COMMENTS ON THE TAXONOMY OF NORTH AMERICAN METOPOSAURS AND A PRELIMINARY PHYLOGENETIC ANALYSIS OF THE FAMILY METOPOSAURIDAE

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Abstract- The Late Triassic metoposaurid Anaschisma has a shallow otic notch. The placement of the lachrymal relative to the orbit is a taxonomically important character. Metoposaurus diagnosticus is the only metoposaur in which the clavicles are united along a common edge anterior to the interclavicle. All metoposaurs except M. ouazzoui lack pleurocentra. A small metoposaur from the American Southwest has been referred to Anaschisma and Dictyocephalus, but it represents a new taxon. Phylogenetic analysis indicates that the metoposaurs are in need of taxonomic revision.

INTRODUCTION

Like phytosaurs, metoposaurs were first described early last century from finds in the Upper Triassic of Germany (Meyer, 1842). The first generic name applied, Metopias, was preoccupied this was replaced by Metoposaurus by Lydekker (1890). Metoposaurs are abundant in some Late Triassic strata of the American Southwest and are also known from Europe, North Africa, India and China. However, no taxonomic review of this important group has been undertaken for over 40 years. The purpose of this paper is to review briefly some aspects of the taxonomy of North American metoposaurs and to present a preliminary phylogenetic analysis of the group.

THE TAXONOMY OF NORTH AMERICAN METOPOSAURS

History of Study

Leidy (1856) was the first to identify and name a metoposaurid (Dictyocephalus) from the Late Triassic of North America, although Metoposaurus diagnosticus was already well known from Germany. Later in 1866 and 1868, Cope described Eupelor, which like Dictyocephalus was from the Newark Supergroup of the eastern United States. The first metoposaur material to be described from the western states was an interclavicle from the Chinle Formation of northwestern Arizona (Lucas, 1904), although Cope (1893) had noted Eupelor in Texas. The next year Branson described the genus Anaschisma based upon two skulls from the Popo Agie Formation in Wyoming. Soon after that Case, (1920) described an interclavicle and clavicles from the Dockum Group of West Texas. In 1922, Case described the first well-preserved cranial material of a metoposaur from the New World as a new genus Buettneria.

Subsequently, many good metoposaur specimens have been collected from New Mexico and Texas, and to a lesser extent from Arizona and Wyoming (Branson and Mehl, 1929; Case, 1931, 1932;

Romer, 1939; Sawin, 1945; Colbert and Imbrie, 1956; Davidow-Henry 1989). Several apparently well-preserved skulls have been found in the last twenty years in strata of the Newark Supergroup, but none have been described (Baird, 1986).

Branson and Mehl (1929) provided the first review of the metoposaurs of North America. They recognised five genera from the western United States, Anaschisma, Buettneria, Borborophagus, Koskinonodon and Kalamoiketor, the latter three being named in that paper. Case (1946) and Romer (1947) both reviewed the genera of metoposaurs. Case (1946) accepted as valid the above five genera. However, Romer (1947) suspected that Anaschisma, Koskinonodon and Borborophagus were congeneric and that Dictyocephalus and/or Anaschisma was a senior synonym of Buettneria.

Colbert and Imbrie (1956) reviewed the metoposaurids and recognized one genus in the western United States, Eupelor, with two species, one of which was divided into two subspecies. The three taxa from the Popo Agie Formation of Wyoming (Anaschisma, Borborophagus and Koskinonodon) were synonymized as Eupelor browni. Buettnaria species, except B. major, became Eupelor fraasi jonesi and Kalamoiketor and B. major became Eupelor fraasi fraasi. Roy Chowdhury (1965) placed all the Eupelor species of Colbert and Imbrie (1956) in the genus Metoposaurus. Gregory (1980) divided the metoposaurs into two genera, Anaschisma for forms with shallow otic notches and Metoposaurus for forms with a deep notch. Davidow-Henry (1989) places shallow-notched specimens in Dictyocephalus.

The Otic Notch of Anaschisma

Much confusion in metoposaur taxonomy stems from interpretion of the form of the otic notch of Anaschisma. Anaschisma was named by Branson (1905), who erected two species A. browni and A. brachygnatha. Branson (1905) included photographs and drawings of the two holotypes that showed broad shallow otic notches. Branson and Mehl (1929, p. 44) re-examined the material and stated that "the posterior margin has been broken from both skulls so as to present a regular edge rather than a notched outline. In one skull a short section of the "finished" margin at the base of the notch is preserved and indicates clearly the location of the incision." Thus, they concluded that Anaschisma had a deep otic notch like Buettneria (Branson and Mehl, 1929). Case (1946), Romer (1947) and Colbert and Imbrie (1956) followed Branson and Mehl (1929) in reconstructing Anaschisma with a deep otic notch. Gregory (1980) preferred to believe the illustrations of Branson (1905) and considered that Anaschisma had a shallow otic notch. This view is followed by Davidow-Henry (1989) and Baird (1986).

The holotypes of the two species of Anaschisma are in the Field Museum of Natural History (FMNH). Both the skull of A. browni (FMNH UC 447) and that of A. brachygnatha (FMNH UC 448) have damaged posterior margins. However, both skulls have been skillfully reconstructed so that it is impossible to detect this repair in photographs and thus it is impossible to judge the

shape of the otic notch from illustrations (cf. Gregory, 1980). The posterior margin of A . browni is totally reconstructed. The only fragment of a posterior margin preserved in the area of the otic notch in either specimen is an approximately one-cm-long segment of the left posterior margin of A. brachygnatha. The preserved margin includes part of the squamosal adjacent to the tabular. This specimen is currently under study, but preliminary assessment suggests that the otic notch of Anaschisma was shallower than in Buettneria-like skulls, perhaps like that of Metoposaurus lyazidi (Dutuit, 1976, plate 49A).

The Relationship of the Lachrymal to the Orbit

Romer (1947) was the first to notice that the German genus Metoposaurus was distinct from all American metoposaurs in excluding the lachrymal from the orbit. Colbert and Imbrie (1956) also noted this difference. However, Roy Chowdhury (1965) pointed out that a population of metoposaur skulls from Scurry County, Texas, assigned to Buettneria bakeri by Case (1932), consisted entirely of forms with the lachrymal excluded from the orbit. Roy Chowdhury (1965) argued that this must be a variable character as it is not displayed by all Buettneria skulls. Therefore, he included all the Eupelor skulls of Colbert and Imbrie (1956) in Metoposaurus. However, the quarry sample described by Case (1932) is consistent in this character, and several other large quarry samples of Colberts and Imbrie's (1956) Eupelor taxa show no variation in the placement of the lachrymal. Thus, it appears more parsimonious to assume that the relationship between the lachrymal and the orbit is taxonomically important.

Dutuit (1976, p. 49) considered the lachrymal position to be a poor taxonomic character as it was difficult to determine in many specimens. However, there are so few taxonomic differences among metoposaurs that it it is not reasonable to discard a apparently important character, especially as it can be recognized in most well-preserved skulls.

Configuration of the Clavicles

Lydekker (1890, p. 153) noted in his diagnosis of Metoposaurus sensu stricto, "lateral plates (clavicles) meeting in a long suture in advance of the median plate [interclavicle]." This feature is evident in articulated specimens of Metoposaurus diagnosticus (e.g., Fraas, 1896, plate 2; 1911, plate 15) and is in marked contrast to all North American taxa (e.g., Case, 1920, plate 1; Sawin, 1945, fig. 9). The Buettneria specimens from Scurry County, which are similar to Metoposaurus diagnosticus in the lachrymal condition, have clavicles like other American forms (Case, 1922). Metoposaurus diagnosticus is unique in its clavicular configuration.

Vertebral Form

Romer (1947) noted that metoposaur vertebrae are distinctive in having fully ossified centra, which are solid discs with no

room for pleurocentral elements. Romer (1947) also pointed out that at least one Metoposaurus diagnosticus specimen from Germany had intercentra consisting of hemicylinders. However, Fraas (1889, plate 11, figs. 5-7) illustrated a "typical" metoposaur intercentrum for Metoposaurus diagnosticus, and it is probable that the specimen referred to by Romer (1947) is a juvenile as he. All large North American metoposaurs have intercentra that are simple shallow discs (e.g., Anaschisma: Branson, 1905, fig. 5, no. 2, 5; Buettneria bakeri: Case, 1932, plate 5, fig. 3; Buettneria howardensis: Sawin, 1945, fig. 7).

There is, however, a small metoposaur, found in the Chinle, Bull Canyon and "Cooper" formations of Arizona, New Mexico and Texas, that has very different intercentra. These centra are distinct in having a length that is subequal to their height, in marked contrast to the shallow discs of other American forms. This taxa is discussed further below.

There is one other metoposaur that has elongate intercentra and that is Metoposaurus ouazzoui from Morocco (Dutuit, 1976, fig. 37). This taxon is distinct from all other metoposaurs in retaining pleurocentral elements (Dutuit, 1976) and thus probably represents the most "primitive" metoposaur.

The New Small Metoposaur From The Southwest

Specimens of this animal were collected in the 1930's by Camp from the Placerias quarry in Arizona and subsequently by Gregory from Apache Canyon in New Mexico in the late 1950's and early 1960's and a variety of other workers in the last ten years (e.g. Bolt, Long, Murry in the Chinle Formation; Hunt in the Bull Canyon Formation; Chatterjee, Davidow-Henry in the "Cooper" Formation). This animal is represented by a number of skulls, several with associated postcrania (Davidow-Henry, 1989; Hunt and Lucas, 1989) and is currently under study by the author. This animal is rare in the lower Petrified Forest Member of the Chinle and its equivalents, whereas Buettneria/Eupelor is common and the representation is reversed in the upper Chinle and equivalents.

Gregory (1980) described the first material of this taxon and assigned it to Anaschisma n. sp. Susequently this metoposaur has been considered to represent a new species of Anaschisma (Lucas et al., 1985; Murry, 1989; Milner, 1989), Kalamoiketor (Murry and Long, 1989) or Dictyocephalus (Davidow-Henry, 1989). However this new taxon differs from Anaschisma in having elongate intercentra, from Dictyocephalus and Anaschisma in exclusion of the lachrymal from the orbit and from Kalamoiketor in having a shallow otic notch. The new animal is not a juvenile of a large Buettneria-like form. A collection of over 1000 identifiable vertebrate fossils at New Mexico Museum of Natural History from the Bull Canyon Formation of eastern New Mexico contains only two questionable fragments of a metoposaur with a skull length greater than 25 cm. This strongly suggests that the new small amphibian is not a juvenile. Furthermore, the elongate intercentra indicate it could not be a juvenile of any currently known taxon.

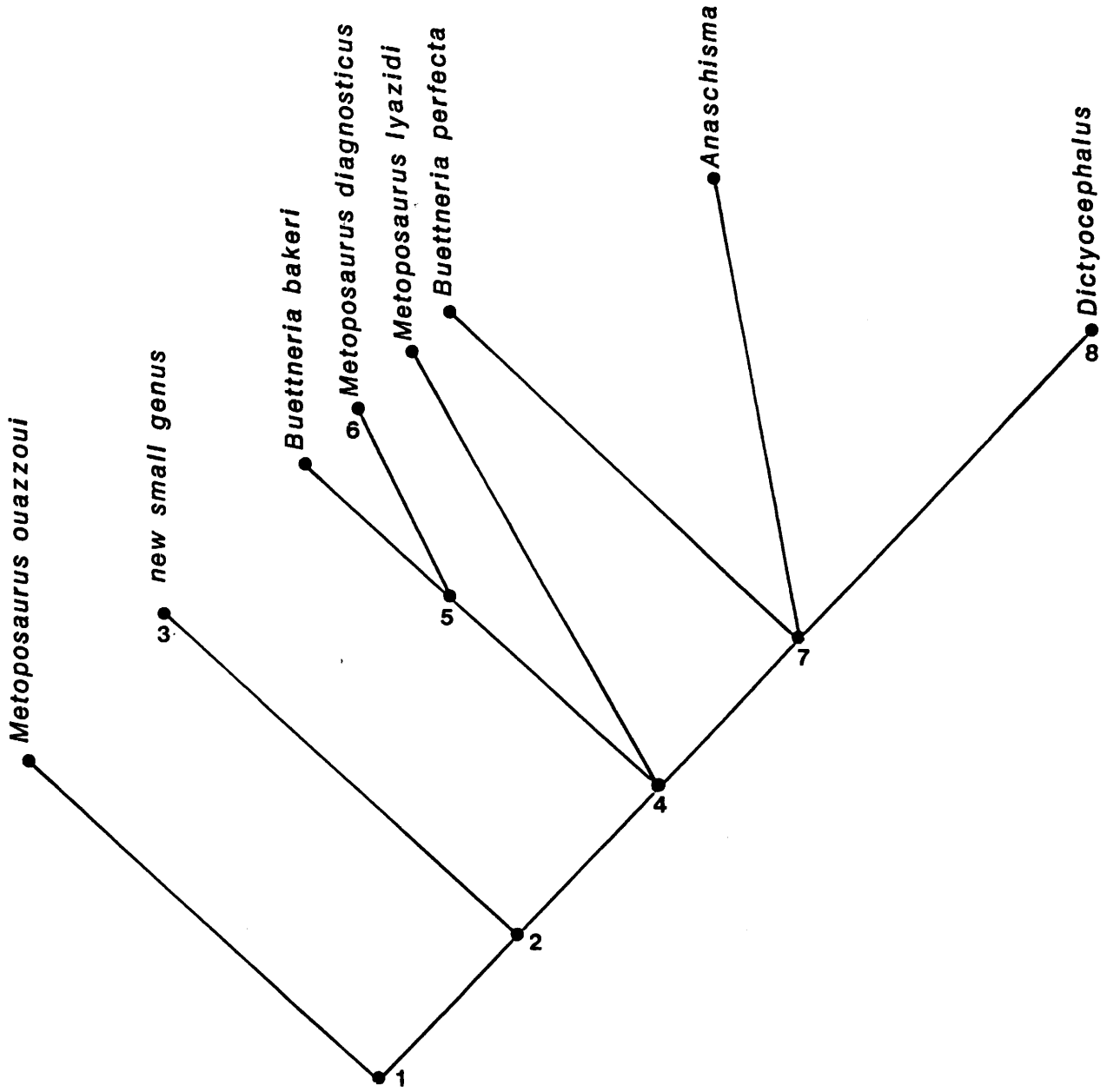

FIGURE 1. Cladogram of metoposaurid amphibians. Nodes are defined by the following characters:
1. Lachrymal close to, but not in, orbit; elongate intercentra; pleurocentral elements present; otic notch deep; clavicles do not have long common margin anterior to the interclavicle.
2. Pleurocentral elements absent.
3. Otic notch shallow and rounded.
4. Intercentra short.
5. Lachrymal not close to the orbit.
6. Clavicles have long common margin anterior to the interclavicle.
7. Lachrymal enters orbit.
8. Otic notch shallow and squared.

PRELIMINARY PHYLOGENETIC ANALYSIS OF THE METOPOSAURIDAE

The characters that have been discussed above, namely the placement of the lachrymal, the form of the intercentra, the shape of the otic notch and the arrangement of the clavicles form the basis for a phylogenetic analysis of the Metoposauridae (Fig. 1). This analysis is very preliminary, and actual specimens of only five of the taxa included have been examined; other information is from the literature. Certain obvious nomen dubia, such as Eupelor and Bogdania (Yang, 1978), are not included, and other species could not be distinguished using these characters. The cladogram assumes convergence of Anaschisma and M. lyazidi on the character of having an otic notch of intermediate depth.

What is immediately apparent from the cladogram is that current metoposaur taxonomy is badly in need of revision. Metoposaurus as used by all recent workers (e.g., to include Buettneria) is a polphyletic taxon of no utility. Hopefully, ongoing studies will clarify some of the many remaining problems in metoposaur taxonomy.

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