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Introduction

The Metoposauridae (Amphibia: Temnospondyli) is a group of large amphibians that is one of the most commonly preserved groups of fossil vertebrates in Upper Triassic strata of Laurasia and northern Gondwanaland (Fig. 1). Since Meyer (1842) named *Metopias diagnosticus*, one of the first described labyrinthodonts, at least 10 generic and 26 specific names have been applied to metoposauroids. However, despite their abundance and long history of study, there has been only one major revision of the taxonomy of metoposaurids in 150 years (Colbert and Imbrie 1956). Colbert and Imbrie (1956) revised the systematics of all metoposaurid taxa then known (except *Metoposaurus ultimus*) based largely on comparative measurement ratios rather than derived character states. Colbert and Imbrie's (1956) taxonomy has been used up to the present time with the only significant change being the lumping of virtually all of their species into the genus *Metoposaurus* by Roy Chowdhury (1965) and the suggestion by Gregory (1980) that *Anaschisma* could be distinguished from *Metoposaurus*.

Several factors have led to a need for a revision of the family. The most important of these is the emergence of phylogenetic systematics that have yet to be applied to metoposaurids except in a preliminary way (Hunt 1989a). A second factor was the discovery and description by J. M. Dutuit (1976) of diverse and exquisitely preserved metoposaurids from Morocco. The placement of the Moroccan metoposaurids in the "waste basket" taxon *Metoposaurus* has stretched this "genus" beyond its breaking point. Finally, on a more personal note, I was drawn to revise the metoposaurids by the description of a new taxon from western North America and a need to place it in an adequate phylogenetic context.

During the course of this study, I have examined most major collections of metoposaurs in North America and Western Europe containing the vast majority of all named taxa outside India. These collections are: American Museum of Natural History, New York (AMNH); Bristol Museum and Art Gallery, Bristol (BMAG); Carnegie Museum of Natural History, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Field Museum of Natural History, Chicago, University of Chicago collection (FMNH UC); Institut für Geologie und Paläontologie der Universität Tübingen, Tübingen (IMGPUT); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of Northern Arizona, Flagstaff (MNA); Museum National d'Histoire Naturelle, Paris (MNHN); University of Missouri,

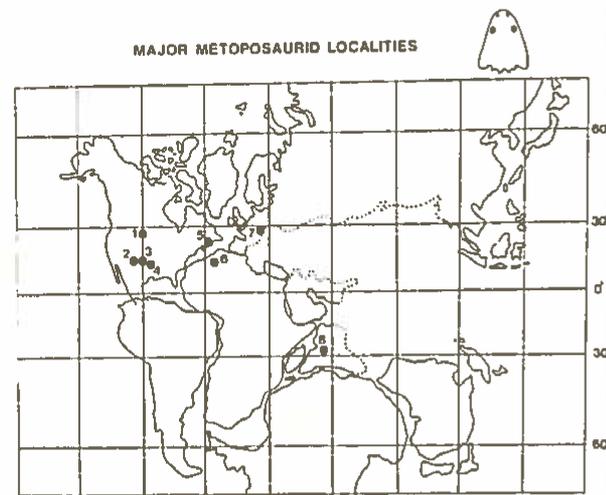


Figure 1. Geographic distribution of major metoposaurid localities. 1. Popo Agie Formation, Wyoming, USA. 2. Bluff Mesa and Painted Desert members of the Petrified Forest Formation, Arizona. 3. Santa Rosa, Garita Creek, Buckhorn Canyon, and Redonda formations, New Mexico, USA. 4. Camp Springs Member, unnamed member and Tecoma and Cooper members of the Dockum Formation, Texas, USA. 5. Wolfville Formation, Nova Scotia, Canada. 6. Argana Formation, Morocco. 7. Schilfsandstein, Blasen sandstein, and Lehrbergschichten, Germany, Maleri Formation, India.

Columbia (MU); Natural History Museum, formerly British Museum (Natural History), London (NHM); New Mexico Museum of Natural History and Science, Albuquerque (NMMNH); Oklahoma Museum of Natural History, Norman (OMNH); Panhandle Plains Museum, Canyon (PPM); Panhandle Plains Museum, Canyon, West Texas State collection (WT); South Dakota School of Mines, Rapid City (SDSM); Staatliches Museum für Naturkunde, Stuttgart (SMNS); Texas Memorial Museum, Austin (TMM); Texas Tech University, Lubbock (TTUP); University of California Museum of Paleontology, Berkeley (UCMP); University of Michigan Museum of Paleontology, Ann Arbor (UMMP); Yale Peabody Museum, New Haven (YPM); Yale Peabody Museum, New Haven, Princeton University collection (YPM PU). Other institutional abbreviations are: ISI, Indian Statistical Institute, Calcutta; UMCZ, University Museum of Zoology, Cambridge University, Cambridge.

Note: Temnospondyli has been shown by many authors to be polyphyletic (e. g., Milner 1988) but is still used for convenience. Temnospondyli is used here in the sense of Milner *et al.* (1986), Panchen and Smithson (1988), and Milner (1990). Stratigraphic nomenclature for western North America follows Lucas (1992).

In the western United States, the first report of a metoposaurid was Cope's (1893) assignment of fragmentary specimens probably from the Tecovas Member of the Dockum Formation of west Texas, to *Eupelor*. In 1904, Lucas described the first new taxon from this region, *Metoposaurus fraasi*, based on an interclavicle. The next year, Branson (1905) named *Anaschisma browni* and *Anaschisma brachygnatha* for two skulls from the Popo Agie Formation of Wyoming. Subsequently, Case (1920) named *Metoposaurus jonesi* for articulated clavicles and an interclavicle and *Buettneria perfecta* for a skull (Case 1922), both from the Tecovas Member of west Texas.

Branson and Mehl (1929) reviewed the metoposaurids of the western United States and named five new taxa, *Koskinodon princeps* and *Borborophagus wyomingensis* from the Popo Agie of Wyoming and *Kalamoiketor pinkleyi* and *Buettneria (?) major* from the Blue Mesa Member of the Petrified Forest Formation of Arizona (lower Petrified Forest Member of the Chinle Formation of older authors). *B. (?) major* was based on clavicles, but all the other taxa were based on skulls or partial skulls. Branson and Mehl (1929) placed *M. fraasi* in the genus *Kalamoiketor*.

Case (1931, 1932) based descriptions of *Buettneria bakeri* on a large quarry sample of skulls and postcrania from the Camp Springs Member of the Dockum Formation of Texas. In the late 1930s and early 1940s, three other large concentrations of metoposaurid specimens were reported. Romer (1939) briefly described a quarry that yielded tens of skulls of *Buettneria perfecta* near Lamy in northern New Mexico. This quarry is now known to be in the Garita Creek Formation (Hunt and Lucas 1989; Lucas and Hunt 1989a). Sawin (1945) described a smaller sample from the unnamed member of the Dockum Formation (sensu Lucas 1992) of Howard County, Texas, under the name *Buettneria howardensis*. A third sample, whose discovery dates from this period, is from the Tecovas Member from near Amarillo, Texas (Colbert and Imbrie 1956; Murry 1989). Colbert and Imbrie (1956) referred these specimens to *Eupelor fraasi jonesi*.

Green (1954, p. 64) named a new species of *Buettneria*, "*B. calgariensis*," in an unpublished dissertation, from the Tecovas Member of the Dockum Formation in Crosby County, Texas. This taxon, which was never published, was based on a skull (TTUP 54-125).

Colbert and Imbrie (1956), who revised the Metoposauridae, considered *Dictyocephalus elegans* and *Eupelor durus* to be valid Newark taxa. They synonymized all the Wyoming taxa as *Eupelor browni*, all the Texas taxa as *Eupelor fraasi jonesi*, and all the Arizona and New Mexico taxa as *Eupelor fraasi fraasi*. It is worth noting at this point that Colbert and Imbrie

(1956) overlooked the fact that in *Buettneria bakeri* the lachrymal does not enter the orbit even though they considered this lachrymal trait to be a valid apomorphy for *Metoposaurus diagnosticus*. Roy Chowdhury (1966) placed the vast majority of Colbert and Imbrie's species and subspecies in the genus *Metoposaurus*. Subsequently, Gregory (1980) suggested that *Anaschisma* may be a distinct genus from *Metoposaurus*. Davidov (1987) and Henry (1987-1989) and Hunt (1989a) have further commented on the taxonomy of North American metoposaurids with special regard to small specimens

Africa

The discovery and detailed description of the spectacular metoposaurid specimens from the Argana Formation of Morocco is due to the efforts of J. M. Dutuit (1967, 1972, and 1976). Dutuit (1976) named three new species of *Metoposaurus*—*M. ouazzoui*, *M. azeroua*, and *M. lyazidi*—from the Argana Formation. Some of the Argana specimens are articulated individuals that represent the most complete specimens of metoposaurids (e.g., Dutuit 1976, pls. 30-34). Dutuit (1976) also described a skull fragment and associated bones from the Isalo II Formation of Madagascar as a new species of metoposaurid, *Metoposaurus boffmani*.

India

Fragmentary labyrinthodont specimens have long been known from the Maleri Formation of India (e.g., Lydekker 1885; Huene 1940). However, only in 1966 did Roy Chowdhury describe abundant metoposaurid specimens, which he assigned to *Metoposaurus maleriensis*. Recently, a large number of new specimens have been discovered that are currently undescribed (Sengupta 1990; pers. comm. 1990).

China

Young (1978) named the supposed metoposaurid *Bogdania fragmenta*, an aptly named taxon, based on very fragmentary specimens from the Huangshanji Formation, Xinjiang Province of China. Some of these specimens do not even pertain to a labyrinthodont (G. Lucas, pers. comm. 1991).

Character Analysis

Introduction

Metoposaurids show limited variation relative to other Triassic temnospondyls. However, there are a large number of robust characters in the Metoposauridae that can be used to assess the monophyly and internal relationships of this family. Polarities of characters are assessed against a series of outgroups comprising

Dentary Tusk

- 5A Dentary tusk is not part of dentary row and has smaller teeth external to it.
- 5B Dentary tusk is enlarged tooth of dentary row with no smaller teeth external to it.

Metoposaurids are unique among temnospondyls in having a symphyseal tusk that is a part of the dentary tooth row and thus does not have any teeth external to it (A. A. Warren, written comm. 1991). M. A. Shishkin (pers. comm. 1991) notes that some adult brachyopoids may approach this condition.

Margin of Posterior Meckelian Foramen

- 6A Posterior coronoid does not form part of dorsal margin of posterior Meckelian foramen.
- 6B Posterior coronoid forms part of dorsal margin of posterior Meckelian foramen.

Metoposaurids are unique among Triassic temnospondyls in having a posterior coronoid that forms part of the dorsal margin of the posterior Meckelian foramen (Jupp and Warren 1986). However, this character occurs in *Trimerorhachis* (Case 1935, Fig. 13) and thus is considered to be a primitive character.

Coronoid Process

- 7A Low coronoid process.
- 7B High coronoid process.

M. A. Shishkin (pers. comm. 1991) noted that the coronoid process of metoposaurids is higher than any other temnospondyls. This is a derived character.

Relationship of Maxilla and Orbit

- 8A Maxilla does not enter margin of orbit.
- 8B Maxilla enters margin of orbit.

Metoposaurus ouazzoui is distinct among metoposaurids in that the maxilla enters the border of the orbit (Dutuit 1972, Fig. 2, pls. 5–7). In other metoposaurs, the posterior of the lachrymal contacts the anterior of the jugal and excludes the maxilla from the orbit. Entry of the maxilla into the orbit is derived relative to the outgroups.

Relationship of Lachrymal and External Nares

- 9A Lachrymal enters margin of external nares.
- 9B Lachrymal does not enter margin of external nares.

Metoposaurus lyazidi is unique among metoposaurids in that the lachrymal enters the margin of

the external nares (Dutuit 1972, p. 181, pls. 48C, 49, 50B). This configuration of the lachrymal is seen in *Trimerorhachis* (Case 1935, Fig. 1) and *Dendroterpeton* (Milner 1980, Fig. 3C) and is considered primitive for metoposaurids.

Relationship of Lachrymal to Orbit

- 10A Lachrymal enters margin of orbit.
- 10B Lachrymal does not enter margin of orbit.

Romer (1947) noted that *Metoposaurus diagnosticus* differs from North American metoposaurids in excluding the lachrymal from the orbit. Colbert and Imbrie (1956) also noted this character in *M. diagnosticus* but failed to note that one of the population samples that they analysed (*Buettneria bakeri*) from North America also had this feature. Thus, Colbert and Imbrie (1956) placed all *B. bakeri* in the same subspecies (*Eupelor fraasi jonesi*) as other metoposaurids having a lachrymal that entered the orbital margin.

It is important to note that the *Buettneria bakeri* sample consists of a quarry (population) sample in which all specimens have a lachrymal excluded from the orbit (Case 1931, Fig. 1 1932, Figs. 2–5, pls. 1, 4). However, Roy Chowdhury (1965) argued that since one of Colbert and Imbrie's subspecies contained individuals with lachrymals both included and excluded from the orbit margin, the position of the lachrymal is therefore a variable character.

The position of the lachrymal relative to the orbit is not variable in any known metoposaurid population sample—for instance the Lamy amphibian quarry (specimens examined at MCZ, OMNH, YPM, NHM (BMJNH)), FMNH, CMNH, SDSM), the *Buettneria bakeri* sample (Case 1931 1932; UMN and MCZ specimens), or the *Metoposaurus ouazzoui* or *Metoposaurus lyazidi* samples from Morocco (Dutuit 1976; MNHN specimens). No metoposaurid specimens show the variability within one individual that is evident in some capitosauroids (e.g. *Parotosuchus wadei*: Cosgriff 1972; Kamphaus and Morales 1981) where cranial bones (frontal in this case) show incorporation and exclusion from the orbital margin on opposite sides of the same specimen.

Dutuit (1976, p. 49) argued that the lachrymal position is of poor taxonomic utility since it is difficult to determine the lachrymal in all specimens. However, in most well-preserved metoposaurid skulls that I have examined the position and shape of the lachrymal is evident. Relative to the outgroups, the primitive condition is for the lachrymal to be incorporated in the orbital margin.

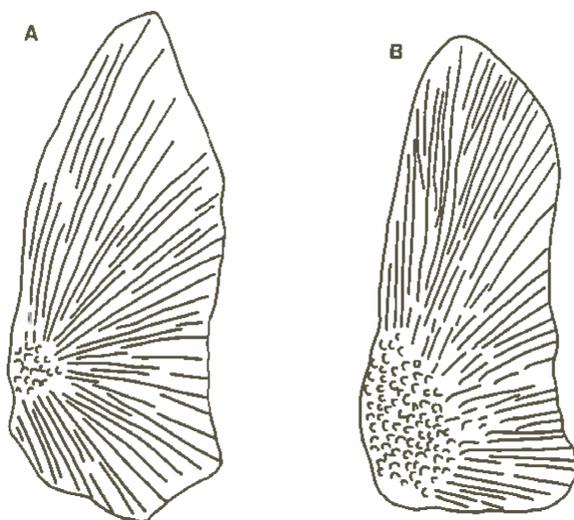


Figure 3. Ornamentation of posterior part of clavicle in metoposaurids. A. *Metoposaurus diagnosticus*. B. all other metoposaurids (after Colbert and Imbrie 1956).

in a partial sunburst pattern (Fig. 3). Colbert and Imbrie noted that the area patterned by pits is much smaller in *M. diagnosticus* than in North American forms.

It is easier to quantify the related character of the extension of the grooved pattern around the circumference of the pitted area (Fig. 3). In *Metoposaurus diagnosticus*, the grooved pattern extends around the posterior margin of the area of pits much further than in other taxa. This can be quantified by measuring the arc incorporated by the grooved pattern around the hypothetical center of the pitted area. The greater radiation of grooves (14B) is the derived state.

Clavicular Articulation

- 15A Clavicles touch anterior to interclavicle with no long union.
- 15B Long linear union of clavicles anterior to the interclavicle.

Lydekker (1890, p. 153) noted in his diagnosis of *Metoposaurus* "lateral plates [clavicles] meeting in a long suture in advance of the median plate [interclavicle]." This feature is evident in an articulated specimen of *M. diagnosticus* (Figs. 8 and 12; Fraas 1889, pl. 15; Fraas 1896, pl. 2) and is in marked contrast to other taxa of metoposaurid. This feature results in a shorter relative segment of the sculptured area of the interclavicle, anterior to its widest point, than in any other metoposaur. This autapomorphy of *M. diagnosticus* is undoubtedly derived.

Fused Neural Arch on "Axis"

- 16A No fused neural arches on second presacral vertebrae.
- 16B Fused neural arches on second presacral vertebra ("axis").

The fusion of neural arches on the second presacral vertebra (e. g., Case 1935, pl. 4 Fig. 2; Sawin 1945, Fig. 6a; Dutuit 1976, Figs. 33–34) is unknown among other temnospondyls (Warren and Black 1985) except for some specimens of *Dvinosaurus* (Bystrov 1938, Fig. 26B) and is a derived character for metoposaurids.

Ossification of Separate Pleurocentral Elements

- 17A Separate ossified pleurocentra in posterior trunk vertebrae.
- 17B No separate ossified pleurocentra in posterior trunk vertebrae.

Romer (1947) noted that metoposaurid vertebrae are distinctive in having fully ossified centra (hypocentra), which are solid discs with no room for pleurocentral elements. This is true for presacral vertebrae in all metoposaurids except *M. ouazzoui*. *M. ouazzoui* is unique in having ossified pleurocentra and slightly wedge-shaped hypocentra in the posterior trunk region (Fig. 9A–B; Dutuit 1976, Figs. 36–37, pl. 19, Fig. E–F). There is no evidence that the pleurocentra and hypocentra are fused as in plagiosaurids (Shishkin 1989). The preserved association of these elements is a result of the exquisite preservation of the *M. ouazzoui* specimens. It should be noted that other metoposaurids have small anterior "shoulders" on the hypocentra of the posterior trunk region (e.g., Roy Chowdhury 1965, Fig. 37–38), indicating the possible presence of small, unossified pleurocentra, but this does not result in wedge-shaped presacral hypocentra as in *M. ouazzoui*.

All metoposaurids have wedge-shaped caudal hypocentra indicating that separate pleurocentra were present. However, even articulated metoposaurid skeletons show no evidence of ossified pleurocentra in the caudal region (Dutuit 1976, pl. 33). Thus, as Shishkin correctly pointed out, there is a distinct cranio-caudal difference in the form of the vertebral centra regarding the presence of separate pleurocentral elements.

Romer (1947) noted that one *Metoposaurus* specimen from Germany, illustrated by Fraas, had hemicylindrical centra. Neither examination of Fraas' plate (e.g., 1889, pl. 15) nor of the SMNS specimen supports Romer's view. Obviously loss of ossified pleurocentra and presence of parallel-ended hypocentra is a derived character state within the Temnospondyli.

wide cultriform process of the parasphenoid (maximum width of skull/minimum width of cultriform process ≤ 13) that forms $\frac{3}{4}$ of the internal border of the palatal vacuities and a corpus of the parasphenoid that is less than twice the maximum width of the cultriform process; large quadrate foramina with a maximum dimension greater than the diameter of an occipital condyle in posterior view; fused neural arches on the second presacral vertebra; dorsal articular surface that is laterally convex; dentary tusk that is enlarged tooth of dentary tooth row with no smaller teeth external to it; high coronoid process.

Metoposaurus (Lydekker 1890)

- Metopias* (Meyer 1842, p. 302.)
Metopias (Meyer and Plieninger 1844, p. 18, plate 10 [reversed], Fig. 1.)
Metopias (Meyer 1855, p. 146, plate 60.)
Metopias (Fraas 1889, p. 137, plate 11, 5-9 12-16.)
Metoposaurus (Lydekker 1890, p. 152, Fig. 35.)
Metopias (Fraas 1896, p. 8, plates 1-2.)
Buettneria (Case 1931, p. 1, Figs. 1, 3-10, plates 1-3.)
Buettneria (Case 1932, p. 1, Figs. 2-45, plates 1-7.)
Metoposaurus (Romer 1947, p. 251, Fig. 41.)
Metoposaurus (Colbert and Imbrie 1956, p. 411, plate 2 1-2.)
Eupelor (in part: Colbert and Imbrie 1956, p. 449.)
Metoposaurus (in part: Roy Chowdhury 1965, p. 42.)

TYPE SPECIES: *Metoposaurus diagnosticus* (Meyer 1842).

INCLUDED SPECIES: *Metoposaurus diagnosticus* and *Metoposaurus bakeri*.

DISTRIBUTION: Late Triassic of Germany, United States, and Canada.

DIAGNOSIS: Metoposaurid which differs from other members of the family in having a combination of a lachrymal and a maxilla that do not enter the orbit.

DISCUSSION: The holotype (SMNS 10825) of *Metopias diagnosticus* is most of the anterior two thirds of a metoposaurid skull (Fig. 5D; Meyer and Plieninger 1844, pl. 10, Fig. 1 [reversed]; Meyer 1855, pl. 60), which preserves none of the posterior margin of the skull and only the orbital area on the right side. The lateral margin of the lachrymal is unclear, but it is obvious that neither the maxilla nor the lachrymal entered the margin of the orbit. Skulls of *Metoposaurus* appear to have relatively narrower skulls than other genera though their shape falls within the range of variation of other metoposaurids.

This genus is only definitely recognised from the Schilfsandstein of Germany; the Wolfville Formation of Nova Scotia, Canada; and the unnamed member of the Dockum Formation of Texas, USA. However, this genus has been reported from England and France (Miall 1875; Corroy 1928).

Metoposaurus diagnosticus (Meyer 1842)

- Metopias diagnosticus* (Meyer 1842, p. 302.)
Metopias diagnosticus (Meyer and Plieninger 1844, p. 18, plate 10, Fig. 1 [reversed].)
Metopias diagnosticus (Meyer 1855, p. 146, plate 60.)
Metopias diagnosticus (Fraas 1889, p. 137, plates 11, 5-9 12-16.)
Metoposaurus diagnosticus (Lydekker 1890, p. 152, Fig. 35.)
Metopias diagnosticus (Fraas 1896, p. 8, plates 1-2.)
Metoposaurus diagnosticus (Romer 1947, p. 251, Fig. 41.)
Metoposaurus diagnosticus (Colbert and Imbrie 1956, p. 411, plate 25 1-2.)
Metoposaurus diagnosticus (Roy Chowdhury 1965, p. 42.)

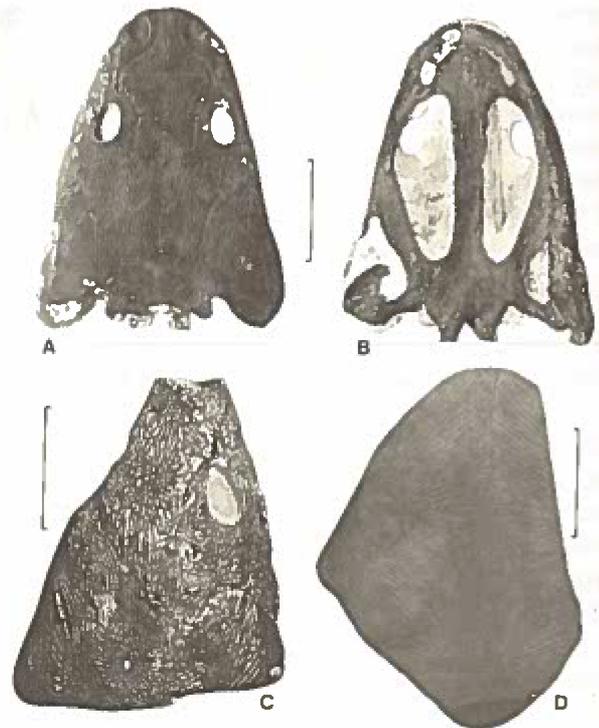


Figure 5. *Metoposaurus diagnosticus* (Meyer 1842). A-B SMNS 4943, skull in dorsal (A) and ventral (B) views. C SMNS 10825, holotype skull in dorsal view. D. SMNS, articulated interclavicle and clavicles in ventral view. Scale bars are 10 cm. A-C courtesy of S. P. Welles (UCMP).

Buettneria (Case 1922)*Metopias* (in part: Miall 1875, p. 157.)*Metoposaurus* (in part Lydekker 1890, p. 153.)*Metoposaurus* (in part: Watson 1919, p. 32, Figs. 18–20.)*Koskinonodon* (Branson and Mehl 1929, p. 203, Figs. 8–9, plates 4–9.)*Borborophagus* (Branson and Mehl 1929, p. 217, Fig. 10, plates 11–12.)*Metoposaurus* (in part: Sawin 1945, p. 362, Figs. 1–12.)*Eupelor* (in part: Colbert and Imbrie 1956, p. 449, Figs. 6–7, plates 25, 3–4, 26 1–2, 27.)*Metoposaurus* (in part: Roy Chowdhury 1965, p. 42.)TYPE SPECIES: *Buettneria perfecta*.

INCLUDED SPECIES: The genus is only known from the type species.

DISTRIBUTION: Late Triassic of North America, Europe, and India.

DIAGNOSIS: Metoposaurid that differs from other members of the family in possessing a lachrymal entering the margin of the orbit.

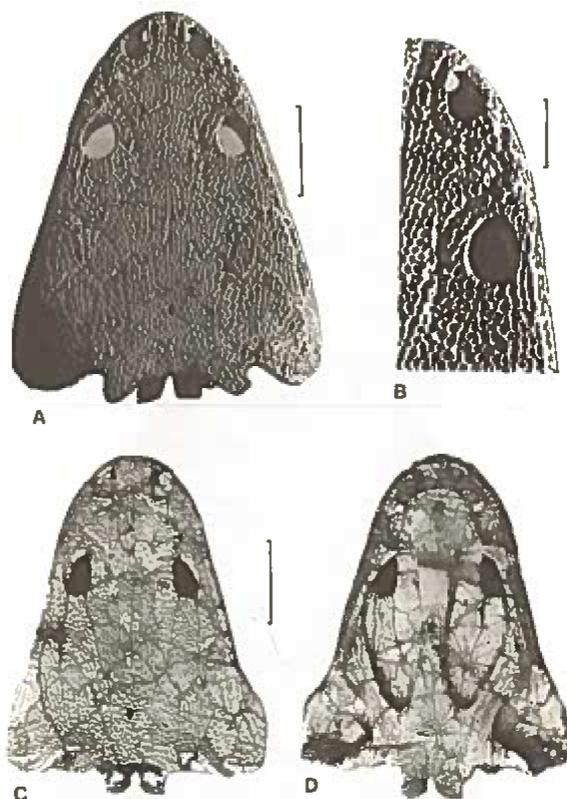


Figure 7. *Buettneria perfecta* Case 1922. A–B. UMMP 7475, holotype skull in dorsal view (A) and close-up of right orbital area (B). C–D. WT 3055, skull in dorsal (C) and ventral (D) views. Scale bars are 10 cm for A, C, and D and 5 cm for B.

Buettneria perfecta (Case 1922)*Metopias diagnosticus* (in part: Miall 1875, p. 157.)*Metoposaurus diagnosticus* (in part: Lydekker 1890, p. 153.)*Metoposaurus diagnosticus* (in part: Watson 1919, p. 32, Figs. 18–20.)*Koskinonodon princeps* (Branson and Mehl 1929, p. 203, Figs. plates 4–9.)*Borborophagus wyomingensis* (Branson and Mehl 1929, p. 217, Fig. 10, plates 11–12.)*Buettneria howardensis* (Sawin 1945, p. 362, Figs. 1–12.)*Eupelor fraasi jonesi* (in part: Colbert and Imbrie 1956, p. 449, Figs. 6–7, plates 25, 3–4, 26 1–2.)*Eupelor fraasi fraasi* (Colbert and Imbrie 1956, p. 449, plate 26, 3–4.)*Eupelor browni* (Colbert and Imbrie 1956, p. 449, plate 26, 3–4.)*Metoposaurus fraasi fraasi* (Roy Chowdhury 1965, p. 42.)*Metoposaurus fraasi jonesi* (in part: Roy Chowdhury 1965, p. 42.)*Metoposaurus browni* (Roy Chowdhury 1965, p. 42.)*Metoposaurus maleniensis* (Roy Chowdhury 1965, p. 21, Figs. 1–2.)

HOLOTYPE: UMMP 7475, complete skull (Fig. 7A–B, Case 1922, pls. 1, 2A–B, Figs. 1–3).

TYPE LOCALITY: Sand Creek, Crosby County, Texas, USA (Case 1922).

TYPE HORIZON: Tecovas Member of Dockum Formation (Late Triassic: late-late Carnian).

DISTRIBUTION: Popo Agie Formation, Wyoming, USA; Tecovas Member of the Dockum Formation, Texas, USA; unnamed member of Dockum Formation, Texas, USA; Blue Mesa Member of Petrified Forest Formation, Arizona, USA; Garita Creek Formation, New Mexico, USA; New Oxford Formation, Pennsylvania, USA; Maleri Formation, India; Schilfsandsstein, Germany.

REFERRED SPECIMENS: Lamy amphibian quarry, New Mexico, USA: MCZ 1674, large slab containing many skulls and dissociated postcrania; AMNH 2994, skull; CM 9547: Popo Agie Formation, Wyoming, USA, 504–505, 527, 537, 517, skulls; Feuerbache Heide, Germany: NHM (BM[NH]) R 37938, large piece of skull (Fig. 8C–D); Otis Chalk, quarry 2, Texas, USA: TMM 31100–122, 31220–1, 31100–47, complete and nearly complete skulls; Sierrita de la Cruz, Texas, USA: WT 3055, skull (Fig. 7C–D), PPM unnumbered, logued, dorsal centra (Fig. 9C–D), caudal interclavicle (Fig. 9E), articulated interclavicle (Fig. 9B), WT 3132 (Fig. 9F–G); Central India: ISI A4, ISI A8, skull roof; TMM 31099–100, small skull with jaws.

DIAGNOSIS: As for genus.

DISCUSSION: *Buettneria perfecta* is undoubtedly the most widespread and best-known metoposaurid taxon. There are three large (>10 skulls) populations of this taxon from the Garita Creek Formation.

which the anterior margin of the orbit is not preserved. However, the lachrymal is very broad in this specimen, close to the inferred margin of the orbit (Roy Chowdhury 1965, Fig. 3), and it can be reasonably assumed that the lachrymal entered the margin of the orbit. Thus, *Metoposaurus maleriensis* is considered a junior subjective synonym of *Buettneria perfecta*.

The holotype of *Metoposaurus maleriensis* (ISI A4) apparently has an ossification in the nasal area that is unique among metoposaurids. In this specimen, the area normally occupied by the nasal bone in metoposaurids contains two ossifications—the more lateral of which Roy Chowdhury (1965, p. 32, Fig. 3) considers to be a septomaxilla. However, the combined area occupied by the nasal and the putative septomaxilla is exactly that occupied by the nasal alone in other metoposaurids (compare Roy Chowdhury 1965, Fig. 3 and Case 1922, pl. 1A) and in paratypes of *M. maleriensis* (Roy Chowdhury 1965, Fig. 4). The putative septomaxilla is present in only one specimen. It appears most parsimonious to consider the unusual ossification of the nasal area in ISI A4 to be a pathology or the misidentification of a broken bone.

Green (1954) informally named *Buettneria calgariensis* with its holotype as TTUP 54–124. The differences cited for this taxon are either taxonomically unimportant (e. g., skull ratios) or are incorrect (only one lateral line canal immediately anterior to the orbit).

The position of the lachrymal flexure of the supraorbital canal of the lateral line system is variable in *Buettneria perfecta*—either crossing the lachrymal bone (Case 1922, pl. 1) or touching its margin (Branson and Mehl 1929, pl. 4).

Dutuitosaurus gen. nov.

Metoposaurus (in part: Dutuit 1976, p. 164, Figs. 1–71, plates 5–34, 44–47, 51–63.)

INCLUDED SPECIES: The genus is only known from the type species.

TYPE SPECIES: *Dutuitosaurus ouazzoui* (Dutuit 1976) new comb.

ETYMOLOGY: For J. M. Dutuit the foremost scholar of metoposaurids in this century.

DISTRIBUTION: Late Triassic of Morocco.

DIAGNOSIS: Metoposaurid that differs from other members of the family, except *Apachesaurus*, in having presacral centra with a diameter:length < 0.8; differs from *Apachesaurus* in having a maxilla that

enters the margin of the orbit, posterior projection of occiput, separate ossified pleurocentra in the posterior trunk vertebrae, and a fused neural arch on the third presacral vertebra.

Dutuitosaurus ouazzoui (Dutuit 1976) new comb.

LECTOTYPE: MNHN XIII/18/66, nearly complete articulated skeleton (Dutuit 1976, pl. 33). The lectotype is the specimen on the right of the block.

TYPE LOCALITY: Locality XIII, Argana Formation, Morocco (Dutuit 1976).

TYPE HORIZON: Lower level of t5, Middle Series, Argana Formation (Late Triassic: early-late Carnian) Morocco (Dutuit 1976).

DISTRIBUTION: Argana Formation, Morocco.

REFERRED SPECIMENS: From the same locality as lectotype: MNHN AZA 276–60 (XIII-14/66), a complete skull; MNHN XIII/13/66, skull with lower jaw and partial vertebral column (Fig. 10C); Dutuit 1976, pl. 5); MNHN XIII/36/66, XI/16/66, XIII/14/66 (specimens), complete skulls (Dutuit 1976, pls. 6–10); MNHN XIII/14/66, two skulls and partial articulated skeleton.

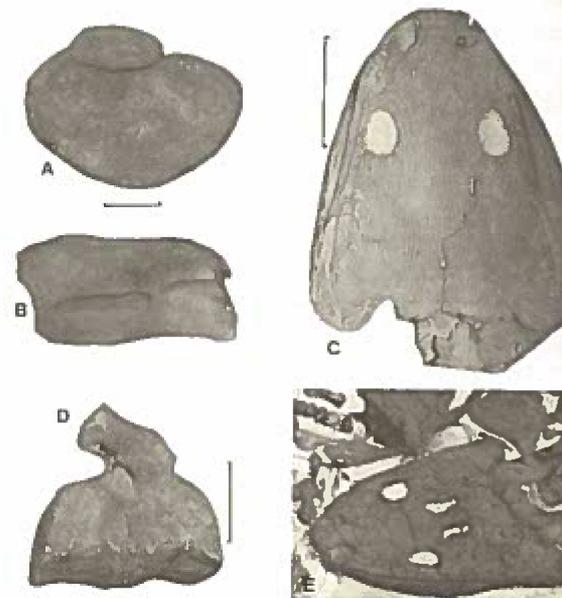


Figure 10. *Dutuitosaurus ouazzoui* (Dutuit 1976). MNHN AZA 177–3, posterior dorsal intercentrum and pleurocentra in posterior (A) and dorsal (B) views. C. MNHN XIII/13/66, skull, dorsal view. D. MNHN AZA 143, posterior dorsal intercentra, pleurocentra and neural arch. E. MNHN XIII/14/66, skull and associated postcrania in dorsal view. Scale bars: 2 cm for A, B, D and 10 cm for C.

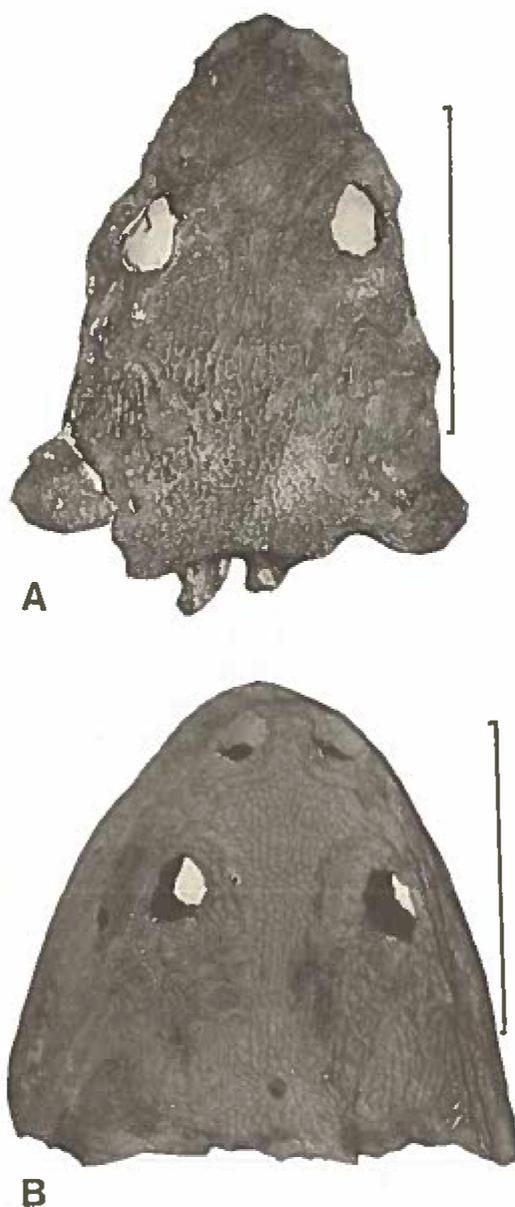


Figure 11. *Arganasaurus lyazidi* (Dutuit 1976). A. MNHN ALM 205. (XIX/3/66), lectotype skull in dorsal view. B. MNHN ALM 215. (XIX/8/66), skull in dorsal view. Scale bars are 10. cm.

Kalamoiketor. *Anaschisma* and *Dictyocephalus* are considered possible senior synonyms for *Apachesaurus* because of their supposedly shallow otic notches and *Kalamoiketor* because of its small size.

The supposed similarity of *Apachesaurus* to *Anaschisma* is based on the assumption, following Gregory (1980), that the illustrations of Branson (1905, Figs. 3a, 9) accurately portray shallow otic

notches in the holotypes of the two species *Anaschisma*. Unfortunately these rather poor specimens (FMNH UC 447, 448) have been heavily reconstructed, and in actuality the shape of the otic notch is not discernable in either specimen (Hunt 1989). Branson and Mehl's (1929, Figs. 6–7) figures are equally misleading in suggesting deep otic notches.

The holotype of *Kalamoiketor pinkleyi* (UM 554) consists of about 114 fragments of a relatively small temnospondyl skull from the Blue Member of the Petrified Forest Formation in the Grand Canyon (Fig. 17B). Branson and Mehl's (1929, Fig. 11) reconstruction is probably as accurate as could be. Unfortunately, UM 554 is undiagnostic at the family level. However, it does possess remnants of a deep otic notch, which indicates that it is not referable to *Apachesaurus*.

Leidy (1856, p. 256) named *Dictyocephalus* from the partial skull of a small labyrinthodont (width of pineal foramen 58 mm) from the Cummock Formation of North Carolina. This monospecific genus has been considered valid by most authors (Romer 1947, p. 317; Colbert and Imbrie 1956, p. 4; Davidow-Henry 1989, p. 290; Hunt 1989a, p. 2) and definitely does possess a shallow otic notch. The type specimen (AMNH 5661) has suffered from much damage since it was collected by Ebenezer Emmons (Fig. 17A). Four illustrations of this specimen show successive stages of disintegration. Emmons (1860, Fig. 162) illustrates a plate missing from the skull fragment extending from the orbits back to, and including, the occipital condyles. Baird (pers. comm. 1990) has an unpublished engraving done for Emmons in about 1856 that shows a smaller fragment missing from the occipital condyles and not extending forward to the orbits. Emmons (1860, Fig. 158.9) illustrates a slightly more damaged specimen with the same general outline. Finally, Colbert and Imbrie (1956, Fig. 1) and Davidow-Henry (1989, pl. 4G) illustrate the specimen in its present state—lacking the occipital region on the left side, much of the bone between the occipitals and the pineal foramen, and some bone anterior to this (Fig. 17A). None of these illustrations shows the fragments that lie to the sides of the main fragment or clearly shows the topography of the upper surface caused by lateral thrusting of various cranial bones over each other. The latter feature is noted by Colbert and Imbrie (1956).

In its present state, there are no features of AMNH 5661 to indicate that it represents a temnospondyl or belongs to any other temnospondyl.

right half of skull (Fig. 13E; Gregory 1980, Fig. 7.2; Lucas *et al.* 1985, Fig. 2A); NMMNH 16948, left posterior skull fragment (Fig. 13C); UCMP 63832, skull roof fragment; UCMP 63047, 66540, 65529, 63848, lower jaw fragments; UCMP 63849, interclavicle (Fig. 14A); UCMP 63854, interclavicle fragment; YPM uncatalogued (field no. 6649/1958/31), clavicle (Fig. 14D); UCMP 63851, clavicle fragment; UCMP 4212, YPM 4217 (Fig. 14B–C) ilia; UCMP 53001, YPM 4214–4216, 4219, limb bones; UCMP 65328, 65550, 65312 (Fig. 14I–J), 65417 (Fig. 14G–H), 65418, 65550 (Fig. 14E–F) NMMNH 17062, centra; UCMP 63856, 65545, YPM 4217, ribs; Revuelto Creek, Bull Canyon Formation, New Mexico, USA: NMMNH 16901, nearly complete skull; NMMNH 4669, lower jaw fragments; NMMNH 4589, 4670, 4855 17491, centra: Lacey Point, Painted Desert Member of the Petrified Forest Formation, Arizona, USA: UCMP 82/39/37, skull (Fig. 13H); Crosby County, Tecovas Member of Dockum Formation, Texas, USA; TTUP 9237, posterior margin of skull (Fig. 13D); Post quarry, Cooper Member of Dockum Formation, Texas, USA: TTUP 9216, skull and lower jaw (Fig. 13F).

ETYMOLOGY: For Dr. J. T. Gregory, who found the holotype and recognised it as a new taxon, for his contributions to Late Triassic vertebrate paleontology in the American Southwest.

DIAGNOSIS: As for genus.

DESCRIPTION: UCMP 63845 is a small, nearly complete, metoposaurid skull. The maximum width is 125 mm with a length of 164 mm from the back of the occipital condyles to the front of a skull that is truncated at the nares. The maximum height of the posterior of the skull is 44 mm.

The arrangement of the bones of the dorsal skull roof is similar to most metoposaurids except anterior to the orbits and along the posterior margin of the skull. The lachrymal is an elongate bone with maximum dimensions of 12 mm and 5 mm. The lachrymal does not enter the margin of the orbit or the external nares. The lachrymal is placed more laterally than in any other metoposaurids; the lachrymal flexure of the supraorbital canal of the lateral line system is placed well medial to it. The jugal and the prefrontal contact each other between the lachrymal and the orbital margin.

The posterior margin of the skull differs from other metoposaurids because of the configuration of the otic notch. The otic notch is wide and shallow (23 mm wide and 5 mm wide on the left side), and there is no development of a tabular horn. Because of the shape of the otic notch, the tabular is more square in outline than in other metoposaurids. The pineal foramen lies two thirds

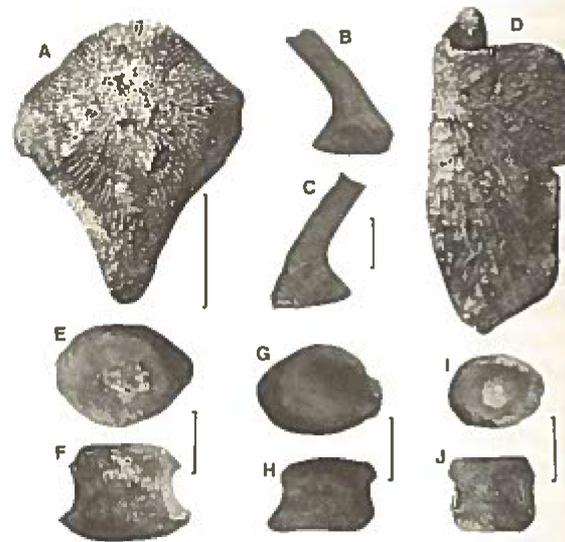


Figure 14. *Apachesaurus gregorii* gen. et sp. nov. A. UCMP 63849, interclavicle in ventral view. B–C. YPM 4217, ilium in external (B) and internal (C) views. D. YPM uncatalogued (6649, 1958/31), right clavicle in ventral view. E–F. UCMP 65550, dorsal intercentrum in anterior (E) and dorsal (F) views. G–H. UCMP 65417, dorsal intercentrum in anterior (G) and dorsal (H) views. I–J. UCMP 65312, dorsal intercentrum in anterior (I) and dorsal (J) views. Scale bars are 1 cm for A and D and 1 cm for B–C and E–J.

the way posterior from the front of the parietal bone. The sensory canals of the lateral line system are not well developed and do not form a complete ring around the orbits. Areas of rapid growth, indicated by grooves in the ornamentation, are poorly developed. In dorsal view, the occiput is only slightly visible.

In palatal view, the organisation of bones is generally typical of metoposaurids except for the width of the cultriform process of the parasphenoid which is broad anteriorly but narrows considerably in the posterior half. Thus, the width of the skull is divided by the minimum width of the cultriform process (Fig. 17). The occipital portion of the skull is not as well preserved as the skull roof or palate, but the arrangement of bones is similar to other metoposaurids. The skull in occipital view is very high and there is no elongate projection of the occipital condyles posteriorly as in other metoposaurids. The quadrate foramen, which has a maximum dimension of 17 mm, is only preserved on the right side.

The best lower jaw (UCMP 63847) is 151 mm long with a maximum height of 23 mm and exhibits no major morphological differences from other metoposaurid taxa. However, the lower jaw is noticeably slender proportionally than in other metoposaurids.

Metoposauridae indet.

- Metoposaurus fraasi* (Lucas 1904)
Anaschisma browni (Branson 1905)
Anaschisma brachygnatha (Branson 1905)
Metoposaurus stuttgartensis (Fraas 1913)
Metoposaurus jonesi (Case 1920)
Buettneria (?) major (Branson and Mehl 1929)
Metoposaurus heimi (Kuhn 1932)
Metoposaurus azerouali (Dutuit 1976)

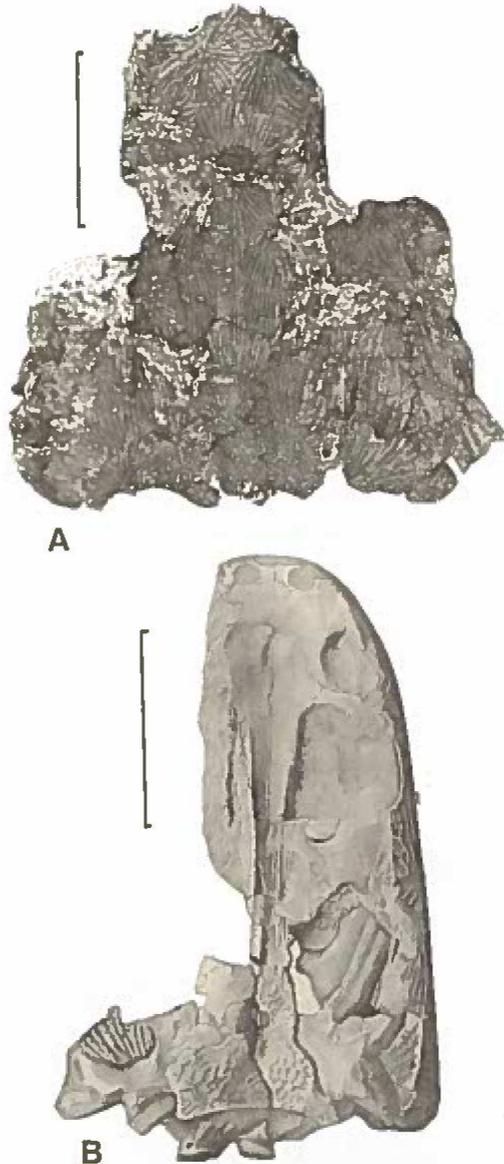


Figure 16. ?Metoposauridae indet. A. IMGPUT, dorsal view of lectotype skull of *Metopias santaecrucis* Koken 1913. (photograph courtesy of F. Westphal, IMGPUT). B. IMGPUT, dorsal view of fragmentary skull of *Metopias santaecrucis* Koken 1913. (from Koken 1913). Scale bars are 10 cm.

DISCUSSION: All of the above taxa are nomina dubia based on skulls (e. g., *Anaschisma browni*; Fig. 15A) or portions of pectoral girdles that are assignable to the Metoposauridae but lacking apomorphies or enough characters to further assess their relationships.

Dutuit (1976) did not designate a holotype for *Metoposaurus azerouali*. Here, I designate a new complete skull (MNHN XV/1/65 D.1) as the lectotype of *M. azerouali* (Fig. 15B). The skull is damaged in a number of areas, notably in the anterior area, and it preserves no diagnostic features. Associated clavicles and interclavicle (MNHN XV/2/65) are designated paralectotypes. None of these specimens are diagnostic below the family level.

Family ?Metoposauridae

Metoposaurus santaecrucis (Koken 1914)

M. santaecrucis (Fig. 16; uncatalogued IMGPUT specimens) does not actually possess an apomorphy of the Metoposauridae but it does have anteriorly placed orbits (though the margins are absent) and a wide cultriform process. However, the ornamentation pattern is very fine and reminiscent more of cyclostosaurs. This taxon is tentatively assigned to the Metoposauridae as a nomen dubium. Koken (1913) did not designate a holotype of this taxon. Here, a skull fragment showing most of the dorsal surface (Fig. 16A; Koken 1914, pl. 1) is designated as the lectotype of *Metopias santaecrucis*.

Temnospondyli indet.

- Dictyocephalus elegans* (Leidy 1856)
Eupelor durus (Cope 1866)
Calamops paludosus (Sinclair 1917)
Kalamoiketar pinkleyi (Branson and Mehl 1929)
Metoposaurus ultimus (Kuhn 1932)
Trigonosternum latum (Schmidt 1931)
Bogdania fragmenta (Yang 1978)
Metoposaurus hoffmani (Dutuit 1978)

DISCUSSION: the taxa listed above have holotypes that are not assignable to the Metoposauridae. Cope (1866) named *Mastodonsaurus durus* for "cranial bones" and referred to it teeth of a labyrinthodont from the Lockatong Formation of Phoenixville town in Chester County, Pennsylvania, USA. No holotype was designated though Baird (1986) notes that AMNH 3927 bears a label in Cope's handwriting.

that all the mainly short-faced temnospondyls (including the Trimerorhachoidea, Trematosauridae, Brachyopidae, and Metoposauridae) might represent one large evolutionary radiation. Shishkin (1973) erected a new suborder, Colosteiformes, for most short-faced temnospondyls, except plagiosaurs, that included the superfamily Trimerorhachidea, which in turn included the families Metoposauridae, Trimerorhachidae, and ?Eobrachyopidae (Saurerpetonidae of most authors). Shishkin (1984) has reaffirmed his support for this taxonomy, but it has not been widely accepted (e. g., Carroll 1988). Several authors believe that colosteids are not even temnospondyls (e. g., Milner 1990). Dutuit (1976) maintained that there was a close relationship between the metoposaurids, plagiosaurids, and brachyopids. Warren and Black (1985) placed the Metoposauridae in their capitosaurian lineage. However, this phylogenetic study relied entirely on Triassic taxa and ignored Paleozoic taxa and thus is of little utility. Milner (1990), in the first comprehensive phylogenetic analysis of the Temnospondyli, places the Metoposauridae as a sister taxon to the Laticopidae—and both as a sister group to the Trematosauridae.

One result of a phylogenetic analysis of Metoposauridae (Fig. 18) shows that the group is undoubtedly monophyletic, few would have expected otherwise. The internal relationships of the Metoposauridae are not totally clear, but the most parsimonious cladogram is shown in Figure 18. *Metoposaurus* and *Buettneria* are the most closely related taxa.

I find it impossible to adequately assess the phylogenetic relationships of the family Metoposauridae based upon the literature. From this study, it is obvious that much of the older literature is at best misleading and at worst inaccurate. Temnospondyl phylogeny is particularly difficult to analyse phylogenetically (e. g., Warren and Black 1985; Morales 1987) because of the conservative nature of the skull and hence a paucity of potential characters and also because of presumed

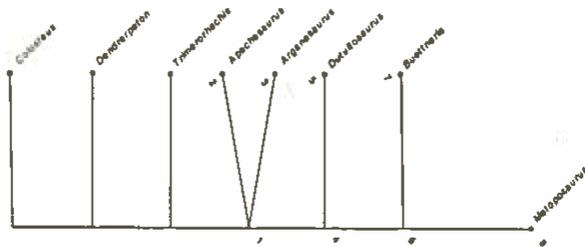


Figure 18. Phylogenetic relationships of metoposaurid taxa. Characters at each node are discussed in text. Nodes are: 1, 1B, 2B, 3B, 4B, 5B, 6B, 7B, 8A, 9B, 10B, 11A, 13A, 14A, 15A, 16B, 17B, 18B, 19B; 2, 2A, 12C, 13B; 3, 9A, 12B; 4, 12A; 5, 8B, 17A, 19A; 6, loss of 18B; 7, 10A, loss 10B; 8, retain 10B.

widespread heterochrony and parallelism. I therefore present two totally incompatible hypotheses of relationships of the Metoposauridae (Figs. 19, 20); one or other could be shown to be correct, it would affect the choice of outgroups for the phylogenetic analysis.

The first hypothesis has its basis in the ideas of Save-Soderbergh and Shishkin and the earlier paper of Romer. It accepts that there is a true phylogenetic relationship between many of the short-faced temnospondyls (Fig. 19). Wilson (1941) explicitly criticized the hypothesis of a close relationship between Metoposauridae and the Trimerorhachidae that has been suggested by Save-Soderbergh (1935). These criticisms were recently addressed by Chorn (1984) in the course of the description of a new trimerorhachid. Wilson (1941) noted that *Trimerorhachis* did not possess ossified prootics or epipterygoid, which are primitive features retained by metoposaurids. These ossified elements are present in the new trimerorhachid (currently not formally named), and the prootic is present in *Trimerorhachis* (Chorn 1984). Wilson (1941) also suggested that the internal carotid artery entered the braincase anterior to the basicranial articulation.

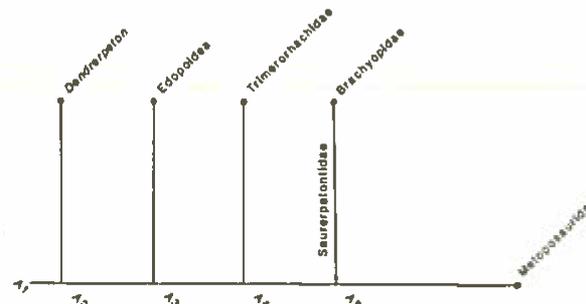


Figure 19. First hypothesis of the phylogenetic relationships of the Metoposauridae. Nodes are: A1. distinct interpterygoid vacuities bordered by triradial pterygoids, struts parasphenoid with long cultriform process overlapping suturing with vomers and with a broad, flat, basal process; broad flat vomers, ribs straight or slightly curved in lateral view; A2. pterygoids no longer form the entire margin of the interpterygoid vacuities and vomers contribute (Godfrey et al. 1987); A3. loss of entepicondyle on humerus, rodlike stapes; A4. broad cultriform process, reduced squamosal embayment, short antorbital region, anterior palatal fenestrae, symphyseal tusks, moderate interpterygoid vacuities (Godfrey et al. 1987; Foreman 1990); A5. quadrate anterior to occipital condyle, occipital slopes back to occipital condyle, accessory teeth reduced, palatal elements, occipital condyles have longest axis horizontal not inclined, high coronoid process, vagus nerve passes through notch outside of exoccipital notch through foramen (Shishkin 1966, 1991, pers. comm. 1991).

There are no strong synapomorphies shared by the Laticopidae and the Metoposauridae, and they are only closely related if the second hypothesis outlined above is correct.

In conclusion, the proposed hypotheses of metoposaurid relationships appear equally parsimonious at our present level of knowledge. More work must be undertaken on temnospondyl phylogenetics before the relationships of this family can be firmly established.

Supposed Middle Triassic Metoposaurids

There are four possible occurrences of metoposaurids in Middle Triassic strata. *Trigonosternum latum* was named for a partial interclavicle from the late Ladinian Lettenkohle of southern Germany (Schmidt 1931). Colbert and Imbrie (1956) rightly noted that the definition of this taxon (essentially as having a broad, short interclavicle) is based on a misinterpretation of the holotype. Colbert and Imbrie (1956) noted that if the holotype is rotated 90° from its orientation in Schmidt's figures (pl. 4, Fig. 20), it is obvious that it is a piece of a "normally proportioned" temnospondyl interclavicle. This specimen is both generically and familialy indeterminate.

SMNS 55385 is a putative metoposaurid skull and lower jaws, also from the Lettenkohle of southern Germany (Kugler and Bartholoma 1985; Morales 1988), under study by M. Morales. This specimen possesses none of the metoposaurid synapomorphies listed above and, in contrast, possesses characters not found in the Metoposauridae as defined here, including a strongly keeled cultriform process (Morales 1988), triangular-shaped skull, large orbits, and a very deep lower jaw. In all these characters, SMNS 55385 is more similar to laticopids such as *Almasaurus habbazi* (Dutuit 1976, pls. 60–68) and *Laticopsis disjunctus* (Wilson 1948, Figs. 1–4). However, a more definite assessment of the relationships of this specimen must await further study of this specimen. In conclusion, this specimen is probably a laticopid.

Gregory (1917) noted that E. C. Case had collected fragmentary vertebrate fossils from the upper Moenkopi Formation (?Spathian-early Anisian) near Holbrook, Arizona, USA. Case identified one of the specimens as a fragmentary interclavicle of *Metoposaurus* close to *Metoposaurus frassi* (sic) (Gregory 1917, p. 35). However, the provenience of the specimen is suspect since the Upper Triassic Shinarump Formation also occurs at this locality (Gregory 1917; Morales 1987c; Welles, pers. comm. 1990). The

identification must also be considered suspect if there are no other metoposaurid specimens among hundreds of temnospondyl bones from the Moenkopi (Morales 1987c). The interclavicle fragment is apparently not extant and was not illustrated or described. Furthermore, a capitosaur interclavicle could easily be mistaken for a metoposaurid interclavicle if it were in a fragmentary condition. (M. Morales, pers. comm. 1990).

Dr. S. P. Welles of UCMP has kindly given me copies of his notes and illustrations of another possible metoposaurid of Middle Triassic age. This specimen (UMZC F. R. Parrington collection no. # 138) is a fragmentary, large interclavicle from the Anisian-Ladinian Manda Formation of Tanzania. This specimen has a maximum preserved breadth of 235 mm and a maximum length of 240 mm. This specimen is unusually large for a Middle Triassic temnospondyl, but it is possible that this large specimen could equally well represent a metoposaurid or a mastodonsaurid. There is much postcranial material that has been assigned to mastodonsaurids (e. g., Fraas, 1889; Huene 1911), but much of it only on the basis of size, and this family is in much need of revision (Milner *et al.* 1990). However, it is likely that even with more study of mastodonsaurid postcrania the Manda specimen will remain indeterminate. In conclusion, there is no unequivocal evidence for the presence of metoposaurs in the Middle Triassic. However, phylogenetic hypotheses outlined above predict the presence of metoposaurids in the Middle Triassic.

Distribution and biochronology

Introduction

Metoposaurids historically have been of little biochronological utility (but see Hunt 1989c). However, with a rigorous new taxonomy for metoposaurids, their utility needs to be reevaluated (Fig. 21).

Europe

Metoposaurids are only known with certainty from Germany and Austria. *Metoposaurus diagnosticus* is restricted to the Schilfsandstein of Württemberg, Germany. Indeterminate metoposaurid postcrania are known from the Lehrbergschichten (*Metopias stuttgartensis*). Recently, a new skull (SMNS 56633) has been found in this stratigraphic unit and is under study by me. There are other indeterminate metoposaurids from the Blasensandstein of southern Germany (*Metoposaurus beimi*) and from Heiligenkreuz, Austria. The Blasensandstein contains the phytosaur *Paleorhinus* and is of the *Paleorhinus*-biochron age (early late Carnian; Hunt and Lucas 1991). The Lehrbergschichten is s

age (Lucas 1990). The fact that *Paleorhinus* is absent in the upper t5 and that no genera are held in common between the upper and lower faunas suggests that the upper fauna may be of younger late-late Carnian age.

India

Buettneria perfecta occurs in the Maleri Formation of India. Kutty and Sengupta (1989) have recently shown that the Maleri contains two distinct faunas. The lower fauna includes *Buettneria perfecta* (specimens assigned to *Metoposaurus maleriensis*), *Hyperodapedon* (*Paradapedon*; Benton 1983) and *Paleorhinus* (*Parasuchus*; Hunt and Lucas 1991). The presence of *Paleorhinus* indicates that this fauna is of early-late Carnian age (*Paleorhinus* biochron of Hunt and Lucas 1991). The upper fauna includes chigutisaurids, a "*Rutiodon*-like form", an *Angistorhinus*-grade phytosaur, and a dicynodont (Kutty and Sengupta 1989). The affinities of the phytosaurs and the presence of a dicynodont suggest a *Rutiodon* biochron age (late-late Carnian; Hunt 1991b). Metoposaurids only occur in the lower fauna (Kutty and Sengupta 1989).

Conclusions

The ranges of the Metoposauridae are: *Metoposaurus diagnosticus*, early-late Carnian; *M. bakeri*, early-late Carnian; *Arganasaurus*, late-late Carnian; *Buettneria*, early-late Carnian to late-late Carnian; and *Apachesaurus*, early-late Carnian to Rhaetian. *Buettneria* and *Metoposaurus* are the only genera to occur on more than one modern continent, and it is clear that metoposaurids did not have as wide a geographic ranges as sympatric phytosaurs. This is possibly a result of the fact that phytosaurs were undoubtedly semiaquatic, whereas metoposaurids were probably confined largely to aquatic environments.

Paleoecology

Metoposaurids generally have been perceived as very inactive animals lying on the bottom of lakes or rivers in wait for prey to swim into their mouth (Colbert and Imbrie 1956; Gregory 1972; Murry 1989b). A number of factors argue against this scenario. Several authors have discussed the problem of how a large animal with weak limbs could open its mouth when the lower jaws rest on the substrate and how the animal could see its prey if it opened its mouth by raising its skull (Howie 1972; Chernin 1974; Chernin and Cruickshank 1978). These problems are solved if metoposaurids were mid-water feeders (cf. capitosaurs; Chernin and Cruickshank 1978).

Several morphological features of metoposaurids also suggest a more active lifestyle. The hydrodynamic shape of the metoposaurid body in longitudinal profile (Long *et al.* 1989, Fig. 2; cf. Chernin and Cruickshank 1972), the lateral placement of the orbits, the increased ossification of the vertebral elements, and the deep body profile (Dutuit 1976, Fig. 85) all suggest an actively swimming mid- upper water feeder. It is interesting to note that Hunt (1989b) suggested that, by analogy with modern crocodilians, the broad U-shaped and flattened skull of metoposaurids indicated that they may have filled the one modern "crocodilian" niche not filled by phytosaurs, namely that of the generalist feeder. Their closest living analog may be the caiman or American alligator. However, poorly ossified lateral bones, strongly braced skull, and well-developed lateral line system all indicate that metoposaurids probably spent most of their life in the water (Case 1937; Bystrow 1947; Olsen 1951) and thus were more aquatic than caimans. This is generally supported by the faunas that are taphonomically associated with metoposaur remains, which are predominantly composed of semiaquatic phytosaurs. However, sites that yield abundant specimens of *Apachesaurus* are always anomalously rich in terrestrial animals (dinosaurs, rauisuchians, sphenosuchians) such as Lacey Point in Petrified Forest National Park (Parrish 1989), quarry 2 in Apache Canyon, and the main quarry at Revuelto Creek (NMMNH L-0001)—both in Quay County, New Mexico. As noted in the taxonomic section, the structure of the ilium and the relatively poorly developed lateral line system suggest that *Apachesaurus* was less aquatic than other metoposaurids. Given the small body size of *Apachesaurus* and its faunal association, it is probable that it inhabited small bodies of water where large aquatic animals were absent.

Dutuit (1983) suggested that metoposaurids might have migrated along saline seaways. Subsequently DeFauw (1989), followed by Milner (1990), has suggested that metoposaurids were fully aquatic and euryhaline. DeFauw (1989) does not explicitly state why she considers metoposaurids to be euryhaline but she states four features that unite her fully aquatic euryhaline ecomorph: (1) heavily incised, continuous lateral line system; (2) reduction in the ossification of the vertebral elements; (3) poorly ossified small limbs; and (4) occur in neritic environments and some are found with fish, ammonites, and marine reptiles. The first three of these features are irrelevant to a euryhaline model, but it is worth noting that metoposaurids do not have continuous lateral line systems and that they have increased rather than reduced ossification

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