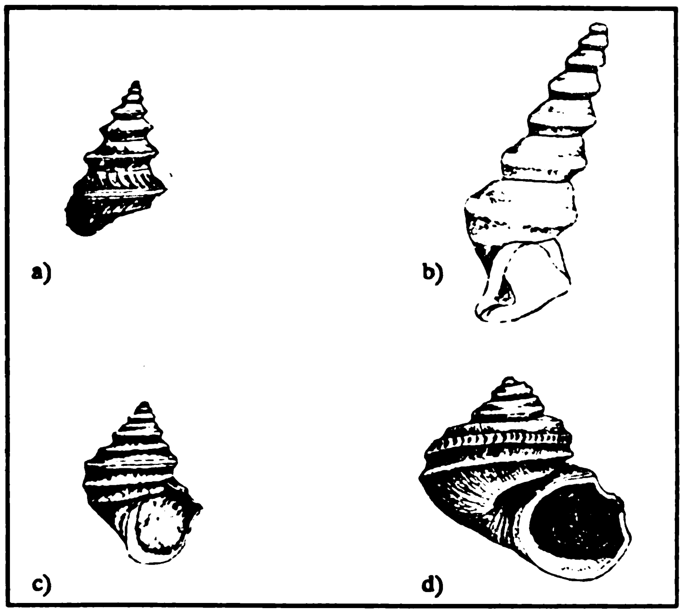

Figure 2 Different styles of whorl stacking
a) primitive b) "right-angle" c) "bisecting" d) rotated
(Figures from Ulrich & Scofield 1897)

Character 55 - 57. Counter-Clockwise Whorl Orientation. The long-axis of the outgroup taxa and early lophospirids such as *Lophospira perangulata* runs 30° adapically of the coiling axis. In species such as *L. milleri* or *L. oweni* the whorl is rotated counterclockwise so that the long axis of the aperture is parallel to the axis of coiling (Fig. 2c)[1]. Further rotation is shown by species of *Trochonemella*, with long axes of the apertures of the earliest and latest species rotated an additional 30° counter-clockwise (Fig. 2d). Caradocian *Trochonemella* species represent the extreme state with a 45° rotation. Transformation series analysis and the relative ages of the different states suggest that the three states represent a morphocline. Therefore species such as *L. milleri* are coded {100}, early and late *Trochonemella* {110} and Caradocian *Trochonemella* {111}.

Characters 58 & 59. Increased Angle between Upper Ramp and Selenizone. Early lophospirid species such as *Lophospira perangulata* and *L. milleri* show an angle between the planes of the upper ramp and selenizone of approximately 45° - 50°. On many *Trochonemella* and some ruedemannid species, this angle increases 90° to 70°. As these

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[1] In the absence of a complete aperture, this can be recognized by the axis of coiling nearly bisecting the apical angle.

states appear significantly later than the one displayed by *L. perangulata* and *L. milleri*, they are considered derived. Character analyses indicate no connection between these different states and they are coded as individual characters.

Characters 60 - 63. Columellar Lip Shape. Early species such as *Lophospira perangulata* display an "upside-down 7" shaped columellar lip. This lip shape appears significantly earlier than any other and is considered primitive. Species such as *L. milleri* have columellar lips with a fuller "L"-shape. More derived species display either a rounded "V"-shaped columellar lip (e.g. *L. helicteres* or *Trochonemella knoxvillensis*) or a well rounded half-circle lip (e.g. later *Trochonemella* species). Character analyses indicate that both the rounded "V"-shaped and half-circle states are derived from the "L"-shaped lip although the relationship between the latter two states could not be clearly resolved. Thus, for Characters 60 - 63 species like *L. milleri* were coded {1000} while species such as *L. helicteres* {1100} and younger *Trochonemella* {1200} (with the states of Character 61 considered unordered). A "U"-shaped columellar lip appears on species such as *L. medialis* with species such as *L. sumnerensis*) showing an extended "U"-shaped lip. Transformation series analyses suggests that "U"-shaped lips were derived from the primitive condition independently of the morphocline described above. Character analyses did suggest that the state shown by *L. sumnerensis* was derived from the state displayed by *L. oweni*. Therefore for Characters 60 - 63, species such as *L. oweni* were coded {0010} while species like *L. sumnerensis* {0011}.

Character 64 (States 1 - 3). Tangential Apertures. Outgroup taxa display radial apertures and this states appears significantly earlier within the Lophospiridae than tangential apertures. Three types of tangential apertures appear among lophospirids. Effectively tangential apertures appear on some open-coiling species such as *Lophospira helicteres* and *L. serrulata* (State 1). *Trochonemella* species display a tangential aperture produced by the tilting of the entire aperture (State 2). Two species, *Lophospira quadrisulcata* and *L.* aff. *L.*

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serrulata (in Rohr 1988) display an "overbite" tangential apertures produced by an extension of the upper whorl (State 3). Transformation series analyses suggest that "overbite" apertures were derived from both of the other types of tangential apertures. Therefore, although no connection was suggested between the first two styles the three conditions had to be coded as an unordered series of states.

Character 65. Apertural Slit. The sinus of early lophospirids culminates in a notch producing the selenizone, with primitive lophospirids lacking an actual slit. While an slit is sometimes described (especially for ruedemannid species), it seems to be inferred much more often than observed in Early Paleozoic species. A strong slit can be seen in only two species, *Schizolopha textilis* and *S. moorei.* The two slits differ and may not be homologous, but given the uniqueness of the trait among Ordovician and Silurian pleurotomariines, they are coded as being the same.

Character 66. Parietal Lip Thickness. On early lophospirids the parietal lip is no thicker than the rest of the shell. On some *Trochonemella* species, the parietal section of the lip is substantially thickened. This feature appears significantly later and therefore is assumed to be a derived trait.

Characters 67 - 68. Columellar Lip Thickness. On early species such as *Lophospira perangulata* the columellar lip is somewhat thicker than the rest of the shell. This state appears significantly earlier than any other involving columellar lip thickness and is presumed to be primitive. Some later species (e.g. *L. oweni* or *L. tropidophora*) display a much thicker columellar lip, often approaching one centimeter in thickness. On species such as *L. tropidophora* the lip fills the umbilicus. As character analyses suggest that the latter state is derived from the former, these states are coded as a morphocline with species such as *L. oweni* coded {10} and those like *L. tropidophora* coded {11}.

Characters 69 & 70. Columellar Lip Extension. The columellar lip of early

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lophospirids extends abapically. This extension is reduced on early *Trochonemella* species and completely lost on later ones. These states appear significantly later than the extended lip state and transformation series analysis suggests that complete loss is derived from the reduced state. Thus for Characters 69 and 70, early *Trochonemella* species are coded {10} and later species {11}.

Character 71 (States 1 & 2). Columellar Lip Reflection. Early species such as *Lophospira perangulata* exhibit some reflection of the inner lip around the umbilicus. This appears significantly earlier than other conditions and presumed to be primitive. Increased reflection resulting in partial covering (not filling) of the umbilicus is seen some species such as *Donaldiella bowdeni* or Silurian *Ruedemannia* species (State 1). Other species, especially Ashgill ruedemannids, show complete covering of the umbilicus by inner lip (State 2). As the first state appears to be derived from both the primitive and second states, this was run as an unordered series.

Character 72. Shell Thickness. The shells of most lophospirids are considered thin (Knight 1941; Peel 1975). Some later species, especially Silurian ones, display significantly thicker shells. The extent of increased thickness was not additively coded owing to possible preservational biases and the difficulty of quantifying the trait.

Character 73 (States 1 & 2). Whorl Expansion Rate[1]. Outgroup taxa and early lophospirids such as *Lophospira perangulata* display an expansion rate between 1.45 and 1.5. This is assumed to be primitive. The high-spired *Donaldiella* species show lower ratios between 1.3 and 1.35 (State 1). Most later species show expansion rates ranging from 1.65 to over 2.2 (State 2). The expansion rates in this higher range may represent two or three separate states, but separating these would required both rigorous morphometrics and prior

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[1] Calculated as described by Raup (1966).

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knowledge of the phylogeny of the group. As transformation series analysis suggests that the higher ratios in that spectrum are derived from the lower ones they are simply coded as a single derived state (State 2). The high and low expansion ratios are coded as unordered states of the same trait instead of individual traits because they represent growth parameters which can be drastically changed with little evolutionary change (Bookstein *et al.* 1985 Chap. 5)

Character 74 & 75. Adult Whorl Numbers. The largest, most complete specimens of early lophospirid species such as *Lophospira perangulata* have seven or eight whorls. This appears significantly earlier among lophospirids than higher or lower numbers and also appears to be shared with the outgroup taxa. Thus it is considered the primitive condition. Many later species such as *L. milleri* or *L. tropidophora* display fewer whorls, with the largest, most complete specimens possessing four or five volutions (Character 74). Other species classified as *Donaldiella* display upwards of nine volutions (Character 75).

Common Descriptive Traits Not Used

The terms used in Appendix A and previous descriptions of fossil gastropods have surprisingly little in common with the characters described above. While some of the more detailed descriptions (especially when accompanied by clear figures) are useful, many produce misleading ideas about gastropod relationships. In some cases, the differences between the descriptive terms and acceptable traits are semantic. For example, growth morphology is often used to infer the depth and shape of lophospirid sinuses (e.g. Ulrich & Scofield 1897; Knight 1944), and descriptions of the sinus are often given in lieu of precise descriptions of the growth lines. While they do reflect the shape and depth of the sinus, growth lines are preserved far more often than sinuses and are therefore used in this study. Thus, even though they are not mentioned, similarities and differences in sinus morphologies are accounted for in this analysis.

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Many features frequently used to compare lophospirid species represent composites of characters used in this study. These features are listed in Table II along with the characters used in this study that determine the final shape and/or size of that feature. For example, apical angles are determined by factors such as whorl expansion rates, suture points, umbilicus sizes and alignments of the whorls relative to the axis. A species with a suture point on the lower carina and a high whorl expansion rate could have an identical apical angle of a species exhibiting a standard expansion rate but with a suture just under the selenizone. The two species could receive identical descriptions in this regard, yet differ in two key traits. Similar examples can be made with shoulder angles, aperture shapes and shell lengths.

The actual size of the gastropods could not be accurately coded. An attempt was made to measure this using the apertural areas of the adult whorls. However, there was significant variation within some species, making sizes almost impossible to qualify. Gap-coding of populations as described by Archie (1985) could be done for some species, but unfortunately many lophospirid species are known from only a few specimens. Therefore size was not accounted for in this study.

Relative selenizone widths have been used to distinguish between lophospirid species (e.g. Grabau & Shimer 1909 or Rohr 1988). However, these authors appear to have given little regard to allometry. Selenizones on juvenile whorls are relatively wider compared to the whorl height than adult selenizones are. Thus selenizone width/whorl height ratios are only meaningful if the either the selenizone width or the whorl height is kept constant between specimens. This was done here by measuring selenizone widths at a set whorl height on different specimens.

The second upper whorl carina of *Ruedemannia humilis* and all *Arjamannia* species was left uncoded for a completely different reason. Based upon the growth line morphology, the carina in the middle of the upper ramp appears to be homologous with the lone carina

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of species such as *Lophospira milleri*. The overall upper whorl morphology of *R. humilis* and early *Arjamannia* does not differ greatly from rare variants of *L. milleri* with two upper whorl carinae. *Schizolopha textilis* and younger *Ruedemannia* species also have an upper whorl carina in the middle of the upper ramp but lack the second upper whorl carina. Initial analyses suggested that these species were all closely related. However, the transformation series analyses and temporal data could not resolve whether the primitive condition in this group was a lone carina in the middle of the upper whorl with a second appearing later or two upper whorl carina with the uppermost one being lost. As the relocation of the primary upper carina to the middle of the upper ramp is involved with the first step of both possible transformation series, the species in question were all coded "1" in Character 26. However, the second step of that series could not be coded as the polarities of the two different states could not be initially resolved.

Table II Some Common Descriptive Features and the Characters Producing Them

Feature	Characters Involved
Apical Angle	Whorl Expansion Rate Suture Points Umbilicus Size Whorl Alignments
Shoulder Angle	Base Width Whorl Expansion Rate Upper Ramp/Selenizone Angle
Aperture Shape	Columellar Lip Shape Sinus Depth (= Growth Line Morphology) Upper Ramp Shape Lower Ramp Shape Base Width Upper Ramp/Selenizone Angle
Shell Length	Whorl Number Suture Points Columellar Lip Extension

Phylogenetic Analysis

The phylogenetic analysis was based on a character matrix (Appendix C) with 94 character states and was analyzed using PAUP 3.0 (Swofford 1985, 1989). Character weighting was not used. Subsets of the matrix were created based on the geologic ages of first known appearance and run in progressively more inclusive sets with subsets of younger species added to subsets of older ones. Later in the study, groups consistently shown to be monophyletic clades were analyzed on their own. Heuristic searches were used for the larger data sets, with exhaustive search and branch-and-bound options used on smaller ones. For

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analyses producing multiple equally parsimonious trees, consensus trees were made, with bootstrapping options used to learn how robust different sister-groups were based upon different randomly generated subsets of the character matrix. This also provides a useful check against faulty or misinterpreted traits.

Statistics such as the number of informative characters and consistency indices were generated by PAUP. Homoplasy excess ratios were calculated as described by Archie (1989b). This statistic was proposed as an alternative to the consistency index, and is derived from a comparison of the mean number of steps per character from random data sets and the actual number of observed steps. A ratio of 1.0 indicates no homoplasy, while a ratio of zero suggests so much homoplasy that the data set is effectively a random one.

The data subsets were created using the following temporal boundaries: 1) Tremadoc through Llandeilo; 2) Tremadoc through Early Caradoc (Black Riveran); 3) Tremadoc through Caradoc; 4) entire Ordovician, and; 5) Tremadoc through Wenlock. While the Llanvirn is the earliest time in which multiple lophospirid species are known to have existed, the Llandeilo is also included in the initial time frame. The Llanvirn and Llandeilo were fairly short stages (11 - 12 million years total, Ross *et al.* 1982), and the stratigraphic relationships between different early lophospirids localities are less clear than those from the Middle and Upper Ordovician. The end of the Black Riveran was chosen because it appears to represent a time of faunal turnover within the Lophospiridae (Tofel & Bretsky 1987). The third and fourth time frames were picked because they represent times of general faunal changes (especially the end-Ordovician), while the last time frame simply includes the youngest species used in this analysis.

Consensus cladograms using only taxa from the older time spans were used as templates in evaluating cladograms including younger taxa. The importance of incorporating older fossil taxa into phylogenetic analyses of contemporaneous organisms has been

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demonstrated (e.g. Donoghue *et al.* 1989). Extending this logic, a phylogeny of Caradocian lophospirids should be more reliable if it was constructed using Llanvirn and Llandeilo species as well. Conversely, the inclusion of younger taxa can confuse the relationships between older taxa by introducing additional homoplasy. The introduction of a Wenlockian species should not change a {1{23}} relationship between three Caradoc species into a {{12}3} relationship. Therefore cladograms including younger taxa were given more credence if the pattern among the older taxa matched the consensus of cladograms generated using only those older taxa.

A lineage originating in the Wenlock can not be the sister group of a clade first known from the Llanvirn (Paul 1982). There are two possible explanations for cladograms that show this. One is that the apparently younger lineage is actually older than thought, with as yet unknown members. The second is sufficient homoplasy linking the younger taxa to some members of the older clade. Character plotting will usually reveal the latter possibility. In analyses using younger species, the stem members of older clades will often display reversals to the primitive conditions for the traits in question with later species maintaining the derived state. However, analyses using only older taxa will demonstrate that those derived traits are not diagnostic of the older clade and that the clades themselves do not share these derived features. Thus, among alternative cladograms including younger taxa greater credence was given to those matching the patterns of character changes seen on the consensus of cladograms produced for only the older species.

This approach relies upon knowing the times of origination for lophospirid species with some degree of confidence. Some (e.g. Nelson 1978) would argue that this is not possible due to the erratic nature of the fossil record. However, as stated in discussing the use of temporal data for the polarization of lophospirid character states, this particular group has an extensive fossil record. Table III lists the known temporal ranges of the species included

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included in this analysis plus the 95% confidence level extensions of those ranges and the level of confidence that the species is younger than the youngest species in the preceding temporal subset (C_Y). The numbers are obviously overly precise given the degrees of uncertainty for the actual ages of the Ordovician stages and their subdivisions. However, what is important is the relative temporal spans represented. A comparison of different time scales indicates general agreement on the relative temporal lengths of the relevant time units. The exception to this is the Ashgill for which estimates are as long as 15 million years (Ross *et al.* 1982) and as short as four million (Harland *et al.* 1989). Using the larger estimate increased the temporal ranges of Ashgillian species and decreased the chance of the species being shown to be younger than all Caradocian ones at higher levels of confidence. Thus, while Harland *et al.*'s more recent time scale may be more accurate, the scale of Ross *et al.* was used here to produce more conservative confidence interval estimates.

Table III Stratigraphic Confidence Intervals of Individual Lophospirid Species

Species	Horizons[1]	Known Temporal Range[2]	95% C.I. of Entire Temporal Range[3]	C_Y[4]
Lophospira perangulata	102	495 - 430 ma	496.25 - 428.75 ma	-
Lophospira manchuriensis	11	483 - 465 ma	487 - 461 ma	-
Lophospira kangyaoensis	2	483 - 473 ma	507.2 - 448.8 ma	-
Lophospira milleri	74	485 - 445 ma	486.0 - 444.0 ma	-
Lophospira pagodai	2	483 - 468 ma	699.2 - 271.8 ma	-
Trochonemella knoxvillensis	1	480 - 476 ma	∞	-
Lophospira centralis	36	471 - 445 ma	472.4 - 443.6 ma	99+%
Pagodospira derwiduii	2	471 - 463 ma	490.3 - 443.7 ma	57%
Pagodospira dorothea	2	471 - 463 ma	490.3 - 443.7 ma	57%
Trochonemella trochonemoides	1	471 - 468 ma	∞	0%
Lophospira helicteres	61	467 - 453 ma	467.5 - 452.5 ma	99+%
Lophospira serrulata	18	467 - 462 ma	467.6 - 461.4 ma	99+%
Trochonemella montrealensis	5	471 - 465 ma	472.4 - 463.6 ma	99%
Trochonemella penguinus	2	468 - 464 ma	525.7 - 406.3 ma	79%
Trochonemella notablis	3	466 - 463 ma	473.25 - 455.75 ma	98%
*Trochonema bellulum**	1	471 - 468 ma	∞	0%
*Trochonema umbilicatum**	83	467 - 447 ma	467.5 - 446.5 ma	99+%
Donaldiella augustina	8	463 - 446 ma	468.8 - 440.2 ma	78%
Lophospira medialis	13	463 - 440 ma	467.1 - 432.5 ma	88%
Lophospira spironema	2	463 - 459 ma	520.7 - 401.3 ma	45%
Lophospira oweni	20	463 - 438 ma	463.6 - 436.4 ma	99%
Lophospira sumnerensis	9	460 - 453 ma	462.0 - 451.0 ma	99+%
Lophospira banksi	2	455 - 450 ma	527.1 - 377.9 ma	73%
Lophospira decursa	2	455 - 453 ma	483.8 - 421.2 ma	87%
Lophospira conoidea	1	455 - 450 ma	∞	0%
Lophospira producta	1	455 - 450 ma	∞	0%
Ruedemannia humilis	1	457 - 453 ma	∞	0%
Schizolopha textilis	1	454 - 449 ma	∞	0%
Donaldiella bowdeni	25	451 - 435 ma	452.4 - 433.6 ma	99+%
Donaldiella filosa	1	451 - 448 ma	∞	0%
Lophospira tropidophora	27	451 - 435 ma	452.2 - 433.8 ma	99+%
Lophospira aff. *L. serrulata*	3	450 - 442 ma	469.3 - 422.7 ma	61%
Lophospira quadrisulcata	5	444 - 441 ma	446.2 - 438.8 ma	99+%
Schizolopha moorei	5	441 - 437 ma	443.9 - 434.1 ma	99+%
Trochonemella churkini	4	450 - 442 ma	459.2 - 432.8 ma	78%
Trochonemella reusingi	4	450 - 442 ma	459.2 - 432.8 ma	78%
Arjamannia thraivensis	1	451 - 441 ma	∞	0%
Ruedemannia lirata	3	450 - 447 ma	457.2 - 429.8 ma	87%
Ruedemannia aff. *R. lirata*	2	450 - 442 ma	565.3 - 327.7 ma	33%
Lophospira ehlersi	1	435 - 433 ma	∞	0%
Arjamannia cancellatula	6	435 - 431 ma	436.4 - 429.6 ma	98%
Arjamannia woodlandi	4	435 - 431 ma	439.6 - 426.4 ma	97%
Arjamannia inexpectans	2	431 - 427 ma	503.1 - 361.9 ma	75%
Arjamannia aulongensis	1	427 - 422 ma	∞	0%
Ruedemannia robusta	2	431 - 427 ma	503.1 - 361.9 ma	75%
Ruedemannia laevissima	1	431 - 427 ma	∞	0%
Longstaffia subulosa	1	427 - 422 ma	∞	0%
Longstaffia laquetta	3	427 - 415 ma	442.3 - 389.7 ma	69%

*: Non-Lophospirid species.

[1]: As the number of horizons per species are based upon published descriptions they likely represent underestimates.

[2]: Calculated from Ross *et al.* (1982) and Harland *et al.* 1989.

[3]: Calculated according to Marshall (1990).

[4]: The minimum confidence level that the species is younger than all of the species in the preceding time frame.

∞: Confidence intervals can not be calculated for species known from single horizons (therefore C_Y = 0%).

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As described above, few horizons and very wide temporal ranges both decrease the confidence of a species temporal range. Notably, the lophospirid species with less robust temporal ranges are all known from few horizons rather than overly wide temporal ranges. Further, these species are usually from regions in Asia or Europe that have been much less thoroughly studied and/or reported than other regions. Lophospirids are often noted in more general paleontological studies of these regions, but they are rarely identified past the generic level. Thus apparently rare lophospirid species may have been found from many sites. However, this could not be assumed when calculating the confidence intervals for those species. This also applies to many Silurian species owing to the less extensive research of Silurian strata compared to Ordovician strata. As with character states, the absence of the Silurian species from Ordovician strata can not be taken into account in confidence interval calculations, but the fact that they are absent from the well-studied Ordovician should be considered significant.

As a final method of testing the results, six cladograms were produced incorporating every sixth taxon with *Lophospira perangulata* used as an outgroup member. Three Trochonematacea species with apparent lophospirid affinities (*Trochonema bellulum*, *T. umbilicatum* and *Eunema strilligatum*) were included both to test their actual relationships and to allow all six groups to include eight taxa. Each cladogram represented an essentially random mix and allowed tests of how well the relationships between those species matched those shown on more inclusive cladograms. This also provides an indication of how important individual species are to the overall analysis. If the patterns of these cladograms varied frequently from the patterns in the more inclusive cladograms, then it is more likely that the discovery and inclusion of a new lophospirid species could drastically change the interpretation of lophospirid relationships. However, if the smaller cladograms consistently matched the patterns seen in the more inclusive cladograms, then it is less likely that the inclu

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inclusion of an additional lophospirid species would greatly disrupt the results of this study.

RESULTS

The results are presented in the order they were generated in.

Llanvirn - Llandeilo Cladograms

The Llanvirn and Llandeilo species used in this analysis are listed in Table IV.

Table IV Lophospirid Species Known from the Llanvirn and Llandeilo

Species	Distribution
Lophospira perangulata (Hall)	Brit., NE Asia, SW, E N.Amer.
L. kangyaoensis Endo	NE Asia
L. manchuriensis Endo	NE Asia, ?N.Amer.
L. milleri (Hall)	Brit., SW, E N.Amer.
L. pagodai (Endo)	NE Asia
Trochonemella knoxvillensis (Ulrich in Ulrich & Scofield)	SE N.Amer.

The taxonomy used in this and subsequent tables reflects in part the sections and subsections of *Lophospira* defined by Ulrich & Scofield (1897) and in part the genera as accepted by Knight (1941).

Fifteen character states were informative in this analysis. A branch-and-bound search generated three equally parsimonious cladograms. Figure 3a is the strict consensus of the three and the majority consensus of 100 bootstrap repetitions is shown in figure 3b. The bootstrap majority consensus matched one of the three equally parsimonious trees while another found *Lophospira pagodai* the sister clade of the *manchuriensis-milleri-knoxvillensis* clade and the third found *L. pagodai* and *L. kangyaoensis* to be sister species with the pair representing the sister clade of the other three species. Bootstrapping linked *Lophospira kangyaoensis* with the *manchuriensis-milleri-knoxvillensis* clade in 36% percent of the replications while *L. pagodai* was linked with the clade 24% of the time and with *L. kangyaoensis* in 18%. The three species clade was found in 88% of the replications with the *milleri-knoxvillensis* sister-pairing found over 98% of the time.

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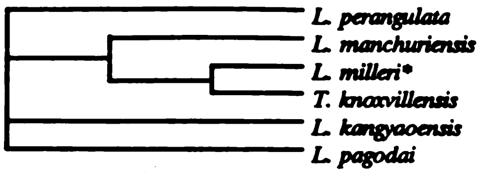
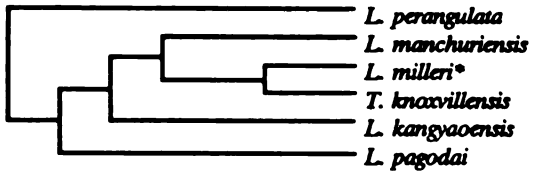


3a) Strict Consensus of Three Cladograms



3b) Majority Consensus of 100 Bootstrap Replications

Figure 3 Consensus Cladograms for Llanvirn-Llandeilo Lophospirids ("*" denotes type species of a genus).

The tree lengths were 26 (minimum possible 24, a maximum 40). The consistency index (CI) was 0.857 which is higher than average for the number of O.T.U.'s and characters states used in previously published studies (Archie 1989b). The homoplasy excess ratio (HER) was calculated to compare the results of this analysis with the predicted results of a random data set of equal dimensions. At 0.783 the HER was also higher than average for a data set of this size. Both figures suggest that the results are at least as robust as the average cladograms of similarly sized data bases in previously published studies.

Species Through the Middle Caradoc (Pre-Shermanian)

Table V Species with First Known Appearances by the Early Caradoc (Black Riveran)

Species	Geographic Range
Lophospira centralis Ulrich & Scofield	MW, E N.Amer.
L. helicteres (Salter)	MW, E N.Amer.
L. serrulata (Salter)	MW, E N.Amer.
Pagodospira derwiduii Grabau	NE Asia
P. dorothea Grabau	NE Asia
Trochonemella trochonemoides (Ulrich in Ulrich & Scofield)	E N.Amer.
T. montrealensis Okulitch	NE N.Amer.
T. penguini n. sp.	E N.Amer.
T. notablis (Ulrich in Ulrich & Scofield)	E N.Amer.

Eight species first appear in the Black River aged strata (see Table V). Two Asian species of early Caradocian age (Grabau 1922; Kobayashi 1930; Shen-Fu 1980) with sufficient descriptions and figures to be included in this study were added here as well as several North

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American species described by Ulrich & Scofield (1897) and others.

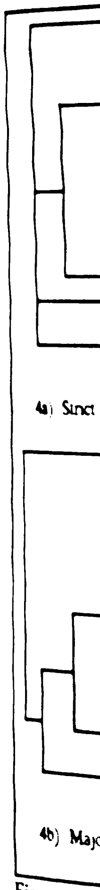
Forty-five character states were informative in this analysis. Eighteen equally parsimonious cladograms were produced using the branch-and-bound option of PAUP. A strict consensus of these trees are shown in Fig 4a, and the majority consensus of 100 bootstrap replications is shown in fig 4b. Some of the differences between the two follow the same pattern as the previous cladograms. The bootstrap consensus again showed *Lophospira kangyaoensis* to be the sister taxon of the *manchuriensis*-clade sharing the *pagodai*-clade as a sister group. However, this occurred on only 28% of the replications. The additional resolutions by the bootstrap consensus were also weak. *Lophospira helicteres* was the sister taxon of *L. centralis* nearly as often as with the *Trochonemella* species (34% vs. 42%). Meanwhile, the clade formed by these taxa was resolved as a sister group to *L. milleri* in 18% of the replications. The previously defined *manchuriensis*-clade was also less robust than before, being found in only 64% of the replications (down from 88%). However, *L. serrulata* was found to be a sister-group to or member of that clade in 92% of the replications.

The length of the cladograms was 72 steps (minimum possible 54, maximum 169). The consistency index (CI = 0.705) and the homoplasy excess ratio was 0.731, both above average for a sample of this size (Archie 1989b). Thus, as with the Llanvirn-Llandeilo results the cladograms here are fairly robust.

Species Known Through the Caradoc

Twelve species first known to appear from the Rocklandian to Shermanian of the Caradoc were added to the analysis (Table VI). All are North American species due to the inadequacy of the descriptions and figures Asian and European material of similar age.

Sixty-one character states were used in this analysis. Only the heuristic search option could be used because of the size of the data set. This produced 184 equally parsimonious cladograms. A strict majority consensus is shown in Figure 5. Owing to the size of the data



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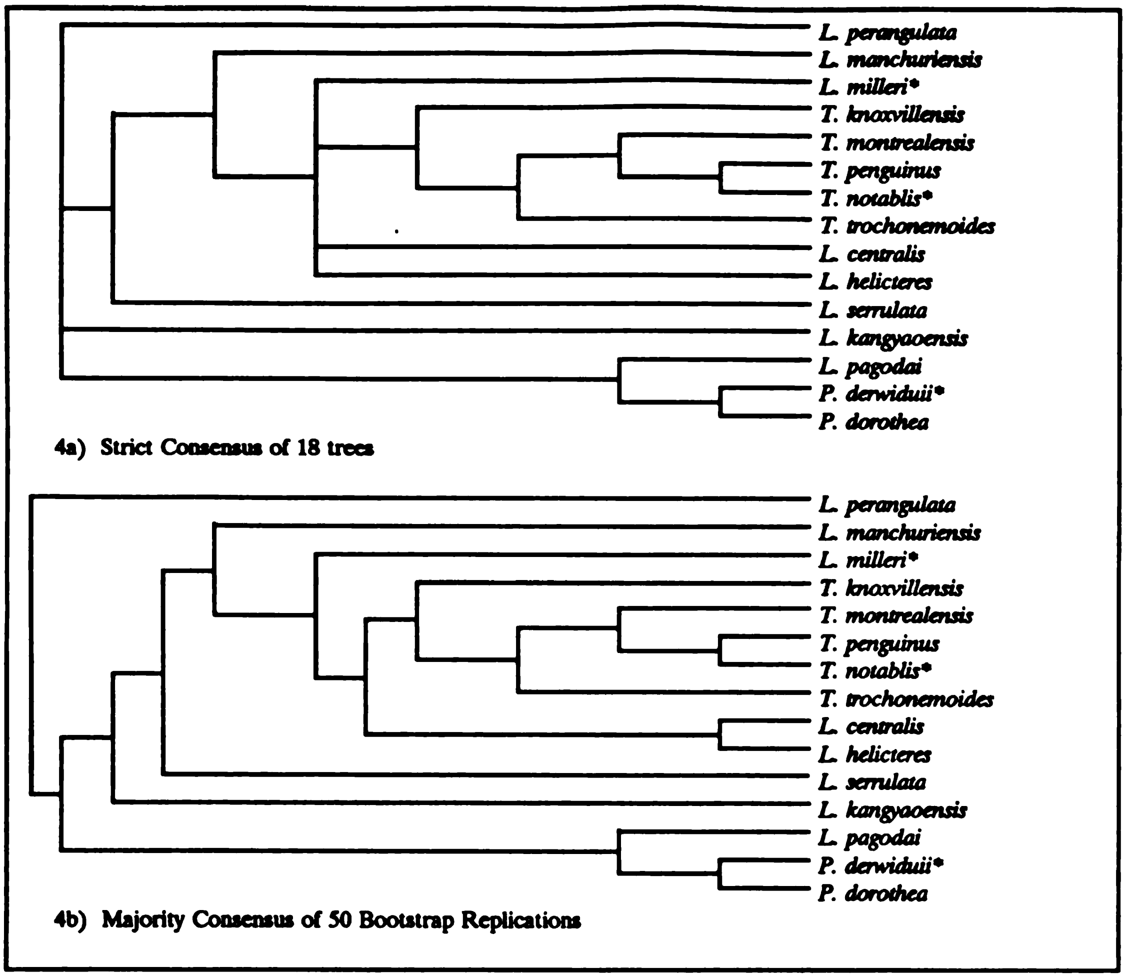

Figure 4 Strict and Bootstrap Consensus Trees for Lophospirids Known through the Lower Caradoc (Black Riveran).

set, significant bootstrapping replications could not be performed without producing computer errors. The tree lengths were 116 (possible minimum 63, maximum 283).

The consistency index (CI = 0.556) and homoplasy excess ratios (HER = 0.600) for the cladograms were again somewhat above average for the number of taxa and characters used (Archie 1989b), although both indicate a decrease in robustness compared to the first two analyses. A major reason for this was PAUP's inability to consistently root five taxa with any others. In an attempt to resolve the possible relations of these "floating" taxa, the five were run with pairs of the major clades in order to find any consistent relationships that might have been obscured in the mass analysis. An example using the two most pertinent clades did unify two previously unlinked taxa, *Donaldiella decursa* and *D. conoidea*. This subset

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Table VI Lophospirid Species First Known from the Upper Caradoc ("Trenton" of N. America)

Species	Geographic Range
Lophospira medialis Ulrich & Scofield	?Brit., ?Asia, W, MW, E N.Amer.
L. spironema Ulrich & Scofield	MW, E N.Amer.
L. oweni Ulrich & Scofield	?Asia, MW, E N.Amer.
L. sumnerensis (Safford)	?Brit., ?Asia, MW, E N.Amer.
L. banksi n.sp.	E N.Amer.
Ruedemannia humilis (Ulrich in Ulrich & Scofield)	E N.Amer.
Schizolopha textilis Ulrich in Ulrich & Scofield	E N.Amer.
Donaldiella conoidea (Ulrich in Ulrich & Scofield)	MW, E N.Amer.
D. decursa Ulrich & Scofield	E N.Amer.
D. augustina (Billings)	MW, E N.Amer.
D. producta (Ulrich in Ulrich & Scofield)	E N.Amer.

analysis used 13 taxa with 18 informative character states. A strict consensus of the 180 trees produced by a heuristic search did not resolve any additional relationships (Fig. 6a) but the consensus of 50 bootstrap replications did pair the species in 23% of the replications Fig. 6b). This is not especially robust as both the *pagodai*-clade and the *medialis-spironema-oweni-sumnerensis*-clade were found in 89% of the replications. *Lophospira banksi* was linked with the *medialis*-clade in 54% of the replications while that group was found to be the sister clade of *D. decursa* and *D. conoidea* in 13% of the replications. That whole group was found to be the sister group of the *pagodai*-clade in 31% of the replications (with *D. producta* the outgroup to that clade). The validity of these differences between the strict consensus cladograms and the results of bootstrapping is discussed below.

Species Known Through the Ashgill

Eleven species first known to appear in the Ashgill were added at this stage of the analysis (Table VII). Most of these are again known from eastern North America, especially from Ctendonta beds and Trenton of Ulrich & Scofield (1897). Specimens and/or sufficiently adequate descriptions and figures of some British and Alaskan material was also available. However, descriptions and figures of Asian material from this time period were not sufficient

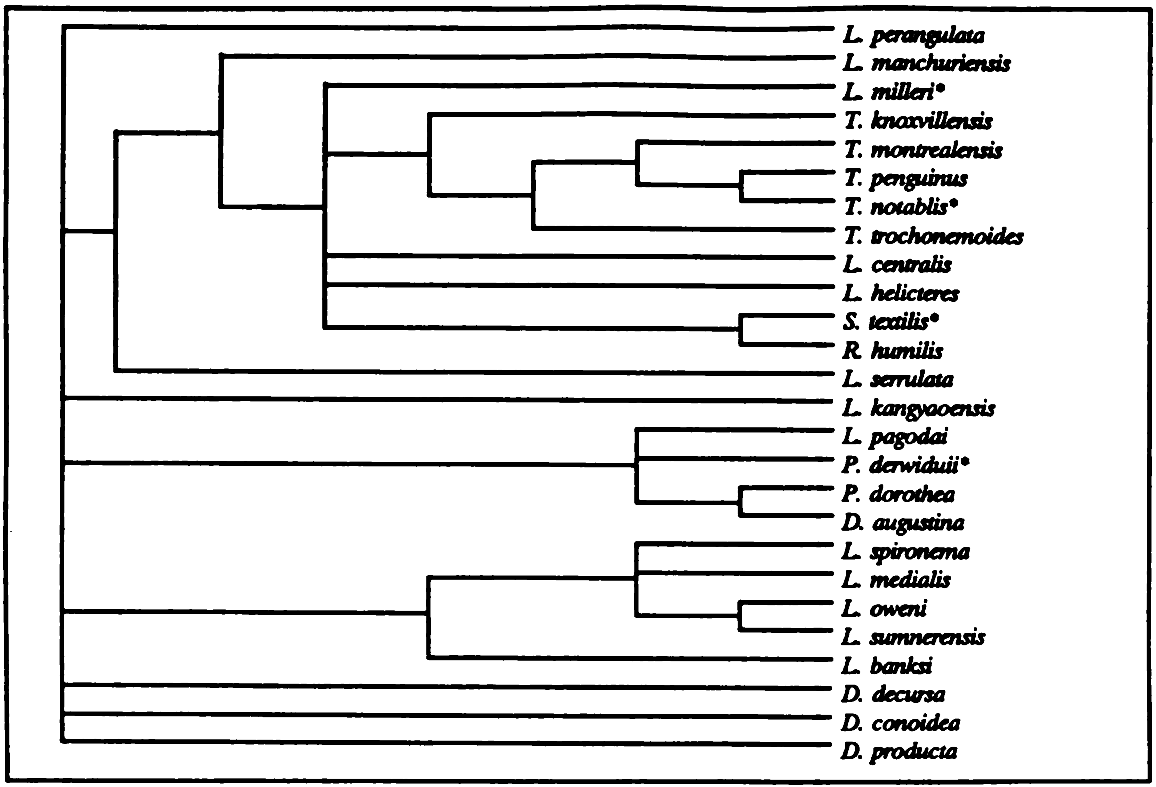

Figure 5 Strict Consensus Cladogram for Species Known through the Caradoc.

Table VII Lophospirid Species First Known from the Ashgill

Species	Geographic Range
Lophospira quadrisulcata Ulrich & Scofield	MW N.Amer.
L. tropidophora (Meek & Worthen)	MW, E. N.Amer.
L. aff. *L. serrulata* (in Rohr 1988)	NW N.Amer.
Schizolopha moorei Ulrich in Ulrich & Scofield	MW N.Amer.
Donaldiella bowdeni (Safford)	E. N.Amer.
D. filosa (Donald)	Brit.
Trochonemella churkini Rohr & Blodgett	NW N.Amer.
T. reusingi Rohr	NW N.Amer.
Ruedemannia lirata (Ulrich in Ulrich & Scofield)	MW N.Amer.
R. aff. *R. lirata* (in Rohr 1988)	NW N.Amer.
Arjamannia thraivensis (Longstaff)	Brit., NE N.Amer.

for inclusion.

As the entire data set could not be run at this point without producing computer systems errors, two groups were used. The first was comprised of nineteen orthocline taxa[1] plus *Lophospira perangulata* and *L. serrulata*. The last species was included because it was the sister taxon of the orthocline clade in the previous analyses and also to test its affinities

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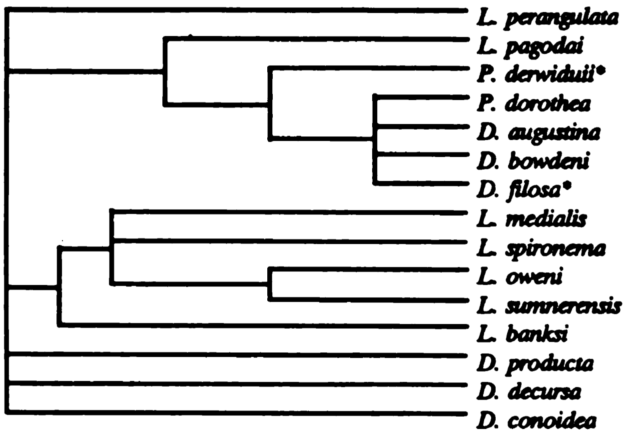
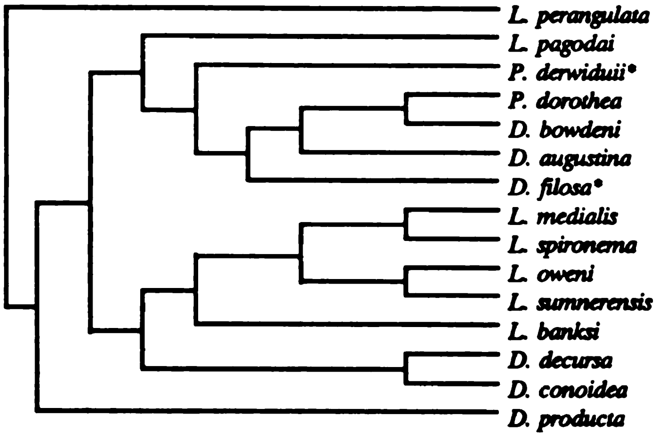
[1] Other synapomorphies of these species includes coarse growth lines, increased whorl expansion rates and "L"-shaped columellar lips.



6a) Strict Consensus of 180 Trees

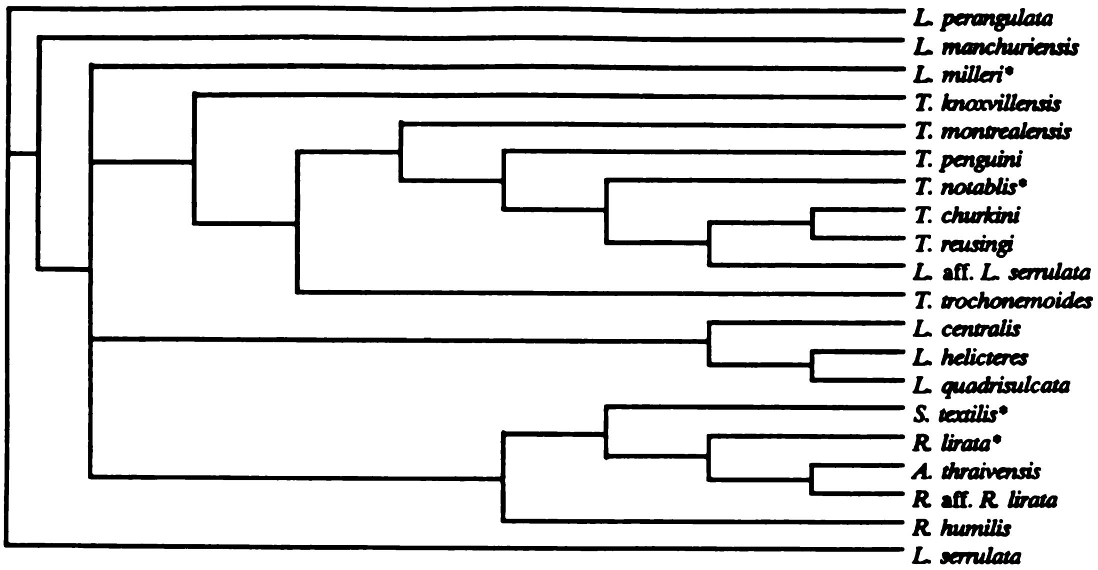


6b) Majority Consensus of 50 Bootstrap Replications

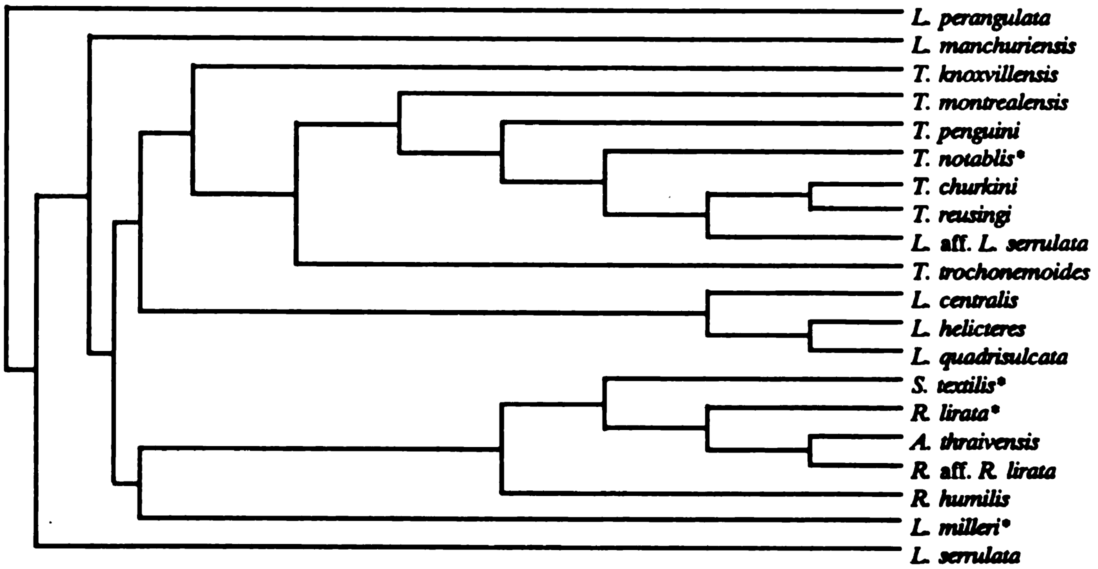
Figure 6 Cladogram of "Floating" Caradoc Taxa

with an Alaskan orthoclinal species tentatively classified as *L. serrulata* (*Loxoplocus* (*Lophospira*) aff. (*L.*) *serrulata* in Rohr 1988). Fifty-one characters were informative in this analysis. Six equally parsimonious cladograms were generated using heuristic search options with the strict majority consensus tree shown in Figure 7a and the majority consensus of 50 bootstrap repetitions in 7b. Analyses using pairs of clades were not necessary, as there were no new "floating" monotypic clades present.

The six trees had lengths of 106 (minimum possible 66, maximum 240). The consistency index (CI = 0.560) and homoplasy excess ratio (HER = 0.617) are both above average for a data set of this size, indicating a fairly robust result. Bootstrapping revealed two fairly robust clades, the *humilis-textilis-lirata-thraivensis* clade (98% of the replications) and the *knoxvillensis*-clade (73% of the replications). The *centralis-helicteres-quadrisulcata* clade was also fairly robust (57%). Notably, *Lophospira helicteres* was linked with *L. centralis* nearly twice as frequently as with the *Trochonemella* species in this analysis. The connections made by bootstrapping absent from the strict consensus cladogram were rather weak - the *centralis-*



7a) Strict Consensus of Six Trees



7b) Majority Consensus of 50 Bootstrap Repetitions

Figure 7 Strict and Bootstrap Consensus Cladogram for Orthoclinal Lophospirids Known through the Ordovician.

and *knoxvillensis*-clades were linked only 24% of the time and *L. milleri* was linked with the *humilis*-clade in only 6% of the replications.

The second set was comprised of the two major groups with strongly swept growth lines known through the Ordovician. This primitive state was chosen because it was apparent by this point that it precluded a species from belonging to the clade analyzed above. Thirteen taxa were included with 22 informative character states. A branch-and-bound search produced three equally parsimonious trees with the strict consensus shown in Figure 8a and the majority consensus of 100 bootstrap repetitions shown in figure 8b.

The tree lengths were 43 (possible minimum 29, maximum 93). The consistency index (CI = 0.611) and homoplasy excess ratio (HER = 0.635) are again both above average for the number of taxa and character states. The only difference between the strict consensus and the majority bootstrap consensus is the linking of *Lophospira medialis* and *L. spironema* in the latter. However, this was found on only 8% of the replications and is not robust. Bootstrapping did indicate the two main clades to be robust as they appeared in over 75% of the replications.

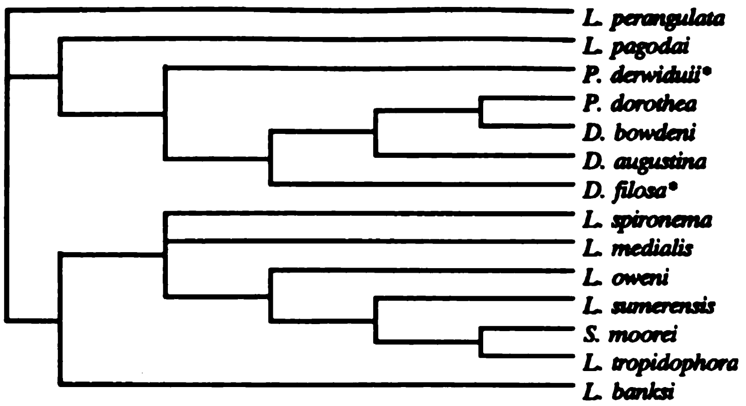
Species Known Through the Wenlock

Table VIII Lophospirid Species First Known from the Silurian

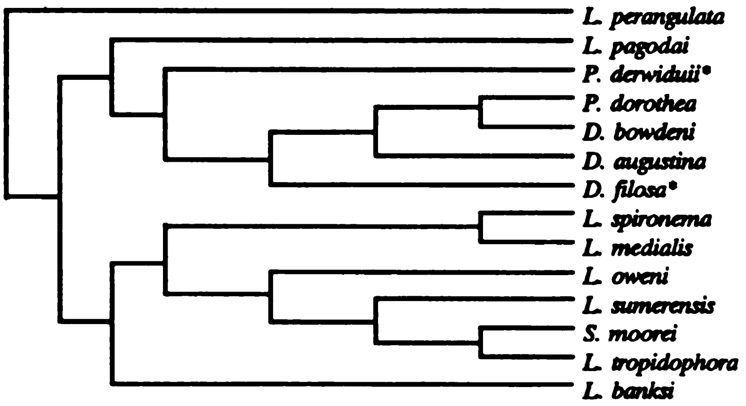
Species	Geographic Range
Lophospira ehlersi Foerste	MW N.Amer.
Ruedemannia robusta (Lindström)	Baltica
R. lævissima (Lindström)	Baltica
Arjamannia inexpectans (Hall & Whitfield)	MW, NE N.Amer.
A. cancellatula (Longstaff)	Brit., NE N.Amer.
A. woodlandi (Longstaff)	Brit., NE N.Amer.
A. aulongensis Peel	NE N.Amer.
Longstaffia tubulosa (Lindström)	Baltica
L. laquetta (Lindström)	Baltica

The Silurian species included in this study are listed in Table VIII. While there are many more Silurian lophospirids than listed here, they have not been adequately described and could not be included in this study. However, some Baltic Silurian species with excellent descriptions and figures by Lindström (1884) were included.

As before, two separate subsets were run based upon growth line morphology. At this point the diagnostic traits of the different clades were well enough known that the new taxa could be run within their respective clades. The first analysis was comprised of 27 taxa



8a) Strict Consensus of Three Trees



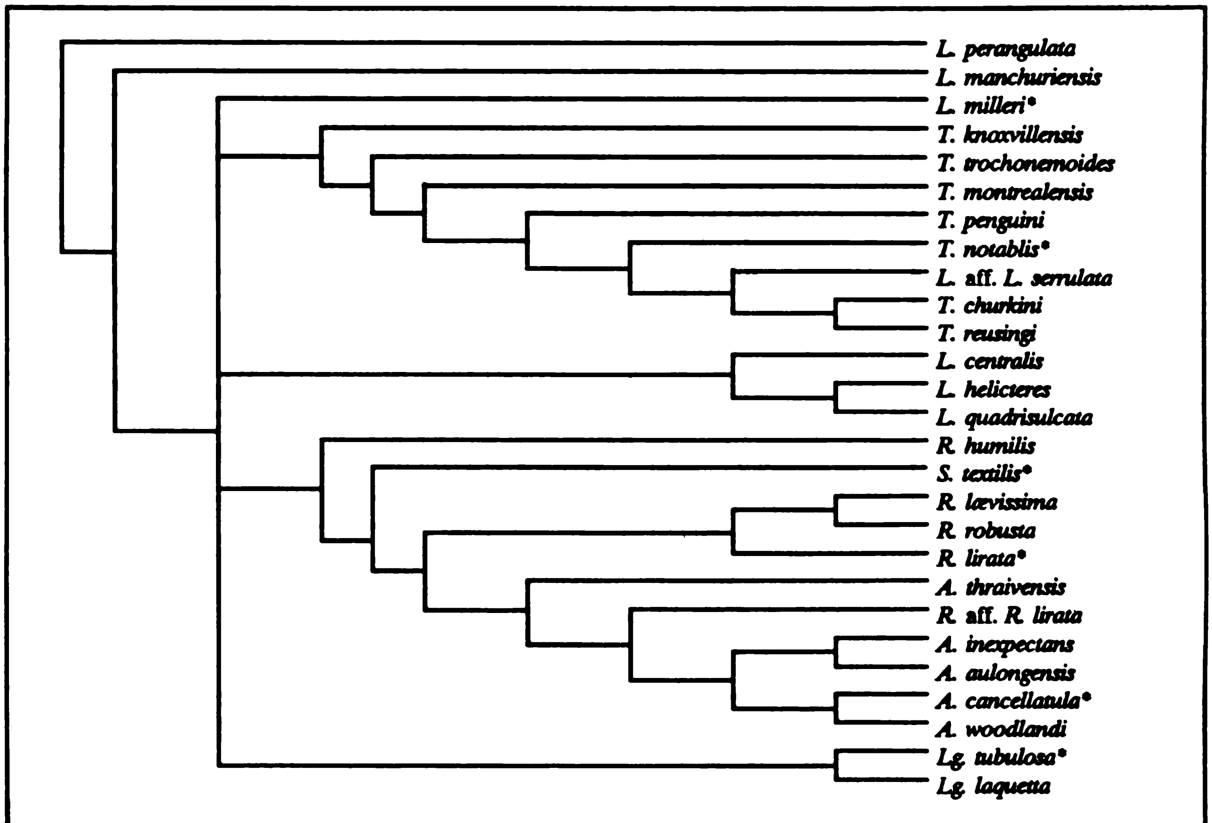
8b) Majority Consensus of 100 Bootstrap Replications

Figure 8 Consensus Trees for Prosoclinal Lophospirid Species Known through the Ordovician.

exhibiting orthocline growth lines plus *Lophospira perangulata*. Sixty-nine character states were informative to this analysis. A heuristic search generated 32 equally parsimonious cladograms, the strict consensus of which is shown in Figure 9. Bootstrapping could not be attempted due to the size of the data set.

The trees produced had a length of 137 (possible minimum 77, maximum 332). The consistency index (CI = 0.524) and homoplasy excess ratio (HER = 0.609) are again above average for the number of taxa and characters used. As six of the Silurian species belonged to one sub-clade within the orthocline group, the sub-clade was analyzed alone using *Lophospira milleri* and *L. perangulata* as outgroup species. Twenty-two character states were informative to this analysis. A branch-and-bound search generated a single cladogram Figure 10. The consistency index (CI = 0.786) is well above average for the number of taxa and characters used while the homoplasy excess ratio (HER = 0.778) is slightly above average (Archie 1989b). Notably the cladogram matches exactly the pattern seen for these species in Figure 9.

The remaining Silurian species was run with the six species of the *medialis*-clade with which it shared obvious synapomorphies with *Lophospira perangulata* included as an outgroup. Fourteen character states were informative with a branch-and-bound search generating three equally parsimonious trees. The strict consensus tree is shown in Figure 11a with the majority consensus of 100 bootstrap repetitions in Fig. 11b. As in previous bootstrap analyses involving these species, the majority consensus paired *L. medialis* and *L. spironema*. However, this pairing occurred in only 22% of the replications and is not very robust. The other difference, the linking of *L. tropidophora* with *L. ehlersi* occurred in 59% of the



(*L.* denotes *Lophospira*, *Lg.* denotes *Longstaffia*)

Figure 9 Consensus Cladogram of Ordovician-Silurian Orthocline Lophospirids.

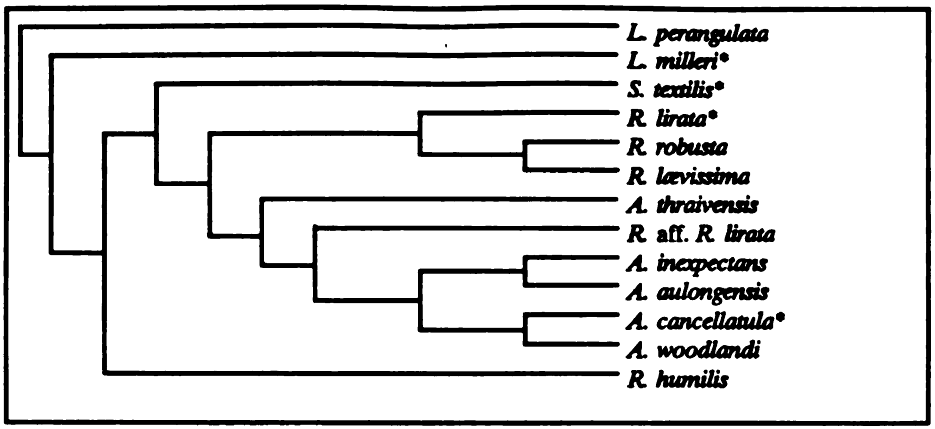
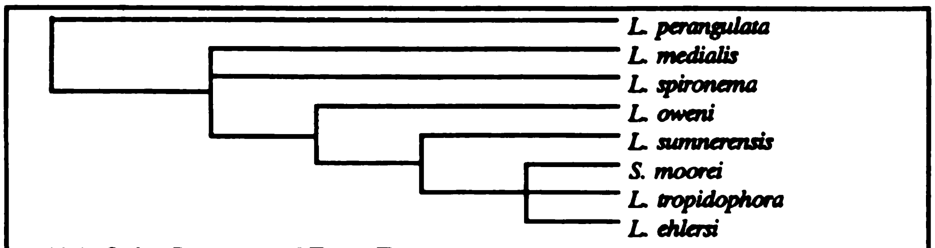
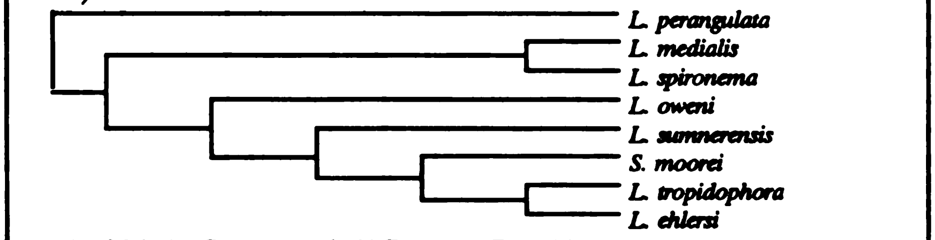


Figure 10 Cladogram for the Orthocline Lophospirid Subclade.



11a) Strict Consensus of Three Trees



11b) Majority Consensus of 100 Bootstrap Repetitions

Figure 11 Cladogram for the *medialis*-clade through the Wenlock

replications while *Schizolopha moorei* was the sister species of *L. tropidophora* in under one percent of the replications and never of *L. ehlersi*. The trees lengths were 30 (minimum possible 24 and maximum 50). The consistency index (CI = 0.667) is again above average for the number of taxa and character states while the homoplasy excess ratio (HER = 0.616) is average.

Random Subset Cladograms

While a full consensus cladogram could not be produced by the computer, Figure 12 was constructed from the above cladograms to provide a consensus for all of the lophospirids. The six subsets composed of every sixth taxon are shown in Figure 13. These can be compared with the relationships shown on a consensus for all of the lophospirids (Figure 12). Two of the six analyses produced single cladograms (13a & 13e). These do not match the vagaries of a consensus cladogram - for example, the first cladogram shows *Trochonemella trochonemoides* and *Lophospira quadrisulcata* as a sister-group and as the sister clade of

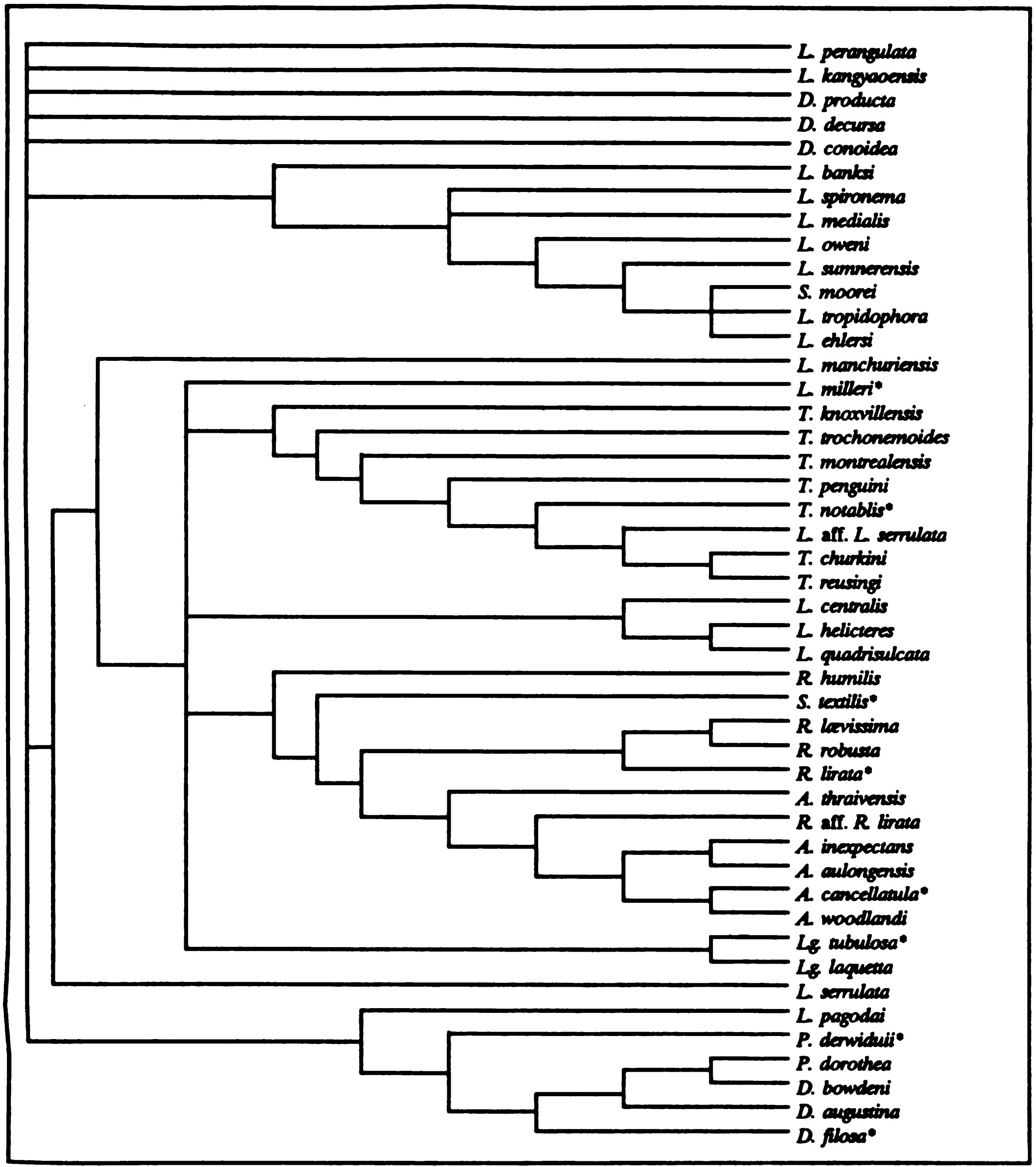


Figure 12 Consensus Cladogram for the Lophospiridae

Arjamannia inexpectans and *Ruedemannia robusta* whereas the consensus shows *T. trochonemoides*, *L. quadrisulcata* and the *A. inexpectans-R. robusta* pair in three sister clades produced by a trifurcation. However, neither cladogram contradicts the consensus cladogram and the relationships shown on both are reasonable given the consensus. The other four analyses produced five or six trees with the consensuses shown (13b - d & f). None matched

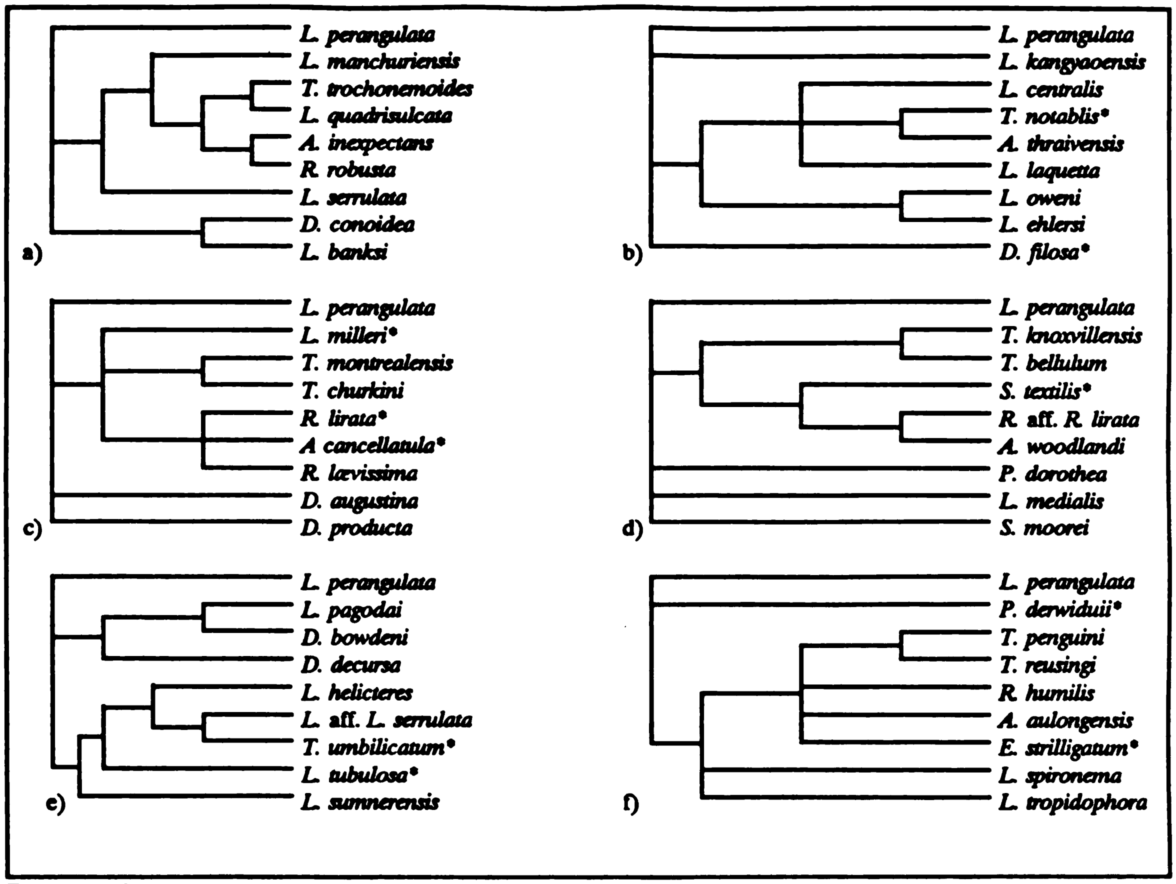


Figure 13 Six Subset Cladograms

the overall consensus exactly. Three failed to pair species that were linked on the consensus. In two of these cases (*L. medialis* and *Schizolopha moorei* in 13d and *R. humilis* and *A. aulongensis* and *L. spironema* and *L. tropidophora* in 13f) the pairs involved one of the most primitive and one of the most derived species from each clade. In these cases, homoplasies between the more derived species produced alternative relationships to the consensus. The same is true to a lesser extent for *R. lirata* and *R. lævissima* in 13c. The final cladogram, 13b, is similar to 13a and 13e in that it shows *T. notablis* and *A. thraivensis* to be a sister pair instead of part of unresolved as on the consensus. The similarities between these subsets and the overall consensus cladogram add further support to the general relationships between lophospirid clades and suggest that they should not be seriously disrupted by as-yet-unknown species. Conversely, these subsets also show the importance of importance of unknown species in resolving specifies-level relationships and also the importance of considering temporal factors when deciphering cladograms.

DISCUSSION

The hypothesized evolutionary tree of the Ordovician and Silurian Lophospiridae are shown in Figure 14. Three major clades, the Bicinctids[1], the Trochiformids[2] and the Donaldiellids[3], four individual species (*Lophospira kangyaoensis*, *L. serrulata*, *L. banksi* and *D. producta*) and one sister-group pair are all thought to have independently evolved from *Lophospira perangulata* at different times from the Arenig or Llanvirn to the Caradoc. None of these groups show any convincing synapomorphies with each other, as the states shared by later species of different clades never represent traits diagnostic of both clades.

The suggestion that *L. perangulata* is ancestral to multiple species is by no means a radical hypothesis, having been suggested as early as 1897 by Ulrich & Scofield and as recently as 1987 by Tofel & Bretsky. *Lophospira perangulata* is an excellent candidate for being ancestral to many lineages. It is a morphologically simple species exhibiting no derived features relative to other lophospirids - its only characters are the most basic derived traits of the Lophospiridae. Also, *L. perangulata* appears to represent the oldest and most primitive known lophospirid, with at least one British species from the Arenig or possibly Tremadoc (*L. borealis* of Donald 1902) fitting the original description of the species (Hall 1847). *Lophospira perangulata* also appears to have been the most widespread lophospirid species temporally and geographically. The combination of these factors might have encouraged a

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[1] Named for the subsection used by Ulrich & Scofield (1897) to classify many of these species.

[2] Named for the general shell shape exhibited by many of the species.

[3] Named for the predominant genus in the clade, *Donaldiella*

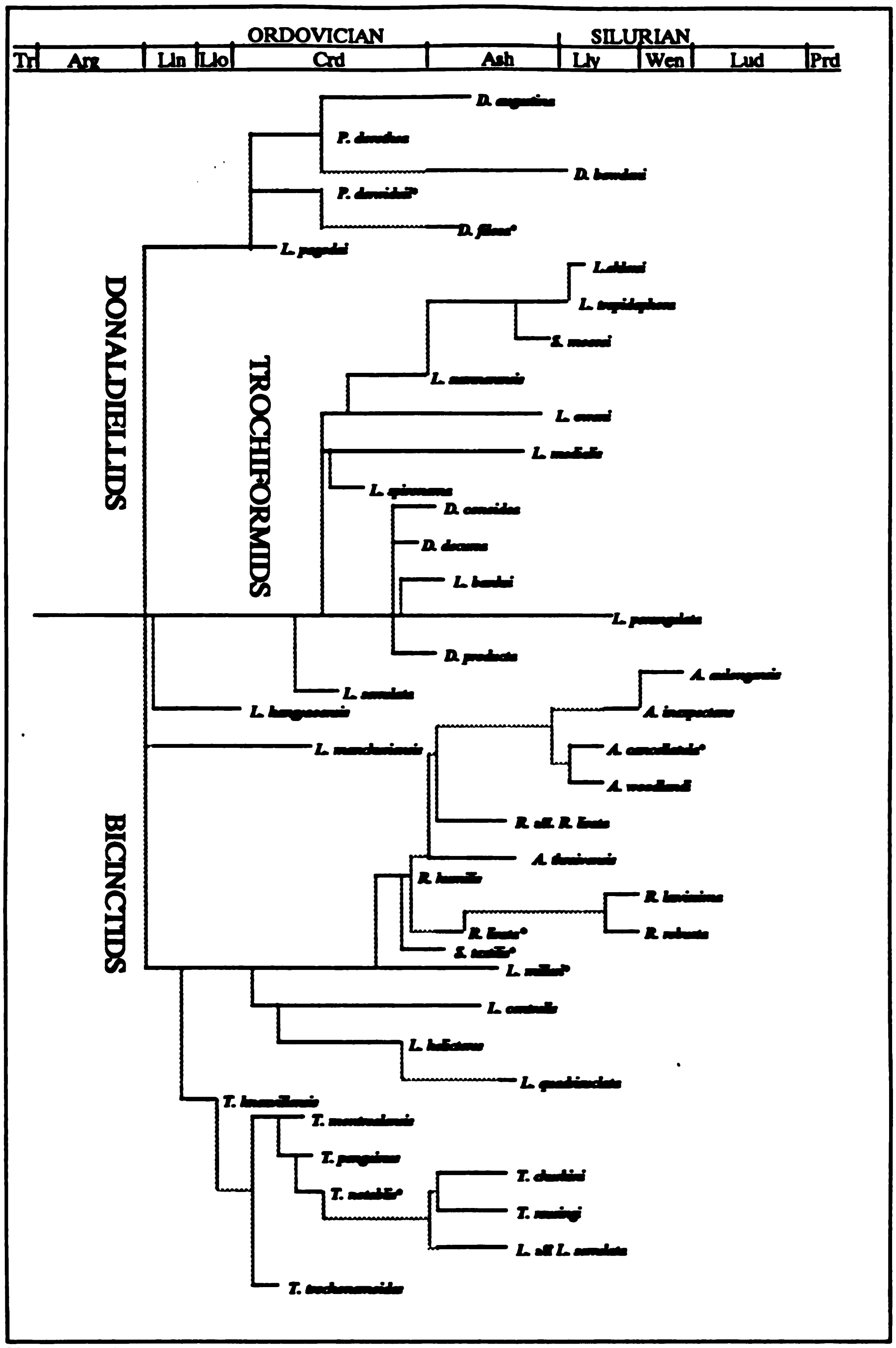

Figure 14 Hypothesized Phylogeny for the Ordovician and Silurian Lophospiridae.

relatively high number of speciation events. I did consider that the specimens classified in Appendix A as *L. perangulata* may represent different lineages that had reverted to the most primitive lophospirid morphology. However, there are lophospirid species displaying more primitive overall morphologies than older relatives, yet all can be easily distinguished from *L. perangulata*. In addition, *L. perangulata* does not display any significant temporal gaps throughout its wide geographic range. I therefore consider the specimens placed in *L. perangulata* to represent a single lineage.

Phylogeny of the Bicinctids

The most diverse clade derived from *Lophospira perangulata* is the Bicinctid clade (Figure 15). Important synapomorphies of this clade include growth lines with much less abapertural sweep than exhibited by *L. perangulata* and an L-shaped columellar lip. The Bicinctid clade has at least four species by the Llandeilo. The Llanvirn-Llandeilo analysis strongly indicates that this clade evolved from *L. perangulata* independent of either *L. kangyaoensis* or *Donaldiella pagodai*. A strict consensus tree linked neither of those two species with the bicinctids while a bootstrap majority consensus was able to link *L. kangyaoensis* with the bicinctid clade on only 37% of the alternate trees compared to 89% of the trees uniting the clade. Any phylogenetic connections closer than *L. perangulata* between the bicinctid clade and either of the other two species requires reversals in the most primitive member of the clade, *L. manchuriensis*. As *L. manchuriensis* represents a good ancestral candidate for all other bicinctid species, this is considered very unlikely. *Lophospira manchuriensis* differs from other bicinctid species only in the absence of more derived traits, being more similar in overall morphology to *L. perangulata*. A very similar species is known from the Llandeilo of North America (*L. rectistriata* Raymond 1908), and while the affinity between the Asian and American species is unclear (see discussion of *L. manchuriensis* in Appendix A), it is probable that a species of this type was ancestral to the rest of the Bicinctids.

Similarly, *Lophospira milleri* shows no autapomorphies itself and represents a likely

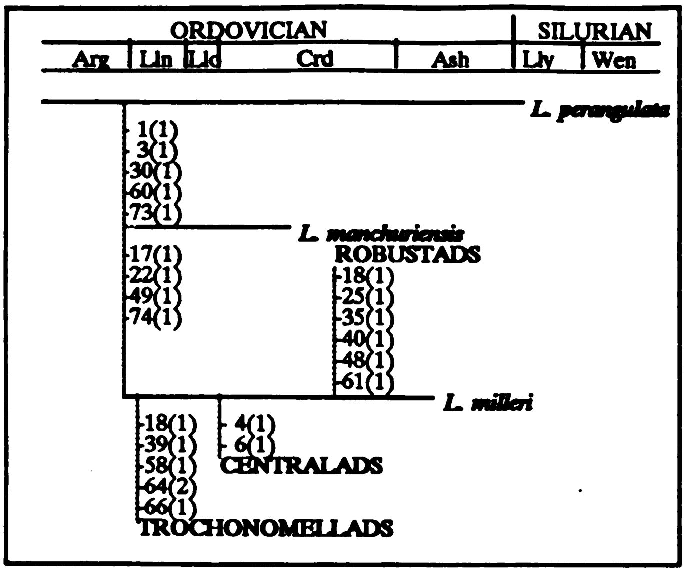

Figure 15 Phylogeny of Bicinctid Species (for character changes, see Appendix B).

ancestor to three independent sub-clades: the trochonemellads[1], the centralads[2] and the robustads[3]. The synapomorphies linking all three sub-clades to *L. milleri* include a sharp upper whorl carina removed from the suture, a less concave upper ramp, a more expanded base producing a sharp intersection between the lower ramp and the base and a decrease in the number of adult whorls. This trichotomy should not be surprising for like *L. perangulata*, *L. milleri* was a temporally and geographically wide-ranging species which might have promoted its chances of producing multiple daughter lineages.

The proposed phylogeny for the oldest apparent bicinctid sub-clade, the trochonemellads, is shown in Figure 16. The earliest known species, *Trochonemella knoxvillensis*, is known from the Llandeilo. The differences between *Lophospira milleri* and *T. knoxvillensis* are the most basic synapomorphies of the trochonemellad clade: a tangential rather than radial aperture, a more rounded inner lip and a strong counter-clockwise rotation of the whorl bringing the upper ramp to a nearly horizontal position. While *T. knoxvillensis* represents a possible ancestor of later *Trochonemella* species, it does appear to have been unusually large. There are poorly understood pre-Caradoc specimens currently placed in

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[1] Named for the predominant genus in the clade, *Trochonemella*.

[2] After *Lophospira centralis*, the apparent stem member of the group.

[3] After the subsection of *Lophospira* used by Ulrich & Scofield to classify these species.

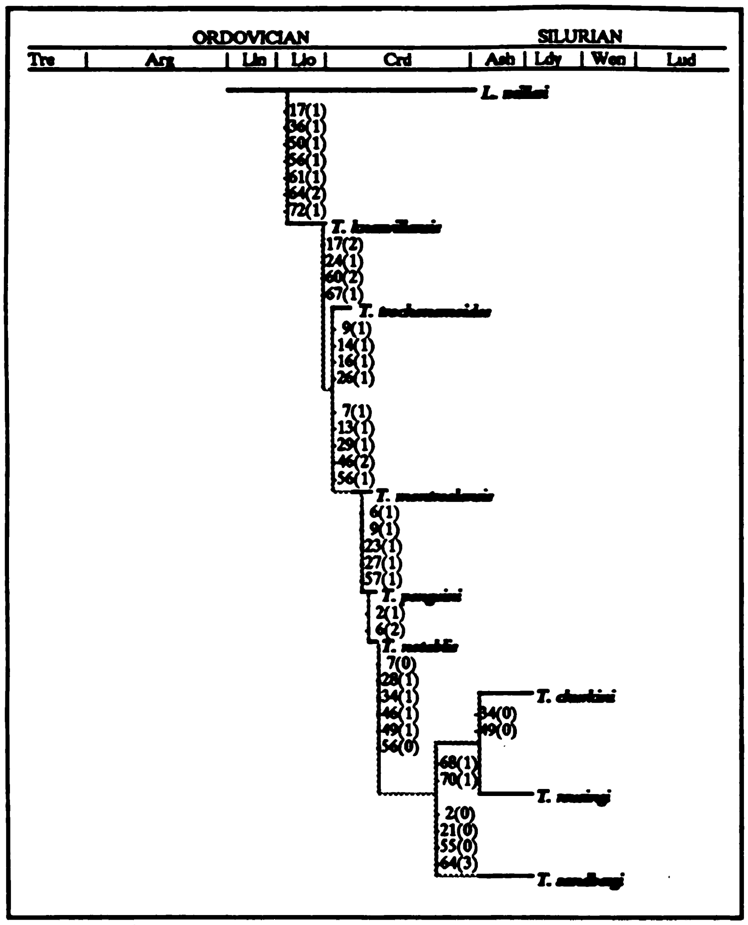

Figure 16 Phylogeny of the Trochonemellads.

either *Lophospira* or *Trochonema* that probably represent early *Trochonemella* and a more thorough examination of those fossils may provide a better last common for later *Trochonemella* than *T. knoxvillensis.*

Two *Trochonemella* lineages are apparent by the Caradoc. One is composed of three species that each represents a step of the development of an imbricated selenizone. The selenizone of *T. montrealensis* lacks a middle thread and is nearly concave. The adult whorls of *T. penguini* display the same selenizone, but the juvenile whorls show sharply imbricated selenizones. The third species, *T. notablis*, exhibits a strongly imbricated selenizone throughout ontogeny. As *T. penguini* n. sp. and *T. notablis* have other synapomorphies such negligible growth line sweep, rounded upper whorl with the upper ramp oriented nearly perpendicular with the selenizone, and a much stronger, abapically oriented upper carina. It was considered that the *T. penguini* and *T. notablis* might represent variants of the same species. However, the continuous selenizone imbrications and lamellose growth lines distinguishing *T. notablis* from *T. penguini* are shared with *Trochonemella* species from the Ashgill. This merits the recognition of *T. penguini* and *T. notablis* as separate species here.

The three Ashgill trochonemellad species appear to be derived from *Trochonemella* *notablis*. This represents one of the only major gaps in the lophospirid fossil record. However, the stratigraphic range of *T. notablis* does overlap with the ranges of the Ashgill *Trochonemella* at the 95% confidence interval (see Table III). *Trochonemella* is associated with an environment absent in eastern North America after the early Caradoc. Later Caradoc faunas from the west have not been well described and it is possible that more intermediate species would be found there.

Two of the Alaskan species, *T. churkini* and *T. reusingi*, share cyclic growth lines with *T. notablis* and are linked more specifically to each other by strongly serrated upper carinae, thickened parietal lips and a very thin columellar lip. The third Ashgillian trochonemellad was originally described as having affinities with *Lophospira serrulata*, but it does not seem to be at all closely related to that species (see cladograms in Figure 6). Therefore, the name *Trochonemella sandbergi* n. sp. is proposed for this species (see description in Appendix A for further comparisons with *L. serrulata*). The relations of this species are more difficult to understand than for the others. The imbricated selenizone, rounded columellar lip, near perpendicular orientation of the upper ramp relative to the selenizone, abapically oriented upper carina and very straight growth lines link *T. sandbergi* with the *notablis-churkini-reusingi* clade while the strongly serrated upper carina links it with both *T. churkini* and *T. reusingi*. The serrated lower carina linking it more specifically with *T. reusingi*. However, *T. sandbergi* displays a very *Lophospira*-like overall form, with even less counter-clockwise rotation of the whorls than either *T. churkini* or *T. reusingi*, and the aperture is only slightly tangential. It is worth noting that the only *Lophospira* species known from the Ashgill of Alaska is *Lophospira perangulata* (Rohr & Blodgett 1985) and *T. sandbergi* may represent a reversion back to a *Lophospira* morphotype made possible by the relative absence of *Lophospira*. The primitive traits of *T. sandbergi* are also displayed by small possibly juvenile specimens identified as *T. churkini* (Rohr 1988 fig. 5.2 & 5.3). If so, *T. sandbergi* may represent a neotenic derivation from *T. churkini* or some related species. While it seems safe to conclude that *T. sandbergi* shares a more recent common ancestor with *T. churkini* and *T. reusingi* than *T. notablis*, more rigorous analysis is necessary to determine if it is more closely related to one than the other.

The traits separating *Trochonemella trochonemoides* from *T. knoxvillensis* and later *Trochonemella* involve the loss of the lophospirid selenizone and the development of a strong internal channel underneath the peripheral carina. These traits link *T. trochonemoides* with the genus *Trochonema* and further discussion on that relationship is given below.

The second bicinctid sub-clade, the centralads, are first known from the base of the Caradoc (Figure 17). This sub-clade is the smallest of the three, with only three species well enough known to include in this study. It is also the least robust, being characterized by very straight growth lines with only a very slight curve above and below the selenizone. This also appears on some derived *Trochonemella* species, and because *Lophospira helicteres* shares other derived traits with those species such as very strong upper and lower carina, an umbilical carina and whorl disjuncture, a bootstrap search of lophospirids known through the early Caradoc linked *L. helicteres* with the Trochonemallads nearly as often as with *L. centralis* (30% vs 36% respectively). However, *L. helicteres* lacks any of the key characteristics of the trochonemallads. The most important trait of the trochonemellads, the tangential aperture, is exhibited by *L. helicteres* but is clearly convergent. *Lophospira helicteres* is strongly associated ecologically with the *Trochonemella* species with which it shares derived states and it is possible that these simply represent similar adaptive responses to the same ecological system.

While *Lophospira helicteres* and *L. centralis* share only a single non-Bicinctid synapomorphy, *L. helicteres* differs from *L. centralis* mostly in traits associated with the open-coiling of the final whorls. On well-preserved specimens, the young close-coiled whorls of *L.*

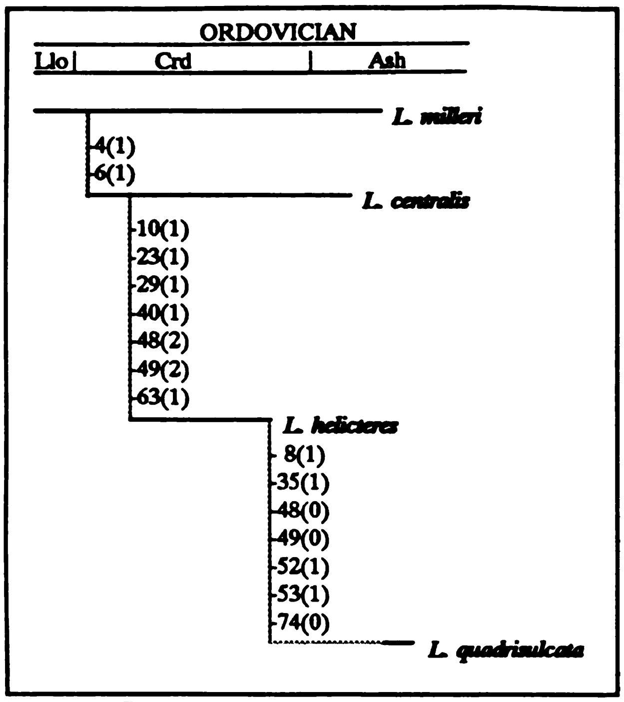

Figure 17 Phylogeny of Centralad Species

helicteres are nearly identical with *L. centralis*, being distinguishable only by the stronger upper carina and bolder selenizone middle lirae. *Lophospira centralis* appears to precede *L. helicteres* and their geographic ranges are nearly identical and as it differs only in the lack of derived traits, it is considered the likely ancestor of *L. helicteres*.

The Ashgill species *L. quadrisulcata* appears to be descended from *L. helicteres*, sharing an umbilical and sutural carina, a more rounded columellar lip and strong upper and lower whorl carinae with the older species. While it lacks the open-coiling and associated traits of *L. helicteres*, *L. quadrisulcata* does display a tangential aperture that may represent a close-coiled fixation of the tangential aperture produced by the open-coiling of *L. helicteres*.

The final bicinctid sub-clade to appear was the robustads (Figure 18). The oldest known species of this group, *Ruedemannia humilis* and *Schizolopha textilis* appear in the upper Caradoc. While *Lophospira milleri* was not as common after the Black Riveran as before, it was still present (*contra* Tofel & Bretsky 1987) and is the most likely ancestor for the group. Important synapomorphies of this clade include thin spiral lirae on the lower whorl, a greatly reduced lower carina, an upper carina halfway between the suture and the selenizone and fuller upper ramp produced by increased convexity and a more vertical angle relative to the selenizone.

Of the two Caradoc species, *Schizolopha textilis* is the more derived, displaying a long thin apertural slit, a higher sutural point and additional spiral lirae on the upper whorl.

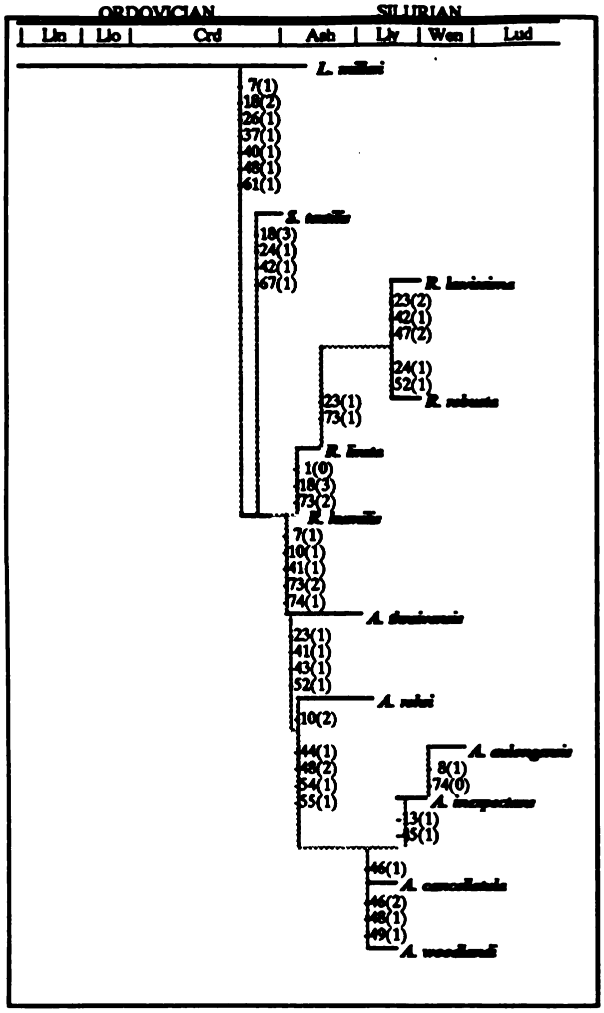

Figure 18 Phylogeny of the Robustads

Ruedemannia humilis would represent the most likely ancestor candidate for *S. textilis* except that species possesses two upper whorl carina while *S. textilis* possesses only one. However, cladograms including younger taxa suggest that other species with single upper carina were derived from *R. humilis*, so *R. humilis* is considered the most likely ancestor for *S. textilis*.

While *Schizolopha textilis* and *Ruedemannia humilis* are sister-taxa in Figure 5, the inclusion of Ashgill and Silurian robustad species places *R. humilis* as the outgroup to *S. textilis* and to two separate infraclades, the ruedemannads and the arjamannads[1]. However, neither the ruedemannads not the arjamannads display the long apertural slit or the same manner of thin upper whorl spiral lirae of *S. textilis* as diagnostic traits, disqualifying that species as a likely ancestor. However, *R. humilis* does not show any synapomorphies relative to the two later clades and serves as a likely ancestral candidate for both. As the arjamannads and the ruedemannads do not share any new synapomorphies with each other, it is supposed that they are separately derived from that species. While the ruedemannads do display a single upper carina similar to *S. textilis*, the clade has other synapomorphies not seen in *S. textilis*. Given that they also first appear after *S. textilis*, there

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[1] Named for the predominant genera in each clade, *Ruedemannia* and *Arjamannia*.

does not appear to be a connection between them closer than *R. humilis*.

The arjamannad infraclade is characterized by thick spiral lirae on the lower whorl forming a cancellate pattern, a prominently extended selenizone and the presence of a second upper whorl carina. *Arjamannia thraivensis* and *A. rohri* n. sp. (*R.* aff. *R. lirata* of Rohr 1988 - see Appendix A) are the oldest known species, both appearing in the Ashgill. Silurian arjamannads display thick cancellate ornamentation on both the upper and lower whorl with the two upper carina being reduced to thin lirae only somewhat stronger than the surrounding ornamentation. *Arjamannia thraivensis* does not exhibit this, but *A. rohri* displays sparse additional lirae on the upper whorl. The Alaskan species also share a more swollen base with the Silurian species. Thus, *A. rohri* or some similar species represents a likely ancestor for all known Silurian *Arjamannia* while *A. thraivensis* or another similar species was likely ancestral to *A. rohri*. Because of it is known only from Alaska while other well known *Arjamannia* species are known from eastern North America and Britain, *A. rohri* itself may be a questionable candidate as the direct ancestor of the Silurian *Arjamannia*. However, *Arjamannia* has been reported from the Silurian of China (Pan 1978), and while the affinities of that species are unknown, this implies a fairly wide biogeographic distribution for the clade. It is possible that more thorough examination of poorly known species currently placed in *Ruedemannia* and *Lophospira* may clarify the situation.

The earliest known Silurian arjamannad species, *Arjamannia cancellatula* and *A. woodlandi* differ by *A. woodlandi* possessing a *Lophospira*-like morphology throughout life rather while *A. cancellatula* displays a similar morphology only while young. *Arjamannia woodlandi* is known from the Brassfield Limestone, a diminutive fauna containing at least one other lophospirid species (*Lophospira ehlersi*) that reverted to a more primitive overall morphotype. It seems possible that this represents a common evolutionary response to similar ecologic circumstances. The other two Silurian species are share an higher spiral lirae density on the whorls and weak selenizone middle lirae. *Arjamannia inexpectans* appears to be a likely ancestor of *A. aulongensis* as it is older and lacks some of the derived features seen on *A. aulongensis*.

The second infraclade, the ruedemannads, are a less robust group as there are fewer species known within the clade. *Ruedemannia lirata* shows no autapomorphies relative to *R. robusta* and *R. lævissima* and represents a good potential ancestor of the two Silurian species. Synapomorphies of the ruedemannads include a very wide selenizones, a convex upper whorl with a single carina in the middle and a strongly reflected columellar lip. Silurian synapomorphies include are a more vertical upper slope relative to the selenizone, a much wider base and a reversion to weaker growth lines. It is worth noting that this analysis supports Ulrich's (1897 in Ulrich & Scofield) original suggestion that *R. lirata* was linked to "more common" *Lophospira* through *R. humilis* (p. 989).

Phylogeny of the Donaldiellids

The oldest known donaldiellid species, *Lophospira pagodai*, is also from Llanvirn. Important synapomorphies of this clade include a "right-angle" whorl stacking with the selenizones perpendicular to the right line of the apical angle, a flat upper ramp, a very low whorl expansion rate and an increased number of adult whorls. While the synapomorphies of the group are fairly well understood, the relations within the donaldiellids are the least well understood of the three major offshoots of *L. perangulata*. This is due both to the relative morphologic simplicity of the group (only 10 character states apply) and the absence of specimens. Abundant specimens were available only for *Donaldiella bowdeni* from the Ashgill of Kentucky. *Lophospira pagodai* is the only pre-Ashgill species for which good specimens were available, and only the descriptions and figures of the Asian *Pagodospira derwiduii* and *P. dorothea* and the British *D. filosa* were detailed enough to merit inclusion in this analysis. Neither the material nor the descriptions and figures of *Donaldiella augustina* were detailed

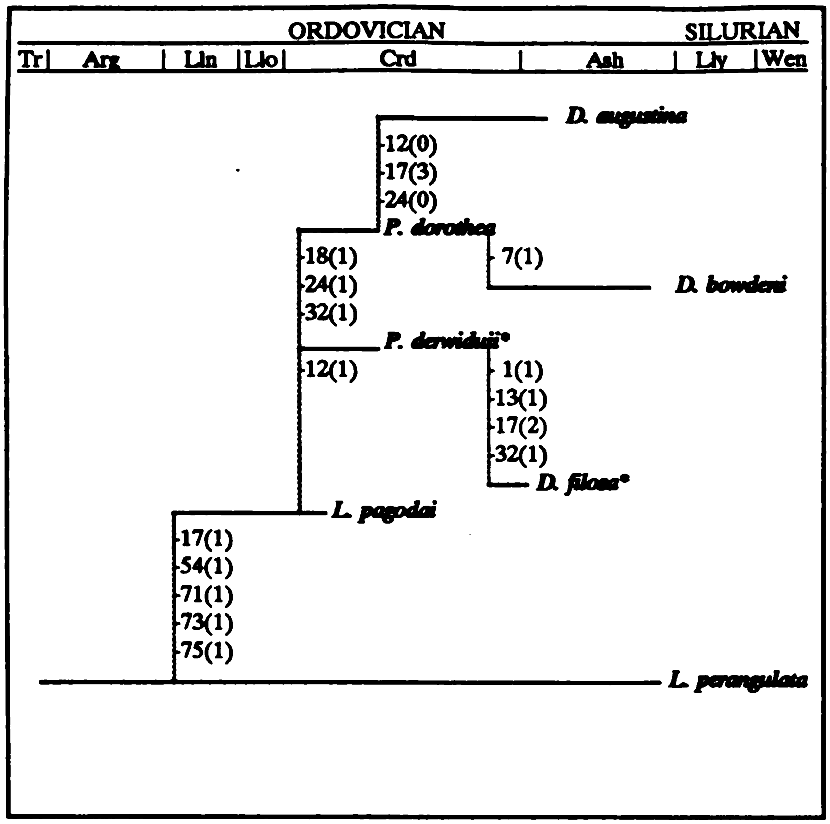

Figure 19 Phylogeny for the Donaldiellids

enough on their own, but combining the two provided adequate information.

The inferred phylogeny for the donaldiellids is shown in Figure 19. Unlike the stem members of other major clades, *Lophospira pagodai* does not appear to have produced abundant daughter lineages. However, the species is a potential ancestor to *Pagodospira derwiduii* from the Early Caradoc of Asia, which in turn is a potential ancestor for all of the other species. Post-*pagodai* synapomorphies include a selenizone unique to lophospirids, being very slightly convex and displaying a very weak middle thread. The Asian *P. dorothea* represents a possible precursor for both of the North American species. *Pagodospira dorothea* shares an extended upper ramp with *Donaldiella augustina* and *D. bowdeni*, and a fine upper whorl carina and strongly reflected columellar lip with *D. bowdeni*. Information about the columellar lip is absent for *D. augustina* and it is not known to have an upper carina. *Donaldiella augustina* is unusual in its huge size relative to other lophospirids, and some of the character states shown by that species may simply be allometric changes. It appears to be a descendant of *P. dorothea* or some related species, and is not thought closely aligned with any later ones.

The affinities of *Donaldiella filosa* are more difficult. It lacks the extended upper ramp and fine upper carina shown by *P. dorothea* and *D. bowdeni*, and it appears to have evolved separately from a *P. derwiduii*-like ancestor via unknown intermediates. To an even greater extent than with the trochonemellads, a detailed study of the many poorly understood high-spired lophospirids of the Early Ordovician could greatly clarify relations within the Donaldiellids.

Phylogeny of the Trochiformids

The phylogeny for the Trochiformids (Figure 20) is much more robust than for the Donaldiellids. This appears to be the last significant clade to diverge from *Lophospira perangulata*, with the earliest known species first appearing in the post-Black Riveran Caradoc. Important synapomorphies of this clade are a U-shaped columellar lip, a weak upper carina and a somewhat elliptical whorl produced by an increased whorl expansion rate without an increase in the base size. The trochiformid upper carina might appear homologous with the stronger feature shown by members of the Bincinctid clade, but the Trochiformids lack the important diagnostic traits of those species such as reduced growth line sweep and an expanded base.

The two oldest known trochiformid species are *Lophospira medialis* and *L. oweni*. Of the two, *L. medialis* appears to be the more primitive, differing from *L. oweni* and later species in the clade in the absence of derived traits. *Lophospira spironema* from the upper Caradoc was temporally and geographically very restricted and may simply have been a regional variant of *L. medialis*. However, *L. spironema* differs in part by possessing spiral ornamentation on the upper and lower whorls and an unusually thin lower lip, so it is considered a separate species here.

While *Lophospira oweni* appeared at the same time as *L. medialis*, it shares a greatly thickened columellar lip, an upper carina that weakens with age and more indistinct selenizone trilineations with younger species such as *L. sumnerensis* and *L. tropidophora*.

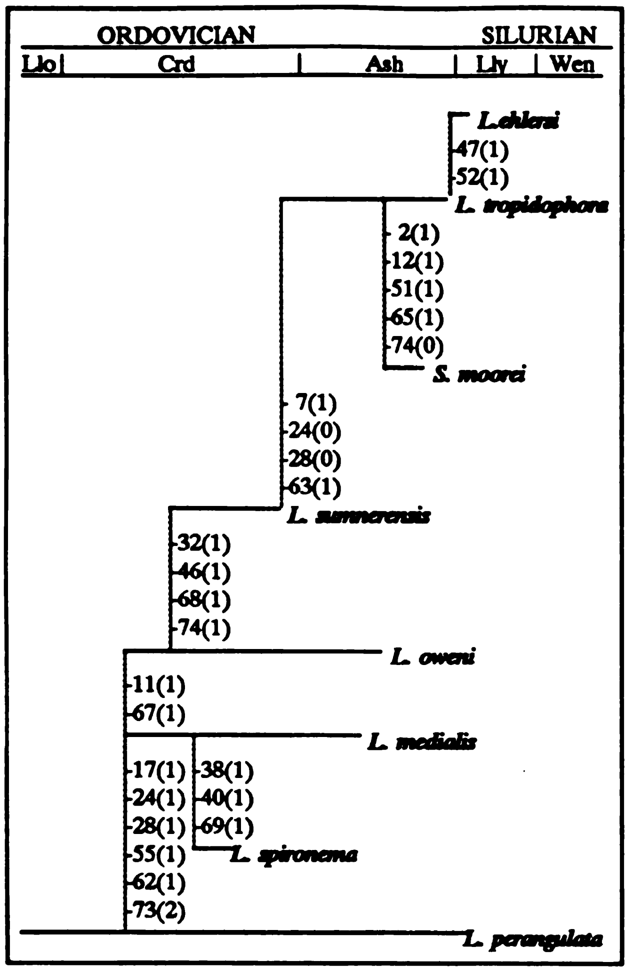

Figure 20 Phylogeny of the Trochiformids.

Even though it appears to have stronger growth lines, *L. oweni* is considered the likely ancestor of those species because of these synapomorphies. The lip is even thicker on later species, being much more extended and completely filling the umbilicus. Because *L. sumnerensis* also shares a high suture point and the loss of the lower carina with the later *L. tropidophora*, and also because it appears to be replaced in the fossil record by that species, it is thought to be ancestral to *L. tropidophora*. The Silurian *L. ehlersi* from the Brassfield formations of the Lower Wenlock is considered a descendant of *L. tropidophora*. I did consider that the younger species might simply represent a younger, smaller version of *L. tropidophora*. However, the suture point of *L. ehlersi* drops over ontogeny and *L. ehlersi* may represent a reversion to a more primitive form.

The final species in this clade, the Ashgillian *Schizolopha moorei*, is thought to have been separately derived from *L. tropidophora*. *Schizolopha moorei* shows the high suture point of *L. sumnerensis* and *L. tropidophora*, with the relatively flat, carina-less upper ramp and wide selenizone with *L. tropidophora*. While it is not clear that the columellar lip is as thick or extended as on those two species, it is comparable. Although *S. moorei* shows the strong growth lines, they are much more widely spaced than those of *L. oweni* and appear to represent an autapomorphic cyclic feature. This species differs from all other Trochiformids in possessing a rather thick apertural slit.

Affinities of Lophospirid Mixospecies

A pair of sister species and four lone species are thought to have independently evolved from *Lophospira perangulata* at different times in the Ordovician. These species all represent what Archibald (1990) termed mixospecies, as they do not have any convincing synapomorphies with other taxa, resulting in unresolved polytomies. The *decursa-conoidea* sister pair are included here as they represent a mixotaxon that can not be linked to any other lophospirid group.

The sister species, *Donaldiella decursa* and *D. conoidea* are linked by only a single trait and therefore were not apparent on even the strict consensus trees of smaller data sets. When the pairing was produced by a bootstrapping search (see Figure 6), they were paired on only 23% of the replications. However, the trait they share is a lower ramp so reduced that the lower carina almost appears to be an umbilical carina. This represents the only change *D. decursa* displays relative to *L. perangulata* with *D. conoidea* also exhibiting a wide protruding selenizone. Therefore I think that *D. conoidea* was derived from *D. decursa* as originally suggested by Ulrich (p. 976 of Ulrich & Scofield 1897). These two species lack any of the synapomorphies of the donaldiellid clade and while they appear superficially similar, there is no close phylogenetic relation.

Neither of the other two high-spired Caradoc species show any convincing synapomorphies with either the Donaldiellids or the *decursa-conoidea* pair. *Donaldiella producta* possesses a greatly increased number of whorls, but it lacks the characteristic "right-angle" whorl stacking of the Donaldiellids and also lacks any of the more derived features found in that group. It also lacks the reduced lower ramp of the *decursa-conoidea* clade. This agrees with Ulrich's suggestion that the species was independently derived from *Lophospira perangulata* (p. 976 in Ulrich & Scofield 1897). Another mixospecies, *L. banksi*, has a wide, prominent selenizone similar to *D. conoidea*, but displays a normal lower ramp. This species also displays a peculiar open coiling not seen in any of the above species. This is a variable merontic trait in *L. perangulata* which may have become fixed in *L. banksi*.

Lophospira kangyaoensis of the Llanvirn of Asia was linked by Endo (1932 p. 53) to the younger *L. sumnerensis* of the Trochiformid clade owing to the shared high suture points. However, the Asian species lacks the U-shaped columellar lip diagnostic of that clade and lack the greatly increased lip thickening characteristic of the later members such as *L. sumnerensis* that show the higher suture points. There are Asian species from the Caradoc (e.g. *L. trochiformis* Grabau or *L. konnoi* Kobayashi) that may be descended from or otherwise closely related to *L. kangyaoensis*, but these are not well enough understood to include in this analysis. As discussed previously, there are no convincing synapomorphies connecting *L. kangyaoensis* with the stem members of either the bicinctid or the donaldiellid clades, supporting the view that it evolved independently from *L. perangulata*.

The final mixospecies, *Lophospira serrulata*, has often been linked to *L. helicteres* as the two share a very similar style of open coiling (e.g. Wilson 1951 p. 39). *Lophospira serrulata* also displays an umbilical carina and a strong upper whorl carina similar to those found on *L. helicteres* and some more derived *Trochonemella* species. Because of this, strict and bootstrap majority cladograms including these species place *L. serrulata* as the sister group of the Bicinctids. However, *L. serrulata* lacks any of the synapomorphies of that clade and the cladograms linking it to some Bicinctids depend upon reversals to primitive states for the stem members of the bicinctid clade. *Lophospira serrulata* is strongly associated with other lophospirids displaying tangential apertures and as suggested previously the similarities may represent common adaptive responses to the same ecological pressures. This appears to be the case for the strong upper carina at least, as the one displayed by *L. serrulata* is formed by a projection from the aperture not seen on any other lophospirid species.

Lophospira serrulata also does not appear to be especially close to the Trochiformids. A species similar to *L. medialis* would represent a likely potential ancestor for *L. serrulata* as they share similar U-shaped columellar lips and increased whorl expansion rate with no corresponding change in the width of the base. However, *L. serrulata* disappears from fossil record before the earliest Trochiformids appear, making such a relationship between *L. serrulata* and *L. medialis* very unlikely. As *L. serrulata* shows many autapomorphies relative to the Trochiformids, it is not a possible ancestor for that group.

TAXONOMIC REVISIONS AND THE RELATIONSHIPS BETWEEN HIGHER LOPHOSPIRID TAXA

Taxonomic Status of *Lophospira*

Lophospira as previously described is an extremely paraphyletic group. As the type species, *Lophospira milleri*, represents a paraphyletic metaspecies as described by Donoghue (1985) and Archibald (1990), it is not possible for the genus to be monophyletic. However, the genus can be made less offensive to taxonomic purists by the erection of two new genera, *Ambilophospira* and *Paralophospira* (see Appendix A). The former is an ambitaxon as a clade of the species included is an unresolvable polytomy with one species (*A. perangulata*) a valid ancestor for both the species in the genus and for other genera (Archibald 1990). *Ambilophospira* is comprised of *A. perangulata* and the mixospecies derived from *A. perangulata*. *Ambilophospira perangulata* is designated as the type species of that genus. As the *decursa-conoidea* sister pairing is not especially robust, these two species are also placed in *Ambilophospira*. The species within the trochiformid clade are re-classified here as the genus *Paralophospira*, with *P. oweni* designated as the type species. Some (e.g. Frey 1987) have classified some species in this clade as *Schizolopha* owing to their similarities to *S. moorei*. While this analysis supports that relationship, the type species of that genus, *S.*

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textilis, does not belong to this clade and trochiformid species therefore should not be classified in that genus.

Unfortunately, the two new genera include some of the better known species placed in *Lophospira*. However, as most stratigraphic studies do not identify these species past the generic level and as the stratigraphic range of *Lophospira* encompasses that of *Paralophospira* and is nearly as old as *Ambilophospira*, this re-classification does not render stratigraphic studies especially obsolete.

This leaves *Lophospira* as only *L. milleri*, *L. manchuriensis*, *L. centralis*, *L. helicteres* and *L. quadrisulcata*. While the genus is still paraphyletic, it now contains only descendants of *L. manchuriensis* that have not changed significantly enought to merit higher taxonomic recognition. Among the descendants of *Lophospira milleri*, higher taxonomic status is recognised for two of the clades, the Trochonemallinae and the Ruedemanniinae, with the third subclade is tentatively retained in *Lophospira* (see discussions below). The assignment of these higher taxonomic rankings may appear to be somewhat arbitrary, for neither of the clades receiving subfamily labels are phylogenetically more significant than the third clade. However, the morphologic change is much greater for these two clades and both have substantial histories after the Silurian - the Trochonemallinae persist until at least the Devonian and probably throughout the Paleozoic while the Ruedemanniinae survived until the Jurassic (Knight *et al.* 1961). The third clade shows neither the substantial change nor the subsequent history of the other two and is therefore left in *Lophospira*. While this goes against strict cladistic taxonomy, to ignore the magnitude of the differences between the clades and their likely ancestors effectively denies the possible evolution of higher taxonomic forms after the initial radiation of a group. Carrying this logic to an extreme, it denies the evolution of anything other than species after the basal Cambrian. While this may be true in a sense, it is not a taxonomic philosophy that can be reconciled with the accepted Linnaean hierarchy and ignores the differences in amounts and types of evolutionary change.

Lophospira-Loxoplocus and Knight's Subgeneric Rankings

Knight (1941 in Shimer & Shrock) reclassified *Lophospira*, *Donaldiella* and the Silurian *Loxoplocus* as subgenera of the genus *Loxoplocus*, thinking that they represented artificial and intergrading morphotypes of the same genus. This has been upheld by some (e.g. Peel 1977; Copper & Grawbarger 1977; Rohr 1980), but rejected by others (e.g. Tofel & Bretsky 1987). The relationship between *Lophospira* and *Loxoplocus* are unclear as there is only one known species of *Loxoplocus*. Without first-hand examination of good examples of that species it was not possible to include it in this analysis.

There has been no consensus on the affinities of *Loxoplocus*. While Knight obviously considered them close, Wenz (1938) did not even classify *Loxoplocus* as a pleurotomariine, placing it instead with the Murchisonids. In a description of the type species, Whiteaves (1886) suggested with reservations that *Loxoplocus* might be related to *Lophospira helicteres* (p. 30). Ulrich & Scofield made a similar suggestion in a footnote to the description of their *Helicteres* sub-section (1897 p. 963). While it is not described as such, the figures seem to indicate a trilineate selenizone and relatively straight growth lines, which would link it with lophospirids in general and Bicinctids in particular. The strong sutural and lower carina and rounded columellar lip further link it with *L. helicteres*. If this relationship could be demonstrated, the species within the centralad subclade could be reclassified as *Loxoplocus*. However, *Loxoplocus* appears to lack the upper ramp and umbilical carinae of the later centralad species, casting some doubts on this relationship. Unfortunately, *Loxoplocus* is not a well understood genus and while it may be descended from species of *Lophospira*, ranking *Lophospira* as a subgenus within *Loxoplocus* is not justified by the existing evidence.

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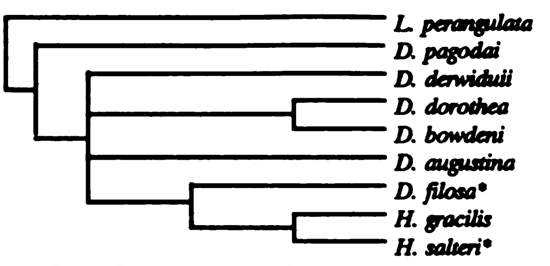
Lophospira - Donaldiella Relationship

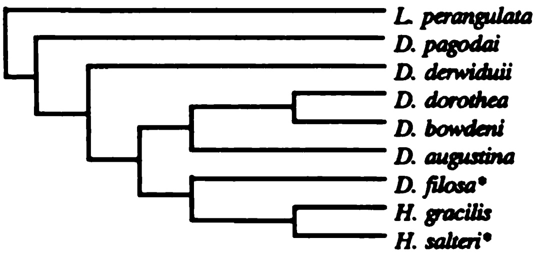
Knight (in Shimer & Shrock 1941) used *Donaldiella* as a sub-generic level morphologic description of high spired lophospirid species. However, the donaldiellid clade in this analysis contains the type species of *Donaldiella*, and as this represents a monophyletic group that can be termed *Donaldiella*, it is re-elevated to generic level here. As the type species of *Pagodospira* also falls in this clade, Knight *et al.*'s (1961) synonymization of *Pagodospira* with *Donaldiella* is maintained. *Donaldiella* is characterized by "right-angle" whorl stacking, low whorl expansion rate and high number of whorls. The oldest known species, *D. pagodai*, extends the genus to at least the Llanvirn of Asia. The upper temporal bound is not as clear. Silurian specimens are known from the United States and Britain showing the diagnostic traits of the genus (Donald 1906; Harrison & Harrison 1975) and an American specimen from the Devonian may also belong here (Linsley 1968).

Even though the exact diversity levels are unknown, it appears that this clade radiated more slowly than other lophospirid clades. There are few species reliably described as either *Donaldiella* or *Pagodospira*, and many of the species placed as those genera may actually be murchisonids. This clade also appears to have spread slowly geographically. Members of other lophospirid clades usually occur throughout the lophospirid geographic range soon after appearing. While *Donaldiella* is known from the Llanvirn in Asia, it is not known in North America until the Upper Caradoc and not until the Ashgill in Britain. This may indicate a change in larval ecology. While protoconchs can serve as an indicator of planktotrophic versus non-planktotrophic larvae (Jablonski & Lutz 1983), lophospirid protoconchs are rarely preserved and could not be compared in this analysis.

The other high spired taxa used in this analysis appear to have evolved separately from *Ambilophospira perangulata* and should not be termed *Donaldiella*. As there is no unity between those species, it is suggested that they be placed in *Ambilophospira* (*A. decursa*, *A.*



a) Strict Consensus of 12 Trees



b) Majority Consensus of 100 Bootstrap Replications

Figure 21 Cladogram of Ordovician *Donaldiella* and early Caradocian *Hormotoma*

conoidea and *A. producta*). As noted above, while *A. decursa* and *A. conoidea* appear to be sister species, this pairing is much less sure than any of the others and a new genus name is therefore withheld at least tentatively.

A possible relationship between this genus and the murchisonid genus *Hormotoma* merits examination. Early pleurotomariines are thought to be the ancestors of the murchisonids (Knight *et al.* 1961). Among lophospirids, *Donaldiella* species share the most in common with murchisonids. *Donaldiella* has at times been classified not only as a murchisonid, but as a subgenus of *Hormotoma* (e.g. Longstaff *née* Donald 1906, 1924; Wenz 1938). Linsley (1968) distinguished *Donaldiella* from murchisonids by the presence or absence of an apertural slit. However, this trait varies between Ordovician lophospirid species and can not reliably characterize higher taxonomic units in the Ordovician. The oldest *Donaldiella* predate the oldest reliable examples of *Hormotoma*[1], which seems to be one of the oldest reliable murchisonids. Like *Donaldiella*, *Hormotoma* is characterized by a right-angle stacking of the whorls and *Hormotoma* species display a selenizone similar to the one of more derived *Donaldiella* species. *Hormotoma* species display more ventricose whorls than *Donaldiella* species, but the older species (e.g. *H. gracilis*) show thinner whorls than later ones (e.g. *H. salteri*). The rate of geographic spreading of *Hormotoma* is uncertain for while it is widely reported, it is not clear that all of the species actually belong in *Hormotoma* (see footnote below).

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[1] Older specimens have been placed in the genus (e.g. Endo 1932 or Flower 1968) but these appear to be based upon poorly preserved specimens lacking the diagnostic whorl stacking pattern of later *Hormotoma*.

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A branch-and-bound search of *Donaldiella* and two of the earliest reliable examples of *Hormotoma* (*H. gracilis* and *H. salteri*) produced twelve trees, the strict consensus of which is shown in Figure 21a. The majority consensus of 100 bootstrap replications is also included. While hardly conclusive, *D. filosa* was found to be the sister group of the two *Hormotoma* species, sharing a more convex upper slope and a similar selenizone. The pairings in the majority consensus are not especially robust - most branches occur in around 50% of the replications save the *gracilis* - *salteri* pairing which occurs in over 80% of the replications. However, the relationships between the *Donaldiella* species matches those seen in previous cladograms. As *D. filosa* is not known before the Ashgill, it is not a likely ancestor for those species. However, it does suggest that *D. filosa* had a common ancestor with *Hormotoma* after its last common ancestor with the other *Donaldiella* species used in this analysis. As mentioned above, the early history of *Donaldiella* is not well understood and a more thorough study of early *Donaldiella* species could give a clearer indications about not only the relations within the genus, but between pleurotomariines and murchisonids.

Lophospira-Trochonemella-Trochonema Relationship

The bicinctid trochonemellad sub-clade was initially classified as the genus *Trochonemella*. However, this subclade does not appear to be restricted to family Lophospiridae. As noted previously, *Trochonemella* is often confused with the genus *Trochonema* which lacks a selenizone. Ulrich (in Ulrich & Scofield 1897) was clearly impressed with the similarities between *Trochonema* and species now classified as *Trochonemella*, but he ascribed this to parallel evolution in two closely related groups (p. 962 & 989). Ulrich provisionally classified *T. notablis*, *T. knoxvillensis* and *T. trochonemoides* in *Lophospira* instead of *Trochonema* because they had selenizones. However, *Trochonema* displays all of the synapomorphies of the trochonemellads: a strongly tangential aperture, rotated whorls and rounded columellar lips. Further, they share more specific traits with

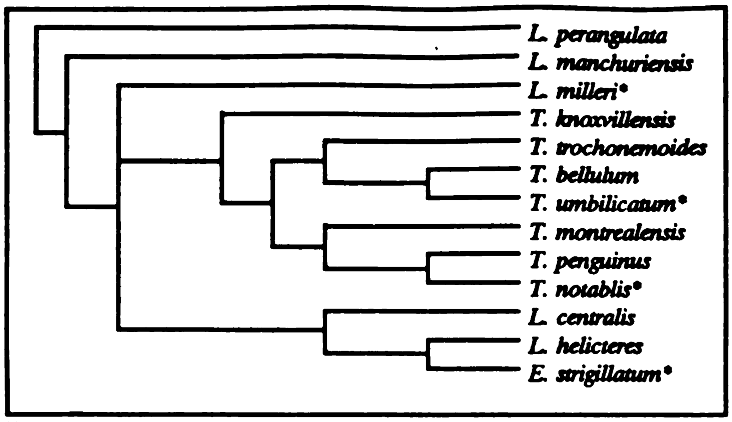

Figure 22 Consensus of Three Trees for early Caradocian Bicinctids plus *Trochonema* and *Eunema*.

higher trochonemellad species such as the location of the upper carina and a thinner columellar lip. Even the strong internal channel underneath the mid-whorl cited by Knight *et al.* (1961) as being diagnostic of the Superfamily Trochonematiina is weakly present in primitive lophospirids and more strongly present in *Trochonemella* species such as *T. trochonemoides*.

As the first reliable members of *Trochonema* appear at the base of Caradoc, an analysis of Bicinctids present through the Black Riveran was run including two *Trochonema* species from the early Caradoc: *Trochonema bellulum*, known from the base of the Caradoc, and the type species of the genus, *Trochonema umbilicatum*. In addition, to test the phylogenetic reality of the superfamily Trochonematiina, the type species of the *Lophospira*-like genus *Eunema* was also included. A branch-and-bounds analysis produced 12 trees, the consensus of which is shown in Figure 22. The results are reasonably robust (CI = 0.667 and HER = 0.681) for the size of the data set. The relationships between the species previously analyzed match those of earlier cladograms which adds further confidence to these results.

The amended phylogeny in Figure 23 shows two infraclades descended from *Trochonemella knoxvillensis*, one discussed above and *T. trochonemoides* plus *Trochonema*. As *T. trochonemoides* has no autapomorphies relative to the two *Trochonema* species, it represents as a potential ancestor for the other two. The species is therefore reclassified here as *Trochonema trochonemoides*. The type species of *Trochonemella* is found in the other infraclade descended from *Trochonemella knoxvillensis*. As *T. knoxvillensis* can not be

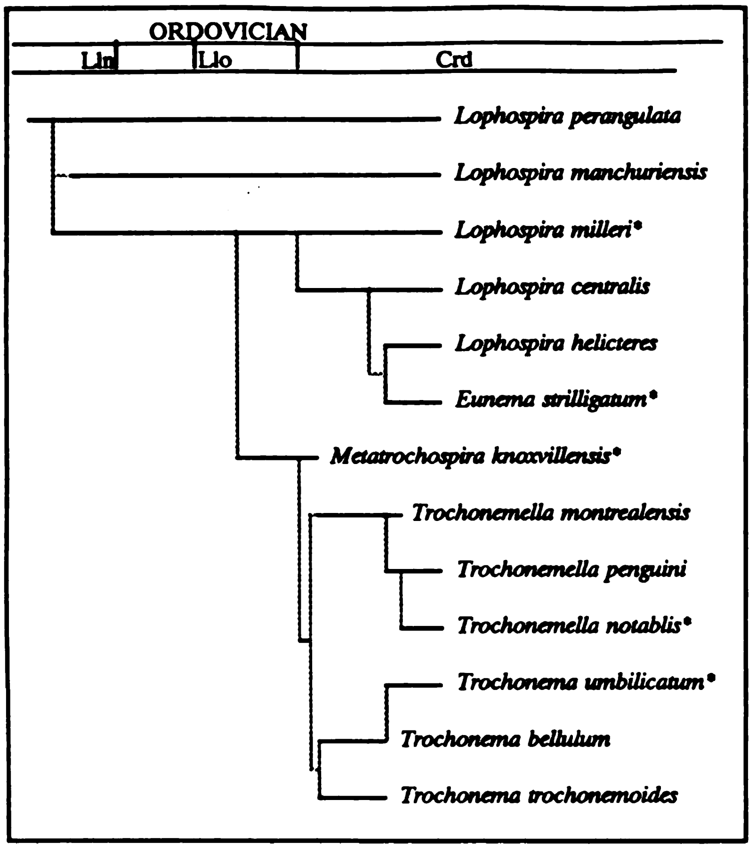

Figure 23 Augmented Phylogeny of the Ordovician-Silurian Lophospiridae with Amended Taxonomy.

properly placed in either *Trochonemella* or *Trochonema*, it is reclassified here as *Metatrochospira knoxvillensis* (see Appendix A).

Eunema strilligatum is related to the centralads, with the bootstrap majority consensus indicating a relationship with *Lophospira helicteres*. The two species share some derived traits such as the sutural carina and open coiling that seem to associated with a common ecology. However, the similarities in the columellar lip shape and in growth line morphology make this connection plausible, and as *E. strilligatum* represents the more derived form, *L. helicteres* is suggested as ancestral to that species.

As there are later Paleozoic genera that appear to be descended from *Trochonema*, this clade merits higher taxonomic recognition as the sub-family Trochonemallinae. *Eunema* is maintained as a separate genus descended from centralad species of *Lophospira*. All are considered to be members of the family Lophospiridae. As the superfamily Trochonematiina is clearly a polyphyletic group, its use should be discontinued.

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Lophospira - Ruedemanniinae Relationship

Both of the Ordovician and Silurian genera classified in the subfamily Ruedemanniinae belong to the robustad subclade. Species of this subfamily are thought to have given rise to *Worthenia*, which extends the subclade into the Mesozoic (Knight *et al.* 1961). This stratigraphic range merits higher taxonomic recognition and Knight's subfamily designation (1956) is upheld here. Each of the three Upper Ordovician-Silurian robustad infraclades include the type species of a genus. These infraclades are therefore recognized as the genera *Schizolopha*, *Ruedemannia* and *Arjamannia*. As presented here, all three represent mixotaxa (Archibald 1990) as there are no diagnostic traits shared by any of the three. As all three appear to be separately derived from *Ruedemannia humilis*, an appropriate generic label for this metaspecies is not obvious. While Knight classified it as *Ruedemannia* (U.S.N.M. 45903 holotype label), it lacks the diagnostic traits of that genus, so there is no good reason to assign it to *Ruedemannia* rather than one of the other two genera. The species was originally classified as *Lophospira* (Ulrich in Ulrich & Scofield 1897), which would be appropriate in the sense that the Ruedemanniinae are presumed to have evolved from *Lophospira*. However, as the species represents the stem-member of a sub-family, it should be included in that sub-family. A genus name can not be applied to species of different sub-families, so the species can not be classified as *Lophospira*. Therefore the species is reclassified as a *Hellermannia humilis*, an effective "meta-genus" stem-member of the sub-family Ruedemanniinae (see Appendix A).

Knight's synonymization of *Schizolopha* with *Lophospira* is reversed, as *S. textilis* represents a mixospecies within the Ruedemanniinae not the Lophospirinae. Accordingly, *S. textilis* is reclassified here into the subfamily Ruedemanniinae. The genus is now monotypic, as *S. moorei* is not at all closely related to the type species and should be reclassified as *Lophospira moorei*. However, as *S. textilis* can not be placed in *Arjamannia* or

Ruedemannia, the genus name is maintained.

Relations of *Longstaffia*

Two species from the Silurian genus *Longstaffia* were included in this study, but beyond being an apparent member of the bicinctid clade, it could not be linked with any of the sub-clades in that group. *Lophospira milleri* is not known in the Silurian, although other apparent bicinctid species are (e.g. *L. gothlandica*). Peel (1977) suggested that this genus was affiliated with the ruedemannids based upon the strong spiral ornamentation exhibited by the species in that genus. The species *L. centervillensis* does exhibit very strong spiral whorl lirae and other ruedemannid features such as an upper carina halfway between the selenizone and suture. It is not clear that the spiral ornamentation of the type species of the genus, *L. tubulosa*, is actually homologous with these lirae. The lower whorl ornamentation of *L. tubulosa* and *L. laquetta* seem to be additional carinae and there are only three actual revolving elements compared to at least ten on the lower whorls of Ruedemanniinae species and *L. centervillensis*. While Lindström (1884) described additional fine lirae on *L. tubulosa*, Knight (1941) did not and there are no extra lirae evident on his photographs of the holotype. However, *L. centervillensis* does share a greatly expanded base with *L. tubulosa* and *L. laquetta*, and it may be that the thick additional carina of the Baltic species represents a derivation of the finer lirae of the Ruedemanniinae. Unfortunately, *Longstaffia* is another poorly defined genus and the only specimen currently classified in the genus available for examination (*L. centervillensis*) was too incomplete to include in this analysis. There are Silurian lophospirid species described by Longstaff *née* Donald (1906, 1924) that may belong to this genus, and a more thorough study of those specimens as well as Lindström's Baltic examples is necessary.

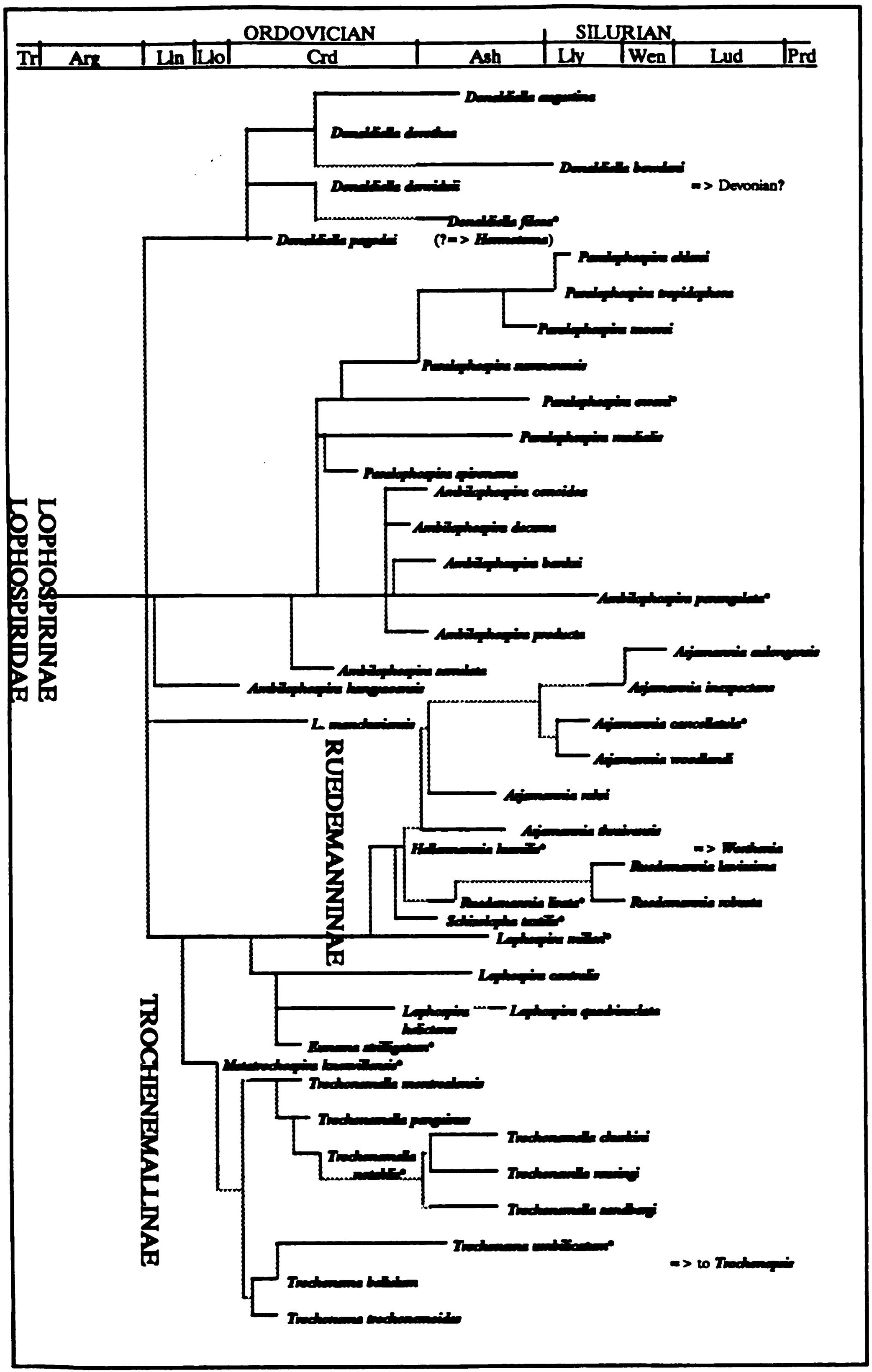

Figure 24 Amended Phylogeny of the Ordovician-Silurian Lophospiridae.

EVOLUTIONARY TRENDS AND PATTERNS WITHIN THE LOPHOSPIRIDAE

One of the historical trends among lophospirids is the tendency for later lophospirid species to display less variability than earlier ones. Many of the distinguishing traits of Upper Ordovician and later species such as extra carina, spiral ornamentation, gerontic open-coiling and suture points are variable features within pre-Caradoc species. This is in part responsible for the high number of species described from Early Ordovician taxa by Donald (1902, 1906), Butts (1926) and Endo (1932). This variation was even recognized by Donald in two species names (*Lophospira variablis* and *L. instabilis*). The specimens described by Butts and Endo appear to represent small population samples of four or five species showing substantial but continuous variation in suture points and ornamentation but not in features such as growth line patterns and columellar lip shapes. It requires very little genetic difference to produce substantial morphological variation in modern gastropods (Palmer 1985) and this may have been even more true for early, morphologically simple lophospirids. The decrease in the apparent intraspecific variation may have been a product of the extensive radiations of the Caradoc. The Llanvirn and Llandeilo appear to have had less complex ecological communities than the Caradoc (Sepkoski & Miller 1985) and it possible that lower levels interspecific competition allowed a greater range of phenotypes to survive than could in the Caradoc.

The difference in intraspecific variation produced the interesting dilemma of valid traits for species of later time periods not being valid for their ancestors. The initial traits and characters were produced by examining specimens from the Middle and Upper Ordovician and the difficulty in applying some to the older specimens was considered a potential flaw in this study. It is possible that more accurate comparisons of the younger and older species could be with detailed morphometric analyses such described by Schindel (1990) on populations of early lophospirids. This is somewhat analogous to McNamara's (1986)

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description of Early Cambrian trilobites, although at a much lower taxonomic level, and a comparison of the variation shown by early lophospirids with that of stem species of other higher taxonomic units could have interesting implications for the evolution of higher taxa.

The evolution of many lophospirid traits appears to have been more gradual than punctuated. Traits such as the ones mentioned above as well as the imbricated lunulae and rotated whorls of *Trochonemella* species, the tangential aperture of *Lophospira quadrisulcata* and the cancellate spiral ornamentation of *Arjamannia* species show one or more intermediate steps from the primitive form to the most derived one. Even changes such as the loss of the selenizone in *Trochonema* have intermediate steps. Only a few traits such as the tangential aperture of the Trochonemallinae "right-angle" whorl stacking of *Donaldiella* appear *de novo*. While phylogenetic analyses can make evolution appear punctuated by portraying character states as simply appearing, this analysis suggests more gradual modes pervaded within the Lophospiridae.

REAL VERSUS APPARENT DIVERSITY LEVELS

The most important aspect of this study is the implication it may have for studies of higher taxic diversity (e.g. Sepkoski 1979, 1985). The elimination of one superfamily and addition of a new subfamily is supported here. This does not greatly effect previous calculations of higher taxic diversity patterns. However, this represents the earliest gastropod group used in a phylogenetic analysis and there have been few analogous studies in other major groups. If phylogenetic studies of other early Paleozoic groups produce similar results then the conclusions of studies such as Sepkoski's may not be applicable to clades in general, only to historical morphotypes. The inclusion of polyphyletic families such as the Trochonematidae causes a loss of information of both the originations and extinctions of unrelated clades. This is also true in regards to information about clade extinctions when paraphyletic taxa are used. There can be little doubt that radiations and extinctions of organisms sharing a particular morphology represent events of historical importance regardless of whether the morphologies in question represent synapomorphies, convergences or symplesiomorphies. However, these do not necessarily reflect the evolutionary patterns of individual clades. It is therefore possible that additional phylogenetic studies of organisms from the early Paleozoic will force a re-appraisal of many diversity studies.

Groups with greater degrees of convergent evolution should have higher numbers of polyphyletic taxa. The evolutionary rates in such groups will appear lower than those in clades with identical rates of morphogenesis but lower amounts of convergence. Convergence-prone groups will have fewer taxa per clade and the evolutionary dynamics of such groups will therefore be underestimated by taxa-counting studies. The Lophospiridae represent an example of this as several traits that have previously been used to distinguish higher gastropod taxa appear multiple times within the family. These include apertural slits, tangential apertures, loss of selenizones and spiral ornamentation. The appearances and disappearances of species in the multiple clades with these features might have been ecologically significant, but are not significant when examining evolutionary patterns at the family level. Because of this, lophospirid genera such as *Donaldiella*, *Schizolopha* and *Ruedemannia* were polyphyletic based upon previous classifications and descriptions of lophospirid diversity at the generic level based upon the previous literature would be inaccurate.

Another potential problem of such studies is the equating of taxonomic units. This is highlighted by this analysis. For example, the two sub-families that evolved within the bicinctid clade are sister-groups of a clade not given even generic recognition. It is also difficult to equate a monotypic genus such as *Schizolopha* or a meta-genus such as *Hellermannia* either with a derived genus such as *Donaldiella* or *Trochonemella* or an

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ancestral one such as *Lophospira*. The history of *Schizolopha* represents the evolution and extinction of a single species, while the history *Hellermannia* represents an evolutionary trifurcation, with the lone species of the genus probably going extinct because of anagenesis. While the history of *Donaldiella* is simply that of a single clade, the history of *Lophospira* involves the history of many other higher taxa.

At the species level, it is difficult to equate long-lived, widely dispersed meta-species such as *Ambilophospira perangulata* and *L. milleri* with more short-lived local species such as *A. banksi* or *A. serrulata*. This does not effect estimates of specific diversity for a short period of time, but might when dealing with longer spans of time. It also raises the question of what percentage of metaspecies should be expected in a clade and what differences exist between clades with many metaspecies and ones with few.

Another problem with species level diversity is the great difference between the number of species described and the actual number of species. The sources listed in Table IX represent some of the most cited sources concerning lophospirids, yet over 50% of the species described in those sources represent previously described species, apparent variants of known species, or non-lophospirids. For *Lophospira*, 115 species[1] have been described of

Table IX Numbers of Invalid Species in Frequently Cited Lophospirid Descriptions

Author(s)		# of New Species Described	# of Apparent Junior Synonyms or Non-Lophospirids
Ulrich & Scofield 1897		30	12
Longstaff *née* Donald 1902, 1906, 1924		17	12
Foerste 1914, 1923, 1924		9	4
Raymond 1908		3	1
Grabau 1922		9	6
Butts 1926		7	6
Kobayashi 1932		6	4
Endo 1932		8	6
	Totals:	89	45

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[1] Not counting species originally described as *Lophospira* but later reclassified in other lophospirid genera.

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which 49 represent probable synonyms and with another 10 based upon either interior molds or specimens too poorly preserved to evaluate. Eight others classified as *Lophospira* appear to belong to other lophospirid genera and another pair likely do not even represent lophospirids. Another 15 could not be judged due to inadequate descriptions and figures and a lack of available specimens. Overall, it appears that only 31 of the described *Lophospira* species clearly represent unique *Lophospira* species. Species within the other genera are more reliable. This is probably due to the fact that all except *Loxoplocus* are newer taxonomic names and greater care has been taken in assigning species to these genera.

There are two main reasons for the over-splitting of lophospirid species. As stated in the introduction, early workers tended to do so in part because they considered age and modern locations to be diagnostic of a fossil species. Thus, fossils matching the description of *Ambilophospira perangulata* were only placed in that species if they were from Chazyan or Black River aged sediments from eastern North America. Fossils otherwise matching its description found either in Asia or Britain or in older or younger North American strata were placed in number of different species. Another problem was that some workers based many of their comparisons upon published descriptions and figures rather than direct comparison of specimens. However, many of these were misleading or simply incorrect. There also appear to have been cases of misunderstood descriptions. With inaccurate bases for comparison, over-splitting of species was inevitable. These factors exacerbate the biases in apparent species richness over time discussed by Signor (1985). Not only will more thoroughly studied strata yield more species, it is probable that a higher percentage of those described will be redundant.

The status of *Lophospira* is somewhat analogous to that of *Pleurotomaria* and *Murchisonia* over a century ago when most Paleozoic gastropod species were classified in one genus or the other. Estimating the specific diversities of either genus based upon classifica

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classifications up to 1870 would yield extremely inflated results. To a lesser extent, the same is currently true of *Lophospira*, as too many of the species classified in that genus are either synonyms or belong in other lophospirid genera. The opposite may be true for more recently described genera such as *Arjamannia*, as there seem be species belonging to that genus still placed in *Lophospira*. There are even specimens still classified as *Murchisonia* or *Pleurotomaria* that probably belong to lophospirid genera. Thus, simply counting descriptions will likely produce overestimates of the specific diversities of long recognized genera and underestimates of the diversities of more recently recognized ones.

It should be pointed out that even with the great number of apparent synonymies, the evolutionary rates for lophospirids were higher than that of recent gastropods as calculated by Stanley (1975). By the Ashgill a minimum of 50 species[1] appeared in a clade that had only a single known species in the Arenig (R = .078/My and t_2 = 8.89 My vs. R = .067/My and t_2 = 10.3 in Stanley 1975). As this does not include several species with inadequate descriptions and figures and no available specimens, these figures could be as much as R = .085/My and t_2 = 8.15 My. While these rates are still low compared to other groups, they do suggest that the evolutionary rates of early lophospirids were higher at the species level than those of modern gastropods.

CONCLUSIONS

The Lophospiridae is composed of at least five major clades and is divided into twelve genera. *Ambilophospira* and *Lophospira* represent polyphyletic metataxa. *Ambilophospira* is thought to be ancestral to *Lophospira*, *Paralophospira* and *Donaldiella*. *Paralophospira* represents a monophyletic genus as likely does *Donaldiella*, although the possibility exists that

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[1] This includes five *Trochonema* and three *Eunema* species but no *Hormotoma*.

Donaldiella is connected to the murchisoniine genus *Hormotoma*. *Lophospira* is thought to be ancestral to *Eunema* plus two sub-families, the Trochonemallinae and the Ruedemanniinae. The Trochonemallinae are composed of the monophyletic genera *Trochonemella* and *Trochonema* plus an ancestral metagenus *Metatrochospira*. The Ruedemanniinae is composed of three monophyletic genera, *Ruedemannia*, *Arjamannia* and the monotypic *Schizolopha*, plus the monotypic metagenus *Hellermannia*. The designation of the metagenera *Metatrochospira* and *Hellermannia* allow *Trochonemella* and *Trochonema*, and *Arjamannia*, *Ruedemannia* and *Schizolopha* to represent a monophyletic sister-groups. *Longstaffia* appears to represent another monophyletic genus descended from *Lophospira* but with uncertain relations to other lophospirid genera. The relations of another early Paleozoic lophospirid genus, *Loxoplocus*, could not be resolved in this study. The paraphyletic subfamily Lophospirinae is retained as a paraphyletic ancestral metataxon and includes *Ambilophospira*, *Lophospira*, *Paralophospira*, *Donaldiella* and *Eunema*. Polytomies are prevalent, with at least eight lineages thought to have diverged from *A. perangulata* and three from both *L. milleri* and *H. humilis*. While attempting to classify evolutionary changes in this manner is frowned upon by some (e.g. Wiley 1981), Ordovician and Silurian lophospirids appear to represent an example of how the relationships between two and possibly three higher taxonomic units can be inferred working with lower level taxa.

APPENDICES

APPENDIX A : SYSTEMATIC PALEONTOLOGY

Order **ARCHAEOGASTROPODA** Thiele 1925
Suborder **PLEUROTOMARIINA** Cox and Knight 1960
Superfamily **PLEUROTOMAROIDEA** Swainson 1840
Family **LOPHOSPIRIDAE** Wenz 1938
Subfamily **LOPHOSPIRINAE** Wenz 1938
Genus ***AMBILOPHOSPIRA*** n. gen.

Type Species: *Ambilophospira perangulata.*

Diagnosis: Trilineate selenizone, strongly swept growth lines and generally concave upper and lower ramps and lacking the diagnostic traits of other lophospirid genera.

Discussion: This represents a paraphyletic metataxon composed of *Ambilophospira perangulata* and the mixospecies thought to be descended from *A. perangulata* but not belonging to any of the more inclusive lophospirid clades. This genus represents an ambitaxon (see Archiabald 1990), as a clade of the species in this genus is an unresolvable polytomy with *A. perangulata* representing a potential ancestor not only for the other *Ambilophospira* species but also other lophospirid genera.

Etymology: "*Ambi-*" to denote the ambitaxon status of this genus as described by Archibald (1990) and *Lophospira* to mark its close relation to that genus.

AMBILOPHOSPIRA PERANGULATA (Hall)

Murchisonia perangulata
1847 Hall, *Pal. New York*, 1, p. 41, pl. 10, fig. 4
Murchisonia perangulata var. *A*
1847 Hall, *Pal. New York* 1, p. 179, pl. 38, fig.s 7a - 7b
Murchisonia bicincta var. *perangulata*
1859 Salter, *Geo. Surv. Can., dec. 1*, p. 19 - 20, pl. 4, fig.s 5 - 7
Lophospira perangulata
1897 Ulrich & Scofield, *Geol. Surv. Minn.* 3 pt. 2, p. 972, pl. 73, fig.s 1 - 7
1908 Raymond, *Ann. Carn. Mus.* 4, p. 188 - 189, pl. 49, fig.s 7 & 8
1909 Grabau & Shimer, *N. Amer. Index Fossils, Vol. 1*, p. 633, fig. 859 a - c
1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 763
1926 Butts, *Geo. Surv. Alab. Spec. Ppr.* 14, p. 30, fig. 11
1938 Twenhofel, *G.S.A. Spec. Ppr.* 11, p. 61, pl. 8, fig. 20
1951 Wilson, *Geol. Surv. Can. Bull.* 17, p. 37, pl. 4, fig.s 7 - 8
1971 Steele & Sinclair, *Geol. Surv. Can. Bull.* 211, p. 15 - 16
1987 Tofel & Bretsky, *J. Paleo. Vol.* 61(4), p. 705, pl 4, fig.s 7 - 8, 10, 13
Loxoplocus (*Lophospira*) *perangulata*
1944 Knight *et al.*, *Index Fossils of N. Amer.*, p. 449, pl. 182, fig.s 3 - 5
1980 Rohr, *Palaeontographica Abt. A, Band 171*, p. 174, pl. 8, fig.s 11 - 14
Murchisonia milleri
(PART) 1884 Walcott, *U.S. Geol. Surv.* 8, p. 79, pl. 1, fig.s 12, 12a-b
(PART) 1888 Walcott, *Amer. J. Sci. Arts* 35, p. 237, fig.s 3 - 4
Lophospira acuminata (or var. of *perangulata*)
1897 Ulrich & Scofield, *Geol. Minn.* 3 pt 2., p. 973, pl. 73, fig. 8
Lophospira acuminata
1909 Grabau & Shimer, *N. Amer. Index Fossils, Vol. 1*, p. 634, fig. 859 d
1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 756
Loxoplocus (*Lophospira*) *acuminatus*
1944 Knight *et al*, *Index Fossils Of N. Amer.*, p. 450, pl. 182, fig. 23
?Lophospira peracuta

1897 Ulrich & Scofield, *Geol. Surv. Minn. 3, pt. 2*, p. 976, pl. 73, fig.s 15 - 17
1915 Bassler, *U.S. Nat. Mus. Bull. 92 Vol. 2*, p. 763
1951 Wilson, *Geol. Surv. Can. Bull. 17*, p. 36 - 37, pl. 3, fig. 4
?Lophospira borealis
1902 Donald, *Quart. Jour. Geol. Soc. Lon.* 58, p. 333, pl. 9,
fig.s 5 & 6
1906 Donald, *Quart. Jour. Geol. Soc. Lon.* 62, p. 559
?Lophospira variablis
1902 Donald, *Quart. Jour. Geol. Soc. Lon.* 58,p. 334, pl. 9, fig.s 7 - 10.
?Lophospira instabilis
1906 Donald, *Quart. Jour. Geol. Soc. Lon.* 62, p. 560 - 561, pl. 18, fig.s 8 - 10
?Lophospira sedgwickii
1906 Donald, *Quart. J. Geol. Soc. Lon.* 62, p. 562, pl. 18, fig.s 11 & 12
?Lophospira pulchelliformis
1922 Grabau, *Pal. Sin. Ser. B* 1 Fas. 1, p. 26, pl. 3, fig.s 3 & 4
?Lophospira acuta
1922 Grabau, *Pal. Sin. Ser. B* 1 Fas. 1, p. 27, pl. 3, fig. 6
1930 Kobayashi, *Jap. J. Geol. Geog.* 7(3), p. 89 - 90, pl. 8, fig. 7
?Lophospira gerardi
1922 Grabau, *Pal. Sin. Ser. B* 1 Fas. 1, p. 28, pl. 3, fig. 7
1930 Kobayashi, *Jap. J. Geol. Geog.* 7(3), p. 89 - 90, pl. 10, fig. 6a
?Lophospira gerardi var. *laxa*
1922 Grabau, *Pal. Sin. Ser. B* 1 Fas. 1, p. 28, pl. 3, fig. 8
Lophospira elongata
1926 Butts, *Geo. Surv. Alab. Spec. Rep.* 14, pl. 19, fig. 25
Lophospira conica
1926 Butts, *Geo. Surv. Alab. Spec. Rep.* 14, pl. 19, figs. 26 & 27
?Lophospira subpulchella
1930 Kobayashi, *Jap. J. Geol. Geog.* 7(3), p. 90, pl. 8, fig. 9
Lophospira aojii
1932 Endo, *U.S. Nat. Mus. Bull.* 164, p. 52, pl. 28 fig.s 1 - 3 & pl. 29 fig. 1
?Lophospira turritiformis
1932 Endo, *U.S. Nat. Mus. Bull.* 164, p. 55, pl. 29, fig.s 12 & 13
Lophospira yentaiensis
1932 Endo, *U.S. Nat. Mus. Bull.* 164, p. 56, pl. 29, fig.s 4 - 6

Description: Small to moderate sized (height 6 - 20 mm, usually around 10 mm), composed of six to eight volutions with a apical angle ranging from <40° to >60° (averaging ~50°). Suture variable, usually on lower carina but sometimes higher or lower, with gerontic coiling often open. Upper ramp concave with some specimens displaying a dull to very rarely thread-like carina next to suture. Moderately wide trilineate selenizone with symmetric threads of equal strength, slightly protruded from sharp angle of upper ramp/lower ramp juncture. Lower ramp flat to dull to (rarely) thread-like carina, shifting slightly to small, nearly flat base. Umbilicus small. Aperture sub-triangular. Slightly thickened columellar lip shaped as an upside-down "7" usually pointing towards umbilicus. Growth lines variable, usually weak, fine, strongly swept abaperturally from suture to selenizone, and swept beneath selenizone to lower carina, then straight to umbilicus. Lunulae V-shaped, very faint.

Discussion: As can be noted, this is morphologically variable species, with variations noticeable within single collections from the same bed and even on individuals. Given its wide temporal and geographic distribution combined with the taxonomic philosophy of early workers, this variation has resulted in a plethora of species names, usually based upon either a single difference between the "new" species and the *Ambilophospira perangulata* holotype (which lacks any derived characters), or because of a presumed difference in geologic age or geographic location. *Ambilophospira perangulata* appears to represent the oldest known lophospirid, as represented by Donald's (1902) *Lophospira borealis* from the Tremadocian Durness Limestone. While Donald thought her species most similar to *L. obliqua* or *L.*

centralis, her description and figures both depict a gastropod with a concave upper ramp instead of flat, strongly swept growth lines instead of straight or nearly so, a dull carina close to the suture instead of a sharp one lower on the upper ramp, and an aperture with a long axis at an angle to the apex instead of nearly parallel - the very differences separating *A. perangulata* from *L. milleri* and *L. centralis*. Similar explanations apply to other *Lophospira* species of Donald's (1902, 1906; Longstaff 1922): *L. variablis* (Llandeilo), *L. instablis* (Ashgill) and *L. sedgwickii* (Llandovery). However, as the types of these specimens were not examined during this study, the connections are considered tentative.

Ulrich and Scofield's (1897) *Lophospira acuminata* shows the hesitancy American workers had in using *L. perangulata* for non-Chazyan or Black Riveran *Lophospira*. While acknowledging that their species might well simply be a Late Ordovician form of *Ambilophospira perangulata* (hence the qualifier "or var. of *perangulata*", p. 973), they chose to separate it based upon its small size, protruding selenizone and more concave whorls. However, in these traits *L. acuminata* matched descriptions of Black Riveran *Murchisonia perangulata* already given by Salter (1859) and since given by Wilson (1951) and Steele & Sinclair (1971), as well as Rohr's (1980) descriptions of Upper Ordovician *A. perangulata* from California. In addition to *L. acuminata*, *L. pulchella* may also represent a another form of *A. perangulata*. Ulrich and Scofield note a strong association between *L. acuminata* and *L. pulchella* in the Ashgill, with the differences between the two being the somewhat larger size of some *L. pulchella* and the presence of a weak thread-like carina just under the suture on *L. pulchella*. While this carina is much stronger than those reported on any *Ambilophospira perangulata*, it is not as strong as the upper carina of species such as *L. milleri* or *L. centralis*, and it is located just beneath the suture like those on *A. perangulata* but unlike those of the other two species. It therefore seems possible that *L. acuminata* and *L. pulchella* represent a dimorphic, Upper Ordovician variation of *A. perangulata*.

Many Asian species of Ordovician *Lophospira* also probably belong within *Ambilophospira perangulata*. Grabau's (1922) *Lophospira acuta* and *L. pulchelliformis* with Kobayashi's (1930) *L. subpulchella*, all from the Llanvirn or early Caradoc of north east Asia, may represent early analogues of the American *L. acuminata* and *L. pulchella*, although it should be noted that none of the three Asian species deviate from the range of variation shown by *A. perangulata*. Endo (1932) described three and possibly four species from a single Llandeilo bed in Manchuria that all likely represent *A. perangulata*. While Endo separated the species based upon differences in size, suture points and upper carinas, the group taken as a whole seems representative of a small *A. perangulata* sample showing characteristic variation. While the holotypes of Endo's material was examined, Grabau's and Kobayashi's was not, thus making the synonymization of those species tentative.

Ambilophospira perangulata differs from species such as *L. milleri* or *L. centralis* in its upper carina being much duller and closer to the suture (if even present), strongly curved, faint growth lines, a weaker lower carina, less swollen whorls and a columellar lip with a more acute angle pointing towards the umbilicus. *Ambilophospira perangulata* is very similar to *Paralophospira medialis*, which differs in having more ventricose whorls and a fuller, more rounded columellar lip. *Ambilophospira perangulata* is also similar to species of *Donaldiella* such as *D. pagodai* or *D. bowdeni*. Members of this genus differ in having reduced apical angles, a generally greater number of whorls, flatter and longer upper ramps, and more "L"-shaped columellar lips. Given its lack of derived traits and its early appearance, *A. perangulata* represents the likely ancestor for at least four separate clades within the Lophospiridae.

<u>Materials</u>: U.S.N.M. 46067 (eight plesiotypes), plus several hundred specimens from

various sites in Kentucky including: 4073-CO, 4852-CO, 4876-CO, 4879-CO, 4880-CO, 5015-CO, 5067-CO, 5074-CO, 5092-CO, 5098-CO, 5107-CO, 6142-CO, 6532-CO, 6909-CO, 6916-CO, 7350-CO, 7783-CO & 75-HCL-JP.

Occurrence: Ordovician to Silurian (?Tremadoc to Llandovery).

AMBILOPHOSPIRA KANGYAOENSIS (Endo)

Lophospira trochoformis
1926 Butts, *Geo. Surv. Alab. Spec. Rep.* 14, pl. 19, fig. 23
NON *Lophospira trochiformis*
1922 Grabau, *Pal. Sin. Ser. B* 1 Fas. 1, p. 24, pl. 3, figs 1, 2a & 2b
Lophospira kangyaoensis
1932 Endo, *U.S. Nat. Mus. Bull.* 164, p. 53, pl. 28, figs 14 - 17
Lophospira cf. *oweni*
1932 Endo, *U.S. Nat. Mus. Bull.* 164, p. 54 - 55, pl. 28, figs 2 & 3

Description: Small to moderate (15 - 21 mm height) composed of five whorls and an apical angle near 60°. Suture above lower carina, near selenizone. Upper ramp slightly concave to flat. Moderately wide somewhat projecting selenizone trilineate with equally strong threads. Lower ramp flat to very weak lower carina, shifting slightly to base. Umbilicus small. Aperture oval. Columellar lip slightly thickened, shaped as an upside-down "7". Growth lines uniform, faint, moderately spaced, with strong abapertural sweep from suture to selenizone, strongly swept beneath, straightening to umbilicus. Lunulae sharp V-shaped.

Discussion: Endo's *A. kangyaoensis* was described after Butt's nearly identical *L. trochoformis*. However, that name of this species is technically an invalid synonym of Grabau's *Lophospira trochiformis* from the Caradoc of Asia. While somewhat similar, the affinities between Grabau's species and Butts' are not understood and they can not be united at this time. Another of Endo's specimens from the Llanvirn of South Manchuria, *L.* cf. *oweni* also matches the holotype.

The high suture of *Ambilophospira kangyaoensis* is similar to that of much later species such as *Paralophospira sumnerensis* and *P. tropidophora*. However, those species can easily be distinguished from *A. kangyaoensis* by their extremely thick columellar regions. Also, complete specimens of the later species show an extended U-shaped lower lip, a feature clearly not present on *L. trochoformis*.
Ambilophospira kangyaoensis differs from *A. perangulata* in the higher suture point and in a more conical stacking of the whorls.

Materials: U.S.N.M. 83654 (Holotype). Also, U.S.N.M. 71482 (holotype of *Lophospira kangyaoensis*) from the Llandeilo of Alabama and U.S.N.M. 83655 (type of *L.* cf. *oweni*) from south Manchuria.

Distribution: Ordovician (Llanvirn - Llandeilo)

AMBILOPHOSPIRA SERRULATA (Salter)

?Murchisonia tricarinata
    1847 Hall (part), *Pal. N.Y. Vol. 1*, p. 178, pl. 38, fig. 6c (?NOT 6a & 6b)
?Lophospira tricarinata
    1915 Bassler (part), *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 765 & 766
Murchisonia serrulata
    1859 Salter, *Geol. Surv. Can., dec. 1*, p. 20, pl. 4, fig. 1
Lophospira serrulata
    1897 Ulrich & Scofield, *Geol Surv. Minn.* 3 pt. 2, p. 968, pl. 72, fig.s 51 -55; pl. 73, fig. 57
    1909 Grabau & Shimer, *N. Amer. Index Fossils, Vol. 1*, p. 636, fig. 862 d - f
    1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 764
    1951 Wilson, *Geol. Surv. Can. Bull.* 17, p. 38, pl. 5, fig.s 8 & 9
    1971 Steele & Sinclair, *Geol Surv. Can. Bull.* 211, p. 16 - 17, pl. 9, fig.s 1 - 6
    1987 Tofel & Bretsky, *J. Paleo.* 61(4), p. 709, pl. 4, fig.s 1 - 6, 9, 11 & 12
Loxoplocus (*Lophospira*) *serrulatus*
    1944 Knight *et al.*, *Index Fossils Of N. Amer.*, p. 449, pl. 182, fig.s 12 & 13
NON *Loxoplocus* (*Lophospira*) aff. *L.* (*L.*) *serrulata*
    1988 Rohr, *J. Paleo.* 62(4), p. 559, pl. 3, fig.s 12 - 16

Description: Large (35 - 45 mm height), composed of six to seven whorls with an initial apical angle around 60°. Suture initially on lower carina covering lower fifth of preceding whorl with open coiling of final whorl. Wide concave sutural shelf to sharp upper carina nearly half-way between suture and selenizone, with concave upper ramp beneath. Trilineate selenizone with strong serrated or wavy middle thread, sharply pronounced from nearly perpendicular angler of upper ramp/lower ramp juncture. Lower ramp concave to sharp carina, with fairly pronounced shift to flat base with thick umbilical carina. Juvenile umbilicus small. "Pseudo"-tangential aperture produced by open coiling. Aperture distorted sub-quadrangular. Thickened columellar lip U-shaped, slightly extended beneath, somewhat reflected. Growth lines uniform young, moderately spaced, moderately strong, trend somewhat adaperturally toward upper carina, the strong swept abaperturally to selenizone with strong sweep beneath to lower carina, straightening to umbilicus. Growth line strength on final whorl exaggerated with erratic spacing.

Discussion: *Ambilophospira serrulata* represents a difficult species to include in a phylogenetic analysis. While this species is highly derived in many ways, *A. serrulata* possesses primarily autapomorphic features not seen in any other species. Both *Lophospira helicteres* and *A. serrulata* display open coiling producing effectively tangential apertures, and both inhabited similar environments. However, this is the extent of the similarities between the two, and there are many more important differences. The presence of a strong upper whorl carina might appear to connect *A. serrulata* with species such as *L. helicteres* and *L. milleri*, the adapertural sweep of the growth lines on either side indicate that some projection from the aperture was associated with the *A. serrulata* upper carina, a feature absent in the upper carinae of any other lophospirid species. The columellar lip shape is similar to that of species such as *Paralophospira medialis* and *P. tropidophora*, but the only other similarities between *A. serrulata* and these species are symplesiomorphic. As *A. serrulata* disappears before those species seem to have originated, the columellar lip shape probably represents a lone convergency. A serrated middle selenizone thread occurs on the Llandoveran *L. pteronoides*. However, while this was used by Longstaff *née* Donald (1924) to place *L. pteronoides* in Ulrich & Scofield's Serrulata section, all the other features of this species indicate that it belongs in the genus *Arjamannia*. A species with suggested affinities to *A. serrulata* from Ashgill of Alaskan (Rohr 1987) also exhibits a serrated middle thread. However, this species also exhibits a severely serrated upper carina and a notably serrated lower one. Further, the growth lines show very little sweep on the later species with no adapertural sweep near the upper carina and the aperture is nearly round with little columellar lip development. As many of these features link the Alaskan species with species of *Trochonemella*, it is considered unlikely that any actual affinity exists between it and *A. serrulata* from the Caradoc.

Materials: U.S.N.M 45925 (several latex casts and internal molds) from the Platteville of Wisconsin and Illinois.

Occurrence: Ordovician (early to mid Caradoc) of Minnesota, Wisconsin, Illinois & Tennessee. Possibly from the basal Caradoc (St. Peters Sandstone) of Minnesota (Sloan 1987).

AMBILOPHOSPIRA BANKSI n. sp.

Diagnosis: Tightly open coiling of fourth through sixth whorls. Prominent, wide flat selenizone. Strong rounded sutural and lower whorl carinae, with weak upper slope one.

Description: Moderately large (35 - 40 mm height) composed of six whorls with an apical angle near 45°. Suture initially on lower carina covering lower fifth of whorl, with tight open coiling beginning by the fourth whorl. Strong sutural carina visible on free whorls. Upper ramp slightly concave to flat, with very weak carina closer to suture than selenizone, becoming weaker with age. Moderately wide, flat selenizone with median thread weakening with age. Selenizone protrudes strongly from nearly perpendicular upper ramp/lower ramp junction. Lower ramp slightly concave to strong, rounded lower carina, with slight shift to flat base. Umbilicus small. Aperture sub-quadrangular. Slightly thickened columellar lip shaped as an upside down seven usually pointing towards umbilicus. Growth lines weak, fine, strongly swept abaperturally from suture to selenizone and swept beneath selenizone to lower carina, straightening to umbilicus. Lunulae sharp U-shape, faint until final whorl.

Discussion: This species is analogous to *Ambilophospira serrulata* in that it possesses many unique traits, but few connecting it to any other species. The open coiling exhibited by *A. banksi* is very different from that of *A. serrulata* or *L. helicteres*, producing a tight cork-screw and maintaining a radial aperture instead of producing wide gaps between whorls and an effectively tangential aperture. The sutural carina of *A. banksi* is much more prominent than that of *L. helicteres*, and the absence of an umbilical carina further distinguishes *A. banksi* from the two Caradoc species.

Ambilophospira banksi may be a precursor of the Wenlockian *Loxoplocus solutus*. However, while the later species exhibits similarly strong sutural and lower carina, its pattern of coiling is more reminiscent of *L. helicteres* or *A. serrulata*, and its aperture more similar to the former species. However, key traits such as the growth line morphology and details about the selenizone have been poorly described or figured, and the affinities of the Silurian species to Ordovician lophospirids requires a more detailed examination of *L. solutus* than has been yet possible.

Ambilophospira banksi can resemble species of *Donaldiella*. However, species of that genus display a greater number of whorls and exhibit whorl stacking so that the selenizones are perpendicular to the right angle of the shell. For *A. banksi* this angle is somewhat acute, as it is for *Lophospira* species such as *A. perangulata*. Most other species such as *L. milleri* showing a very acute angle between the selenizones and right angles. In this and other traits such as growth line morphology and columellar lip shape, *A. banksi* is more similar to *A.*

perangulata than any other species. Most of the main distinguishing traits between the species being weakly expressed variants in *A. perangulata*. *Ambilophospira banksi* also resembles *L. producta*, but differs from that species in its open coiling and having fewer whorls. *Ambilophospira conoidea* and *A. decursa* are also somewhat similar but differ in having a greatly reduced lower ramps and closed coiling. It is likely that *A. banksi* represents nothing more than a descendant of *A. perangulata* with some of that species more extreme variations fixed and exaggerated.

It is possible that casts described as being from the upper Trenton of Kentucky and doubtfully assigned to *Lophospira elevata* by Ulrich & Scofield (1897) belong in to this species.

Materials: Six specimens fairly complete silicified specimens and fragments from U.S.G.S. C-72-3-7350 from the Shawan quadrangle, Kentucky plus another from U.S.G.S. 7812 in the same quadrangle.

Occurrence: Ordovician (late Caradoc) of Kentucky. Specimens from the Clays Ferry Formation, which extends into the Ashgill.

Etymology: Named for Ernest Banks, the greatest shortstop never to play in the World Series.

Genus *LOPHOSPIRA* Whitfield 1886

LOPHOSPIRA MANCHURIENSIS Endo

?*Lophospira subabbreviata*
1906 Raymond, *Ann. Carn. Mus., 3*, p. 501
NON 1850 d'Orbigny, *Prodome de Paleontolgie, Tome 1*, p. 8 (see *R. abbreviata*)
?*Lophospira rectistriata*
1908 Raymond, *Ann. Carnegie Mus. 4*, p. 187, pl. 49, fig.s 3 - 6
1909 Grabau & Shimer, *N. Amer. Index Fossils*, Vol. 1, p. 632, fig. 835
1915 Bassler, *U.S. Nat. Mus. Bull.* **92** Vol. 2, p. 764
?*Loxoplocus* (*Lophospira*) *rectistriatus*
1944 Knight *et al.*, *Index Fossils Of N. Amer.*, p. 449, pl. 182, fig.s 6 - 7
?*Lophospira morrisi*
1922 Grabau, *Pal. Sin. Ser. B* 1, Fas. 1, p. 24, pl. 3, fig.s 1, 2a & 2b
1930 Kobayashi, *Jap. J. Geol. Geog.* 7(3), p. 87 - 89, pl. 9, fig. 6
?*Lophospira grabaui*
1932 Endo, *U.S. Nat. Mus. Bull.* 164, p. 52 - 53, pl. 28, fig.s 4 5
Lophospira manchuriensis
1932 Endo, *U.S. Nat. Mus. Bull.* 164, p. 54, pl. 28, fig.s 6 - 11

Description: Small (15 mm height) composed of five whorls with an apical angle of 60°. Suture on lower carina covering lower fourth of whorl. Upper ramp concave. Moderately wide selenizone trilineate with thread of equal strength, barely protruding from acute angle of upper ramp/lower ramp juncture. Lower ramp flat to weak carina with slight shift to flat base. Umbilicus very small. Aperture sub-quadrangular. Slightly thickened columellar lip "upside-down 7" shape, somewhat reflected over umbilicus. Growth lines sharp, evenly spaced, uniform, running straight from suture curving abaperturally half-way to selenizone, running nearly straight adapically beneath, straightening at lower carina to umbilicus. Lunulae sharp U-shaped.

Discussion: This species appears to represent an intermediate between

Ambilophospira perangulata and *Lophospira milleri*. While more like the former in overall morphology, *L. manchuriensis* can be distinguished by its growth lines running straight over the suture with a very weak abapertural sweep compared to that shown by *A. perangulata*. *Lophospira manchuriensis* can be easily distinguished from *L. milleri* by its lack of an upper carina, a weaker lower whorl carina, a narrower base and a sharper columellar lip.

Lophospira manchuriensis may well by the junior synonym of two other species names. *L. manchuriensis* and *L. grabaui* are from the same limestone unit and differ only in the points of suture on the whorl. However, while suture points are very consistent within species from the Caradoc onwards, this seems to be a somewhat variable trait in earlier lophospirids. Endo (1932) linked *L. grabaui* with *Paralophospira tropidophora* and *L. trochiformis* Grabau. However, the growth lines of *L. grabaui* are much straighter than Endo's description implies (see Endo 1932 pl.28 fig.s 4 - 5), and the number of whorls and suture point seems to be the only traits *L. grabaui* shares with the much younger *P. tropidophora*. Comparison with Grabau's *L. trochiformis* is more difficult, as no types of that species were available for examination, and Grabau's descriptions and figures (1922, p.27, pl. 3 figs. 5a-b) are too vague to compare with *L. grabaui* or any other species.

Regardless of the relationship between *Lophospira manchuriensis* and *L. grabaui*, *L. manchuriensis* is very likely a junior synonym of *L. rectistriata* Raymond. The Asian species is very similar Raymond's (1908) description of the contemporaneous American species. While Raymond's figures were incomplete, what detail shown also agrees with the specimen and the figures published by Endo. However, as no types of that species were examined during this study and no figures of *L. rectistriata* beyond Raymond's incomplete drawings have ever been published, it is difficult to be certain of the relationship.

Materials: U.S.N.M. 83655 (holotype of *Lophospira manchuriensis*). Also, U.S.N.M. 83653 (holotype of *L. grabaui*). Both from the black banded limestone bed of the Kangyao formation, which appears to equal Machiakou Limestone of Lai Tsai-ken *et al.* 1975 (in Section VIII of Shen-Fu 1980).

Distribution: Ordovician (Llanvirn - ?Llandeillo). Found with trilobites *Isostelloides* and *Nileus* and cephalopod species *Actinoceras richtofeni*, which occur at and under the *Glyptograptus austrodentus* graptolite zone. The absolute ages given for these rocks by the Chinese differ greatly from the ages given by Americans (e.g. Ross *et al.* 1982), the *G. austrodentus* zone occurs just under the appearance of *G. teretiusculus* in the Ordovician of China, which marks the onset of the Llandeillo (Ross *et al.* 1982). The similar *L. rectistriatus* occurs in Chazyan sediments (Llanvirn - Llandeillo) in America.

LOPHOSPIRA MILLERI (Hall)

Murchisonia bicincta
  NON 1846 M'Coy, *Syn. Char. Carb. Lime. Foss. Ire.*, p. 16
  NON 1862 M'Coy, *Syn. Sil. Foss. Ireland*, pl.1, fig. 7
  1847 Hall, *Pal. New York 1*, p. 177, pl. 38, fig.s 5a - 5h
  NON 1859 Salter, *Geo. Surv. Can., dec 1*, p. 19 - 20, pl. 4, fig.s 5 - 7
    [see *A. perangulata*]
?Murchisonia aspera
  1859 Billings, *Can. Nat. Geol.* 4, p. 458 - 459
?Lophospira aspera
  1908 Raymond, *Ann. Carn. Mus.* 4, p. 189 - 190, pl. 55, fig. 2
  1938 Twenhofel, *G.S.A. Spec. Ppr.* 11 p. 60, pl 9 fig.s 4 - 5

Lophospira bicincta
1906 Donald, *Quart. Jour. Geol. Soc. Lon.* 62, p. 563 - 564, pl. 44, fig. 2
1915 (part) Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 757 - 758
NON 1897 Ulrich & Scofield, *Geol. Minn.* 3 pt. 2, p. 964, pl. 72, fig.s 1 - 5
[see *L. centralis*]
NON 1909 Grabau & Shimer, *N. Amer. Index Fossils* Vol. 1, p. 632
[see *L. centralis*]
Murchisonia milleri
1877 Hall in Miller, *Amer. Pal. Foss.*, p. 244
(PART) 1884 Walcott, *U.S. Geol. Surv.* 8, p. 79, pl. 1, fig.s 12, 12a-b
(PART) 1888 Walcott, *Amer. J. Sci. Arts* 35, p. 237, fig.s 3 - 4
Lophospira milleri
1941 Knight, *Geol. Soc. Am. Sp. Ppr.* 32, p. 179, pl. 39, fig.s 4a - 4b
1951 Wilson, *Geol. Surv. Bull.* 17, p. 36, pl.5, fig. 4
1971 Steele & Sinclair, *G.S.C. Bull.* 211, p.14 - 15, pl 8, fig.s 6 - 12
1987 Tofel & Bretsky, *J. Paleo. Vol.* 61(4), p. 715, pl. 5, fig.s 4 - 5
Loxoplocus (*Lophospira*) *milleri*
1944 Knight *et al.*, *Index Fossils of N. Amer.*, p. 449, pl. 182, fig.s 1 - 2
1960 Knight *et al.*, *Treatise on Invert. Paleo (I)* Vol. 1, p. 208, fig. 121 #2
Lophospira obliqua
1897 Ulrich, *Geol. Surv. Minn.* 3 pt. 2, p. 965, pl 72, fig.s 6 -8
1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 762
?*Lophospira bicincta* var. *scotica*
1906 Donald, *Quart. Jour. Geol. Soc. Lon.* 62, p. 564, text-fig. 2, pl. 44,
fig.s 3 & 4
?*Lophospira scotica*
1922 Longstaff, *Quart. Jour. Geol. Soc. Lon.* 80, p. 409.
?*Lophospira seelyi*
1908 Raymond, *Ann. Carn. Mus.* 4, p. 190 - 191, pl. 55, fig. 3
?*Lophospira belli*
1924 Foerste, *Can. Geo. Surv. Mem.* 138, No. 121, p. 212, pl. 37, fig.s 3 a - c
?*Lophospira dutchtownensis*
1938 Cullison, *J. Paleo. Vol.* 12(3), p. 223 - 224, pl. 29, fig.s 8a-b;
?*Lophospira basicarinata*
1938 Cullison, *J. Paleo. Vol.* 12(3), p. 223, pl. 29, fig.s 7a-b;
?*Lophospira corrugata*
1938 Cullison, *J. Paleo.* 12(3), p. 223, pl. 29, fig. 6
Lophospira saffordi
1951 Wilson, *Geol. Surv. Can. Bull.* 17, p. 36, pl. 5, fig. 4

Description: Moderate sized (20 - 25mm height), composed of five whorls with an apical angle around 60°. Suture on lower carina, covering lower fourth of preceding whorl. Upper ramp slightly concave with thread-like carina closer to suture than selenizone, sometimes varying in strength between and upon individuals. Moderately wide selenizone trilineate with lirae of equal strength, slightly pronounced from obtuse angle of upper ramp/lower ramp juncture. Lower ramp flat to thread-like carina somewhat weaker than the upper whorl, with similar variance. Whorl shifts moderately sharply to slightly convex base. Umbilicus very small. Aperture sub-quadrangular. Thickened L-shaped columellar lip somewhat reflected, partially covering umbilicus. Growth lines sharp, trending straight from aperture over upper carina, sweeping abaperturally near halfway towards selenizone, running straight adaperturally beneath selenizone, straightening towards umbilicus with weak concave lunulae.

Discussion: As discussed by Tofel & Bretsky (1987), the taxonomic history of *Lophospira milleri* is convoluted. Many descriptions of *L. bicincta* apply to *L. milleri*. A notable exception is the description given by Ulrich & Scofield (1897) which matches instead the holotype specimen of *L. centralis* (see discussion below). However, their description of

L. obliqua matches the holotype of *L. milleri* as described by Knight (1944). As it is very possible that Llandeillo specimens described by Billings (1859) as *Murchisonia aspera* also belong to this species, *L. milleri* may itself be a junior synonym. While the descriptions and figures of Billings, Raymond (1908) and Twenhofel (1938) appear to fit this species, Billings did not include figures with his description and Hall may not have been sufficiently aware of *M. aspera* when he was forced to rename his *L. bicincta* to *L. milleri*. However, as first hand examination of the holotypes of *L. aspera* and the clearly similar *L. seelyi* was not done during this study, the connection is considered tentative.

This species can be distinguished from the contemporaneous *Ambilophospira perangulata* by its straighter growth lines, prominent carina and more ventricose whorls, among other features. *Lophospira milleri* is most similar to *L. concinnula*, juvenile *L. helicteres* and *L. centralis*, differing from each by having more strongly curved growth lines. It is also seems similar to *L. rectistriata*, but based upon Raymond's (1908) description and figures, that species lacked a prominent upper carina. Tofel & Bretsky (1987) considered the frequently asymmetrical selenizone common on Platteville *L. milleri* from the Wisconsin area to be significant feature distinguishing *L. milleri* from other *Lophospira* species, but this seems to be a variable trait in similar and later aged specimens from Kentucky, and is also observed occasionally on other *Lophospira* species.

Lophospira milleri is superficially similar to well preserved specimens of the younger *Paralophospira oweni* (mistakenly called *L. saffordi*) and the two have been confused (e.g. Wilson 1951). Distinguishing between the two is important, as *P. oweni* appears to replace *L. milleri* as the dominant moderate sized lophospirid in later Ordovician sites in Kentucky. However, *P. oweni* differs by having consistently very strongly swept growth lines, a much weaker upper carina and often no lower one, a more U-shaped, much thicker columellar lip, and much narrower shoulder angles. It bears noting that the growth lines of *L. milleri* are sometimes much more strongly swept on areas of disrupted growth, which can appear similar to the growth line pattern of *P. oweni*. As such disruptions are accompanied by a change in shell texture and frequently oscillations of carina strengths, this can usually be recognized.

As with *Ambilophospira perangulata*, the wide temporal and geographic distribution of this species has resulted in a large number of synonyms. While *Lophospira milleri* has been thought by some to have existed only during the early to mid Caradoc (e.g. Tofel & Bretsky), older specimens appear to have existed. One of the two U.S.N.M 17326 specimens labeled *Lophospira milleri* from the Pogonip Limestone represents a perfectly good example of the species, dating the species to the Llanvirn or Llandeillo (Walcott 1884; Ross *et al.* 1980). As mentioned above, the descriptions and figures of *L. aspera* and *L. seelyi* from the Chazyan of Canada and New York (Raymond 1908) fall within the range of variation seen in the Kentucky specimens from the Caradoc, as do *L. bicincta* and *L. scotica* from the Llandeillo of Scotland (Donald 1906) and *L. morrisi* from the Llandeilo of northern China (Grabau 1922). The description and figures of *L. dutchtownensis* (Cullison 1938) from the Dutchtown Limestone (early Caradoc) also fits here.

Lophospira milleri is considered very significant in that early members of the species are considered as likely ancestors to a number of latter lophospirid species.

Materials: USNM 17326 (paratype) from Pogonip Ridge, Nevada, U.S.N.M. 45910 (holotype plus four paratypes of *Lophospira obliqua*). Several hundred silicified specimens from U.S.G.S. site 6419-CO (= 42-66 JP) from the Wilmore quadtrangle, Kentucky plus additional specimens from sites D-1206-CO, 5023-CO, 5080-CO, 5092-CO, 5100-CO (= 7-66), 6131-CO, 7348-CO, 7791-CO (= 41-66 JP) and Ulrich-308K.

Occurrence: Ordovician (late Arenig to Caradoc)

LOPHOSPIRA CENTRALIS Ulrich in Ulrich & Scofield

Lophospira centralis
  1897 Ulrich in Ulrich & Scofield, *Geol. Minn.* 3 pt. 2, NON p. 979, pl. 73, fig. 9
  1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 758
Lophospira bicincta
  1897 Ulrich & Scofield, *Geol. Minn.* 3 pt. 2, p. 964 - 965, pl 72, fig.s 1 - 5
  1926 Butts, *Geol. Surv. Alab.* 14 pl. 30, fig. 10
Lophospira delicata
  1987 Tofel & Bretsky, *J. Paleo.* 61(4), p. 717, pl. 5, fig.s 10 - 11

Description: Moderate sized (16 - 20 mm height), composed of five volutions with an apical angle of 58 - 65°. Suture on lower carina, covering lower fourth of previous whorl. Upper ramp flat with thread-like carina closer to suture than selenizone. Moderately wide trilineate selenizone with threads of equal strength, slightly pronounced from obtuse angle of upper ramp/lower ramp juncture. Lower ramp flat to thread-like carina, shifting sharply to slightly convex base. Umbilicus very small. Aperture sub-quadrangular. Thickened L-shaped columellar lip somewhat reflected. Uniform growth lines closely spaced, moderately strong, trending straight from suture over carinae to selenizone, and straight from selenizone to umbilicus, with barely concave lunulae.

Discussion: The holotype differs drastically from Ulrich's (1897) original description and figure in several ways. Ulrich's describes a species very similar to *Ambilophospira perangulata*, with strongly swept, irregular growth lines, concave upper and lower ramps, no upper carina and a weak lower one, and a strongly pronounced, only faintly trilineate selenizone. Instead, this specimen comes much closer to matching Ulrich & Scofield's description of *L. bicincta*. As both are recorded from the Central Limestone of the Stones River Group, it is possible that some sort of mix-up occurred - however, if this is the case it happened not long after Ulrich's description, for the holotype bears the same U.S.N.M. number that Bassler (1915) recorded fewer than twenty years later. As *L. bicincta* is not valid due to taxonomic priority (see Knight 1944), *L. centralis* assumes priority. This species also matches Tofel & Bretsky's (1987) description and figures of *L. delicata*, making the latter a junior synonym of *L. centralis*.

This species is most similar to *Lophospira milleri*, differing in the nearly complete straightening of the growth lines. In this, *L. centralis* appears to represent the culmination of a trend observed in a major clade of lophospirids. While it was considered that *L. centralis* might simply represent a straight-lined variant of *L. milleri*, the co-occurrence of the two in the early to mid Caradoc in some areas (Ulrich & Scofield 1897; Tofel & Bretsky 1987) but not in others (e.g. Wilson 1951) as well as indications of separate long-term population trends (Tofel & Bretsky 1987) suggest that they represent individual entities. *Lophospira concinnulla* and juvenile *L. helicteres* differ in having a much more pronounced middle thread on the selenizone and a slightly greater growth line sweep. *Lophospira centralis* is also very similar to the Ashgillian *L. quadrisulcata*, which differs in having a slightly tangential aperture, a much stronger upper carina somewhat lower on the upper ramp, a narrower selenizone and a second lower carina.

Materials: U.S.N.M. 46064 (holotype) plus 30+ specimens from U.S.G.S. site 5023-Co, 20+ from KY-7-69 and four specimens from site 7349-CO, all in Kentucky.

<u>Occurrence</u>: Ordovician (Caradoc to early Ashgill).

LOPHOSPIRA HELICTERES (Salter)

?Murchisonia tricarinata
1847 Hall (Part), *Pal. New York* 1, p. 178, pl. 38, figs. 6a & 6b (not 6c)
?Lophospira tricarinata
1915 Bassler (part), *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 765 & 766
Murchisonia helicteres
1859 Salter, *Geol. Surv. Can., dec. 1*, p. 21, pl. 4, fig.s 2 - 4
Lophospira helicteres
1909 Grabau & Shimer, *N. Amer. Index Fossils, Vol. 1*, p. 632, fig. 857
1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 760
1951 Wilson, *Geol. Surv. Can. Bull.* 17, p. 34, pl. 5, fig.s 1 - 3
1987 Tofel & Bretsky, *J. Paleo.* 61(4), p. 711, pl. 5, fig.s 1 - 3, 6
Lophospira helicteres var. *wisconsinensis*
1897 Ulrich & Scofield, *Geol. Minn.* 3 pt. 2, p. 971, pl. 72, fig.s 25 - 28
1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 760
Lophospira concinnula
1897 Ulrich & Scofield, *Geol. Minn.* 3 pt. 2, p. 966, pl. 72, figs. 16 - 19
?Lophospira fillmorensis
1897 Ulrich & Scofield, *Geol. Minn.* 3 pt. 2, p. 967, pl. 72, figs. 20 - 24
Lophospira wisconsinensis
1909 Grabau & Shimer, *N. Amer. Index Fossils, Vol. 1*, p.633, fig. 858
Loxoplocus (*Lophospira*) *wisconsinensis*
1944 Knight *et al.*, *Index Fossils Of N. Amer.*, p. 449, pl. 182, fig.s 8 - 9
Lophospira sexlineata
1938 Raasch in Schrock & Raasch, *Am. Mid. Nat.* 18, p. 564, pl. 8, fig. 13

<u>Description</u>: Large (50 - 70 mm height), composed of six volutions with an close-coiled apical angle of 55°- 60°. Suture initially on lower carina covering lower fourth of whorl, dropping by fourth whorl with open coiling of final two or three whorls. Weak sutural carina visible on open coiled whorls. Upper ramp slightly concave with strong thread-like carina closer to suture than selenizone. Moderately wide selenizone with median thread somewhat stronger than bordering ones on juvenile whorls, becoming variable on open coils. Selenizone protrudes slight from juvenile upper ramp/lower ramp junction, increasing on open coils. Lower ramp flat to strong thread-like carina, shifting sharply to slightly convex base with moderate umbilical carina. Juvenile umbilicus very small. "Pseudo"-tangential aperture produced by open coiling. Aperture sub-rhombohedral young, becoming oval to circular on open whorls. Thickened columellar lip with extended lower corner, somewhat reflected. Growth lines uniform young, closely spaced, moderately strong, trending straight from suture over carina with slight abapertural sweep just above selenizone, slightly stronger sweep below straightening by lower carina to umbilicus. Growth line strength on final whorls greatly exaggerated. Lunulae widely concave.

<u>Discussion</u>: While superficially similar to *Ambilophospira serrulata*, that species displays very strongly swept growth lines, a different shaped columellar lip, a much more weakly developed base, a more strongly concave upper ramp, no sutural carina and a thinner selenizone with a serrated middle thread. The main similarity between the two species - open coiling producing an effectively tangential aperture in adult stages - probably represents a convergent aptation for living on soft mud substrates of subtidal zones. Therefore, the two species are not considered closely related.

Lophospira helicteres is most similar to *L. concinnula*, differing primarily in exhibiting open coiling, an umbilical carina and attaining a larger size. The upper whorls of *L. helicteres* are nearly indistinguishable from those of *L. concinnula* and it has been suggested that the two represent the same species (Tofel & Bretsky 1987). However the type specimens of *L.*

concinnula exhibit a full set of whorls with no opening of the coiling, and while it is possible that open coiling could simply represent ecophenotypic variation, the ecologic differences involved would probably have necessitated speciation. The upper whorls of *L. helicteres* are also very similar to *L. milleri* and *L. centralis*, differing from them in the same manner as does *L. concinnula*. *Lophospira helicteres* is also very similar to *L. quadrisulcata* from the Ashgill. While the later species does not exhibit open coiling, it does exhibit a tangential aperture and may represent a close-coiled fixation of the "pseudo" tangential aperture of *L. helicteres*.

Materials: Thirty nine silicified specimens from U.S.G.S. site 6034-CO in the Little Hickman Quadrangle and site D-1138-CO in the Valley View Quadrangle (Marble Creek Section), Lexington County Kentucky. Also U.S.N.M. 45901 & 45902 (types of *Lophospira helicteres* var. *wisconsinensis*), U.S.N.M. 45892 (*L. concinnula* holotype plus several paratypes), U.S.N.M. 45899 & 45900 (holotype and paratypes of *L. fillmorensis*) and U.S.N.M. 158282 (*L. sexlineata* holotype).

Occurrence: (Ordovician, early to middle Caradoc). Apparently fairly common in the upper part of the Tyrone Limestone in Kentucky. Associated with archaeogastropods *Trochonemella penguini*, *Trochonema umbilicatum* (Hall), *Murchisonia* (*Hormotoma*) *gracilis* Hall and *Liospira* species.

LOPHOSPIRA QUADRISULCATA Ulrich & Scofield

Lophospira quadrisulcata
1897 Ulrich & Scofield, *Geol. Surv. Minn.* 3 pt.2, p. 967 - 968, pl. 72, fig.s 10 - 11
1909 Grabau & Shimer, *N. Amer. Index Fossils, Vol. 1*, p. 632, fig. 856 e & f
1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 764

Description: Moderate sized (16 - 21 mm height) composed of six volutions with an apical angle of 64° - 67°. Suture on upper of two lower carina covering the lower third of the preceding whorl. Upper ramp flat with strong thread-like carina nearly half-way from suture to selenizone. Trilineate selenizone with middle lirae slightly stronger than bordering ones, somewhat produced from obtuse angle of upper/lower ramp juncture. Lower ramp flat to strong thread-like carina, shifting dully to a short ramp flat to a second, weaker carina, then shifting sharply to slightly convex base with strong umbilical carina. Umbilicus very small. Slightly tangential sub-quadrangular aperture. Columellar lip L-shaped, thickened with little reflection. Growth lines fine but sharp, closely and evenly spaced, trending straight abaperturally from suture past upper carina with a slight abapertural sweep just above selenizone, slightly swept beneath selenizone then straight to umbilicus.

Discussion: This specimen agrees closely with Ulrich & Scofield (1897) original description. While similar in overall appearance, *L. quadrisulcata* differs from the older *L. milleri* in having straighter growth lines, a tangential aperture and two extra carina. *Lophospira quadrisulcata* is actually much more similar to young, close coiled *L. helicteres*. While that species also lacks the second lower carina and has a radial aperture, *L. helicteres* effectively had a tangential aperture during the early stages of coil opening. The tangential aperture of the later *L. quadrisulcata* may therefore simply represent a fixation of the tangential stage life style of *L. helicteres*. By possessing a second lower carina, *L. quadrisulcata* is somewhat similar to the Silurian genus *Longstaffia*, which expands the lower whorl with a second and third lower carina. However, members of this genus do not display a tangential aperture or an umbilical carina, and have somewhat more curved growth lines, so it is not likely that *L. quadrisulcata* was ancestral to these later lophospirids. The possession of a tangential aperture and an umbilical carina might appear to link *L. quadrisulcata* to species of *Trochonemella*. However, no close relationship is likely as the aperture of *L. quadrisulcata* is not as oblique and as those of *Trochonemella*, and its umbilical carina is much thicker. Further, *L. quadrisulcata* lacks any of the other derived traits shown by that genus.

Materials: Holotype (U.S.N.M. 45919) from the Maquoketa Formation in Fillmore county, Minnesota.

Occurrence: Ordovician (middle Ashgill)

Genus *PARALOPHOSPIRA* n. gen.

Type Species: *Paralophospira oweni.*

Diagnosis: Prosocline growth lines, thin upper whorl carina becoming weaker on older whorls, U-shaped columellar lip often greatly thickened.

Discussion: This represents a monophyletic clade arising in the middle Caradoc and consisting of many of the better known Upper Ordovician species previously placed in *Lophospira*. However, *Paralophospira* appears to have evolved from *Ambilophospira perangulata* much later than did *Lophospira* and as such *Paralophospira* species are not especially closely related to *Lophospira*.

Etymology: To denote the historical affinity of the species in this genus with *Lophospira*.

PARALOPHOSPIRA OWENI (Ulrich & Scofield)

Lophospira oweni
1897 Ulrich & Scofield, *Geol. Surv. Minn.* 3 pt. 2, p. 980, pl. 73, fig.s 41 - 45
1909 Grabau & Shimer, *N. Amer. Index Fossils, Vol. 1*, p. 634, fig. 860 a - c
1915 Bassler, *U.S. Nat. Mus. Bull.* **92** Vol. 2, p. 762
NON *Lophospira* cf. *oweni*
1932 Endo, *U.S. Nat. Mus Bull.* **164**, p. 54 - 55, pl. 29, fig.s 2 & 3
Loxoplocus (*Lophospira*) *oweni*
1944 Knight, *et al.*, *Index Fossils of N. Amer.*, p. 449, pl 182, fig.s 10 - 11
Lophospira saffordi
1897 Ulrich in Ulrich & Scofield, *Geol. Surv. Minn.* 3 pt. 2, p. 982, pl. 73, fig.s 49 - 51
1915 Bassler, *U.S. Nat. Mus. Bull.* **92** Vol. 2, p. 764
NON 1951 Wilson, *Geol. Surv. Can. Bull.* 17, p. 36, pl. 5, fig. 4
[see *L. milleri*]
?*Lophospira tenuistriata*
1897 Ulrich in Ulrich & Scofield, *Geol. Surv. Minn. 3, pt. 2*, p. 983, p. 72, fig.s 48 - 50
1915 Bassler, *U.S. Nat. Mus. Bull.* **92** Vol. 2, p. 765
?*Lophospira manitoulinensis*
1924 Foerste, *Can. Geo. Surv. Mem.* 138, No. 121, p. 213, pl. 34, fig.s 5 a - d
?*Loxoplocus* (*Lophospira*) *manitoulinensis*
1977 Copper & Grawbarger, *Can. J. Earth Sci.* 15, p. 1992

Description: Moderate sized (25 - 30 mm height), composed of six whorls with an apical angle usually around 55° but ranging as high as 70°. Suture usually on lower carina covering lower fifth of whorl, but higher on specimens with wider apical angles. Upper ramp slightly concave with most specimens displaying a fine, often faint carina near the suture, usually fading with age. Moderately wide selenizone trilineate with middle thread somewhat thicker than bordering ones, often becoming indistinguishable with age. Selenizone protrudes slightly from nearly perpendicular angle between upper and lower ramps. Lower ramp slightly concave to flat to dull lower carina representing a slight extension of ramp/base juncture and often disappearing on larger specimens. Shift to slightly convex base slight. Umbilicus small, usually partially filled by greatly thickened, U-shaped columellar lip. Growth lines moderately sharp, closely spaced, strongly swept abaperturally from suture to selenizone, with strong sweep below straightening towards umbilicus. Lunulae stronger on older whorls, with sharp U-shape.

Discussion: Ulrich (1897) initially distinguished between *Paralophospira oweni* and *Lophospira saffordi* based upon the sharper growth lines and carina of the *L. saffordi*, as well as the supposed retention of the upper carina by *L. saffordi*. However, examination of the syntypes of *L. saffordi* and of over 100 Kentucky specimens that otherwise match Ulrich's description of *L. saffordi*, it is apparent that the upper carina weakens with age on that species as well. Specimens identified as *L. saffordi* are known from rocks deposited in quiet water environments (e.g. the Clays Ferry formation in Kentucky) while *P. oweni* is known from sites such as the Decorah and Utica shales. Interestingly, Ulrich and Scofield report a hiatus in the temporal range of *P. oweni*, stating that no examples were known from what they termed Trenton rocks. *Lophospira saffordi*, meanwhile, is known only from Trenton aged rocks. Therefore, it appears that *P. oweni* and *L. saffordi* represent preservational variations of the same species. As *P. oweni* has taxonomic priority, it is proposed that the two species be united under *P. oweni*.

Paralophospira oweni appears to represent an intermediate step between the earlier *P. medialis* and the later *P. sumnerensis* and *P. tropidophora*. Some of the important invariant diagnostic traits of the later species appear as more variable ones on *P. oweni*. *Paralophospira oweni* can be distinguished from *P. medialis* by its much thicker columellar lip region that often partially fills the umbilicus. On well preserved specimens, *P. oweni* can also be distinguished by its stronger growth lines and the loss of the upper carina with age. In addition, *P. oweni* is usually somewhat larger than *P. medialis*. While sharing very similar overall morphologies, *Paralophospira oweni* is much larger than *P. spironema* and *P. tennuistriata*, and lacks the additional spiral lirae observed on those species. However, it is possible that those species represents a small, ornate localized variants of *P. oweni*. This is especially probable for *P. spironema*, which is known from only one site. *Paralophospira oweni* can be distinguished from *P. tropidophora* by its generally narrower apical angle, produced by the consistently higher suture points on the two younger species. The columellar lip is also thinner on those two species, and it does not fill the umbilicus as well or as often. There also appears to have been an ecologic differences, as *Paralophospira tropidophora* seem to have been more restricted to more shale-rich environments. As mentioned above in regards to *Lophospira saffordi*, *P. oweni* appears to have been more cosmopolitan in its environmental preferences.

In the Ordovician of Kentucky, *Paralophospira oweni* appears to replace *Lophospira milleri* as the dominant lophospirid during the late Caradoc.

Materials: Over 100 silicified specimens from U.S.G.S. 7812-CO in the Shawan quadrangle, Kentucky plus another thirty specimens from U.S.G.S. C-72-3-7350 in the same quadrangle. Also, U.S.N.M. 45911 and 45912 (nine syntypes), and U.S.N.M. 45920 and U.S.N.M. 45921 (six syntypes of *L. saffordi*).

Occurrence: Ordovician (late Caradoc). Specimens from the Clays Ferry Formation, which extends into the Ashgill.

PARALOPHOSPIRA MEDIALIS (Ulrich & Scofield)

Lophospira medialis
    1897 Ulrich & Scofield, *Geol. Minn.* 3 pt 2, p. 973, pl. 73, fig.s 23 - 29
    1909 Grabau & Shimer, *N. Amer. Index. Fossils, Vol. 1*, p. 634, fig. e - h
    1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 761
Lophospira medialis var. *burginensis*
    1897 Ulrich, *Geol. Minn.* 3 pt 2, p. 974, pl. 73, fig.s 30 - 31
Lophospira medialis burginensis
    1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 76

?Lophospira pulchella
    1897 Ulrich & Scofield, *Geol. Surv. Minn.* 3 pt. 2, p. 982, pl. 73, fig.s 46 - 48
    1909 Grabau & Shimer, *N. Amer. Index Fossils, Vol. 1*, p. 634, fig. 859 i - k
    1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 763
Loxoplocus (*Lophospira*) cf. *L.* (*L.*) *medialis*
    1980 Rohr, *Palaeontographica Abt. A, Band 171*, p. 174 - 175, pl. 8, fig.s 8 - 10
?Lophospira obliquestriata
    1924 Longstaff, *Quart. J. Geol. Soc. Lon.* 80, p. 417, pl. 33, fig. 8

Description: Small to moderate sized (height 10 - 30 mm), composed of six to seven volutions with an apical angle ranging from usually around 60°. Suture on lower carina covering lower third of preceding whorl. Upper ramp slightly concave with weak upper carina near suture. Moderately wide trilineate selenizone with symmetric threads of equal strength, slightly protruded from sharp angle of upper ramp/lower ramp juncture. Lower flat to weak lower carina, shifting slightly to small, nearly flat base. Umbilicus small. Aperture subquadrangular. Columellar lip thickened, "U"-shaped. Growth lines weak, fine, strongly swept abaperturally from suture to selenizone and swept beneath selenizone to lower carina, then straight to umbilicus. Lunulae V-shaped, faint.

Discussion: As noted by Rohr (1980), the holotype has a stronger upper carina than depicted in the original description (Ulrich & Scofield 1897). As a result, it seems that many later Caradoc specimens of *Ambilophospira perangulata* have been identified as *Paralophospira medialis* (e.g. McFarlan & White 1948; Wilson 1951). *Paralophospira medialis* differs from *A. perangulata* in the consistent presence of this upper carina as well as in the "U"-shaped columellar lip and a generally wider apical due to an increased whorl expansion rate. This species differs from *Lophospira milleri* in having a finer, more strongly swept growth lines, a weaker upper carina, a different columellar lip shape and a less expanded base. *Paralophospira medialis* is most similar to *P. oweni*, which differs by having stronger growth lines, a thicker columellar lip and an upper carina that weakens with age. However, juvenile *P. oweni* would be very difficult to separate from *P. medialis*.

Five specimens from the Ashgill of California that Rohr (1980) as being very similar to *Paralophospira medialis* appear to belong to the species as they differ only in having stronger upper carinae.

Materials: U.S.N.M 45906 (holotype); also U.S.N.M. 45907 (paratypes) and U.S.N.M. 253141 (*Loxoplocus* cf. *L.* (*Lophospira*) *medialis* in Rohr 1980).

Distribution: Ordovician (middle Caradoc through Ashgill).

PARALOPHOSPIRA SUMNERENSIS (Safford)

Murchisonia sumnerensis
    1869 Safford, *Geol. Tenn.*, pl. 3G, fig.s 1a - 1f (no description)
Lophospira sumnerensis
    1897 Ulrich & Scofield, *Geol. Surv. Minn.* 3 pt. 2, p. 978, pl. 73, fig.s 18 - 20
    1909 Grabau & Shimer, *N. Amer. Index Fossils, Vol. 1*, p. 635, fig. 860 i & j
    1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 765
Loxoplocus (*Lophospira*) *sumnerensis*
    1944 Knight *et al.*, *Index Fossils of N. Amer.*, p. 449, pl. 182, fig.s 14 & 15
?Loxoplocus cf. *L.* (*Lophospira*) *sumnerensis*
    1980 Rohr, *Palaeontographica Abt. A, Band 171*, p. 173 - 174, pl. 8, fig.s 15 - 17

?Lophospira compacta
1961 Yü, *Acta Palaeont. Sin.*, p. 349 (370), pl. 4, fig.s 1 & 2

Description: Moderate sized (25 - 35 mm height) composed of five whorls with an apical angle 65° - 70°. Elongate form with height 35 - 45 mm and apical angle near 45°. Suture above lower ramp/base junction, covering lower third of whorl, lower on more elongate specimens. Upper ramp slightly concave on upper whorls, very concave on final one. Extremely weak thread just below suture rare. Selenizone moderately wide, faintly trilineate, with middle thread somewhat wider than bordering lirae. Lower ramp flat to slightly convex, with slight shift to base. Umbilicus small, partially filled by columella. Aperture sub-ovular. Greatly thickened columellar lip U-shaped, with strong abapical projection. Growth lines moderately strong, strongly swept from suture to selenizone and below, straightening to umbilicus. Lunulae sharp U-shaped, very faint.

Discussion: While this species is fairly consistent, a more elongate variety produced by a lower suture point on the whorl is not infrequent among specimens from the Devils Hollow Member of the Lexington Limestone. This member is noted for coquinas rich in high spired gastropods such as *Hormotoma salteri*. As the presence of specimens with normal suture locations suggests that this is probably not ecophenotypic variation, it is possible that the higher spired individuals simply represent phenotypic variants that were a survivable alternative in the high energy environment suggested for the Devil's Hollow (Cressman 1973).

Paralophospira sumnerensis is in many ways intermediate between the older *P. oweni* and the younger *P. tropidophora*. The suture of *P. sumnerensis* is generally higher than that of *P. oweni*, but not as high as that of *P. tropidophora*. All three display very similar lip shapes, but the lip of *P. sumnerensis* is further extended than that of *P. oweni*, as is that of *P. tropidophora*. Also, the thickness of the columellar lip thickness of *P. sumnerensis* is intermediate, filling the umbilicus to a greater degree and with a greater frequency than seen on *P. oweni*, but not to the extent or frequency as *P. tropidophora*. While *P. oweni* possesses weak upper and lower carinae that usually weaken further with age, there appear to be no trace of either on *P. sumnerensis*, a featured shared with *P. tropidophora*. However, *P. sumnerensis* and *P. oweni* are very similar in size, both being much smaller than *P. tropidophora*. The preservation of this species suggests that it also may have been an ecological intermediate, for as on *P. tropidophora* the finer details are only rarely preserved. This is also the case for the specimens originally described as *P. oweni* by Ulrich & Scofield (1897), but well preserved specimens of that species originally described as *Lophospira saffordi* appear to have also lived in more quiet water environments.

Specimens from the Klamath Mountains described by Rohr (1980) probably belongs to this species, as does a species from north west China described by Yü (1961). The age for Rohr's specimens is uncertain, but the Chinese specimens appear to be Caradocian (Sheng-Fu 1980).

Materials: Seventeen fairly complete silicified specimens plus many fragments often encased in coquina from U.S.G.S. sites 6915-Co and 6916-CO from the Perryville quadrangle, Kentucky. One fairly complete elongate specimen plus smaller specimens fragments in coquina from U.S.G.S. site 5095-CO from the East Frankfort Quadrangle, Kentucky and additional smaller specimens and fragments from U.S.G.S. site 5036-CO Colestown quadrangle Kentucky.

Distribution: Ordovician (middle to late Caradoc).

PARALOPHOSPIRA TROPIDOPHORA (Meek)

Pleurotomaria (Scalites?) tropidophora
    1872 Meek, *Amer. Jour. Sci, 3rd ser., 4*, p. 278
    1873 Meek, *Geol. Surv. Ohio, Pal.* 1, p. 154, pl. 13, fig.s 6a - 6c
Lophospira tropidophora
    1909 Grabau & Shimer, *N. Amer. Index Fossils* Vol. 1, p. 635, fig. 860 f - h
    1915 Bassler, *U.S. Nat. Mus. Bull.* 92, Vol. 2, p. 766
    1924 Foerste, *Can. Geol. Surv. Mem.* 138, No. 121, p. 212 - 213, pl. 34, fig. 15
Schizolopha tropidophora
    1987 Frey, *Palaios* 2(1), p. 19
Murchisonia multigruma
    1873 Miller, *Jour. Cin. Soc. Nat. Hist.* 1, p. 104
Lophospira multigruma
    1897 Ulrich & Scofield, *Geol. Surv. Minn* 3 pt. 2, p. 978, pl. 72, fig.s 36 - 39
Lophospira ampla
    1897 Ulrich in Ulrich & Scofield, *Geol. Minn.* 3 pt. 2, p. 981 pl. 73, fig.s 52 - 54
    1909 Grabau & Shimer, *N. Amer. Index Fossils* Vol. 1, p. 635, fig. 860 d & e
    1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 757

Description: Moderate to large (35 - 50 mm height) composed of five whorls with an apical angle from 75° to 80°. Sutures high, often just below selenizone covering nearly the lower half of the preceding whorl. Upper ramp very slightly concave to flat. Wide selenizone weakly trilineate, protrudes slightly from nearly perpendicular angle of upper ramp/lower ramp junction. Lower ramp flat shifting slightly to flat to slightly convex base. Very small umbilicus almost always filled by extremely thick columella. Aperture sub-ovate. Extremely thick columellar lip U-shaped, extended abapically. Growth lines moderately strong, strongly swept abaperturally to selenizone, strongly swept beneath, straightening and of greatly exaggerated strength towards umbilicus. Lunulae sharp U-shapes when visible.

Discussion: This species is very common in Cincinnatian. Broken pieces of the larger whorls of *Paralophospira tropidophora* look similar those of the strongly associated *Donaldiella bowdeni*. However, single whorls can be distinguished by the columellar lip - those of *P. tropidophora* fill the umbilicus while on *D. bowdeni* the lip is reflected around the umbilicus. Given the drastic difference in whorl expansion rates it would be difficult to confuse any specimens bearing more than a single whorl. A single specimen from the Millersburg member of the Lexington formation from the late Caradoc may belong to this species. However, this may simply be an enlarged *P. oweni*.

Ulrich (in Ulrich & Scofield 1897) originally distinguished *Lophospira ampla* from *Paralophospira tropidophora* due to the former possessing a weak upper carina and a columellar lip that was slightly extended and twisted rather than simply filling the umbilicus. This appears to be nothing more than a variation of *P. tropidophora* produced by the suture being closer to the selenizone, which distorts the shell so that the columellar lip does not fill the umbilicus as fully, projecting instead around it. The weak carina of *L. ampla* appears to represent the sutural carina of *P. tropidophora*, slightly displaced by the higher suture point. This variation co-occurs with specimens matching Ulrich's description of *P. tropidophora* in Kentucky, as well as in Ohio and Indiana.

Paralophospira tropidophora is most similar to species such as *P. oweni* and *P. sumnerensis*. Features distinguishing those species are listed in the discussions above. *Paralophospira tropidophora* is also very similar to *P. ehlersi* of the early Llandovery. The younger species differs in being smaller and in having a lower suture point on the adult whorls.

Materials: One hundred twenty two (122) fairly complete specimens plus fragments from U.S.G.S. site 6139-CO from the New Point quadrangle, Indiana (Dillsboro Formation); Ten more fragmentary specimens from Lancaster quadrangle, Kentucky (Gilbert member of the Ashlock Formation); Single possible specimen from U.S.G.S. 7344-CO from the Shawan quadrangle, Kentucky (Millersburg tongue of Lexington Limestone). Also, U.S.N.M. 45930, 45931 and 45932 (hypotypes) and U.S.N.M 45887 and 45888 (five paratypes of *Lophospira ampla*).

Distribution: Ordovician (Ashgill, possibly late Caradoc).

PARALOPHOSPIRA EHLERSI Foerste

Lophospira ehlersi
1923 Foerste, *J. Sci. Lab. Den. U.* 20, p. 82 - 83, pl. 14, fig. 16

Description: Small to moderate size (14 - 18 mm height) shell with five volutions and an average apical of 80°. Initial sutures cover half of the preceding whorl, dropping to lower carina and covering the lower third of the penultimate whorl. Upper ramp flat with no carina. Selenizone trilineate with fine but sharp lirae, pronounced from sharp angle of upper ramp/lower ramp juncture. Lower ramp flat to weak, extremely dull lower carina, shifting slightly to wide convex base. Umbilicus small, partly filled by columellar lip. Columellar lip U-shaped, extremely thick. Growth lines faint, closely spaced, being strongly curved abaperturally from the suture to selenizone.

Discussion: *Paralophospira ehlersi* is very similar to the Ashgillian *P. tropidophora*, which differs in being much larger and having suture points consistently just beneath the selenizone. *Paralophospira tropidophora* differs from in having a wider angle between the upper and lower ramps on the adult whorls. In this, *P. ehlersi* is similar to the variation of *P. tropidophora* described by Ulrich and Scofield as *Lophospira ampla*. However, young *P. tropidophora* specimens also show sharper upper ramp/lower ramp junctures, so the difference between the two species is probably due largely to size. The fauna *P. ehlersi* is described in association with (Foerste 1923) is notable for being relatively diminutive, with *P. ehlersi* representing possibly the largest fossil species present. Notably, this fauna is not diminutive to the extreme found the Brassfield fauna immediately above it (Harrison & Harrison 1975), and *P. ehlersi* does not seem to be the unspecified *Lophospira* described from the site. However, it is highly probable that *P. ehlersi* represents simply a diminutive form of *P. tropidophora* that carried on into the Silurian.

Materials: Over twenty specimens from below the Brassfield Formation, Centerville Ohio.

Occurrence: Silurian (early Llandovery).

Genus Donaldiella Cossman 1903

DONALDIELLA PAGODAI (Endo)

Lophospira producta pagodai

1932 Endo, *U.S. Nat. Mus. Bull.* 164, p. 55, pl. 29, figs 8 - 11

Description: Small (height 20 - 26mm) composed of at least eight whorls with an apical angle around 30°. Suture on the lower carina covering lower sixth of preceding whorl. Upper ramp wide, slightly concave. Trilineate selenizone symmetrical, protruding slightly from nearly perpendicular angle between upper and lower ramps. Lower ramp slightly concave to flat to weak lower carina. Slight shift to flat base. Umbilicus small. Slightly thickened columellar lip extended, upside-down "7" shape. Growth lines weak, sharply swept abaperturally, straightening on base to umbilicus. Lunulae weak, V-shaped.

Discussion: *Donaldiella pagodai* exhibits the "right-angle" whorl stacking pattern and increased whorl numbers characteristic of *Donaldiella*. As such it represents the oldest known species of that genus. While Endo (1932) suggested a relation between this species and species now placed in *Donaldiella*, he instead classified it as a variant of *Lophospira producta*. While Ulrich (1897) to place *L. producta* in the *Bowdeni* subsection of *Lophospira* (which was composed of species later placed in *Donaldiella*), Ulrich suggested a separate origin for *L. producta* as that species shares little with the other species except for an increased number of whorls.

Donaldiella pagodai is very similar to *Ambilophospira perangulata*, but can be distinguished by the perpendicular alignment of the selenizones and the right-side of the apical angle.

Materials: U.S.N.M. 83657 (Holotype plus paratype) from southern Manchuria.

Distribution: Ordovician (Llanvirn)

Subfamily RUEDEMANNIINAE Knight 1956

Genus *HELLERMANNIA* n.gen.

Type Species: By monotypy, *Hellermannia humilis*.

Diagnosis: Weak spiral lirae on lower whorl, two upper whorl carina, absence of traits diagnosing *Arjamannia*, *Ruedemannia* or *Schizolopha*.

Discussion: This represents a metataxon thought to be ancestral to all later Ruedemanniinae. As it lacks the diagnostic traits of any of its three daughter lineages, and as *Lophospira* is restricted to the sub-family Lophospiridae, a new generic name is erected for this species.

Etymology: After Joseph Heller, author of *Catch-22* and the ending used for other ruedemannid species.

HELLERMANNIA HUMILIS (Ulrich in Ulrich & Scofield)

Lophospira humilis

1897 Ulrich in Ulrich & Scofield, *Geol. Surv. Minn.* 3 pt 2, p. 968, pl. 72, fig.s 12 - 15
1915 Bassler, *U.S. Nat. Mus. Bull.* 92 Vol. 2, p. 761
<u>NON</u> Butts, *Geol. Surv. Alab. Spec. Rep.* 14, pl. 19, fig. 21

<u>Description</u>: Small (height 7 - 14 mm) composed of four to five whorls with an apical angle around 80°. Suture on lower carina covering lower third of preceding whorl. Upper ramp flat with a carina next to the suture and a second half way between the suture and selenizone. Moderately wide selenizone trilineate, symmetric, protruding slightly from wide angle of upper/lower ramp juncture. Lower ramp flat to weak fine lower carina, with additional very fine spiral lirae present. Shift sharp to expanded, somewhat convex base. Umbilicus small, partially covered by reflected "L"-shaped columellar lip. Fairly sharp growth lines straight over both upper carina, slightly swept abaperturally two selenizone, swept beneath but straightening on base to umbilicus.

<u>Discussion</u>: This species differs from the type description (Ulrich in Ulrich & Scofield 1897) by possessing faint spiral lirae on the lower whorl similar to although somewhat weaker than those seen on *Ruedemannia* and much weaker than those of *Arjamannia* species. Knight reclassified the species on the type label owing to its strong similarity to the younger *R. lirata*. However, the later species differs in possessing a wider selenizone, more convex upper and lower ramps and only one upper carina. As these traits can be used to diagnose the genus *Ruedemannia*, *Hellermannia humilis* should not be classified here. *Arjamannia* species share a bicarinate upper ramp with *H. humilis*, but are diagnosed by cancellate ornamentation produced by the growth lines and very strong spiral lirae. The contemporary *Schizolopha textilis* has similarly strong spiral lirae, but exhibits them on the upper whorl as well. That species also has only one upper carina and displays a long thin apertural slit.

Butts (1926) figures but does not describe a Llandeilo species he termed *Lophospira humilis*. However, he labeled this a new species and it has little in common with Ulrich's species. Given the poor condition of the single fossil, the affinities of Butt's specimen are unknown.

U.S.N.M. 60648 is identified as a paratype of this species but belongs instead to *Ruedemannia lirata*.

<u>Materials</u>: U.S.N.M. 45903 (holotype plus five paratypes) from the Trenton of New York.

<u>Distribution</u>: Ordovician (upper Caradoc).

Genus *ARJAMANNIA* Peel 1975

ARJAMANNIA ROHRI n. sp.

Ruedemannia aff. *R. lirata*
1988 Rohr, *J. Paleo Vol* 62(4), p. 561, pl. 4, fig.s 24 - 27

<u>Diagnosis</u>: Two strong upper whorl carina with additional weaker spiral lirae on the upper and lower whorls.

<u>Description</u>: Small (height 11 - 15 mm) composed of five whorls with an apical angle around 75°. Suture covers lower third of preceding whorl. Upper ramp flat with thread-like carina beneath suture and a second slightly stronger half way between the suture and

selenizone and sparse, thin spiral lirae between the carinae. Moderately wide selenizone trilineate, protruding strongly from upper ramp (but less strongly from lower ramp owing to its increased width). Lower ramp slightly convex, descending nearly vertically from selenizone, with strong spiral lirae forming a cancellate pattern with the growth lines. Sharp shift to very wide base. Umbilicus small, covered by reflected "L"-shaped columellar lip. Growth lines sharp, straight over both upper carinae, swept abaperturally to selenizone, swept beneath to lower carina then straight to umbilicus. Lunulae faint, fairly straight.

Discussion: Rohr (1988) tentatively linked this species with *Ruedemannia lirata*. However, the species has much more in common with *Arjamannia thraivensis*, differing from that species primarily in having spiral lirae on the upper whorl as well as the lower and in having a more full produced base resulting in the lower ramp descending vertically from a produced selenizone. *Arjamannia rohri* shares the latter trait with Silurian *Arjamannia*, but can be distinguished from any of those species by its retention of both upper carinae as distinct threads rather than being incorporated into the cancellate pattern produced by abundant spiral lirae and equally strong growth lines.

Materials: U.S.N.M. 422388 (holotype) plus 36394 and 422389 from the Seward Peninsula of Alaska.

Occurrence: Ordovician (Ashgill)

Etymology: After David Rohr, in honor of his work with northwestern North America Paleozoic gastropods.

Subfamily TROCHONEMALLINAE Zittel 1895
METATROCHOSPIRA n. gen.

Type Species: By monotypy, *Metatrochospira knoxvillensis*.

Diagnosis: Displaying tangential aperture, rotated whorls and umbilical carinae of both *Trochonemella* and *Trochonema*, but retaining a *Lophospira*-like placement of upper carina and trilineate selenizone with no imbrications or enlargement of the midwhorl internal channel.

Discussion: This represents a metataxon thought to be ancestral to all later Trochonemallinae. As it lacks the diagnostic traits of either of its daughter lineages a new generic name is erected for this species. Other Llanvirn and Llandeilo species currently classified as either *Lophospira* (e.g. *L. belli* Raymond) or *Trochonema* (e.g. *T. tricarinatum* Billings) may belong to this genus.

Etymology: "Meta" for its metataxon status and "trocho" and "spira" to reflect its intermediate status between *Lophospira* and later Trochonemallinae.

METATROCHOSPIRA KNOXVILLENSIS (Ulrich in Ulrich & Scofield

Lophospira (?) *knoxvillensis*
1897 Ulrich in Ulrich & Scofield, *Geol. Surv. Minn.* 3 pt. 2, p. 989 - 990, pl 75,

fig.s 38 - 40
Trochonemella knoxvillensis
1935 Okulitch, *Ottawa Field Nat.* 49(6), p. 101.

Description: Large (width up to 40 mm) with seemingly few whorls and an apical angle over 100°. Upper ramp slightly concave with sharp upper carina next to suture. Moderately wide selenizone trilineate with middle thread stronger than bordering threads. Selenizone protrudes moderately from nearly perpendicular angle of upper/lower ramp juncture. Lower ramp flat to sharp thread-like lower carina that becomes more obtuse with age. Sharp shift to flat base. Umbilicus large with faint carina around it. Aperture tangential. Thickened columellar lip rounded "L"-shape with little projection and no reflection. Parietal lip thickened. Growth lines sharp, straight over upper carina, rather sharply swept to selenizone, swept beneath with abapertural trend on base to umbilicus.

Discussion: This represents the most primitive known trochonemellid species. While the aperture is tangential and warped like *Trochonemella* and *Trochonema*, the thickened blunt L-shaped columellar lip is more similar to the lip of a species such as *L. milleri* than to *T. notablis*. Unlike either *Trochonemella* or *Trochonema*, this species retains a trilineate selenizone, although the middle thread of *M. knoxvillensis* is stronger than the bordering ones (but not to the extent depicted by Ulrich's figures). *Metatrochospira knoxvillensis* also differs from later Trochonemallinae species in that the upper carina is nearly under the suture owing to the rotation of the whorl instead of between the suture and the midwhorl. However, the carina is in the same position relative to the columellar lip and selenizone as the upper whorl carina of *L. milleri* and similar *Lophospira* species. The sharpness of this carina distinguishes it from the dull sutural carina shown by later trochonemallids with upper carina lower on the upper ramp.

Materials: U.S.N.M. 46064 (holotype and paratype) from the Lenoir Limestone, near Knoxville Tennessee.

Occurrence: Ordovician (Llanvirn).

Genus *TROCHONEMELLA* Okulitch 1935

Discussion: There has been some confusion about the relationship between members of this genus and the Silurian *Ulrichospira* (e.g. Knight 1941; Wilson 1951). Why this occurred is not at all clear as *Trochonemella* and *Ulrichospira* have very little in common. *Ulrichospira* is a poorly understood genus with only one well-described species. However, it clearly lacks the tangential aperture and rotated whorls characteristic of *Trochonemella* species and displays a much different selenizone and a lower lip apparently more reminiscent of more primitive *Lophospira*. *Ulrichospira* is more similar to some members of *Arjamannia* although the lack of spiral ornamentation, a much thicker lower carina and stronger bordering selenizone lirae represent possibly important differences separating *Ulrichospira* from *Arjamannia*.

TROCHONEMELLA PENGUINI n. sp.

Diagnosis: Strongly imbricated lunulae limited to juvenile whorls with adult selenizone slightly concave. Growth lines nearly straight to trilineate selenizone. Strong upper and lower whorl carina. Aperture tangential.

Description: Moderate to large shell averaging 27 mm in height (maximum 33 mm) with five volutions and an apical angle averaging 85°. Initial sutures on lower carina covering lower third of preceding whorls, with coiling opening with age. Upper ramp slightly convex with a strongly pronounced thread-like carina near half-way from suture to selenizone. Selenizone wide, flat to narrowly concave, with fine thread-like bordering lirae and somewhat pronounced from obtuse angle of upper ramp/lower ramp junction. Lower ramp short, flat to (rarely) slightly convex with strong thread-like lower carina shifting markedly at this point to a convex base. Umbilicus large. Fine thread-like umbilical carina becoming dull or extinct on later whorls. Strongly tangential circular aperture. Columellar lip thickened and rounded, with no extension or reflection. Wide, fairly deep U-shaped sinus culminating in selenizone on outer lip. Uniform growth lines closely spaced, moderately strong and sharp, trending straight in an abapertural direction from the suture over the upper carina curving abaperturally close to selenizone. Beneath selenizone growth lines curve away at approximately the same degree as above, straightening at the lower carina and curving on base abaperturally to the umbilicus. Strong concentric lunulae on adult whorls showing somewhat wider and more erratic spacing than the growth lines, with juvenile lunulae on many specimens noticeable imbricated.

Discussion: *Trochonemella penguini* most strongly resembles the somewhat younger *T. notablis* differing chiefly in that the strongly imbricated lunulae are found throughout the whole shell rather than just the juvenile whorls of some specimens. In this trait, *T. penguini* also differs from the Ashgillian *T. churkini* and *T. reusingi*. Also, the upper and lower carina of *T. notablis* are of identical strength, while the lower carina of *T. penguini* is somewhat weaker. In all other respects the two species are nearly identical. It is also very similar to the Canadian *T. montrealensis*. However, *T. montrealensis* is much smaller, being nearly half the size of the Kentucky species, a narrower, more produced selenizone with more widely spaced lamellae, stronger abapertural curve to the growth lines and a flatter upper ramp with a weaker upper carina closer to the suture. Also, the strongly imbricated lunulae seen in the juvenile whorls of *T. penguini* has not been reported on *T. montrealensis*.

Materials: Over 100 silicified specimens from U.S.G.S. site 6034-CO in the Little Hickman Quadrangle and site D-1138-CO in the Valley View Quadrangle (Marble Creek Section), Lexington County Kentucky.

Occurrence: (Ordovician, middle Caradoc). Apparently fairly abundant in the upper part of the Tyrone Limestone in Kentucky. Associated with archaeogastropods *Trochonema umbilicatum* (Hall), *Lophospira helicteres* (Hall), *Murchisonia* (*Hormotoma*) *gracilis* Hall and *Liospira* species.

Etymology: In honor of the great third-baseman of the Los Angeles Dodgers and Chicago Cubs.

TROCHONEMELLA NOTABLIS (Ulrich in Ulrich & Scofield)

Lophospira (?) *notablis*
1897 Ulrich in Ulrich & Scofield, *Geol. Surv. Minn. 3, pt. 2*, p. 990 - 991, pl 72, fig.s 33 - 35.
1915 Bassler, *U.S. Nat. Mus. Bull. 92, Vol. 2*, p. 762
Trochonemella notablis
1935 Okulitch, *Ottawa Field Nat. 49(6)*, p. 101.
1941 Knight, *G.S.A. Spec. Ppr. 32*, p. 358 - 359. pl. 40, fig.s 1a - 1d
1960 Knight *et al.*, *Treatise on Inv. Paleo. (i), Vol. 1*, p. 208, fig. 121 #6
Ulrichospira notablis
1944 Knight *et al.*, *Index Fossils of N. Amer.*, pg.451, pl 182, fig. 28

Description: Moderate sized consisting of five volutions with an apical angle of ~88°. Initial sutures on lower carina covering the lower third of preceding whorls, with coiling opening by the final whorl. Upper ramp slightly convex, flat between upper carina and selenizone. Upper carina a very strongly produced thread nearly half-way between selenizone and suture. Selenizone wide, flat to slightly convex, with fine bordering lirae, and strongly pronounced from obtuse angle of upper ramp/lower ramp junction. Lower ramp short, flat with a slightly concave appearance owing to the pronouncement of the selenizone and strong, thread-like carina, with whorl shifting markedly at this point to convex base. Umbilicus large. Extremely weak, dull umbilical carina on base. Strongly tangential, circular aperture. Columellar lip thickened and rounded with no extension or reflection. Wide, fairly deep U-shaped sinus culminates in selenizone on outer lip. Moderately strong growth lines evenly spaced, trending straight abaperturally from suture over upper carina, with a weak abapertural curve just above selenizone. Beneath selenizone growth lines curve away at approximately the same degree as above, straightening at the lower carina and curving on base abaperturally to the umbilicus. Lunulae on selenizone are strongly imbricated and widely spaced on the entire shell.

Discussion: The specimens housed at the U.S. National Museum all show somewhat exaggerated features due to silicification and/or weathering, especially in making the growth lines on either side of the selenizone appear much stronger than they are at the top or bottom of the whorl. *Trochonemella notablis* is most similar to *T. penguini*, although there are some key differences (see above discussion of *T. penguini*). *Trochonemella notablis* is also very similar to the Upper Ordovician species from Alaska and California, differing from those species in its lack of serrated upper carina and less pronouncement of the selenizone imbrications.

Materials: Three specimens, the holotype and two plesiotypes from Maury County Tennessee labeled as U.S.N.M. 45909, plus U.S.N.M. 47568, another plesiotype of a juvenile, U.S.N.M. 47658, from the Carters Limestone (formerly Carters Creek Limestone [source]) at High Ridge Kentucky, all housed in the U.S. National Museum.

Occurrence: Ordovician (middle Caradoc).

TROCHONEMELLA SANDBERGI n. sp.

Loxoplocus (*Lophospira*) aff. *L.* (*L.*) *serrulata*
1988 Rohr, *J. Paleon.* 62(4), p. 559 - 561, fig.s 3.12 - 5.16

Diagnosis: Moderate sized shell with serrated trilineate selenizone and serrated upper and lower carina, a round columellar lip and a tangential aperture.

Description: Moderate sized (height 20 - 30 mm) composed of four to five whorls with apical angles around 70°. Suture covers lower fifth of preceding whorl. Upper ramp flat to slightly convex with strong, severely serrated upper carina pointed abapically near suture. Moderately wide selenizone with sharply imbricated lunulae bordered by thin lirae and protrudes noticeable from wider angle of upper/lower ramp juncture. Lower ramp descends nearly vertically from selenizone, flat to strong, serrated lower carina. Sharp shift to wide base with weak umbilical carina. Umbilicus small. Aperture tangential. Columellar lip rounded, slightly thickened with no extension or reflection. Growth lines trend straight but abaperturally over upper carina to selenizone, with very slight curve above and below. Straight on lower ramp to umbilicus.

Discussion: Rohr (1988) tentatively linked this species with *Ambilophospira serrulata* due of the serrated appearance of the selenizone middle thread of the Alaskan species. However, upon closer examination these serrations appear more like the imbrications of *Trochonemella* species that occur with *T. sandbergi*. There are no other similarities between *T. sandbergi* and *A. serrulata*. The growth lines of *T. sandbergi* are straight from the sutures to just above and below the selenizone instead of strongly swept as on *A. serrulata*, the columellar lip is thin and rounded instead of thick and "U"-shaped, and there is no apparent sutural carina, adapertural sweep growth line sweep around the upper carina or gerontic open-coiling as on *A. serrulata*. While both species exhibit an umbilical carina, this is also seen on *Trochonemella* species. In addition to the imbricated selenizone, *T. sandbergi* shares with other *Trochonemella* species serrated upper and lower carinae, columellar lip shape, growth-line morphology and a high angle between the selenizone and upper ramp. *Trochonemella sandbergi* differs from all other *Trochonemella* in showing no counter-clockwise rotation of the whorls compared to *Lophospira* species. It also shows a tangential aperture similar to that of *L. quadrisulcata* rather than other *Trochonemella*. However, *T. sandbergi* lacks the strong sutural carina and second lower whorl carina of that species and is more heavily ornate. However, *T. sandbergi* shares it *Lophospira*-like features with small, similarly aged lophospirids possibly representing juveniles of the Alaskan *T. churkini*.

Materials: U.S.N.M. 36433 (18 silicified specimens).

Occurrence: Ordovician (Ashgill).

Etymology: In honor of Ryne Sandberg's record errorless streak.

Genus *TROCHONEMA* Salter 1859.

TROCHONEMA TROCHONEMOIDES (Ulrich in Ulrich & Scofield)

Lophospira (?) *trochonemoides*
1897 Ulrich in Ulrich & Scofield, *Geol. Surv. Minn.* 3 pt. 2, p. 990, pl 75, fig.s 41 - 44.
Trochonemella trochonemoides
1935 Okulitch, *Ottawa Field Nat.* 49(6), p. 101.

Description: Moderately sized, with five volutions and an apical angle of 100’. lophospirid, with a height of 22 mm, an apical angle of 100° and 5 volutions. Sutures cover approximately lower third of preceding whorl, with no noticeable ontogenetic shift. Upper ramp flat, with thread-like carina closer to suture than periphery. Thick, strong carina at mid-whorl pronounced from obtuse angle of upper ramp/lower ramp junction, overlaying a shallow channel on the inner portion of the shell. Lower ramp flat, wide with thread-like carina somewhat weaker than the upper whorl carina and becoming somewhat weaker adaperturally. Whorl shifts gently to convex base with weak umbilical carina that weakens with age. Umbilicus moderately large. Strongly tangential, sub-ovoid aperture. Columellar lip thickened and round, with little extension and no reflection. Sinus apparently V-shaped and very shallow. Growth lines easily consistently fine and evenly spaced, trending straight and abaperturally from the suture over upper carina, curving abaperturally halfway between the upper and middle carina. Beneath mid-whorl carina, growth lines curve away at approximately the same degree as above, straightening at the lower carina and curving on base abaperturally to the umbilicus. Lunulae are on middle carina concentric.

Discussion: The description given by Ulrich (Ulrich & Scofield 1897) is somewhat misleading. While Ulrich states that the lower carina is "extinct" by the aperture, it is present albeit somewhat weakened. Also, while Ulrich describes the growth lines and aperture as being similar to *Trochonemella knoxvillensis* there are important differences. Penciled in approximations of the growth lines on U.S.N.M. 46069 match those of Ulrich's figures, but close examination shows that these drawn lines are exaggerated. In actuality the growth lines of *T. trochonemoides* show a weaker sweep than those of *T. knoxvillensis* (~20° vs. ~30°), although this is due to the much higher location of the upper carina (see description above). Meanwhile, the aperture of *T. knoxvillensis* is much less rounded than that of *T. trochonemoides* owing to a much more produced columellar lip. The latter difference is not easily recognized from Ulrich & Scofield's illustrations alone, as the aperture of *T. trochonemoides* is shown at an angle making it appear less round than it actually is with a more angled columellar lip as on *T. knoxvillensis*. However, the difference in lip extension is noticeable in Ulrich & Scofield's figures. The extended, somewhat reflected columellar lip of *T. knoxvillensis* is common to its contemporary *Lophospira* species of but absent in *T. trochonemoides* and other *Trochonemella*.

Trochonema trochonemoides differs from all *Trochonemella* in the absence of the two bordering lirae of the lophospirid selenizone, and in the seeming retention of the middle carina that is absent in all save *T. walpolius* and *T. knoxvillensis*. In this and in its possession of an internal channel at the mid-whorl *T. trochonemoides* is more similar to contemporaneous early species of *Trochonema* such as *T. bellum*. The chief differences between *T. trochonemoides* and its contemporary *Trochonema* species is in the more strongly developed middle carina, and the less strongly developed internal channel. Ulrich placed *T. trochonemoides* in *Lophospira* instead of *Trochonema* because of the strength of the middle carina and because of his association of the taxa with *T. knoxvillensis* with its clearly lophospirid selenizone. However, given the apparent relationship between *Trochonemella* and *Trochonema*, and the apparent sister-group relationship of *T. trochonemoides* to all *Trochonema*, it becomes clear that Ulrich placed *T. trochonemoides* in *Lophospira* due to its retention of primitive lophospirid traits. Therefore it is recommended that *T. trochonemoides* be reclassified as *Trochonema*.

This species differs from all other *Trochonemella* and *Trochonema* in the constant point of whorl embrasure throughout its ontogeny. However, this observation is based upon a single specimen, and examination of multiple specimens of other *Trochonemella* and *Trochonema* species indicates that while rare, some individuals do exhibit constant embrasure. Therefore, it is possible that this lone *T. trochonemoides* specimen was an exception to the norm for its species in this regard.

Materials: Single specimen, the holotype, stored as U.S.N.M. 46069 in the U.S. National Museum from the Murfreesboro Central Limestone, Tennessee.

Occurrence: Ordovician (Earliest Caradocian)

APPENDIX B: LOPHOSPIRID TRAITS AND CHARACTER STATES

Growth Lines[1]

1. Growth Line Strength
    - 0: Fine
    - 1: Coarse
2. "Foliaceous", "Lamellose" or "Varix-Like" Growth Lines (Cyclic Variation in Strength)
    - 0: Absent
    - 1: Present
3. General Growth Line Attitude I
    - 0: Strong Sweep beginning at Sutural/Upper and Lower Carina -> Selenizone
    - 1: Straight over Carina with Weak Sweep -> Selenizone, Running Straight Adapertually Beneath
4. General Growth Line Attitude II
    - 0: "0" or "1" for Trait #5
    - 1: Straight over Carina with Very Weak Sweep just before Selenizone, Same Under
5. Lunulae Shape
    - 0: Sharp Crescentic
    - 1: Straightened Crescent

O[2] 6. Lunulae Imbrications
    - 0: Absent
    - 1: Present on Juvenile Whorls Only
    - 2: Present Throughout

Selenizone

7. Selenizone Width
    - 0: Narrow
    - 1: Wide (>1mm)
8. Selenizone Loss
    - 0: Narrow
    - 1: Loss
9. Selenizone Prominence
    - 0: Slight Protrusion
    - 1: Strong Protrusion

U 10. Selenizone Mid-Carina A
    - 0: Equal with Bordering Lirae
    - 1: Sharper than Border Lirae
    - 2: Very Thick Thread

11. Selenizone Mid-Carina B
    - 0: Equal with Bordering Lirae
    - 1: Broad, Dull Lirae

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[1] Gerontic whorls disregarded.

[2] O: Ordered Series; U: Unordered Series.

12. Selenizone Mid-Carina Weakening
    0: Strong Thread
    1: Weaker than Bordering Lirae
13. Selenizone Mid-Carina Loss
    0: Presence
    1: Loss
14. Loss of Bordering Lirae
    0: Present
    1: Absent
15. Serrated Mid-Carina
    0: Absent
    1: Present
16. Internal Channel Underneath Peripheral Carina
    0: Weak
    1: Strong

General Whorl Traits

U 17. Upper Ramp Shape (Discounting Upper Carina)
    0: Distinctly Concave
    1: Slightly Concave
    2: Flat
    3: Convex
18. Upper Ramp Length
    0: Half of Whorl Height
    1: Lengthened (>60% whorl height)
U 19. Lower Ramp Shape (Down to Start of Base)
    0: Flat
    1: Somewhat Convex
    2: Extremely Convex
20. Lower Ramp Length
    0: Half of Whorl Height
    1: Greater than 50% whorl height
21. Lower Ramp Length
    0: Half of Whorl Height
    1: Reduced (< 30% Whorl Height)

Upper Whorl Carina

22. Sharp Upper Whorl Carina I
    0: Sutural Carina Only ("Lump")
    1: Sharp Thread
23. Sharp Upper Whorl Carina II
    0: "0" or "1" in 23
    1: Thick Sharp Thread
24. Fine Upper Whorl Carina
    0: "0" in 23 & 24
    1: Weak Thread
25. Ontogenetically Weakening Upper Whorl Carina
    0: Absent
    1: Present

26. Relative Position of Upper Whorl Carina
    - 0: Carina under Suture
    - 1: Carina Half-Way between Suture and Selenizone
27. Attitude of Upper Whorl Carina
    - 0: Perpendicular to Ramp
    - 1: Abapical Attitude
28. Serrated Upper Whorl Carina
    - 0: Absent
    - 1: Present
29. "Second" Sutural Carina (Replacement of Upper Carina) I
    - 0: Absent
    - 1: Weak Lump
    - 2: Strong Lump

<u>Lower Whorl Carina</u>

30. Lower Whorl Carina I
    - 0: "Lump" (Slight extension of Bend between Lower Ramp and Base)
    - 1: Sharp Thread
31. Lower Whorl Carina Ia
    - 0: "Lump" or Sharp Thread
    - 1: Stronger Sharp Thread
32. Derived Lower Whorl Carina Ib
    - 0: "Lump"
    - 1: Very Weak Thread
33. Derived Lower Whorl Carina II
    - 0: "Lump" or Sharp Thread
    - 1: Thick Dull Lower Whorl Carina
34. Serrated Lower Whorl Carina
    - 0: Absent
    - 1: Present
35. Second Lower Whorl Carina
    - 0: Absent
    - 1: Present
36. Third Lower Whorl Carina
    - 0: Absent
    - 1: Present
37. Umbilical Carina
    - 0: Absent
    - 1: Present

<u>Additional Ornamentation</u>

38. Lower Whorl Spiral Lirae
    - 0: Absent
    - 1: Present
39. Lower Whorl Spiral Lirae Thickness
    - 0: Thin (or Absent)
    - 1: Easily Visible

40. Fine, Non-Subsuming Spiral Lirae on Upper Whorl
    0: Absent
    1: Present
41. Thick Spiral Lirae on Upper Whorl IA
    0: Absent
    1: Sparse (Between Carinae)
42. Thick Spiral Lirae on Upper Whorl IA
    0: "0" or "1" in 41
    1: Dense (Including Carinae)
43. Thick Spiral Lirae on Upper Whorl IA
    0: "0" or "1" in 41 & 42
    1: Increased Number of Threads

O 44. Return of Upper Carina
    0: Subsumed into Spiral Lirae
    1: Thread-like on Juvenile Whorls only
    2: Thread-like on Adult Whorls

Whorl Suture Point

45. Juvenile Whorl Suture Point
    0: At Bend between Lower Ramp and Base (usually = Site of Lower Carina)
    1: Below Bend

O 46. Juvenile Whorl Suture
    0: At Bend between Lower Ramp and Base (usually = Site of Lower Carina)
    1: Between Bend and Selenizone
    2: On Selenizone

U 47. Ontogenetic Change in Suture Point
    0: Constant Throughout Shell
    1: Lower Suture Point on Older Whorls
    2: Disjuncture of Older Whorls

U 48. Onset of Disjuncture
    0: Disjuncture Absent or Inconsistent
    1: Final Whorl Only
    2: Penultimate Whorl

Base

49. Base Width
    0: Nearly Straight
    1: Widened, with Fairly Sharp Base/Ramp Intersection & Lower Ramp Closer to Perpendicular with Selenizone

U 50. Further Widening of Base
    0: "0" or "1" in 49
    1: Lower Ramp Vertical with Selenizone
    2: Lower Ramp Projecting from Selenizone

Umbilicus

51. Umbilicus Size
    0: Very Small
    1: Small

52. Umbilicus Loss
    - 0: Present
    - 1: Absent
53. Pseudo-Umbilicus
    - 0: "0" or "1" in Trait #51
    - 1: Present

Aperture[3]

54. Warping of Aperture I
    - 0: Long Axis ~45‘ Adapical to Coiling Axis
    - 1: Clockwise Warpage (Selenizones Perpendicular Right Line of Apical Angle)
55. Warping of Aperture IIA
    - 0: "0" or "1" in Trait #54
    - 1: Long Axis Parallel to Coiling Axis
56. Warping of Aperture IIB
    - 0: Long Axis Parallel or Adapical to Coiling Axis
    - 1: Long Axis ~30‘ Abapical to Coiling Axis
57. Warping of Aperture IIC
    - 0: "0" or "1" in Traits #55 & #56, "0" in Trait #54
    - 1: Long Axis ~45‘ Abapical to Coiling Axis
58. Angle between Upper Ramp and Selenizone
    - 0: Sharp (~45‘)
    - 1: Very Wide (nearly 90‘)
59. Angle between Upper Ramp and Selenizone
    - 0: Sharp (~45‘)
    - 1: Wide (~70‘)
60. Shape of Lower & Inner Lip IA
    - 0: Upside-Down "7"-shape
    - 1: "L"-shape (filling out of Columellar Lip)

U 61. Shape of Lower & Inner Lips IB
    - 0: "0" or "1" in 60, "0" in 62 - 63
    - 1: Rounded "V"-shape pointing -> Umbilicus (rounding of Parietal Lip)
    - 2: Half-Circle

62. Shape of Lower & Inner Lips IIA
    - 0: "0" or "1" in 60 - 61
    - 1: "U"-shape (filling out of Columellar Lip w/ rounding of Parietal Lip)
63. Shape of Lower & Inner Lips IIB
    - 0: "0" or "1" in 60 - 62
    - 1: Extended "U"-shape

U 64. Tangential Aperture
    - 0: Absent
    - 1: Effectively Tangential from Open-Coiling
    - 2: Wholly Tangential
    - 3: "Overbite" Tangential

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[3] Non-Gerontic Whorls only.

65. Apertural Slit
    - 0: Absent
    - 1: Present

67. Parietal Lip Thickness
    - 0: Same as Rest of Shell
    - 1: Thicker

67. Columellar Lip Thickness
    - 0: Somewhat Thicker than Rest of Shell
    - 1: Much Thicker

68. Filling of Umbilicus by Columellar Lip
    - 0: None
    - 1: Partially or Totally Filled

69. Columellar Lip Length
    - 0: Extended
    - 1: Reduced Extension and Thickness

70. Columellar Lip "Loss"
    - 0: Extended with Greater Thickness
    - 1: Same Thickness as Rest of Shell

U 71. Columellar Lip Reflection
    - 0: Reflected without Obscuring Umbilicus
    - 1: Partial Covering of Umbilicus
    - 2: Total Covering of Umbilicus

<u>General Shell Traits</u>

72. Shell Thickness
    - 0: Thin
    - 1: Thick

U 73. Whorl Expansion Rate
    - 0: $H/(H-1) > 1.4$
    - 1: $H/(H-1) < 1.4$
    - 2: $1.6 < H/(H-1) < 1.8$

74. Number of Whorls
    - 0: 6-8
    - 1: 3-5

75. Number of Whorls
    - 0: 6-8
    - 1: ≥ 9

APPENDIX C: DATA MATRIX

Species[4]	000000000111111111122222222223333333333444444444455555555556666666666777777 123456789012345678901234567890123456789012345678901234567890123456789012345
L. perangulata	000000000000000000000000000000000000000000000000000000000000000000000000000
L. manchuriensis	101000000000000000000000000001000000000000000000000009900001000000000000200
L. kangyaoensis	000000000000000000000000000000000000000000000010000009900009000000000000010
_L. milleri_*	101000000000000010000100000001000000000000000000100000100001000000000000210
T. knoxvillensis	101000000100000010000100000001000000100000000000100010001100011002000000001210
L. pagodai	000000000000000010000000000000000000000000000000000001000000000000000010101
_P. derwiduii_*	000000000001000010000000000000000000000000000000000001000000000000000090101
T. trochonemoides	101000001000010120000100010011000000100000000000101000110001200200001001210
L. centralis	101110000000000010000100000001000000000000000000100000100001000000000000210
T. montrealensis	101000100000100020000100010001100000100000000000211010001110012002009010009210
P. dorothea	000000000001000011000000100000001000000000000000000001000000000000000010101
L. helicteres	101110101000000010000110000011100000100000000000221000001000011001000000000200
T. penguini	101101101000100030000110011001100000100000000000211010001111012002000010001210
L. serrulata	100000000100001000000000000000100000100000000000210010001000000101000000000200
_T. notablis_*	111102101000100030000110011001100000100000000000211010001111012002000010001210
D. augustina	000000100000000021000000000000001000000000000000000001000000000000000010101
L. medialis	000000000000000010000000100000000000000000000000000000100000010000000000200
D. decursa	000000000000000010001000000000000000000000000000000000000000000000000000000
L. spironema	000000000000000010000000100000000000010100000000000000100000010000000000200
D. conoidea	000000101100000010001000000000000000000000000000000000000000000000000000100
L. oweni	100000000010000010000000100000000000000000000000000000100000010000100000200
D. producta	000000000000000000000000000000000000000000000000000000000000000000000000001
_S. textilis_*	101000000000000030000110010009001000010100000100100000100019090100900000210
L. sumnerensis	000000000100000000000000100000001000000000000010000000100000011000110000210
R. humilis	101000000000000010000100010001001000010000000000100000100011000000909000210
L. banksi	000000100010000010000001000020000000000000000022000000100000000000000000000
_D. filosa_*	100000000001100020000000000000001000000000000000000090100000900000000010101
_R. lirata_*	001000100000000030000100010001001000010000000100100000100011000000000020210
S. moorei	100000100091000000000000000000001000000000000010000010001000090990109900090200
D. bowdeni	000000100001000011000000100000001000000000000000000001000000000000000010101
L. tropidophora	000000100010000010000000000000001000000000000010000000100000011000110000210
L. quadrisulcata	101110001000000010000110000011000010100000000000100110100001003000000000210
A. thraivensis	101000101000000020000100010001001000011000000100100000100011000300000021210
T. churkini	111102001000100020000110011101100000100000000011101000110101200201001109210
_R._ aff. _R. lirata_	101000101100000020100100010001001000011010000100110000100011000000000020210
_L._ aff. _L. serrulata_*	101102001900900020000110001101100100100000000011110000100901200300001000210
T. reusingi	111102101000100020000110011101100000100000000011111000110101200201001109210
A. inexpectans	101000101001000020100100010001001000011011100200110110100011000000000021210
L. ehlersi	000000100010000010000000000000001000000000000011000001001000000190001100000210
_A. cancellatula_*	101000101000000020100100010001001000011011010210110110100011000000000021210
A. woodlandi	101000901000000020100100010001001000011011020110110110100011000000000021210
_L. tubulosa_*	111000001200100020210110010001100011000000009000120000100001990000001000200
A. aulongensis	101000100100100002010010010001009000099011100200110990100011900000099990210
R. robusta	001000100000000030100110010001001000010000000100110000100011000000000010210
L. laquetta	101010000200100010110100010001000011000000001000110000100001990000000010200
R. lævissima	001000900000000030200100010001001000010010000200100000100011000000000010210
T. bellulum	101000010000010120000110010011000000100000000002110100011000120020000100101210
_T. umbilicatum_*	101100010000010120000110010011000000100000000002110100011100120020000110101210
_E. strilligatum_*	101190019000010010000101000011000000100000000002110000100001100100000000200
H. gracilis	000000000000100020100000000000001000000000000000000001000000000000000001001101
_H. salteri_*	000000000000100030200000000000001000000000000000000000100000000000000000100110
	000000000111111111122222222223333333333444444444455555555556666666666777777 123456789012345678901234567890123456789012345678901234567890123456789012345

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[4] All genus and species names used reflect the nomenclature accepted previous to this study except for the retention of *Pagodospira* and *Schizolopha* for the reasons stated in the text.

APPENDIX D: DESCRIBED LOPHOSPIRID SPECIES

SPECIES	STATUS[5]
Ambilophospira conoidea (Ulrich in Ulrich & Scofield)	Good
Ambilophospira decursa (Ulrich in Ulrich & Scofield)	Good
Ambilophospira kangyaoensis (Endo)	Good
Ambilophospira perangulata (Hall)	Good
Ambilophospira producta (Ulrich in Ulrich & Scofield)	Good
Ambilophospira serrulata (Salter)	Good
Lophospiraa abbreviata (Hall)	Insufficiently Known
Lophospira abnormis Ulirch in Ulrich & Scofield	Poor Specimens
Lophospira acuminata Ulrich & Scofield	see *A. perangulata*
Lophospira acuta Grabau	see *A. perangulata*
Lophospira ampla Ulrich in Ulrich & Scofield	see *P. tropidophora*
Lophospira angulata Butts	Good
Lophospira angulocincta (Murchison)	Insufficiently known
Lophospira aojii Endo	see *A. perangulata*
Lophospira aspera (Billings)	?see *L. milleri*[6]
Lophospira bantatsuensis Kobayashi	Good
Lophospira basicarinata Cullison	?see *L. milleri*
Lophospira beatrice Foerste	see *D. bowdeni*
Lophospira belli Foerste	see *L. milleri*
Lophospira bellicarinata Donald	see *L. milleri*
Lophospira billingsi Raymond	*Trochonemella* species

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[5] Good: species in good standing; see .. : junior synonym; Insufficiently Known: either inadequate descriptions and figures to judge; Poor Specimens: description based upon internal casts or specimens too poorly preserved to evaluate.

[6] If so, *L. aspera* assumes taxonomic priority.

Lophospira bispiralis **(Hall)**	Good
Lophospira borealis **Donald**	see *A. perangulata*
Lophospira bucheri **Foerste**	*Arjamannia* species
Lophospira centralis **Ulrich in Ulrich & Scofield**	Good
Lophospira cicelia **(Billings)**	?see *A. perangulata*
Lophospira compacta **Yü**	Insufficiently Known
Lophospira concinnulla **Ulrich & Scofield**	Juvenile *L. helicteres*
Lophospira conica **Butts**	?see *A. kangyaoensis*
Lophospira conradana **Ulrich & Scofield**	Good
Lophospira conradi **(Hall)**	*Donaldiella* species?
Lophospira corrugata **Cullison**	?see *L. milleri*
Lophospira delicata **Tofel & Bretsky**	see *L. centralis*
Lophospira dutchtownensis **Cullison**	Good
Lophospira elevata **Ulrich & Scofield**	see *P. medialis*
Lophospira elongata **Butts**	see *A. perangulata*
Lophospira excavata **Donald**	see *A. perangulata*
Lophospira ferruginea **Donald**	*Donaldiella* species?
Lophospira fillmorensis **Ulrich & Scofield**	see *L. helicteres*
Lophospira gerardi **Grabau**	see *A. perangulata*
Lophospira grabaui **Endo**	see *L. manchuriensis*
Lophospira grandis **Butts**	?see *A. perangulata*
Lophospira gothlandica **Ulrich & Scofield**	Good
Lophospira guelphica **Whiteaves**	Poor Specimens
Lophospira gumbinenses **Saladzhius**	Insufficiently Known
Lophospira gyrogonia **(M'COY)**	Good

Lophospira helicteres **(Salter)**	Good
Lophospira hermoine **(Billings)**	Poor Specimens
Lophospira hespelerensis **(Whiteaves)**	Poor Specimens
Lophospira humilis **Ulrich in Ulrich & Scofield**	*Hellermannia* species
Lophospira hyacinthensis **Foerste**	Poor Specimens
Lophospira instabilis **Donald**	see *A. perangulata*
Lophospira kindlei **Foerste**	Good
Lophospira kodairai **Kobayashi**	Insufficiently Known
Lophospira konnoi **Kobayashi**	see *L. bantatsuensis*
Lophospira laticarinata **Foerste**	Good
Lophospira manchuriensis **Endo**	Good
Lophospira manitoulinensis **Foerste**	see *P. oweni*
Lophospira milleri **(Hall)**	Good
Lophospira modesta **(Billings)**	Insufficiently Known
Lophospira morrisi **Grabau**	see *L. milleri*
Lophospira mylitta **(Billings)**	Insufficiently Known
Lophospira nigrum **(Perner)**	Poor Specimens
Lophospira obliqua **Ulrich in Ulrich & Scofield**	see *L. milleri*
Lophospira obliquestriata **Longstaff**	see *P. medialis*
Lophospira obscura **Grabau**	Poor Specimens
Lophospira peracuta **Ulrich & Scofield**	?see *A. perangulata*
Lophospira perforata **Ulrich & Scofield**	Poor Specimens
Lophospira perlamellosa **Ulrich in Ulrich & Scofield**	see *P. tropidophora*
Lophospira procera **Ulrich in Ulrich & Scofield**	see *L. milleri*
Lophospira pteronoides **Longstaff**	*Arjammania* species

Lophospira pulchella **Ulrich & Scofield**	see *A. perangulata*
Lophospira pulchelliformis **Grabau**	see *A. perangulata*
Lophospira pulchra **(M'COY)**	Good
Lophospira quadrisulcata **Ulrich & Scofield**	Good
Lophospira rectistriatus **Raymond**	??see *L. manchriensis*[7]
Lophospira saffordi **Ulrich in Ulrich & Scofield**	see *P. oweni*
Lophospira scotica **(Donald - Longstaff)**	see *L. milleri*
Lophospira sedgwickii **Donald**	see *A. perangulata*
Lophospira seelyi **Raymond**	see *L. milleri*
Lophospira sexlineata **Raasch in Shrock**	Good
Lophospira shallockensis **Longstaff**	Poor Specimens
Lophospira sinensis **Yü**	?see *A. perangulata*
Lophospira songkanensis **Pan**	Insufficiently Known
Lophospira sororcula **(Billings)**	Insufficiently Known
Lophospira subcylindrica **Yü**	Insufficiently Known
Lophspiraa subglobosa **(Donald)**	see *L. abbreviata*
Lophospira subpulchella **Kobayashi**	see *A. perangulata*
Lophospira superba **Butts**	Poor Specimens
Lophospira tenuistriata **Ulrich in Ulrich & Scofield**	?Var. of *P. oweni*
Lophospira terrassa **Grabau**	see *A. perangulata*
Lophospira tesakovi **Kurushin**	Insufficiently Known
Lophospira tienshanensis **Yü**	?see *L. angulata*
Lophospira tongxinensis **Guo**	Insufficiently Known

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[7] If true, *L. rectistriatus* assumes taxonomic priority.

***Lophospira tongziensis* Pan**	Insufficiently Known
***Lophospira tricariniata* (Hall)**	see *L. helicteres* or *A. serrulata*
***Lophospira trispiralis* Donald**	?Non-Lophospirid
***Lophospira trochiformis* Grabau**	Good
***Lophospira trochoformis* Butts**	see *A. kangyaoensis*
***Lophospira turritiformis* Endo**	see *A. perangulata*
***Lophospira uniangulata* (Hall)**	see *A. perangulata*
***Lophospira variabilis* Donald**	see *A. perangulata*
***Lophospira ventricosa* (Hall)**	Good
***Lophospira vostokova* Kurushin**	Insufficiently Known
***Lophospira xanthippe* (Billings)**	Insufficiently Known
***Lophospira xiazhenensis* Yü**	?Ruedemannid species
***Lophospira yentaiensis* Endo**	see *A. perangulata*
***Donaldiella augustina* (Billings)**	Good
***Donaldiella bowdeni* (Safford)**	Good
***Donaldiella derwiduii* (Grabau)**	Good
***Donaldiella dorothea* (Grabau)**	Good
***Donaldiella filosa* (Donald)**	Good
***Donaldiella pagodai* (Endo)**	Good
***Donaldiella perneri* Longstaff**	*Hormotoma*?
***Donaldiella sakamotoi* (Kobayashi)**	Non-lophospirid?
***Donaldiella tetracarina* (Kobayashi)**	Good
***Loxoplocus solutus* (Whiteaves)**	Good
***Paralophospira ehlersi* (Foerste)**	Good
***Paralophospira medialis* (Ulrich & Scofield)**	Good

Paralophospira moorei **(Ulrich in Ulrich & Scofield)**	Good
Paralophospira oweni **(Ulrich & Scofield)**	Good
Paralophospira spironema **(Ulrich & Scofield)**	Good
Paralophospira sumnerensis **(Safford)**	Good
Paralophospira tropidophora **(Meek)**	Good
Eunema arctatum **Ulrich in Ulrich & Scofield**	Good
Eunema cerithioides **(Salter)**	Non-Lophospirid
Eunema erigone **Billings**	Insufficiently Known
Eunema fatuum **(Hall)**	Good
Eunema nitidium **Ulrich & Scofield**	*Trochonema* species
Eunema obsoletum **Ulrich in Ulrich & Scofield**	Insufficiently Known
Eunema robbinsi **Ulrich & Scofield**	Insufficiently Known
Eunema salteri **Ulrich & Scofield**	*Trochonema* species
Eunema simile **Ulrich & Scofield**	Insufficiently Known
Eunema strilligatum **(Salter)**	Good
Eunema ventricosa **Yü**	Insufficiently Known
Metarochospira knoxvillensis **(Ulrich in Ulrich & Scofield)**	Good
Trochonemella arachne **(Billings)**	Insufficiently Known
Trochonemella churkini **Rohr & Blodgett**	Good
Trochonemella mikulici **Rohr**	?Non-Lophospirid
Trochonemella montrealensis **Okultich**	Good
Trochonemella notablis **(Ulrich in Ulrich & Scofield)**	Good
Trochonemella reusingi **Rohr**	Good
Trochonemella sinensis **Yü**	Good

Trochonemella trochonemoides **(Ulrich in Ulrich & Scofield)**	*Trochonema* species
Trochonema abruptum **(Billings)**	Insufficiently Known
Trochonema altum **Ulrich & Scofield**	Poor Specimens
Trochonema beachi **Whitfield**	see *T. umbilicatum*
Trochonema bellulum **Ulrich & Scofield**	Good
Trochonema beloitense **Whitfield**	Good
Trochonema eccentricum **Ulrich in Ulrich & Scofield**	Good
Trochonema fragile **Ulrich & Scofield**	Good
Trochonema madisonense **Ulrich in**	?see *T. umbilicatum*
Trochonema niota **(Hall)**	Poor Specimens
Trochonema ovoides **Grabau & Sherzer**	Poor Specimens
Trochonema ozawai **Kobayashi**	Insufficiently Known
Trochonema retrorsum **Ulrich & Scofield**	?see *T. umbilicatum*
Trochenema rugosum **Ulrich & Scofield**	?see *T. umbilicatum*
Trochonema subcrassum **Ulrich & Scofield**	Good
Trochonema tricarinatum **Billings**	Poor Specimens
Trochonema umbilicatum **(Hall)**	Good
Trochonema vagrans **Ulrich & Scofield**	?see *T. beloitense*
Trochonema wilsonae **Steele & Sinclair**	?see *T. umbilicatum*
Longstaffia centervillensis **(Foerste)**	Good
Longstaffia cyclonema **(Salter)**	?*Ruedemannia* species
Longstaffia laqueata **(Lindström)**	Good
Longstaffia tubulosa **(Lindström)**	Good
Schizolopha textilis **Ulrich in Ulrich & Scofield**	Good
Ruedemannia lævissima **(Lindström)**	Good

Ruedemannia lirata **(Ulrich in Ulrich & Scofield)**	Good
Ruedemannia robusta **(Lindström)**	Good
Arjamannia aulangonensis **Peel**	Good
Arjamannia cancellatula **(M'COY)**	Good
Arjamannia inexpectans **(Hall & Whitfield)**	Good
Arjamannia songkanensis **Pan**	Insufficiently Known
Arjamannia thraivensis **(Longstaff)**	Good
Arjamannia woodlandi **(Longstaff)**	Good

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