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Cacops (Amphibia: Labyrinthodontia) From the Fort Sill Locality, Lower Permian of Oklahoma

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ABSTRACT

The armored dissorophid (Superfamily Dissorophoidea) labyrinthodont amphibian *Cacops aspidephorus* is unusual in having a large otic notch closed posteriorly by the tabular. *Cacops* was previously known only from the "*Cacops* Bone Bed," Lower Permian of Texas. Poor preservation makes this material difficult to study. Excellently preserved, though disarticulated, *Cacops* material has now been recovered from the Fort Sill fissure fills, which are probably very close in age to the "*Cacops* Bone Bed." Identification of the Fort Sill material as *Cacops* is based on palatines (primarily), armor scutes, and quadrates; the latter are here described for the first time from Fort Sill. The *Cacops* quadrate resembles that of other dissorophoids in having a posterodorsal process, which is unusual in the marked anterior expansion of its dorsal end. Comparison with other dissorophoids having a closed otic notch shows that *Cacops* is not unique in this anterior expansion of the process. Orientation of the process can apparently be used to distinguish trematopsids with a slit-like, closed (by the tabular) otic notch, from dissorophids. At least one such trematopsid occurs at Fort Sill, and resembles *Cacops* in anterior expansion of the process.

Ontogeny of *Cacops* is discussed, and it is concluded that: 1. Closure of the otic notch by the tabular occured early in ontogeny; 2. Exclusion of the laterally-exposed portion of the palatine from the orbital rim, a feature unique to *Cacops* among known dissorophids, also developed early in ontogeny; 3. Growth-stages of *Cacops* available at Fort Sill were all probably post-metamorphic. All were dentitionally normal labyrinthodonts, with no trace of the "lissamphibian" dental features found in the related *Doleserpeton*. This may be due, however, to the fact that *Doleserpeton* is represented by less-mature specimens than is *Cacops*.

INTRODUCTION

Cacops aspidephorus is a large armored dissorophid amphibian. Dissorophids belong to the labyrinthodont Superfamily Dissoro-

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phoidea, consisting of Dissorophidae, Doleserpetontidae, and Trematopsidae (Bolt, 1969), plus Branchiosauridae and Micromelerpetontidae (Boy, 1972). All definitely identifiable *Cacops* material comes from the Lower Permian "*Cacops* Bone Bed" (hereafter CBB), Baylor County, Texas. The CBB was exhausted long ago, according to Williston (1911); in any case, it is now inaccessible beneath Lake Kemp.

Cacops material from the CBB includes three complete and several partial skulls. The skull is unusual in having the large otic notch closed posteriorly by a ventral extension of the tabular (fig. 1). This tabular extension meets a tall postero-dorsal process from the quadrate, and overlaps part of the lateral face of the process. Presence of a postero-dorsal process (hereafter abbreviated PDP) on the quadrate is common, perhaps universal, in dissorophoids (Bolt, 1969). In *Cacops,* however, the PDP is markedly expanded anterodorsally (figs. 1, 3, 4), a feature not known in any other dissorophoids. This unusual otic region and the skull as a whole, have never been well described due to the hard matrix of the CBB and the near-impossibility of tracing sutures in the available material.

Two localities other than the CBB have been mentioned as possibly producing *Cacops*. Olson (1956, p. 320) tentatively referred two humeri from his locality FA to *Cacops*. This identification cannot be confirmed; the humeri are probably dissorophid, but generically diagnostic characters in dissorophid humeri are not known at present. I have suggested the possible presence of *Cacops* at the Fort Sill locality, near Lawton, Oklahoma, based on scutes (detailed description and comparison in Bolt, 1974a) and a highly distinctive type of dissorophid palatine (briefly described in Bolt, 1974b). Positive identification was not possible at that time; possible ontogenetic changes in taxonomically important characters precluded definite identification using armor alone, even though the armor resembles that of *Cacops* quite closely. Evidence for assignment of the palatines to *Cacops* was only indirect, and thus inconclusive, because of the difficulty of tracing sutures in then-available CBB specimens.

In an effort to find suitable comparative material, preparation of the last of Williston's CBB collection was undertaken during this study. Several useful specimens of *Cacops* (among other genera) were discovered, including two separated palatines and a quadrate. Most of the CBB material has now been at least rough-prepared.

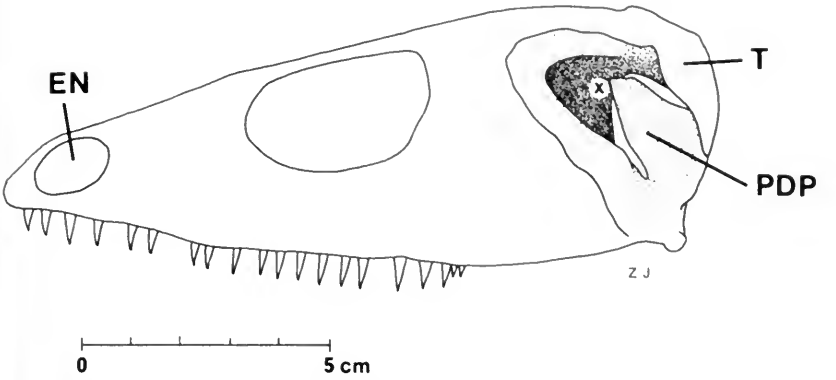

FIG 1. *Cacops aspidephorus* from the *Cacops* Bone Bed, FM UC 649. Outline drawing of skull in left lateral view; based on right side, reversed. Area within otic notch (shaded) is roughly cone-shaped, with base of cone directed laterally. Sutures within the otic notch are unknown, but most of the area anterior to the postero-dorsal process of the quadrate is occupied by the squamosal. Abbreviations: EN, external naris; PDP, postero-dorsal process of quadrate; T, tabular; X, location of distal end of stapes.

In addition to previously-reported material, possible *Cacops* quadrates have now been identified at Fort Sill. This paper compares the CBB palatines and quadrates with those from Fort Sill, and concludes that the evidence supports identification of the Fort Sill specimens as *Cacops*. Although all Fort Sill *Cacops* material recovered to date is disarticulated, it is very well preserved and covers a considerable size-range; it can thus make a significant contribution to our knowledge of osteology and ontogeny in *Cacops*.

As a dissorophoid, *Cacops* is part of a radiation that may have given rise to some or all of the living amphibians (lissamphibians; this is a collective term which does not imply monophyly). The possibility of relationship was originally supported mainly by the presence of bicuspid, pedicellate (*sensu* Parsons and Williams, 1962) marginal and fang teeth in *Doleserpeton* (Bolt 1969). This genus, sole member of the Doleserpetontidae, is known only from Fort Sill. Similar dental features have recently been found in some dissorophids (Bolt, in press), and in *Doleserpeton* itself at least some of the palatal denticles are now known to be pedicellate (Bolt, ms.). A survey of dissorophoids for such "lissamphibian" characters is desirable, but very difficult with most types of preservation. The fine preservation of Fort Sill specimens has made it possible to study the palatine denticles of *Cacops;* and, as explained below, the morphology of marginal teeth can at least be inferred.

"Skull length" in this paper refers to length as measured in the midline and in the plane of the skull table. Measurements were taken between the tip of the snout and the posterior ends of the postparietals on the skull table.

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MATERIALS

Specimen repositories are indicated as follows: AMNH—American Museum of Natural History; FM—Field Museum of Natural History; KU—Kansas University Museum of Natural History; MCZ—Museum of Comparative Zoology, Harvard University.

The Fort Sill locality is a commercial limestone quarry in SW¼ section 31, T4N, R11W, Comanche County, Oklahoma. Quarry operations periodically expose clay-filled fissures, some of which contain great numbers of small tetrapod bones. The fissure fills are discarded as waste by the quarry operators, and most specimens recorded from Fort Sill have come from the clay dumps. The age of the fissure fills is unquestionably Lower Permian, and probably close to that of the Arroyo Formation of Texas (Olson, 1967). Bones from Fort Sill are usually disarticulated, but otherwise excellently preserved.

The CBB is on Indian Creek in Baylor County, Texas. The fauna is of Lower Permian age; according to Olson (1958), the CBB is in either the upper Arroyo formation or the lower part of the Vale. The original size of the pocket was about 6 ft. by 10 ft., and 2 ft. thick (Williston, 1910, 1911).

MORPHOLOGY AND COMPARISON

Palatine—Dissorophid palatines from Fort Sill, tentatively referred to *Cacops,* were described and figured previously (Bolt, 1974b, text-figure 8); the figure is reproduced here in Figure 2. These palatines have a laterally-exposed portion (LEP), as do most (perhaps all) dissorophoids. A unique feature is exclusion of the LEP from the orbital rim. This presumably occurred by means of a secondary union of the lacrimal and jugal dorsal to the LEP. Two partial skulls from the CBB (FM UR 2431 and UC 900) show a LEP shaped like that in Figure 1, with a sutural separation between the LEP and bone dorsal to it. The orbital rim is not preserved in

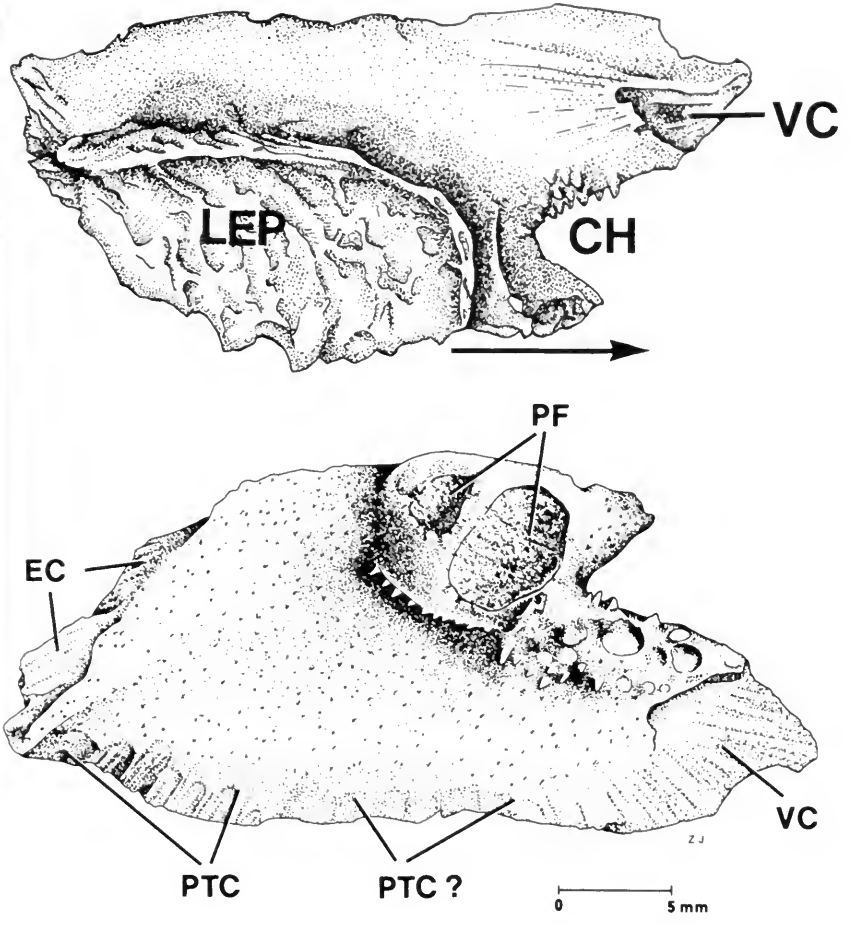

FIG 2. Right palatine of *Cacops*, from the Fort Sill locality; FM PR 1034. Top, in dorsolateral view; arrow indicates anterior. Bottom, in palatal view. Large denticles occur medial and anterior to the fang teeth; small denticles (indicated only schematically) cover most of the palatal surface. Abbreviations: CH, area bordering choana; EC, contact area for ectopterygoid; LEP, laterally-exposed portion of palatine; PF, area occupied by fang tooth (two such areas are shown); PTC, contact area for pterygoid; VC, contact area for vomer.

either case, but the LEP was clearly excluded from it. Similarly, two parallel cuts 5 mm. apart through the orbital floor of FM UR 2430 show a LEP outlined by sutures and separated from the orbital rim by bone. Finally, a separated palatine (FM UR 2433) recently recovered from the CBB collection very closely resembles the Fort

Sill palatines in shape of the LEP and its apparent exclusion from the orbital rim. A second *Cacops* palatine from the CBB (FM UR 2432) is exposed only in ventral view.

Thirteen *Cacops*-like palatines are presently known from Fort Sill. The largest, FM PR 1034, is complete (fig. 2) and about 3.5 cm. long. This is about the same size as the separated palatines from the CBB; exact comparison is impossible, since the thin anterior and posterior portions of both CBB specimens are apparently somewhat damaged. Most of the Fort Sill specimens are broken, some consisting of little more than the LEP. The smallest measurable specimen is about 2.3 cm. long, and is considerably smaller in all dimensions than the CBB palatines. Some of the less-complete specimens were much smaller, probably about a centimeter long. The LEP is similarly-shaped in all Fort Sill palatines, and was clearly not exposed within the orbit.

Most of the ventral surface of each *Cacops*-like palatine from Fort Sill is covered with monocuspid denticles (fig. 2); preparation has necessarily removed denticles from the CBB specimens, so no comparison is possible. No trace of pedicely is visible in the Fort Sill specimens. This was confirmed by examining a small palatine with the scanning electron microscope. The denticles are largely intact, but show no trace of pedicely.

The palatal surface shows clear contact areas for the ectopterygoid (presumably) and vomer (fig. 2). At least the posterior part of the pterygoid contact area is coarsely striated; the original description (Bolt, 1974b) concluded that the pterygoid did not extend much beyond that area, and thus did not reach the vomer. This conclusion now seems less probable; the very thin medial border of the palatine suggests that it may have been supported along its length by a narrow anterior extension of pterygoid. The CBB specimens are not well enough preserved to provide a check on this suggestion. If *Cacops* does have a pterygoid-vomer contact, it may not be the only dissorophid with this primitive condition. Only in *Tersomius texensis* is it certain that there is no pterygoid-vomer contact (and even here there is uncertainty as to the exact position of all sutures around the pterygoid—cf. Carroll, 1964; Bolt, 1974b). The anterior relationships of the pterygoid are obscure in all other described dissorophids.

Quadrate—A total of 14 quadrates has been found which probably pertain to *Cacops;* all have a strong postero-dorsal process

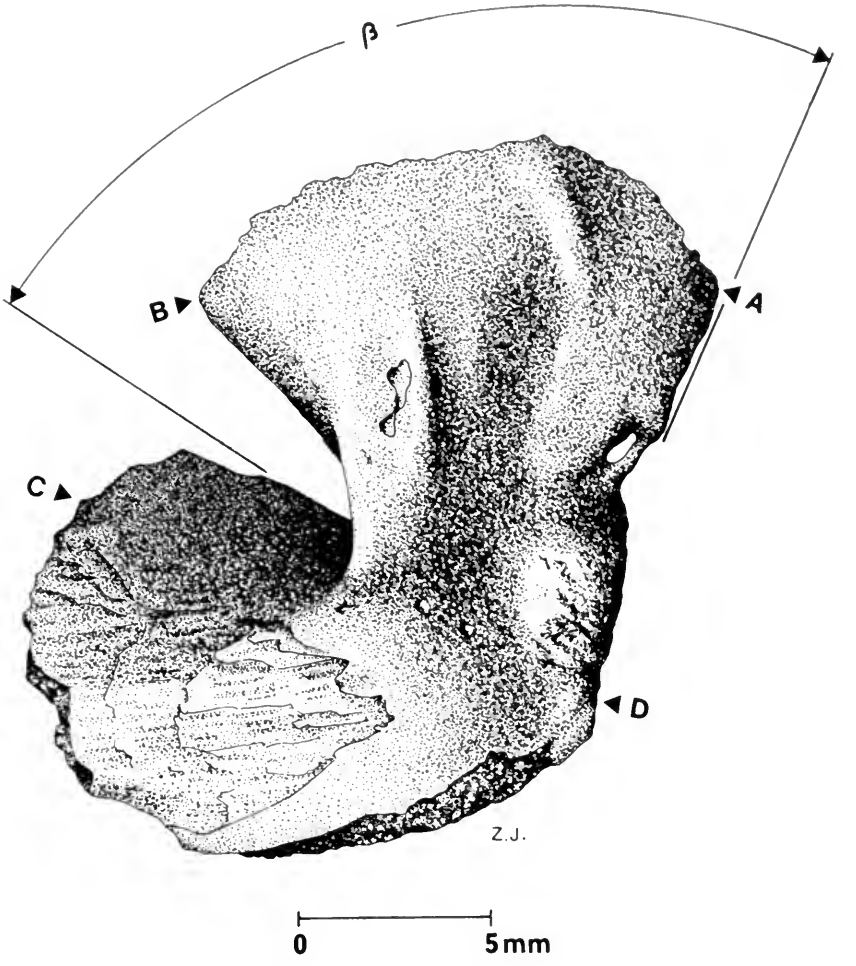

FIG. 3. *Cacops* quadrate from Fort Sill, FM PR 1032, medial view in plane of postero-dorsal process. Abbreviations: AB, points between which (maximum) process length was measured; CD, points between which basal length was measured; β, the process angle, is measured between the posterior border of the postero-dorsal process, and the line formed by the junction of contact areas for the pterygoid (medially) and the squamosal + quadratojugal (laterally).

(PDP). In the largest of the quadrates, the PDP is markedly expanded anteriorly (fig. 3). Some expansion is visible even in the smallest examples (fig. 4). This type of expanded PDP can be seen in the *Cacops* skull (FM UC 649) figured by Williston (1910), and in a separated quadrate from the CBB (FM UR 2434) which is about

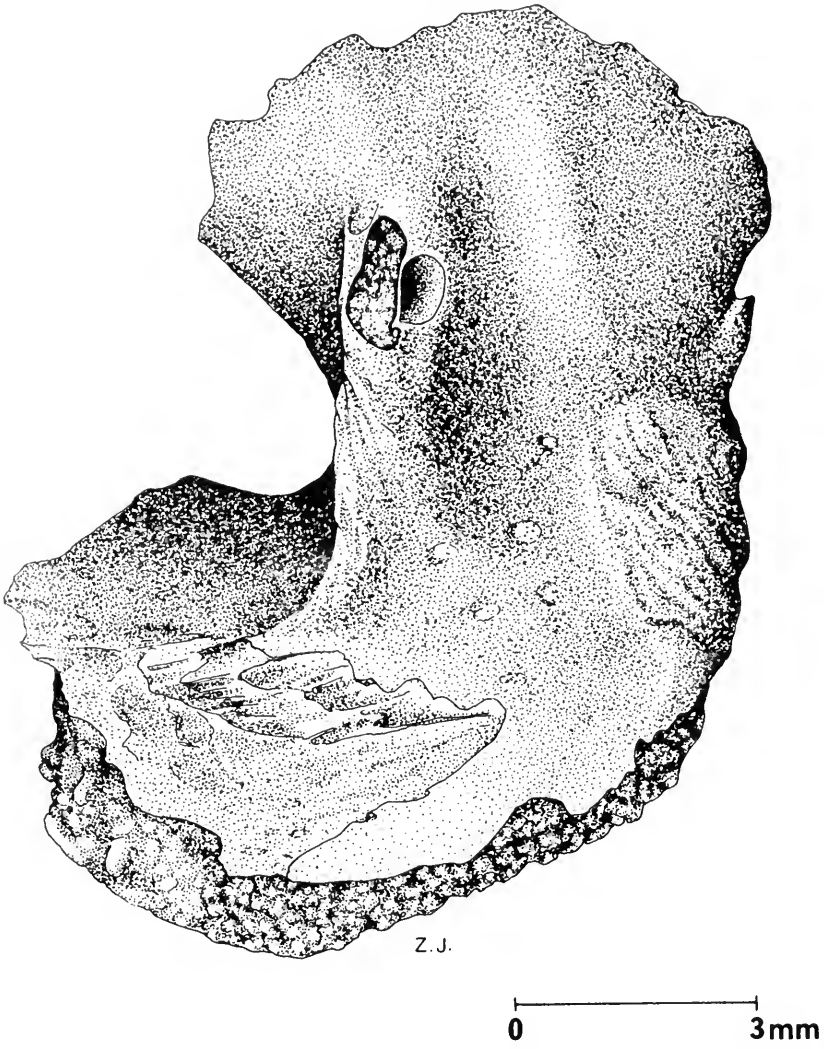

FIG. 4. *Cacops* quadrate from Fort Sill, FM PR 1033, medial view in plane of postero-dorsal process.

the same size as that in the skull. The Fort Sill quadrates are considerably smaller with, for example, a process length in the largest (FM PR 1032; see fig. 3) of 1.2 cm. as compared to about 2.1 cm. in FM UR 2434. Similarly, FM PR 1032 has a maximum basal length (see fig. 3) of about 1.5 cm., compared to 2.1 cm., for FM UR 2434 from the CBB. Both the CBB and Fort Sill quadrates have a process

angle (see fig. 3) of about 75-85°, as measured in FM PR 1032 and 1033 and UR 2434.

The quadrate is sufficiently well preserved in a number of dissorophoids, to establish the presence of a PDP. It is usually not possible to be certain whether the process is expanded as in *Cacops*, and no similar examples have been reported. Such an expansion is clearly absent in *Doleserpeton* which is, however, a much smaller animal than *Cacops* and has an open otic notch. *Cacops* is more appropriately compared with other large dissorophoids having a closed otic notch. There are only three such species: *Longiscitula houghae, Dissorophus multicinctus* (both dissorophids), and *Trematops milleri* (a trematopsid). These are also the *only* dissorophoids known to have a closed otic notch, with the exception of the Russian dissorophid *Zygosaurus lucius* which I cannot consider because there is no useful published information on it and the only known specimen has been lost. The three dissorophids (including *Cacops*) have very large otic notches closed by a tabular extension which, in lateral view, stands at about 90° to the skull table. *Longiscitula* (FM UR 430; skull length about 12 cm.) has a PDP, and there is some indication of expansion, but the area is very poorly preserved. *Dissorophus multicinctus* (MCZ 2122-1; skull length about 13.5 cm.) has an expanded postero-dorsal process, but the quadrate is so damaged that the process angle and length cannot be obtained. The process in *D. multicinctus* seems much thicker than that of *Cacops*, and not as high. The latter feature could be partly due to breakage; however, *D. multicinctus* has a considerably lower skull than *Cacops*, and therefore a lower PDP would be expected. The process angle in *Longiscitula* and *D. multicinctus* is probably close to that of *Cacops*, since all have a nearly-vertical tabular extension. A high process angle may be characteristic of dissorophids, based on these genera plus *Tersomius texensis* (unexpanded, relatively low PDP on small skull associated with holotype, AMNH 4719; process angle about 85°, like that in *Doleserpeton*). In contrast to the dissorophids, *Trematops milleri* (fig. 5) has a slit-like otic notch and the posterior tabular extension is at about 45° to the skull roof. The quadrate in such trematopsids should be readily distinguishable from that in all dissorophids, based only on process angle. This seems to be the case: the process angle in *T. milleri* FM UC 1760 is about 35°. There is apparently no anterior expansion of the process in *T. milleri*. Some trematopsids may, however, have an expanded process: a single quadrate from Fort Sill (KU 34652)

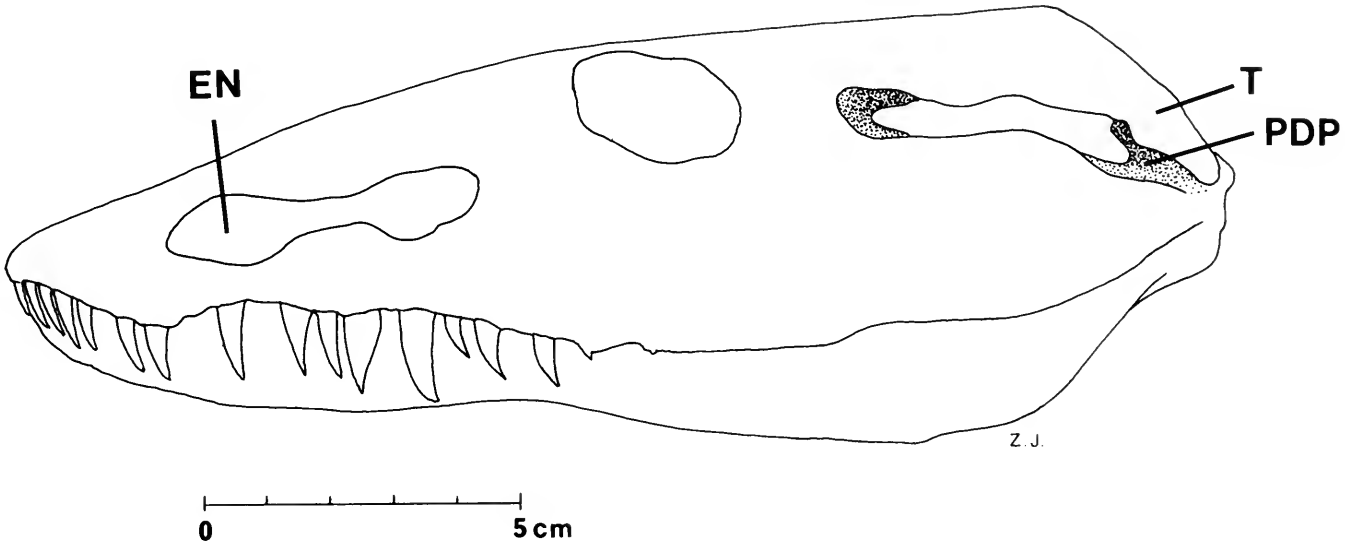

FIG. 5. *Trematops milleri,* FM UC 1760. Outline drawing of skull in left lateral view. Sutures within the otic notch are not shown; most of the area anterior to the postero-dorsal process of the quadrate is occupied by the squamosal. The postero-dorsal process is largely hidden in this view by the descending process of the tabular. Abbreviations: EN, external naris; PDP, postero-dorsal process of the quadrate; T, tabular.

has an anteriorly-expanded PDP with a process angle of 35°, which suggests trematopsid rather than dissorophid affinities.

DISCUSSION AND CONCLUSIONS

Identification of Cacops.—I believe that the palatine provides convincing evidence for identification because it is a unique type on the basis of comparison with most other dissorophoids (the relationships and shape of the LEP cannot be determined in some species). The armor is also good evidence, because it is reasonably distinctive and can be compared with that of other armored dissorophids (cf. Bolt, 1974a). The quadrate provides the weakest evidence due to lack of comparative information for other dissorophoids, although so far as known it resembles that of *Cacops* most closely. The quadrate region of dissorophoids and labyrinthodonts in general will be treated in greater detail in a future paper.

In addition to the comparisons given above, another line of reasoning suggests that the isolated bones described are best assigned to *Cacops:* The palatine and quadrate are easily distinguished from those of the unarmored *Doleserpeton,* the most common dissorophoid at Fort Sill. The next most common dissorophoid elements (although actually rare) are those here assigned to *Cacops.* Other dissorophoid armor scutes, quadrates, and palatines are extremely rare in collections made to date. It is thus likely that the elements assigned to *Cacops* at least belong to the same species. Identification of the *Cacops* palatine makes it virtually certain that the species is *Cacops* cf. *C. aspidephorus.*

Ontogeny of Cacops—The Fort Sill specimens, with the exception of the largest palatine, represent animals considerably smaller and therefore probably younger than those known from the CBB. Just as clearly, the Fort Sill animals were not larval-sized; as a rough estimate, skull lengths probably lay in the range from about 12.5 cm. (the size of most CBB specimens) to 6 or 7 cm.

The shape and (especially) the relationships of the LEP are potentially valuable taxonomic characters, but LEP ontogeny must be better known before they can be used with confidence. It is interesting that over a considerable size range, these characters are stable in *Cacops.* It is therefore most unlikely that any of the numerous dissorophid species with skull lengths of about 6 cm., and a LEP which participates in the orbital rim, are juveniles of *Cacops.*

As noted above, a closed otic notch is restricted to the larger dissorophoids. (Not all large dissorophoids appear to have closed otic notches, but this requires further study.) This may simply reflect failure to find juvenile skulls of the species with closed otic notches. On the other hand, it seems at least as likely *a priori* that otic-notch closure may have occurred rather late in ontogeny; some of the species with open otic notches may thus be represented only by juveniles. Two types of evidence suggest that *Cacops,* at least, developed otic notch closure at a rather small skull size: direct evidence comes from FM UR 2435, a partial left half of a *Cacops* skull from the CBB discovered in the course of this study. The tip of the snout is damaged in this specimen, but the position of the orbit and the posterior end of the postparietal is clear. Skull length can be estimated as about 6 cm., or no more than half the size of the *Cacops* skulls described by Williston (1910) which were until now the only ones available. This skull is thus smaller than that of most other dissorophoid species (see text-figure 1 in DeMar, 1968; also Olson, 1941). Although the quadrate is missing in this specimen, the presence of a long ventral extension from the tabular indicates that it almost certainly had a closed otic notch. Indirect evidence comes from the Fort Sill *Cacops* quadrates. All have a rugose area, V-shaped in outline, on the lateral face of the PDP. This area begins at the dorsal border of the process and runs less than one-third of the way down; it probably marks the contact of the tabular extension with the quadrate. Presence of this area in even the smallest quadrates, thus suggests that the otic notch was closed even in small *Cacops* specimens.

Presence of pedicellate denticles in *Doleserpeton* may be transitory, and characteristic of a juvenile, early post-metamorphic stage (Bolt, in press). The non-pedicellate palatine denticles of *Cacops* do not indicate whether or not that genus passed through a similar stage, in as much as the available palatines are all probably from more mature individuals than are the *Doleserpeton* specimens.

Isolated marginal tooth-bearing bones of *Cacops* are not identifiable at present in the Fort Sill material. It is virtually certain, however, that at least some of the labyrinthodont maxillae, premaxillae, and dentaries at Fort Sill pertain to *Cacops.* None of the labyrinthodont teeth (except those of *Doleserpeton*) at Fort Sill are either bicuspid or pedicellate. Thus *Cacops* was probably a dentitionally normal labyrinthodont, in the growth-stages preserved. This does not exclude the possibility of a more or less *Doleserpeton*-like mar-

ginal dentition at younger stages as observed in *Tersomius* and "cf. *Broiliellus* sp." (Bolt, in press).

REFERENCES

BOLT, J. R.

1969. Lissamphibian origins: possible protolissamphibian from the Lower Permian of Oklahoma. Science, **166**, pp. 888-891.

1974a. Armor of dissorophids (Amphibia: Labyrinthodontia): an examination of its taxonomic use and report of a new occurrence. Jour. Paleontol., **48**, pp. 135-142.

1974b. Evolution and functional interpretation of some suture patterns in Paleozoic labyrinthodont amphibians and other lower tetrapods. Jour. Paleontol., **48**, pp. 434-458.

In press. Dissorophoid relationships and ontogeny, and the origin of the Lissamphibia. Jour. Paleontol.

BOY, J. A.

1972. Die Branchosaurier (Amphibia) des saarpfälzischen Rotliegenden (Perm, SW-Deutschland). Abhandl. hess. L.-Amt. Bodenforsch, **65**, pp. 1-137.

CARROLL, R. L.

1964. Early evolution of the dissorophid amphibians. Bull. Mus. Comp. Zool., **131**, pp. 161-250.

DEMAR, R. E.

1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the family Dissorophidae. Jour. Paleontol., **42**, pp. 1,210-1,242.

OLSON, E. C.

1941. The family Trematopsidae. Jour. Geol., **49**, pp. 149-176.

1956. Fauna of the Vale and Choza: 11. *Lysorophus:* Vale and Choza. *Diplocaulus*, *Cacops* and *Eryopidae:* Choza. Fieldiana: Geol., **10**, pp. 313-322.

1958. Fauna of the Vale and Choza: 14. Summary, review and integration of the geology and the faunas. Fieldiana: Geol., **10**, pp. 397-448.

1967. Early Permian vertebrates. Okla. Geol. Survey, Circular 74, pp. 1-111.

PARSONS, T. S., and E. E. WILLIAMS

1962. The teeth of Amphibia and their relation to amphibian phylogeny. Jour. Morphol. **110**, pp. 373-390.

WILLISTON, S. W.

1910. *Cacops, Desmospondylus;* new genera of Permian vertebrates. Jour. Geol., **21**, pp. 249-284.

1911. American Permian vertebrates. Univ. Chicago Press, Chicago. 145 pp.