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New Material of *Trematochampsa oblita* (Crocodyliformes, Trematochampsidae) from the Late Cretaceous of Madagascar, with a Review and Cladistic Analysis of the Family Trematochampsidae

presented by

Erin Lynn Rasmusson

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NEW MATERIAL OF *TREMATOCHAMPSA OBLITA* (CROCODYLIFORMES, TREMATOCHAMPSIDAE) FROM THE LATE CRETACEOUS OF MADAGASCAR, WITH A REVIEW AND CLADISTIC ANALYSIS OF THE FAMILY TREMATOCHAMPSIDAE

By

Erin Lynn Rasmusson

A THESIS

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ABSTRACT

NEW MATERIAL OF *TREMATOCHAMPSA OBLITA* (CROCODYLIFORMES, TREMATOCHAMPSIDAE) FROM THE LATE CRETACEOUS OF MADAGASCAR, WITH A REVIEW AND CLADISTIC ANALYSIS OF THE FAMILY TREMATOCHAMPSIDAE

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Recent study of new material of the trematochampsid crocodyliform *Trematochampsa oblita*, from the Late Cretaceous of Madagascar, has provided additional data for a cladistic analysis of the Family Trematochampsidae, an enigmatic group of metasuchian crocodyliforms known from the Cretaceous of Gondwana and the Tertiary of Europe. Among the questions addressed were: (1) Is the Family Trematochampsidae monophyletic? (2) How do trematochampsids relate to other crocodilian groups that have been hypothesized to be closely related, notably peirosaurids? (3) Is the genus *Trematochampsa* monophyletic with respect to other trematochampsids? and (4) What are the implications for biogeography?

For the cladistic analysis, PAUP*4.0 was employed, using a variety of search algorithms on a data matrix that included thirty unordered characters and thirteen total taxa, including two outgroups (*Araripesuchus patagonicus* and *Notosuchus terrestris*), two peirosaurids (*Peirosaurus tormini* and *Lomasuchus palpebrosus*), and the nine named trematochampsid species. Strict and Adams consensus trees were obtained with the data, one set including and another excluding the two peirosaurids. A monophyletic Trematochampsidae was recovered in both options, and the peirosaurids, when included, fall within Trematochampsidae. The genus *Trematochampsa* itself, however, was found to be paraphyletic, with *Trematochampsa oblita* closer to the European taxa on the consensus tree that does not include the peirosaurids. The two European Tertiary taxa, *Bergisuchus dietrichbergi* and *Iberosuchus macrodon*, were found to be sister taxa and to occupy a relatively crownward position in the clade.

The results of the analysis support the use of a vicariance biogeography model to explain the distribution of Gondwanan trematochampsids. However, a dispersal model best explains the presence of the Tertiary forms in Europe.

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Mike Gottfried, for all his assistance and guidance throughout this project, as well as my committee members: Dr. Al Holman and Dr. Danita Brandt, for their many insights. Thank you to Dr. Greg Buckley, my honorary committee member, for letting me work on his specimens.

There are many people associated with the Mahajanga Basin Project that I'd like to acknowledge. First, Dr. David Krause (Stony Brook University) for his support and generosity; also, the many participants of the Mahajanga Basin expeditions for their efforts in the field; the people of Berivotra; our colleagues at the Université d'Antananarivo; and the Institute for the Conservation of Tropical Environments in Antananarivo.

I would not have been able to finish this project without the help of many people. Especially, John and Anita Campeau for their dedicated French translations; Sunny Wang at the MSU Museum and his staff for their computer expertise; the generous petrologists and hydrogeologists for allowing a paleontologist to invade their computer labs; and Dr. Tom Vogel for the last minute use of his digital camera.

Finally, I am most grateful for the support of my fellow graduate students, who have become my very good friends, as well as that of my family and Mark.

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KEY TO ABBREVIATIONS

a, an	angular
ar	articular
d, de, den	dentary
ec	ectopterygoid
exo	exoccipital
f, fr	frontal
fme	mandibular fenestra
fti	infratemporal fenestra
fts	supratemporal fenestra
j, ju	jugal
l, la	lacrimal
m, mx	maxilla
n, na	nasal
ne	external nares
or	orbit
ot	otic notch
p, pa	parietal
pal	palpebral
pfr, prf	prefrontal
pm	premaxilla
po, por	postorbital
q, qu	quadrate
qj	quadradojugal
sa	surangular
so	supraorbital
soa	anterior supraorbital
soc, socc	supraoccipital
sop	posterior supraorbital
sq	squamosal
sur	surangular

INTRODUCTION

The Family Trematochampsidae comprises extinct, relatively poorly known metasuchian crocodyliforms. Most fossil material of the species in this family consists of fragmentary cranial remains. Nine species are currently assigned to the trematochampsids, but the monophyly of the family has been questioned. New material has been discovered of one of the most enigmatic trematochampsid species, *Trematochampsa oblita,* from the Late Cretaceous of Madagascar. Description of these remains adds to the knowledge of this species, and leads into a cladistic analysis of the phylogenetic interrelationships of the Family Trematochampsidae. The new information on *T. oblita* and the relationships within trematochampsids allows for a discussion of the biogeography of this family, whose members are found in Cretaceous and Tertiary deposits of South America, Africa, Madagascar, and Europe. The purpose of this thesis is to expand our knowledge of *T. oblita,* to address the related questions of monophyly within and interrelationships among trematochampsids, and to examine trematochampsid biogeography.

The trematochampsids are classified as metasuchian crocodyliforms. Crocodyliforms are part of a larger group within archosaurians, the Crocodylomorpha (Table 1), which includes all crocodilians and their immediate Triassic and Jurassic relatives (Benton and Clark 1988). Within crocodyliforms, three groups are traditionally recognized: the Protosuchia, "Mesosuchia," and Eusuchia. The Protosuchia is basal to the other two and includes small forms from the Early Jurassic (Clark 1986). The mesosuchians apparently arose from the protosuchians and were common during the Jurassic and Cretaceous (Clark 1986). Because of the paraphyletic status of the

- **Infraclass Archosauromorpha**
  - **Superorder Crocodylomorpha**
    - **Order Crocodyliformes**
      - **Division Protosuchia**
      - **Division Mesoeucrocodylia**
        - **Subdivision Thalattosuchia**
        - **Subdivision Metasuchia**
          - **Family Notosuchidae**
            - ***Notosuchus***
            - ***Uruguaysuchus***
            - ***Araripesuchus***
            - ***Libycosuchus***
          - **Family Sebecosuchidae**
            - ***Sebecus***
            - ***Baurusuchus***
          - **Family Peirosauridae**
            - ***Peirosaurus tormini***
            - ***Lomasuchus palpebrosus***
          - **Family Trematochampsidae**
            - ***Amargasuchus minor***
            - ***Itasuchus camposi***
            - ***Hamadasuchus rebouli***
            - ***Trematochampsa taqueti***
            - ***Trematochampsa oblita***
            - ***Itasuchus jesuinoi***
            - ***Eremosuchus elkoholicus***
            - ***Iberosuchus macrodon***
            - ***Bergisuchus dietrichbergi***

Table 1. Classification of the Trematochampsidae and other discussed taxa within the Archosauromorpha. Based in part on Benton and Clark (1988). Classification adapted from Benton (1998).

mesosuchians, the group is joined with the eusuchians, the modern crocodilian clade, to form the Mesoeucrocodilia (Whetstone and Whybrow 1983).

The Mesoeucrocodilia is divided into two groups: thalattosuchians and metasuchians (Benton and Clark 1988). The Thalattosuchia are longirostrine marine forms whose precise phylogenetic position is questionable. The metasuchians include the families: Notosuchidae (e.g. *Notosuchus*, *Uruguaysuchus*, *Araripesuchus*, and *Libycosuchus*), Sebecosuchidae (e.g. *Sebecus* and *Baurusuchus*) (Benton and Clark 1988), Peirosauridae (Gasparini 1982) and Trematochampsidae (Buffetaut 1974).

Trematochampsids are freshwater/terrestrial metasuchians found in the Cretaceous of South America, Africa, and Madagascar, and the Eocene of Europe and Algeria. The paleogeographic distribution of the group suggests that it is Gondwanan in origin. Buckley and Brochu (1999) have hypothesized that trematochampsids are most closely related to *Araripesuchus* and the Peirosauridae. It has been suggested that the latter group is a junior synonym of the Trematochampsidae (Buffetaut 1988, 1989) (Table 1); however, Gasparini et al. (1991) argued that there are not sufficient data to support this grouping.

The genus *Araripesuchus* includes four species: *A. gomesii* Price 1959, from the middle Albian of northeastern Brazil; *A. wegeneri* Buffetaut 1981, from the Aptian of Niger; *A. patagonicus* Ortega et al. 2000, from the Albian of Argentina; and an unnamed species from the Campanian/Maastrichtian of Madagascar (Buckley and Brochu 1996). These are small crocodilians with short snouts, large orbits, large antorbital fenestrae, and robust dentaries (Hecht 1991) (Figure 1).

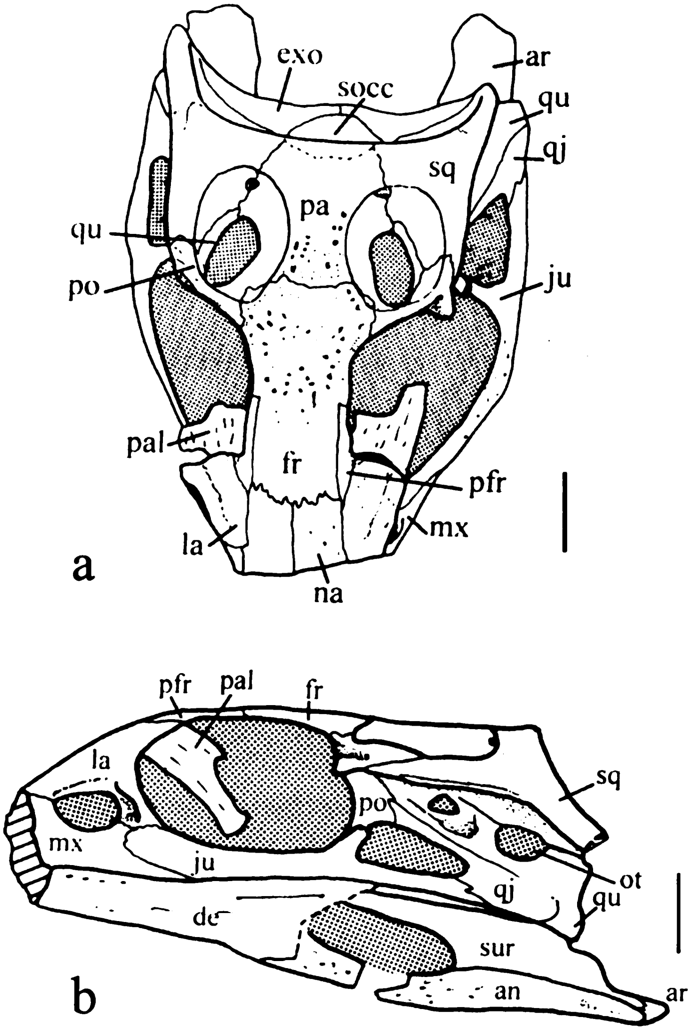

Figure 1. Skull of *Araripesuchus patagonicus* in a) dorsal and b) left lateral view. Scale bar equals 1 cm. From Ortega et al. 2000.

The Peirosauridae includes two species: *Peirosaurus tormini* Price 1955, from the Campanian of Brazil; and *Lomasuchus palpebrosus* Gasparini et al. 1991, from the Campanian of Argentina. Both species possess a somewhat elongate, narrow snout (with a small antorbital fenestra preserved in *Lomasuchus*), and teeth that are compressed and serrated (Gasparini et al. 1991) (Figure 2).

Crocodyliforms placed in the Family Trematochampsidae share the following combination of distinguishing characteristics: In the dentary (Figure 3a), an enlarged fourth tooth is followed by four to five small teeth, and then a group of larger posterior teeth. The posterior teeth are bulbous in shape and ornamented with fine irregular ridges. Alveoli are close-set and nearly circular, except in ziphodont (teeth laterally compressed and serrated) forms (Buffetaut 1989). There is a depression lateral to the posterior dentary teeth to accommodate a large maxillary tooth (Buffetaut 1994). The ventral edge of the maxilla (Figure 3b) has an undulating appearance. An antorbital fenestra is present (Chiappe 1988). The snout is deep, with forward-facing external nares (Buffetaut 1991).

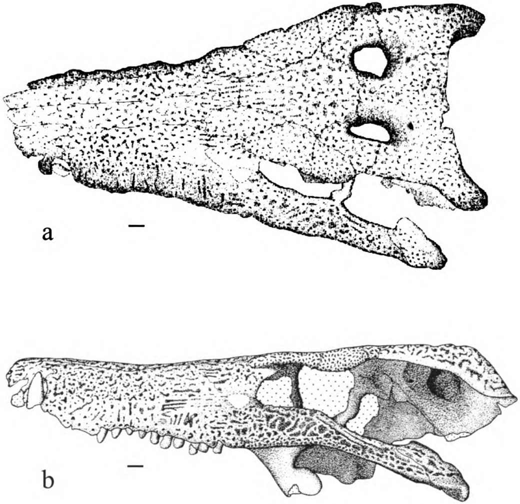

Figure 2. Skull of *Lomasuchus palpebrosus* in a) dorsal and b) left lateral view. Scale bar equals 1 cm. From Gasparini et al. (1991).

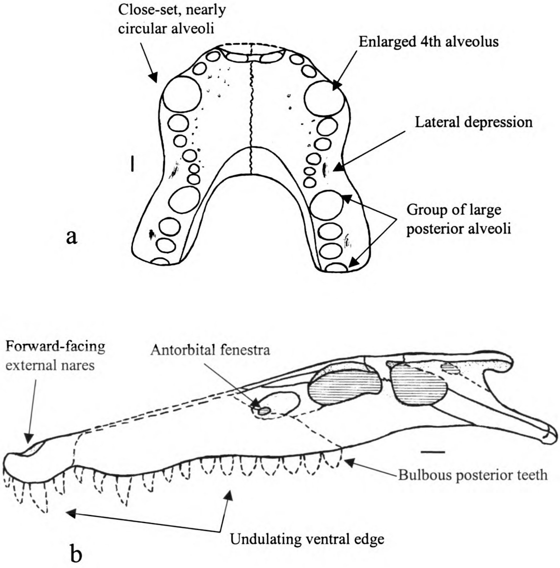

Figure 3. Select distinguishing characteristics of the Family Trematochampsidae. a) Anterior portion of lower jaw of *Trematochampsa oblita* in dorsal view. From Buffetaut and Taquet (1979). b) Skull of *Trematochampsa taqueti* in left lateral view. From Buffetaut (1976). Scale bars equal 1 cm.

FAMILY TREMATOCHAMPSIDAE

Nine species are currently assigned to the Trematochampsidae, summarized below from oldest to youngest. The geographic distribution of these species is shown in Figure 4.

Amargasuchus minor CHIAPPE, 1988

The oldest species in the family is *Amargasuchus minor* from the Early Cretaceous (Hauterivian) of northwest Patagonia, Argentina. The species is described on the basis of an incomplete right maxilla that suggests that *A. minor* had a more slender, elongate snout than other trematochampsids (Chiappe 1988) (Figure 5). Viewed laterally, the maxilla is moderately high with an undulating ventral edge. An antorbital fenestra appears to have been present. In ventral view (Figure 6) the maxillary wall and alveolar row is almost straight and all teeth are laterally compressed. Thirteen alveoli are preserved, with the fifth and sixth, as preserved (which may correspond to the sixth and seventh maxillary alveoli), being slightly larger and the rest nearly equal in size (Chiappe 1988). The skull of *A. minor* is estimated to be 9-10 centimeters in length (Chiappe 1988).

Itasuchus camposi (KELLNER), 1987

Itasuchus camposi is known from the Albian of Brazil, and was originally described as *Caririsuchus camposi* by Kellner (1987). The holotype of *Caririsuchus camposi* studied by Kellner is a nearly complete skeleton (Figure 7). Unaware of Kellner's work, Buffetaut (1991) studied the holotype specimen (unfortunately, now in

Figure 4. Distribution of trematochampsid species, shown on a map depicting Late Cretaceous paleogeography:
★ *Amargasuchus minor,* ▼ *Itasuchus camposi,* ● *Hamadasuchus rebouli,* □ *Trematochampsa taqueti,* ■ *Trematochampsa oblita,* ▲ *Itasuchus jesuinoi,* ⬢ *Eremosuchus elkoholicus,* ◆ *Iberosuchus macrodon,* ○ *Bergisuchus dietrichbergi.*

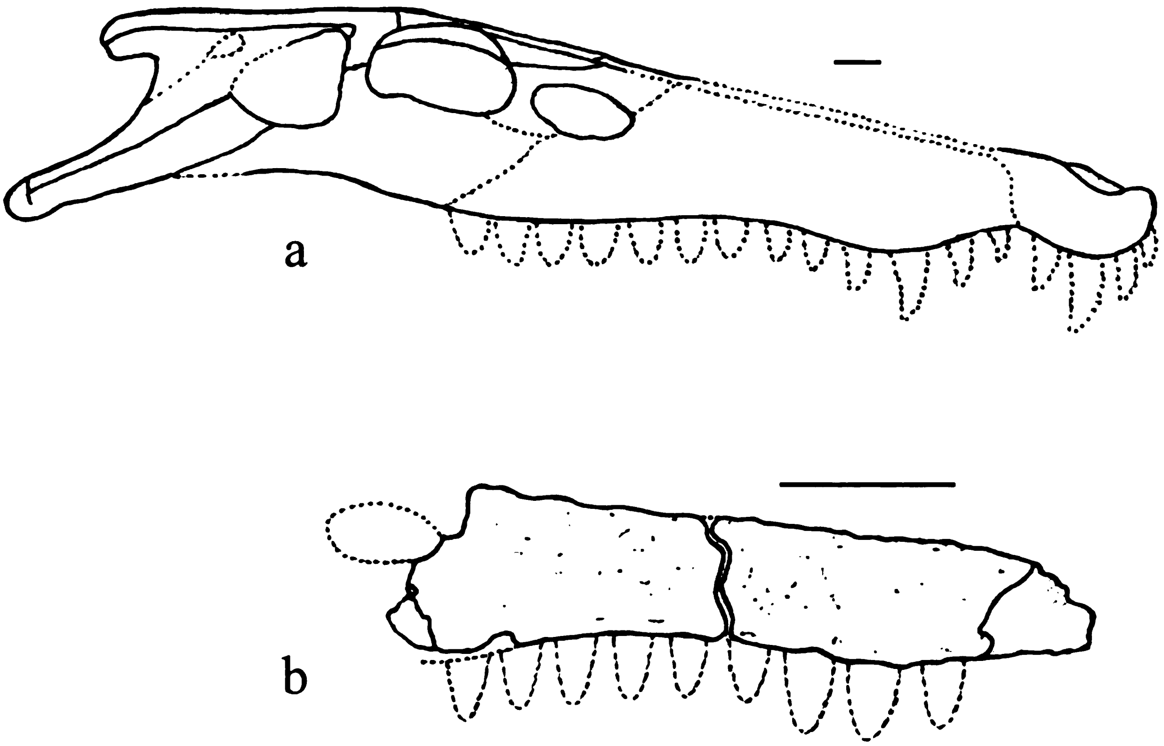

Figure 5. a) Skull of *Trematochampsa taqueti* for comparison with b) Fragmentary right maxilla of *Amargasuchus minor* in right lateral view. Scale bar equals 1 cm. From Chiappe (1988).

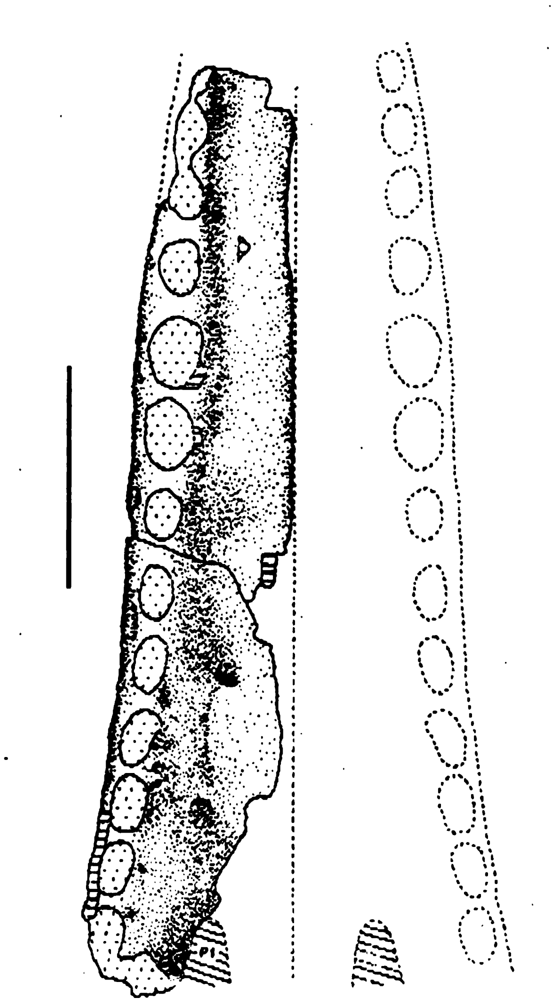

Figure 6. Right maxilla of *Amargasuchus minor* in ventral view. Scale bar equals 1 cm. From Chiappe (1988)

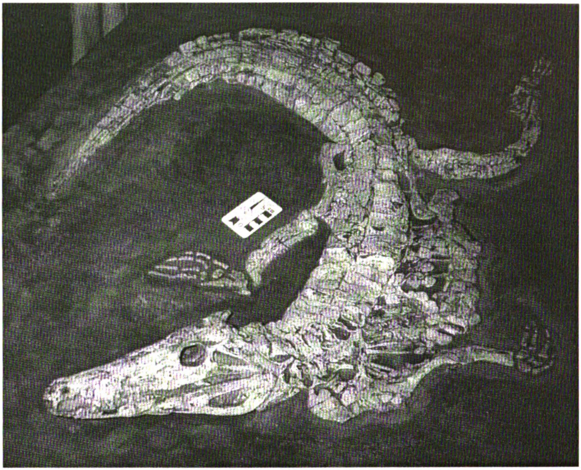

Figure 7. Nearly complete skeleton of *Itasuchus camposi*. Scale bar is 5 cm. From Buffetaut (1991).

private hands) and found that it closely resembles *Itasuchus jesuinoi* Price, 1955. Both species possess a deep snout, and a maxilla with an undulating ventral edge and forward-facing external nares (Figure 8). The shape of the skull, jaws and teeth, as well as the shared presence of preorbital swellings formed by the nasals and prefrontals, indicate that the two specimens are likely congeneric (Buffetaut 1991), with minor differences in the number and sizes of the teeth providing the basis to separate them at the species level. Kellner (1987) estimated there to be 21 teeth present in the upper jaw of his *C. camposi,* and a similar number in the lower jaw. The largest teeth are the second and third premaxillary teeth, the second maxillary tooth, and the third dentary tooth. Teeth in the posterior part of the jaws are shorter, more uniform in size, and laterally compressed. All teeth are finely serrated.

Taking the above into account, *Caririsuchus* is considered to be a junior synonym of *Itasuchus*, and the specimen is therefore named *Itasuchus camposi* (Buffetaut 1991).

Hamadasuchus rebouli BUFFETAUT, 1994

Hamadasuchus rebouli is found in the Late Albian to Early Cenomanian red beds of southern Morocco. This species is described from an incomplete left dentary (Figure 9). The dentary has an undulating dorsal edge and is interpreted to have fifteen teeth, all close-set and ziphodont in form (Buffetaut 1994). Four small alveoli are positioned between the enlarged fourth and ninth alveoli, a trait common to trematochampsids. In medial view, the mandibular symphysis extends to the posterior rim of the seventh alveolus. The splenial is interpreted to have extended to the symphysis (Buffetaut 1994).

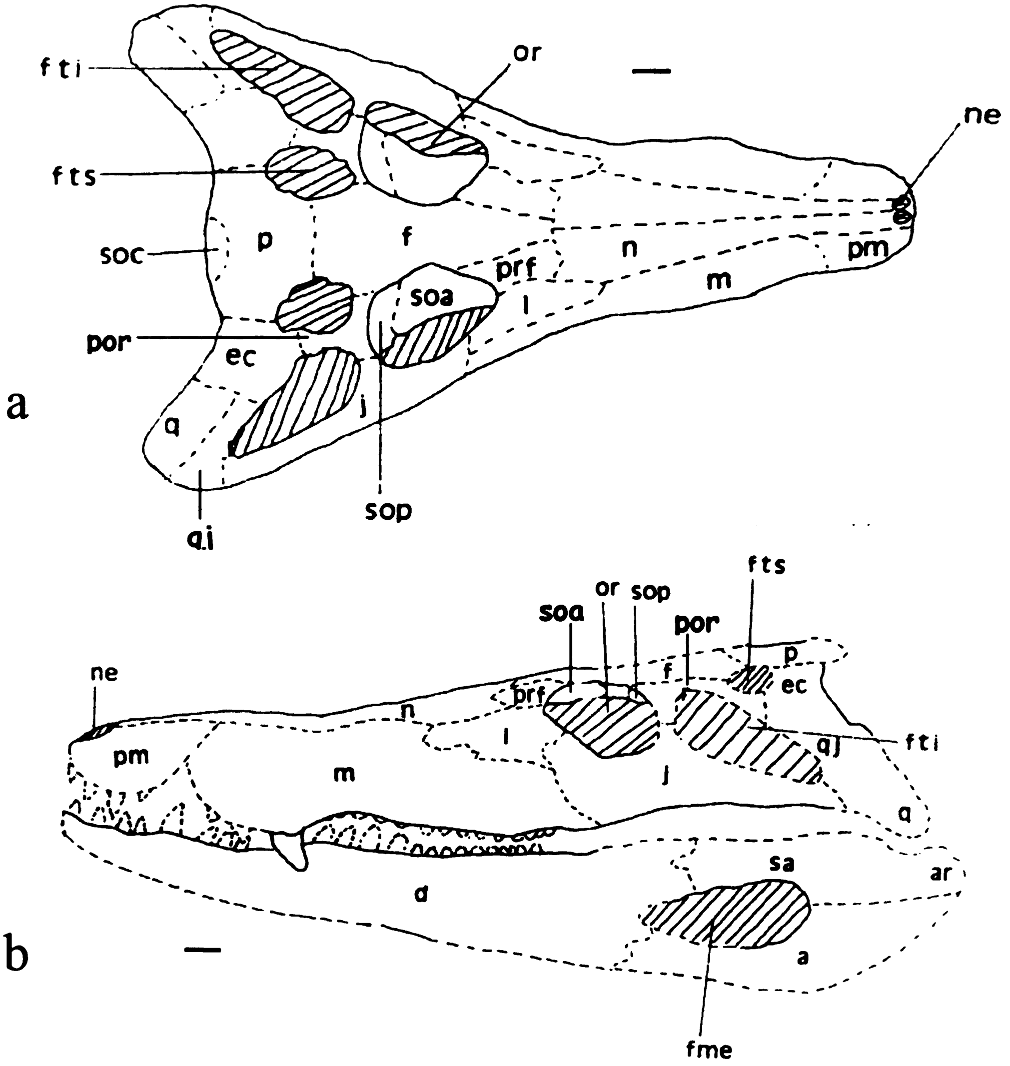

Figure 8. Reconstruction of the skull of *Itasuchus camposi* in a) dorsal view and b) left lateral view. Scale bar equals 1 cm. From Kellner (1987).

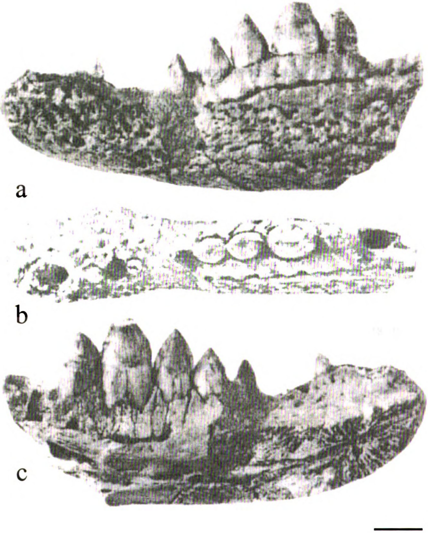

Figure 9. Left dentary of *Hamadasuchus rebouli* in a) lateral, b) dorsal, and c) medial view. Scale bar equals 1 cm. From Buffetaut (1994).

Trematochampsa taqueti BUFFETAUT, 1974

Trematochampsa taqueti is a relatively well-known species from the Early Senonian of Niger. This small to medium-sized trematochampsid (approximately 1-3 meters in length) had a moderately elongate skull with robust jaws (Buffetaut 1974). The dentary (Figure 10) shows a large fourth tooth and displays a depression lateral to the smaller seventh and eighth alveoli to accommodate the large third maxillary tooth (Buffetaut 1976). Thirteen total teeth are found in the maxilla, which has an undulating ventral edge (Figure 11). All teeth are uncompressed, but the orientation of the wrinkles in the enamel gives the teeth a serrated appearance. The morphology of the maxilla indicates the presence of an antorbital fenestra, and the postorbital pillar of the jugal is moved slightly toward the interior (Buffetaut 1976).

Trematochampsa oblita BUFFETAUT AND TAQUET, 1979

Trematochampsa oblita is the focal species of this study. It is found in the Campanian/Maastrichtian of Madagascar and will be described and discussed in detail in the next section.

Itasuchus jesuinoi PRICE, 1955

Itasuchus jesuinoi is known from the Maastrichtian of Brazil. This species is very similar to *I. camposi* in skull, jaw, and tooth shape. Both species display preorbital swellings formed by the nasals and prefrontals (Figure 12). There is a difference, however, in the number and sizes of the teeth (Buffetaut 1991). The dentary of *I. jesuinoi*

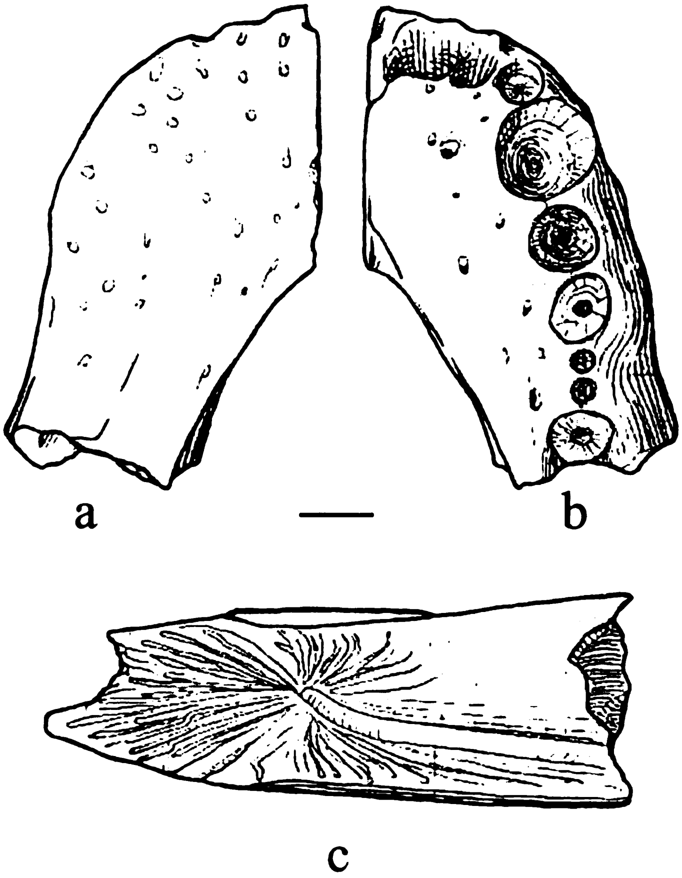

Figure 10. Fragmentary right dentary of *Trematochampsa taqueti* in a) ventral, b) dorsal, and c) medial views. Scale bar equals 1 cm. From Buffetaut (1976).

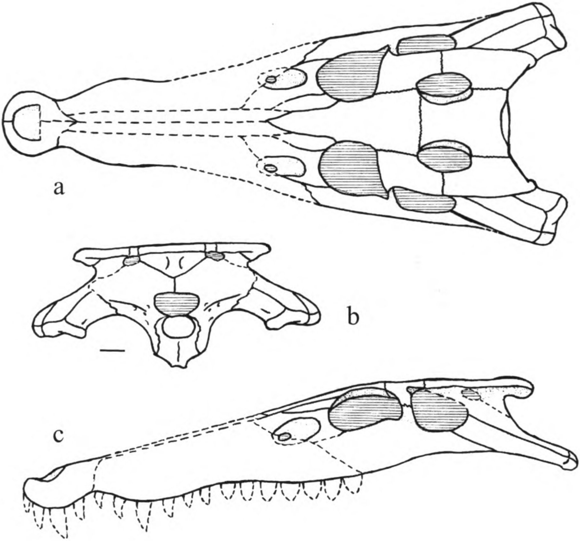

Figure 11. Skull of *Trematochampsa taqueti* in a) dorsal, b) occipital, and c) left lateral view. Scale bar equals 1 cm. From Buffetaut (1976).

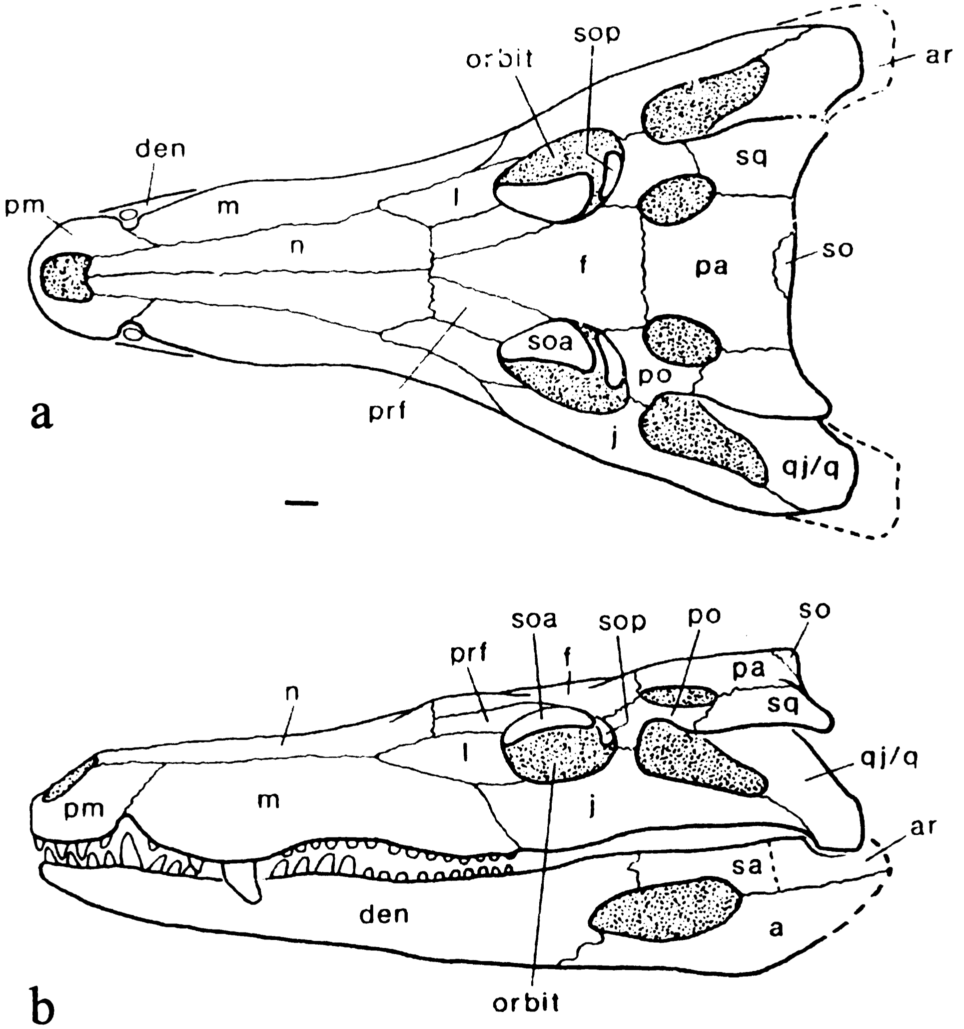

Figure 12. Reconstruction of the skull of *Itasuchus jesuinoi* in a) dorsal and b) left lateral view. Some features shown in this reconstruction may be inaccurate. Scale bar equals 1 cm. From Buffetaut (1985).

holds 17 teeth, the largest being the third and eleventh, while alveoli five through nine are much smaller. The anterior maxillary teeth are conical and pointed, the posterior teeth have a rounded tip, dense ornamentation, and slight lateral compression. In comparison, the dentary of *I. camposi* holds an estimated 21 teeth (Kellner 1987). As with *Trematochampsa taqueti*, the postorbital pillar of the jugal of *I. jesuinoi* is moved slightly toward the interior, and an antorbital fenestra is present (Buffetaut 1985).

Eremosuchus elkoholicus BUFFETAUT, 1989

Three trematochampsid species have been described from the Eocene, extending the family's stratigraphic range past the K/T boundary. *Eremosuchus elkoholicus,* from Algeria (Buffetaut 1989), is known from a very deep, narrow right dentary (Figure 13). Twelve ziphodont teeth are present in the dentary; the alveoli are close-set, and nearly circular (Figure 14). The first and fourth teeth are the largest. Although this species is placed within Trematochampsidae, the characteristic small teeth between an enlarged fourth and ninth/tenth are not seen. The dentary of *E. elkoholicus* does possess a lateral depression. Also known from *E. elkoholicus* are amphicoelous vertebral centra considered to be thoracic in origin, and small caudal centra that possess longitudinal ridges along their ventral surfaces (Buffetaut 1989).

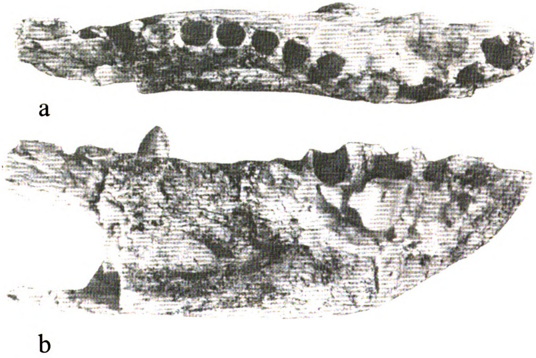

Figure 13. Right dentary of *Eremosuchus elkoholicus* in a) dorsal and b) right lateral view. From Buffetaut (1985b).

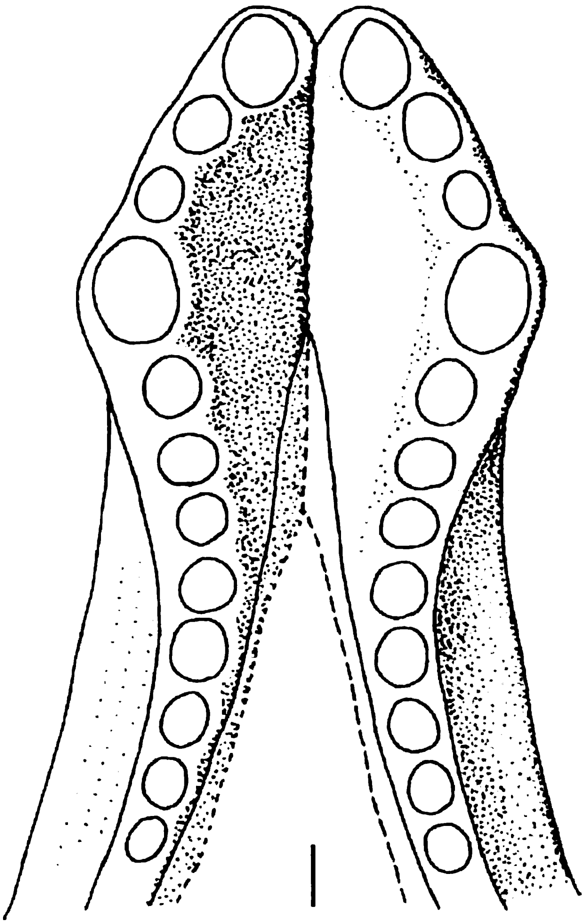

Figure 14. Reconstruction of the lower jaw of *Eremosuchus elkoholicus*, dorsal view. Scale bar equals 1 cm. From Buffetaut (1989).

Iberosuchus macrodon ANTUNES, 1975

Iberosuchus macrodon, from the Eocene of Portugal and Spain, is described from upper jaw fragments (Figure 15), which show close-set, nearly circular alveoli and relatively long, strongly developed ziphodont teeth (Antunes 1975). The second and third premaxillary and second maxillary teeth are the largest and are nearly conical in cross-section; the smaller teeth are laterally compressed. A notch is present at the suture of the premaxilla and maxilla to accommodate a large dentary tooth. The nasal openings face forward and an antorbital fenestra is present (Antunes 1975).

Bergisuchus dietrichbergi KUHN, 1968

Bergisuchus dietrichbergi, from the Eocene of Messel, Germany, was originally described by Berg (1966) as "aff. *Sebecus*? n.sp." The specimen consists only of fragments of the upper jaw and dentary, so Berg chose not to give it a formal name, but wanted to note its similarities to the South American Tertiary genus *Sebecus* (Buffetaut 1988). Kuhn (1968) later named the specimen *Bergisuchus dietrichbergi*. The fragmentary maxilla has a large third tooth; the other alveoli are smaller. All maxillary teeth are slightly compressed laterally and seem to have fine serrations (Buffetaut 1988). The antorbital fenestra is present. The dentary is slender and narrow with a lateral depression for the large third maxillary tooth. The dentary most likely held thirteen teeth, the largest being the laterally compressed, slightly recurved fourth; smaller, less compressed teeth are posterior. The splenial is preserved and likely reached the mandibular symphysis (Buffetaut 1988).

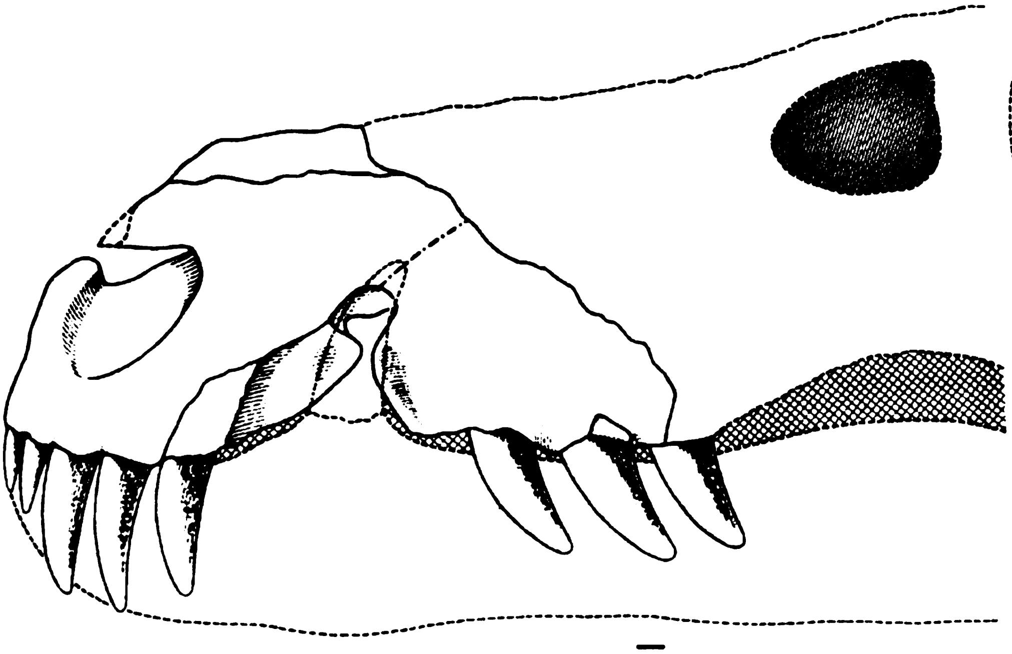

Figure 15. Reconstruction of *Iberosuchus macrodon* from upper jaw fragments. Scale bar equals 1 cm. From Antunes (1975).

PREVIOUS MATERIAL OF *TREMATOCHAMPSA OBLITA*

The holotype of *Trematochampsa oblita* is housed at the Muséum National d'Histoire Naturelle in Paris. It was collected from Upper Cretaceous strata in the region of "Maevarana," south of Mahajanga, near the beginning of the 20th century (Buffetaut and Taquet 1979). The precise type locality is unknown. The holotype consists of three mandibular fragments; a reconstruction (from Buffetaut and Taquet 1979) of the anterior portion of the lower jaw based on these fragments is shown in Figure 16a. Anterior and posterior ends of both dentary bones are missing. The fourth and tenth alveoli are the largest. Alveoli 5-9 are small and associated with lateral depressions to accommodate large maxillary teeth. The splenial is preserved and takes part in the posterior portion of the mandibular symphysis. The teeth are poorly preserved but are nearly circular in cross-section with ornamented enamel (Buffetaut and Taquet 1979). The lower jaw is wider and deeper than that of *T. taqueti* (Figure 16b).

NEW MATERIAL OF *TREMATOCHAMPSA OBLITA*

Recent expeditions to the Mahajanga Basin of northwest Madagascar (Figure 17) conducted by the State University of New York at Stony Brook and the University of Antananarivo (Madagascar) have greatly increased the known diversity of the island's tetrapod fauna. The two universities started the Mahajanga Basin Project in 1993 and have recovered a rich assemblage of well-preserved vertebrates, including frogs, turtles, snakes, sauropods, theropods, mammals, fishes, and a number of crocodyliforms, primarily from the Maevarano Formation, a terrestrial/freshwater Upper Cretaceous (Campanian-Maastrichtian) unit (Krause et al. 1997, Krause et al. 1999, Rogers et al.

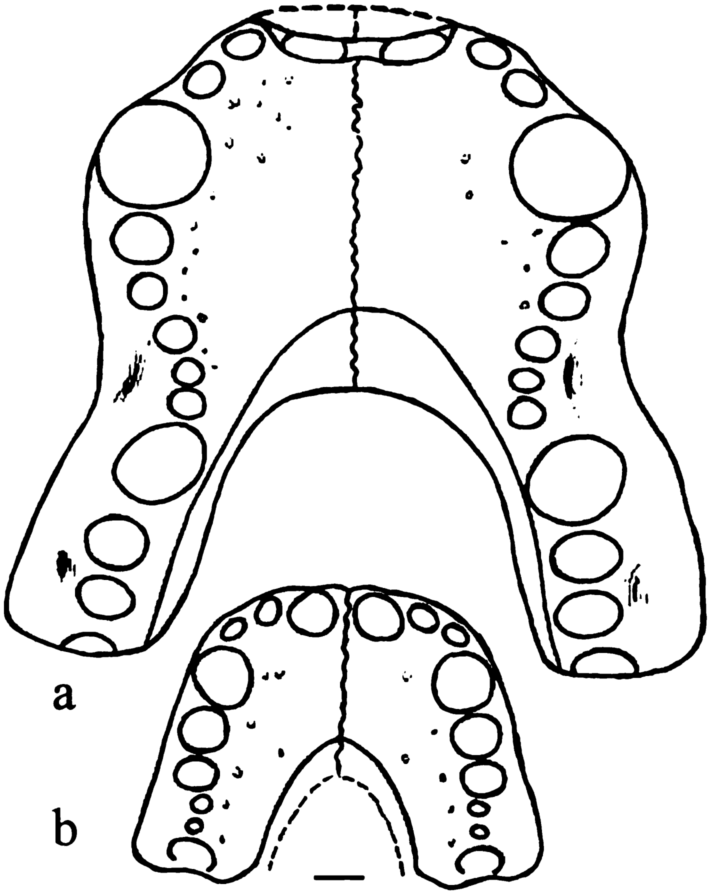

Figure 16. Reconstruction of the anterior portion of the lower jaws of a) *Trematochampsa oblita* and b) *Trematochampsa taqueti*. From Buffetaut and Taquet (1979).

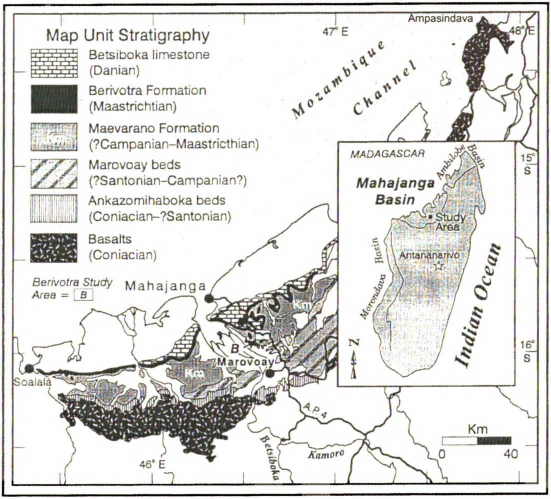

Figure 17. Map of the Mahajanga Basin in northwest Madagascar, showing study area and geologic setting. From Rogers et al. (2000).

2000). The seven crocodyliform species found suggest crocodyliforms were the most diverse tetrapods in the fauna (Buckley and Brochu 1999). Some of the crocodyliform remains belong to the poorly known trematochampsid species, *Trematochampsa oblita*.

The new material of *Trematochampsa oblita* described here was collected in the late 1990s from the Maevarano Formation, near the village of Mangapaika, in the Mahajanga Basin (Figure 17). The Mahajanga Basin contains two Maastrichtian-age formations: the terrestrial Maevarano Formation, which may also be in part Campanian, and the overlying and partially interfingering marine Berivotra Formation (Rogers et al. 2000). *Trematochampsa oblita* was found in the uppermost part of the Anembalemba Member of the Maevarano Formation. The locality from which the material was collected, around the Miadana Hills, is approximately 4-5 kilometers southeast of the main collecting areas (near the village of Berivotra). The Miadana Member of the Maevarano Formation is only known in the region of Miadana Hills, where it overlies the Anembalemba Member and is overlain by the marine Berivotra Formation. Matrix, similar to a coarse sandstone found near the top of the Anembalemba Member, formed a hardened crust around the fossils. This coarse, poorly sorted sandstone was interpreted by Rogers et al. (2000) to have been deposited in a channel-belt system (a broad, shallow braided stream). To date, *T. oblita* has not been found in the main field area, nor has the most common large crocodyliform from the main field area, *Mahajangasuchus insignis*, been found in the Miadana region (Rasmusson and Buckley 2001).

The *Trematochampsa oblita* material was borrowed from the Field Museum of Natural History in Chicago, Illinois and brought to Michigan State University for detailed study. The five fragments were measured, described, photographed, and drawn through the use of a Leica M28 binocular zoom microscope with camera lucida attachment.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Hay, 1930
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
Family TREMATOCHAMPSIDAE Buffetaut, 1974
Genus *TREMATOCHAMPSA* Buffetaut, 1974
Trematochampsa oblita Buffetaut and Taquet, 1979

LOCALITY AND HORIZON. The material of *Trematochampsa oblita* described here was collected from the Maastrichtian-age Miadana Member of the Maevarano Formation, near the village of Mangapaika, in the Mahajanga Basin, Madagascar.

MATERIAL. The new *T. oblita* specimen (catalogued at the Field Museum of Natural History as MAD 98301) consists of a partial right dentary, fragmentary left dentary, frontal, one vertebra, and six other fragmentary pieces tentatively assigned to *T. oblita*.

Dentary. The right dentary (Figures 18, 19, and 20) has twelve preserved alveoli; the posterior part of the bone, behind the twelfth alveoli, is missing. The dentary is quite deep, reaching 66 mm at both the fourth and tenth alveoli. The depth varies little posterior to the position of the fourth alveolus. The maximum width of the dentary is 68 mm at the level between the fourth and fifth alveoli. Posterior to the seventh alveoli the dentary becomes much narrower (33 mm). In medial view (Figure 18), the dentary displays a large mandibular symphysis, oriented at a 40-degree angle relative to the horizontal. The posterior edge of the symphysis is missing, but if complete the sutural surface would extend to the sixth or seventh alveolus. The splenial is absent but likely contributed to the posterior edge of the symphysis.

The lateral surface of the dentary (Figure 19) is ornamented with prominent pits and grooves. The anterolateral portion of the bone is convex from alveoli 3 to 5, and concave from 6 to 9, which forms an embayment for a large maxillary tooth. In dorsal view (Figure 20), the alveolar row displays an S-shaped curvature. The largest alveoli are the fourth and tenth; much smaller alveoli are positioned in between, as is characteristic of trematochampsids. Nine of the twelve alveoli have preserved teeth, although they are broken at the level of the alveolar rim. The spaces between the alveoli are small (1-4 mm). Alveoli 1 and 10 appear slightly laterally compressed, the rest are nearly circular. The anteroposterior diameters of the alveoli are as follows:

Alveolus position:	1	2	3	4	5	6	7	8	9	10	11	12
Diameter (in mm):	17	12	10	23	9	8.5	7	7	7	26	10	10

A fragment of the left dentary (Figure 21) includes alveoli 3, 4, and 5, with teeth preserved in 3 and 4. The preserved teeth are 12 and 17 mm above the alveolar rim, respectively, and are conical in shape. A series of longitudinal lines are present on the enamel surfaces of both teeth.

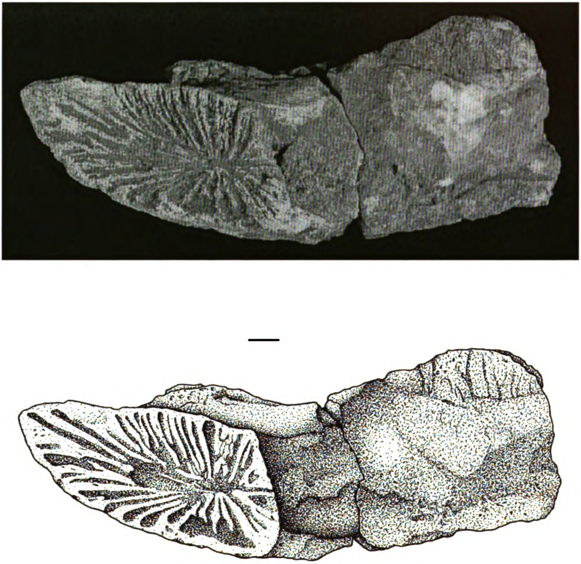

Figure 18. Right dentary of *Trematochampsa oblita* in medial view showing large mandibular symphysis. Scale bar equals 1 cm.

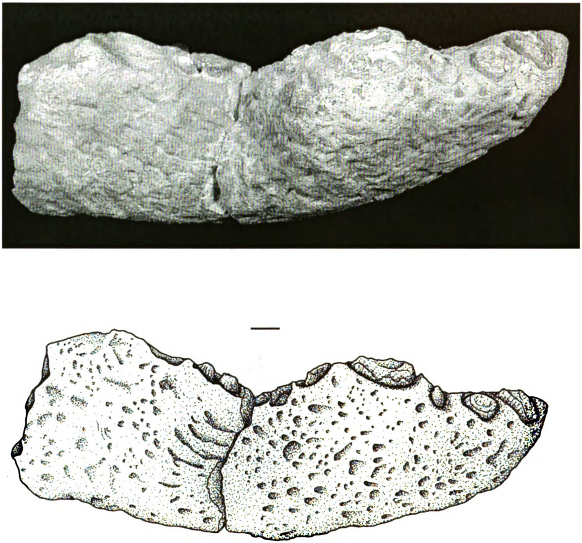

Figure 19. Right dentary of *Trematochampsa oblita* in lateral view showing degree of ornamentation and smooth lateral depression. Scale bar equals 1 cm.

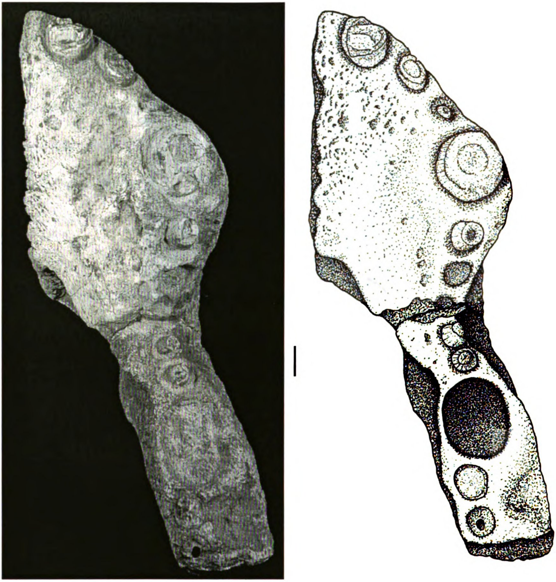

Figure 20. Right dentary of *Trematochampsa oblita* in dorsal view showing large 4th and 10th alveoli and lateral depression. Scale bar equals 1 cm.

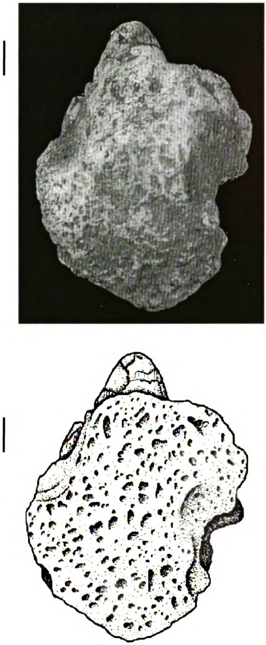

Figure 21. Fragment of left dentary of *Trematochampsa oblita* in lateral view showing the small third and large fourth tooth. Scale bar equals 1 cm.

Frontal. The frontal is roughly triangular in shape; the anterior end and left edge are broken. The ventral side (Figure 22) shows a broad, open groove (8 mm wide) positioned midway between the two orbits. The bone within the groove and forming the rim of the orbits is smooth. In contrast, the dorsal side is heavily sculpted (Figure 23). A convex ridge runs along the midline of the bone, mirroring the groove on the ventral side. The bone as preserved measures 64 mm anteroposteriorly and an estimated 47 mm at its widest point.

Vertebra. The vertebra (Figure 24) has an amphicoelous centrum, and a neural arch. The centrum is 35 mm in length and, although the ventral half is missing, the circular shape of the anterior and posterior ends can be seen. The body of the centrum is laterally constricted. The neural arch is high (extending 30 mm above the centrum), but the neural spine is not preserved. The left transverse processes are more complete than those on the right side. The left postzygapophysis extends 10 mm beyond the posterior edge of the centrum. The anterior end of the prezygapophysis is missing. It is not certain to what part of the column this vertebra belongs.

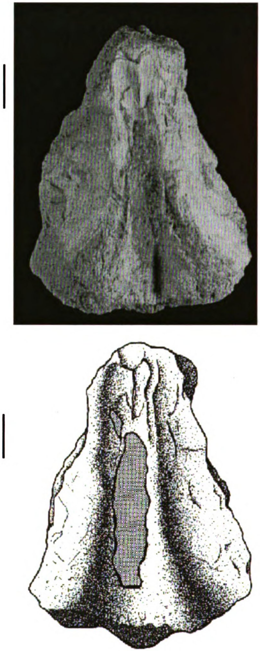

Figure 22. Frontal of *Trematochampsa oblita* in ventral view showing broad groove between orbits. Stippled patches indicate matrix. Scale bar equals 1 cm.

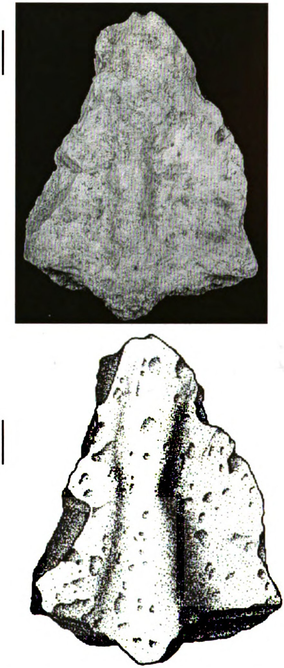

Figure 23. Frontal of *Trematochampsa oblita* in dorsal view showing ornamentation. Scale bar equals 1 cm.

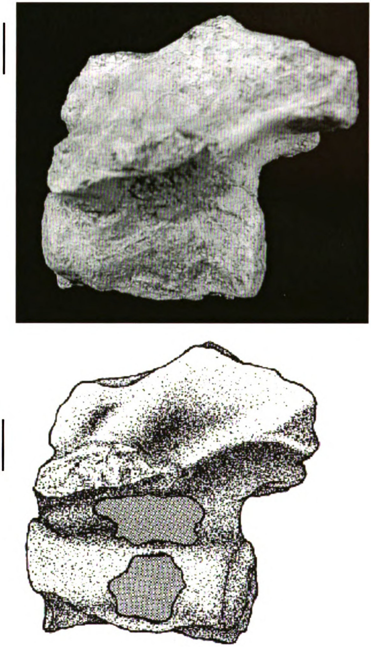

Figure 24. Vertebra of *Trematochampsa oblita* in lateral view. Stippled patches indicate matrix. Scale bar equals 1 cm.

PHYLOGENETIC ANALYSIS

To assess the phylogenetic relationships of the Family Trematochampsidae, a data matrix of thirty unordered and unweighted characters was scored for trematochampsids, peirosaurids, and two outgroup taxa, and subjected to a maximum parsimony analysis using PAUP* version 4.0 (Swofford 2000) (Table 2). Information on all species, with the exception of *T. oblita*, was obtained from the literature. Due to the fragmentary nature of many of the trematochampsid species, only cranial characters were used, focusing on the lower and upper jaw and dentition. The majority of characters were adapted and modified from Clark (1986 and 1994), Buscalioni and Sanz (1988), Buckley and Brochu (1999), and Ortega et al. (2000); select others were added to reflect information derived specifically from the trematochampsid species. A list of characters used can be found in the appendix.

To assess the relationships within a group (the ingroup), a number of closely related outgroup taxa must also be considered (Maddison 1984). The outgroup taxa chosen for this analysis are *Notosuchus terrestris* and *Araripesuchus patagonicus,* which, on the basis of recent studies (Buckley and Brochu 1999), have been interpreted as related to but distinct from trematochampsids. The outgroup taxa provide a means of assessing the polarity of characters found in the ingroup (the Family Trematochampsidae). Because of the questionable phylogenetic position of the peirosaurids (*Peirosaurus tormini* and *Lomasuchus palpebrosus*), an analysis including these species was also performed.

Three search algorithms were used from the PAUP* 4.0 program: heuristic, branch-and-bound, and exhaustive. The algorithms for both a heuristic and branch-and-bound search select a representative example of possible most parsimonious trees, while

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Amargasuchus minor	?	?	?	?	?	?	?	?	1	?	1	?	1	?	0	?	2	?	?	?	?	?	0	?	?	?	?	?	?	?
Itasuchus camposi	1	1	1	0	0	1	1	1	1	0	1	1	2	1	1	1	1	0	1	0	1	?	0	0	0	1	1	1	1	1
Hamadasuchus rebouli	0	1	0	1	1	1	?	?	?	?	?	1	?	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trematochampsa taqueti	1	1	0	0	0	1	?	?	1	1	1	1	2	1	1	0	1	1	1	0	1	1	0	0	0	0	1	0	1	1
Trematochampsa oblita	1	1	1	1	1	1	?	?	?	?	?	1	?	1	1	1	?	?	?	?	?	?	?	1	?	?	?	?	?	?
Itasuchus jesuinoi	1	1	1	0	0	1	1	1	1	0	1	1	2	1	1	1	1	0	1	0	1	?	0	?	?	1	1	1	1	1
Eremosuchus elkoholicus	1	0	1	0	0	1	?	?	?	?	?	0	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Iberosuchus macrodon	?	?	0	?	?	1	0	?	0	1	?	0	?	0	0	0	?	0	0	1	1	1	0	?	?	0	?	?	?	1
Bergisuchus dietrichbergi	0	0	0	?	1	1	?	?	0	?	0	0	2	0	0	0	1	0	?	?	?	?	0	1	?	?	?	0	?	0
Lomasuchus palpebrosus	1	1	1	0	1	1	0	?	1	1	1	1	2	0	0	1	1	?	1	0	?	1	0	1	0	0	0	0	0	0
Peirosaurus tormini	1	1	1	0	1	1	1	1	1	1	1	1	2	0	0	1	1	0	1	0	?	1	1	0	?	0	0	0	0	0
Araripesuchus patagonicus	0	1	0	0	0	1	0	1	0	0	0	?	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0
Notosuchus terrestris	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	2	0

Table 2. Data matrix of nine trematochampsid species, two peirosaurids, and the two outgroups coded for 30 unordered, unweighted characters. A list of characters can be found in the appendix. Information on all species, with the exception of *T. oblita*, was obtained from the literature.

an exhaustive search examines every possible tree configuration to give a complete list of most parsimonious trees. Both Strict and Adams consensus trees were obtained from the resulting most parsimonious trees. MacClade 4.03 (Maddison and Maddison 2001) was used to further manipulate the topology of the trees.

RESULTS

Two analyses were performed with the data matrix. The first analysis contained data from the nine trematochampsid species and the two outgroups. The three search algorithms all produced two equally parsimonious trees, each 40 steps long with a consistency index of 0.725 and a retention index of 0.7027 (Figure 25). The Strict and Adams consensus trees have the same topology (Figure 25a).

The second analysis included the two peirosaurid species. The three search algorithms all produced 24 equally parsimonious trees, each 47 steps long with a consistency index of 0.6596 and a retention index of 0.7037. Strict and Adams consensus trees were obtained and differ only slightly in their topology (Figure 26).

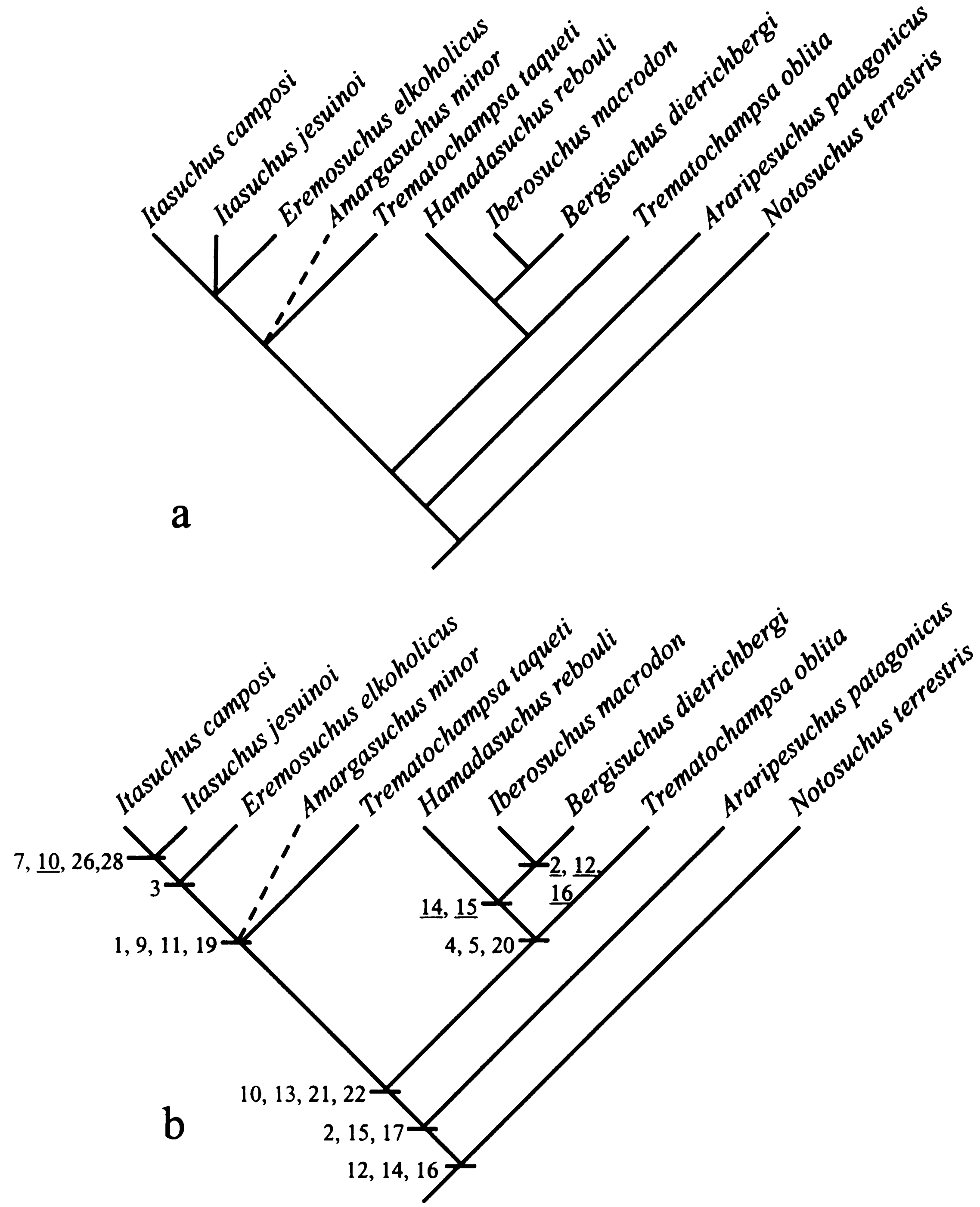

Figure 25. Equally parsimonious trees, 40 steps long, resulting from the first analysis: a) is also the consensus tree, b) shows character changes. Underlined numbers indicate reversal to primitive state. *Amargasuchus minor*, which is known only from fragmentary material, was speculatively mapped onto the tree on the basis of 5 characters.

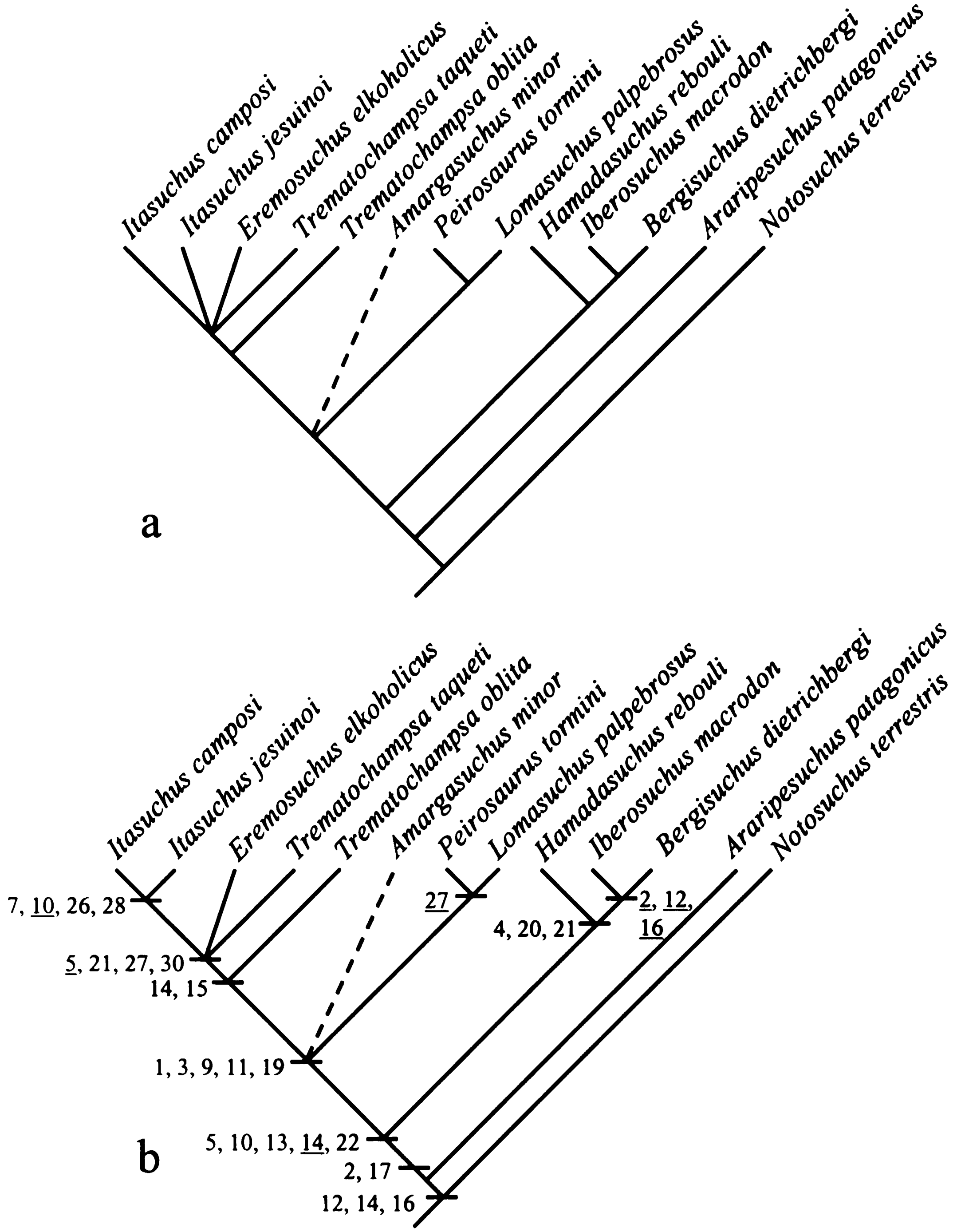

Figure 26. Consensus trees, 47 steps long, from second analysis, with the two peirosaurids included. a) Strict. b) Adams with character changes. Underlined numbers indicate reversal to primitive state. *Amargasuchus minor*, which is known only from fragmentary material, was speculatively mapped onto the tree on the basis of 5 characters.

DISCUSSION OF PHYLOGENETIC ANALYSIS

RELATIONSHIPS WITHIN TREMATOCHAMPSIDS

Both trees resulting from the first analysis show the Family Trematochampsidae to be monophyletic (Figure 25). The difference between the trees lies in the placement of *Eremosuchus elkoholicus*, a species that lacks data for many of the characters. The monophyly of trematochampsids is supported by: five teeth present on the premaxilla (character 10), heterodonty in the maxillary teeth (character 13), a quadrate that is inclined less than 45 degrees (character 21), and a basisphenoid almost hidden in ventral view (character 22). Characters that support other nodes are mapped on the tree in Figure 25b.

The monophyletic Trematochampsidae is divided into two distinct clades, one including *Trematochampsa taqueti, Eremosuchus elkoholicus, Itasuchus jesuinoi,* and *Itasuchus camposi,* and the other including *Trematochampsa oblita, Hamadasuchus rebouli, Iberosuchus macrodon,* and *Bergisuchus dietrichbergi.* The monophyly of the first clade is strongly supported by the following characters: a large occlusion pit lateral to the seventh dentary alveolus (character 1), a sinusoidal maxillary edge (character 9), more than twelve teeth on the maxilla (character 11), and a quadratojugal not exposed beneath the jugal (character 19). *I. camposi, I. jesuinoi, and E. elkoholicus* all possess a sigmoidal lateral contour of the dentary (character 3). The sister-taxon relationship between the two species of *Itasuchus* is supported by: a forked projection of the surangular (character 7), fewer than five teeth on the premaxilla (character 10), and preorbital swellings formed by the nasals and prefrontals (character 28).

The exclusion of *T. oblita* from the above clade renders the genus *Trematochampsa* paraphyletic. However, *T. oblita* also possesses a derived state in characters 1 and 3. Only one additional step is added to the tree when *T. oblita* is considered to be basal to this clade. Two additional steps are required to make *Trematochampsa* a monophyletic genus (Figures 27).

The trematochampsid species *Amargasuchus minor* was not included in the phylogenetic analysis. The specimen for this species is a single fragmentary maxilla, and therefore only five characters could be coded. The species has, however, been mapped onto the tree and is placed in the clade including *T. taqueti*, *E. elkoholicus*, *I. jesuinoi*, and *I. camposi* on the basis of a sinusoidal maxillary edge (character 9) and more than twelve teeth on the maxilla (character 11).

The second clade (*H. rebouli, I. macrodon, B. dietrichbergi,* and *T. oblita*) is supported by: a mandibular symphysis extending beyond the posterior rim of the fifth dentary alveolus (character 4), a dentary robustness ratio equal to or greater than 1 (character 5), and a dorsally oriented squamosal surface (character 20). *H. rebouli, I. macrodon,* and *B. dietrichbergi* form a monophyletic group defined by possessing serrated, laterally compressed maxillary and dentary teeth (characters 14 and 15). The two Tertiary European forms are joined based on shared reversal to three primitive states: a straight dorsal edge of the dentary (character 2), homodont post-caniniform dentary teeth (character 12), and caudally curved caniniform maxillary and dentary teeth (character 16).

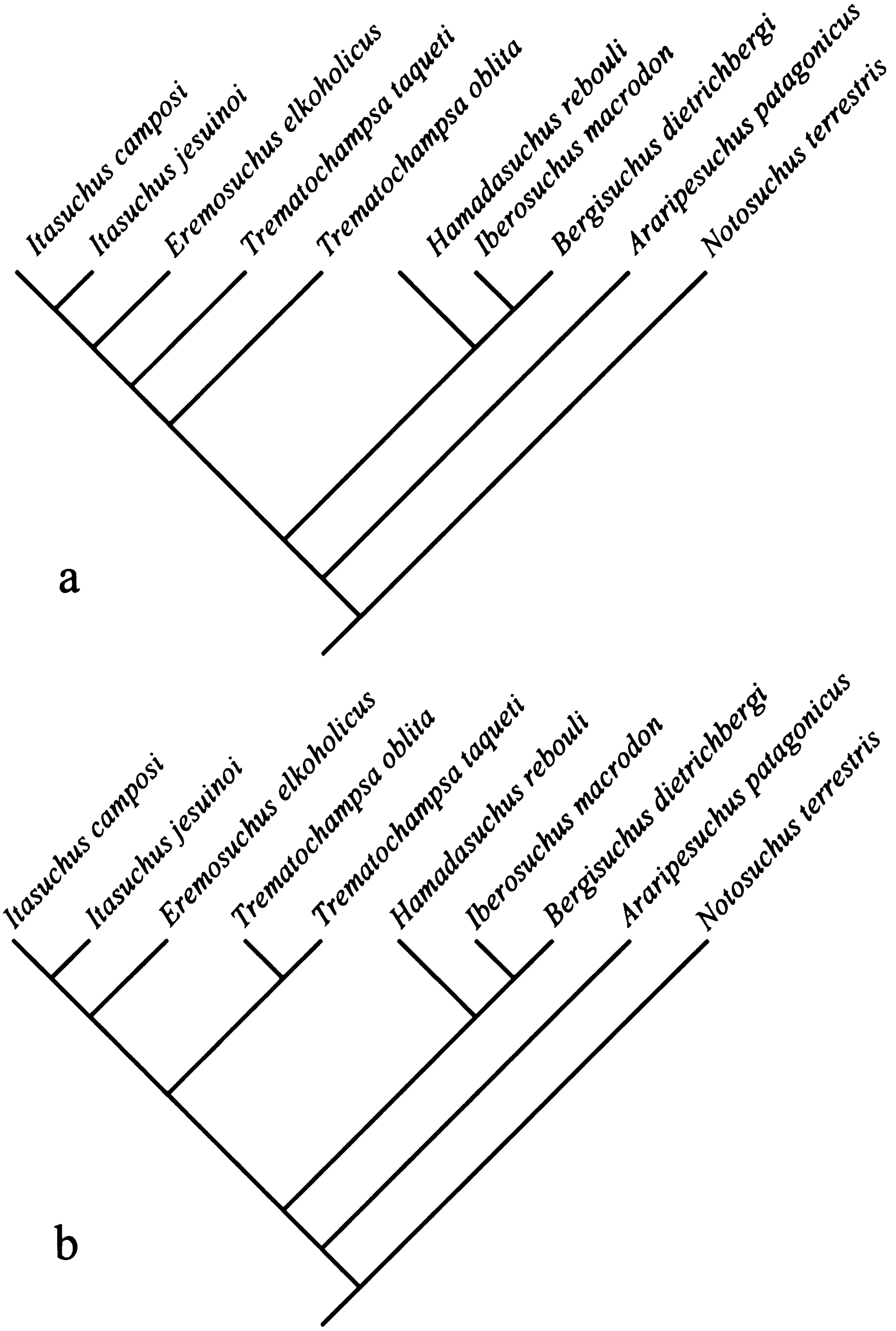

Figure 27. Two possible tree topologies. a) *T. oblita* is basal to Gondwanan clade, 41 steps. b) *T. oblita* and *T. taqueti* form a monophyletic genus, 42 steps.

RELATIONSHIPS INCLUDING PEIROSAURIDS

The second analysis included the two peirosaurid species *Lomasuchus palpebrosus* and *Peirosaurus tormini*. The two consensus trees differ only in their placement of *E. elkoholicus* (Figure 26). The morphology of the trees shows three distinct clades, one grouping the two peirosaurids, which supports the findings of Gasparini et al. (1991). However, the peirosaurid clade falls within the trematochampsids. The Family Peirosauridae is thus subsumed within a monophyletic Trematochampsidae, which supports the suggestion of Buffetaut (1988, 1989). Interestingly, in this analysis *T. oblita* falls closer to the clade containing *T. taqueti, E. elkoholicus,* and the two *Itasuchus* species. Node-defining characters are mapped onto the Adams consensus tree (Figure 26b).

IMPLICATIONS FOR BIOGEOGRAPHY

Current plate tectonic reconstructions suggest the breakup of Pangaea to have begun at the end of the Triassic (Scotese 1998). In the early-to-mid Jurassic, Europe separated from North America and by the Late Jurassic, the Central Atlantic Ocean had opened up between North America and Gondwana. Also in the Late Jurassic, Madagascar and India began to rift from Africa (Scotese 1998). By the middle Cretaceous (about 100 Mya), South America had separated from Africa, and Madagascar had separated from India at about 80 Mya (Smith et al 1994, Scotese 1998). The timing of separation between India and Antarctica-Australia is more controversial. Classical plate interpretations suggest that India separated from Antarctica-Australia around 120 Ma (Roeser et al. 1996, Lawver et al. 1992). However, a new model from Hay et al.

(1999) suggests a much longer connection between Antarctica and Indo-Madagascar, through the Kerguelen Plateau (Figure 28). According to this new reconstruction, the continents may have remained connected until as recently as 80 Mya (Hay et al 1999).

Two biogeographic models can be used to help explain the distribution of trematochampsid crocodyliforms. According to dispersal biogeography, a group of related organisms originates from one point and disperses beyond geographic barriers. Alternately, in vicariance biogeography a group originally has a large range and is fragmented by barriers (Prothero 1998), such as those created by drifting landmasses. Taking into account the range of trematochampsids and the plate tectonic reconstructions discussed above, both models can be invoked to explain the distribution of these species.

Figures 29 and 30 show the phylogenetic trees from the two analyses superimposed on maps of Late Cretaceous continental positions. In both cases, vicariance biogeography seems to have played a large role in the distribution of trematochampsids. The oldest trematochampsids lived while Gondwana was still largely intact, so crocodylomorphs basal to trematochampsids must have been present in Gondwana before the rifting of South America and Africa. As the continents separated, the Gondwanan trematochampsids were divided, with clades evolving in South America and Africa.

The presence of *T. oblita* on Madagascar can be potentially explained using either model. If the range of more basal trematochampsids encompassed Antarctica and India prior to Gondwanan fragmentation, a vicariance model can explain the presence of *T. oblita* on Madagascar. It is also possible that the early southern South American trematochampsids dispersed to Madagascar through Antarctica and the Kerguelen

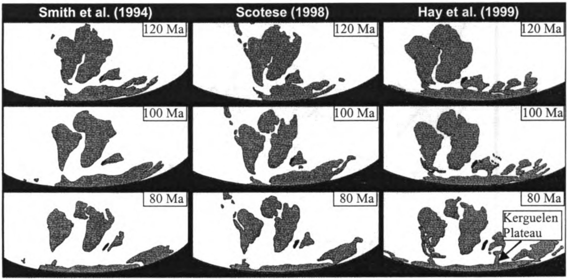

Figure 28. Paleogeographic reconstructions of Gondwanan landmasses according to three authors. Continents are gray, with Madagascar shown in black. Modified from Krause et al. (1999)

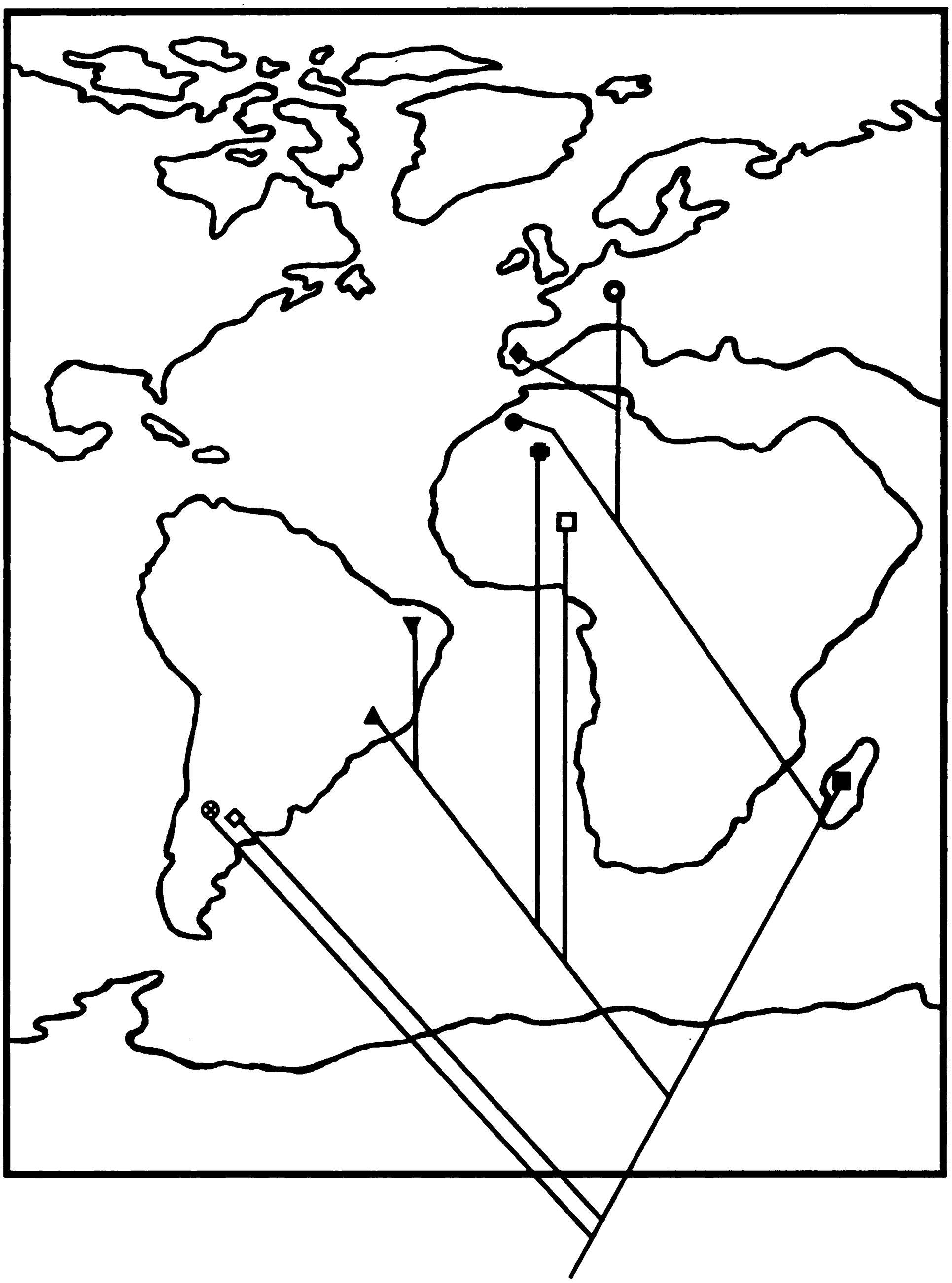

Figure 29. Late Cretaceous map showing cladistic and biogeographic relationships: ▼ *Itasuchus camposi,* ● *Hamadasuchus rebouli,* □ *Trematochampsa taqueti,* ■ *Trematochampsa oblita,* ▲ *Itasuchus jesuinoi,* ⬢ *Eremosuchus elkoholicus,* ◆ *Iberosuchus macrodon,* ⊙ *Bergisuchus dietrichbergi,* ⊗ *Araripesuchus patagonicus,* ◇ *Notosuchus terrestris. Amargasuchus minor* is not included due to the fragmentary nature of the material.

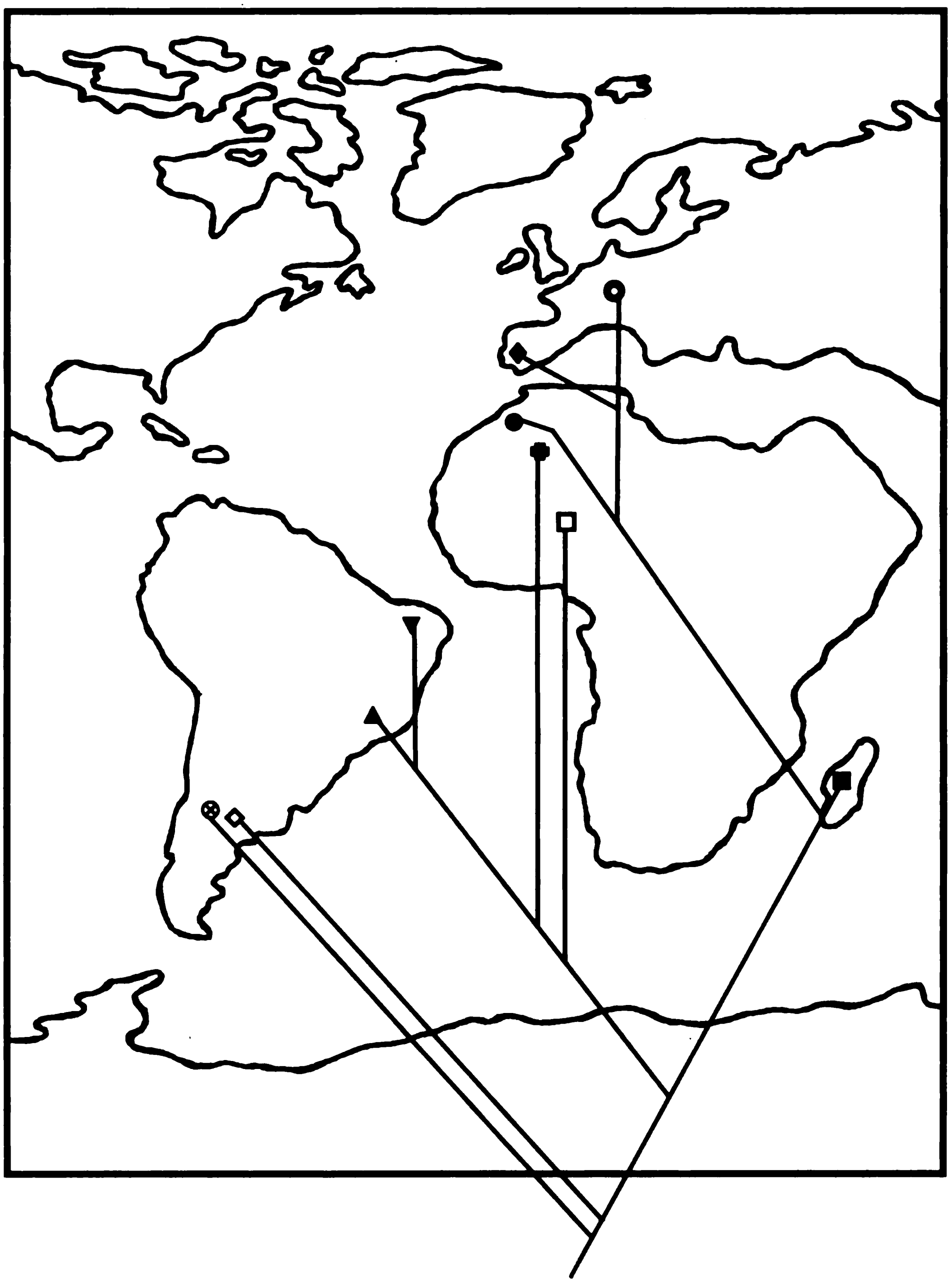

Figure 29. Late Cretaceous map showing cladistic and biogeographic relationships: ▼ *Itasuchus camposi,* ● *Hamadasuchus rebouli,* □ *Trematochampsa taqueti,* ■ *Trematochampsa oblita,* ▲ *Itasuchus jesuinoi,* ✚ *Eremosuchus elkoholicus,* ◆ *Iberosuchus macrodon,* ○ *Bergisuchus dietrichbergi,* ⊗ *Araripesuchus patagonicus,* ◇ *Notosuchus terrestris. Amargasuchus minor* is not included due to the fragmentary nature of the material.

Plateau, consistent with the Hay et al. (1999) paleogeographic model. It seems unlikely, however, that these terrestrial/freshwater crocodyliforms were able to disperse across the Mozambique Channel from Africa.

The occurrence of the two Tertiary forms in Europe (*I. macrodon* and *B.* dietrichbergi) may best be explained by dispersal. These two species are most closely related to *H. rebouli*, a late Albian form from Morocco. It seems likely that a relative of the Moroccan form dispersed from Africa to Europe. Invoking vicariance biogeography to explain the European forms would suggest that the predecessors of trematochampsids were present before the Early Jurassic and had a range spanning North America and Europe. This is possible, but to date no remains of trematochampsid-like crocodyliforms have been found in North America, or in pre-Cenozoic Europe.

CONCLUSION

The new material of *Trematochampsa oblita* adds to the knowledge of this enigmatic species, and has provided more data for a phylogenetic analysis of the Family Trematochampsidae. The analysis shows the family to be monophyletic and to include the peirosaurids. The most parsimonious trees show two distinct clades: one including the Gondwanan species (*I. camposi, I. jesuinoi, E. elkoholicus*, *T. taqueti,* and *A. minor*) and the other including the Moroccan and European species *(H. rebouli, I. macrodon*, and *B. dietrichbergi*). The Malagasy species, *T. oblita*, groups with each of the clades in the two separate analyses. In both, however, the genus *Trematochampsa* is found to be paraphyletic. The results of the phylogenetic analysis and current plate tectonic reconstructions are consistent with using a vicariance model to explain the distribution of Gondwanan trematochampsids. The location of *T. oblita* on Madagascar can be explained using both vicariance and dispersal biogeography, taking into account the Kerguelen Plateau. The presence of Tertiary forms in Europe is best explained using a dispersal model. The trematochampsids remain a relatively poorly known group; each new discovery will lead to a better understanding of the interrelationships and biogeography of this family.

APPENDIX

CHARACTERS

Upper and Lower Jaw/Dentition:

1. Dentary smooth lateral to seventh alveolus (0), dentary with large occlusion pit lateral to seventh alveolus (1).
2. Dorsal edge of dentary straight (0), dorsal edge of dentary sinusoidal, with two concave waves (1).
3. Lateral contour of dentary straight in dorsal view (0), sigmoidal (1).
4. Length of dentary symphysis is shorter than or just reaches the posterior rim of fifth alveolus (0), symphysis extends posteriorly beyond the posterior rim of the fifth alveolus (1).
5. Dentary robustness: ratio of depth of dentary at 4th alveolus to length from center of 4th alveolus to anterior end is less than 1 (0), ratio is equal to or greater than 1 (1).
6. Splenials not involved in mandibular symphysis (0), splenials involved in symphysis (1).
7. Anterior projection of surangular is simple in lateral view (0), forked (1).
8. Medial shelf of retroarticular process is vertical and facing medially (0), facing dorsally (1).
9. Ventral edge of maxilla in lateral view is straight or convex (0), sinusoidal (1).
10. Number of teeth on premaxilla less than five (0), five (1).
11. Number of teeth on maxilla less than twelve (0), twelve to eighteen (1).
12. Post-caniniform dentary teeth are approximately homodont in size (0), heterodont (1).

13. All maxillary teeth approximately homodont in size (0), with largest teeth at middle of maxillary tooth row (1), heterodont (2).
14. Crowns of maxillary and dentary teeth with distinct denticulate carinae (0), without carinae or with carinae smooth or crenulated (crenulation is made of enamel wrinkles) (1).
15. Maxillary and dentary teeth labiolingually compressed in cross-section (0), subcircular (1).
16. Tips of caniniform maxillary and dentary tooth crowns are caudally curved (0), dorsally directed or lingually curved (1).
17. Enlarged anterior maxillary teeth are absent(0), borne anteriorly in 2nd, 3rd alveoli (1), borne in 4th, 5th alveoli (2).

Other Cranial:

18. External nares facing strongly anteriorly (0), displaced slightly dorsal (1).
19. In lateral view, quadratojugal visible beneath jugal (0), quadratojugal is not exposed (1).
20. Outer surface of squamosal laterodorsally oriented (0), dorsally oriented (1).
21. Quadrate inclination with respect to a horizontal plane including the cranial roof: craniocaudal axis of quadrate inclined more that 45 degrees (0), craniocaudal axis of quadrate inclined less than 45 degrees (1).
22. Basisphenoid widely exposed in ventral view (0), almost excluded from ventral view and hidden by pterygoid and basioccipital (1).
23. Antorbital fenestra is present (0), secondarily absent (1).

24. Dorsal surface of frontal relatively flat (0), with narrow midline ridge (1).
25. Dorsal surface of parietal relatively flat (0), dorsal surface of parietal with narrow midline ridge (1).
26. Palatal surface is concave (0), planar (1).
27. Postorbital pillar is external to outer surface of dermal skull bones (0), internal (1).
28. Preorbital swellings (made by nasals and prefrontals) are absent (0), present (1).
29. Quadrate without fenestrae (0), with single fenestra (1), or with three or more fenestrae on dorsal and posteromedial surfaces (2).
30. Nasals contribute to external nares (0), nasals do not contribute to external nares (1).

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