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SKULL OF THE LOWER PERMIAN DISSOROPHID AMPHIBIAN *PLATYHYSTRIX RUGOSUS*

DAVID S BERMAN

Associate Curator, Section of Vertebrate Fossils

ROBERT R. REISZ¹

Research Associate, Section of Vertebrate Fossils

MICHAEL A. FRACASSO²

ABSTRACT

Description of the skull of the labyrinthodont amphibian *Platyhystrix rugosus*, presented for the first time, is based primarily on a specimen collected by David Baldwin in 1881 in the Lower Permian Cutler Formation near Arroyo del Agua of north-central New Mexico. The specimen is the greater part of a skull and associated partial axial skeleton. Additional skull fragments of *P. rugosus* provide further information on the structure of the skull. The skull of *P. rugosus* exhibits a structural pattern that confirms previous tentative assignments of this genus to the Dissorophidae based solely on vertebral structure. *Astreptorhachis ohioensis* from the Upper Pennsylvanian Conemaugh Group of Ohio, considered closely related to *P. rugosus* on the basis of its vertebral structure, can similarly be assigned to the Dissorophidae. As previously suspected, both species are probably members of a distinct and widely divergent assemblage of armored dissorophids that separated from the central stock during the Middle or Late Pennsylvanian. The occurrence of armored vertebrae within the dissorophids is otherwise unknown until the Early Permian, but its early appearance in this lineage is consistent with the advanced state of the skull of *P. rugosus*.

¹ Address: Department of Biology, Erindale Campus, University of Toronto, Mississauga, Ontario, Canada L5L 1C6.

² Address: Division of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06511.

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INTRODUCTION

Platyhystrix rugosus is one of the more frequently encountered Lower Permian rhachitinous amphibians. Its anatomy and phylogenetic relationships have been until now poorly known, however, because only the dorsal portion of the axial skeleton has been adequately described (Langston, 1953; Lewis and Vaughn, 1965). With the exception of the distinctive neural spines, the dorsal vertebrae have the typical rhachitinous pattern. The spines are greatly elongated, laterally compressed, and distally expanded in the sagittal plane; except for a short proximal portion, the spines exhibit a nodular sculpturing or ornamentation that is presumably dermal in origin (Vaughn, 1971). Dermal sculpturing of the same type but heavier has also been reported on the outer surface of the ribs (Langston, 1953). A series of *Platyhystrix* neural spines illustrated by Lewis and Vaughn (1965) from the Lower Permian Cutler Formation of southwestern Colorado shows clearly that in lateral view the spines formed a greatly expanded sail with a strongly convex dorsal edge. This structure is somewhat analogous to the sail of some pelycosaurian reptiles. To date, only a few cranial fragments from the Lower Permian Cutler Formation of north-central New Mexico have been confidently assigned to *Platyhystrix*; they also exhibit a sculpturing similar to that seen on the neural spines and ribs (Langston, 1953).

The unusual neural spines of *Platyhystrix* have been found in nearly all Lower Permian (Wolfcampian) collecting areas of the Four Corners region of the United States; these include southeastern Utah, southwestern Colorado, and widely scattered areas of New Mexico (Olson and Vaughn, 1970). Carroll (1964) has described several dissorophid spines from two localities in the Lower Permian of Texas that he assigned to *Aspidosaurus* without specific designation. The armor on these neural spines varies in structure from the short, roof-shaped pieces capping the swollen tops of the spines, as in *Aspidosaurus chiton*, to that approaching the armor seen in *Platyhystrix*. Vaughn (1971) noted, however, that the armor of these spines, in which the ornamentation tends to form anastomosing ridges separated by large pits, differs from that of *Platyhystrix*, in which large tubercle-like protuberances tend to be separate; he considered the Texas spines as probably not *Aspidosaurus* but representing an unnamed genus. Lewis and Vaughn (1965) suspected that the same sort of confusion led Langston (1953:405) to state that "Somewhat differently sculptured spines from Texas mentioned by several authors under various names probably belong to other species of *Platyhystrix*." There is at present no evidence to indicate that more than one species of *Platyhystrix* existed or that its distribution extended beyond the Four Corners region. All

occurrences of *Platyhystrix* can be considered Lower Permian with one possible exception—El Cobre Canyon in Rio Arriba County of north-central New Mexico. The Cutler Formation beds in this rather limited area have been judged both Early Permian (Vaughn, 1963) and Late Pennsylvanian (Fracasso, 1980). Both assignments merit serious consideration and this controversy can only be satisfactorily resolved through better collections and detailed stratigraphic studies.

Langston (1953) has summarized concisely the taxonomic history of *Platyhystrix* and its confusion with other, non-dissorophid genera. On the basis of the vertebral materials available to him, he concluded that the genus probably represents an unnamed family perhaps allied to the eryopoids. In a phylogenetic chart of the Dissorophidae, Carroll (1964) showed *Platyhystrix* as an offshoot of the *Aspidosaurus* assemblage; this was done presumably on the basis of their similar vertebrae. He further suggested that the *Aspidosaurus-Platyhystrix* assemblage separated from the remainder of the dissorophids late in the Pennsylvanian or early in the Permian. A somewhat more conservative view was taken by Lewis and Vaughn (1965), who considered *Platyhystrix* to be either closely related to or a member of the Dissorophidae. This was based partly on the observation that within the wide structural variety of neural spines possessed by *Aspidosaurus* are some that approach those of *Platyhystrix*. DeMar (1968) also noted the similarities between the neural spines of *Platyhystrix* and those of some species of *Aspidosaurus*, particularly *A. chiton*, but included *Platyhystrix* in the Dissorophidae as an independent armored lineage of unknown derivation. He also extended the fossil record of *Platyhystrix* into the Late Pennsylvanian on the basis of a report by Lewis and Vaughn (1965) of a *Platyhystrix*-like specimen of that age. This specimen, consisting of neural arches and spines from the Upper Pennsylvanian Conemaugh Group of Ohio, was described by Vaughn (1971) as a new genus and species, *Astreptorhachis ohioensis*. Vaughn pointed out that these two taxa are closely related and probably represent an early armored dissorophid lineage, but cautioned that future discoveries may prove them to belong to a family other than the Dissorophidae.

All of the *Platyhystrix* specimens described here were collected from the Lower Permian Cutler Formation near Arroyo del Agua, Rio Arriba County, of north-central New Mexico. Langston (1953) listed five small *Platyhystrix* skull and jaw fragments that were among field collections made by parties from the University of California, Berkeley, in 1934 and 1935. His assignment was based on their extremely papillose sculpturing which matches that seen on ribs belonging to this genus. Three cranial or mandibular fragments, and five probably associated neural spines and a rib were collected from the Quarry Butte

locality and catalogued as UCMP 39090. One of the skull fragments was illustrated (Fig. 22e; mistakenly referred to UCMP 39092 in the legend) and described by Langston but not identified; it may be an angular. The most revealing UCMP 39090 fragment contains the left postorbital and most of the squamosal, and preserves most of their contributions to the posterior orbital rim and otic notch. The third fragment appears to be from the orbital rim and may be part of the right postorbital. The remaining two fragments, UCMP 39092, were found isolated and their precise locality is unknown. One, illustrated (Fig. 22f) and described by Langston as possibly belonging to the articular region of the lower jaw, is probably a left surangular. The second fragment, neither described nor illustrated, is a right tabular.

The most significant cranial specimen of *Platyhystrix* was discovered by David Baldwin in 1881. He collected the greater part of a large skull, AMNH 11545, that was apparently closely associated with a large portion of an axial skeleton of *Platyhystrix*, AMNH 11544. Neither specimen has been described. Although the skull is not in direct articulation with the postcranial skeleton, there is good reason to believe that these belonged to one individual. This is supported not only by the presence of a fragmentary *Platyhystrix* neural spine on the ventral surface of the skull, but also by the fact that one of the spine fragments assigned to AMNH 11544 can be fitted to this spine. AMNH 11545 and AMNH 11544 are also of appropriate sizes to be part of a single individual. The only specific locality data accompanying this material states, "east side of Rito Puerco." It is very likely that "Rito Puerco" is a synonym for Rio Puerco, a small river that flows northeast through the classic Cutler Formation collecting beds of the Arroyo del Agua area. It is probable that the specimens were collected in the vicinity of the well known quarries about ½ mi southeast of the village of Arroyo del Agua (Langston, 1953).

The skull materials show a structural pattern similar to that of dissorophid amphibians, confirming previous tentative assignments based on vertebrae that *Platyhystrix*, and very probably *Astreptorhachis*, belong in the Dissorophidae.

Abbreviations AMNH and UCMP are used to refer to collections of the American Museum Natural History and the Museum of Paleontology, University of California, Berkeley, respectively.

Key to abbreviations used in the figures:

bo = basioccipital
cp = cultriform process
ect = ectopterygoid
ex = exoccipital
f = frontal
fo = fenestra ovalis

pal = palatine
pf = postfrontal
pm = premaxilla
po = postorbital
pop = paroccipital process of opisthotic
pp = postparietal

j = jugal
 l = lacrimal
 m = maxilla
 n = nasal
 ns = neural spine
 oc = occipital condyle
 op = opisthotic
 p = parietal
 pa = parasphenoid

prf = prefrontal
 pt = pterygoid
 qj = quadratojugal
 sph = sphenethmoid
 sq = squamosal
 st = supratemporal
 t = tabular
 v = vomer
 IX-X, XII = cranial nerve foramina

SYSTEMATIC PALEONTOLOGY

Class Amphibia

Order Temnospondyli

Suborder Rhachitomi

Superfamily Dissorophoidea Bolt, 1969

Family Dissorophidae Boulenger, 1902

Platyhystrix Williston, 1911

Type species.—*Platyhystrix rugosus* (Case, 1910).

Revised diagnosis.—Large dissorophid temnospondyl that differs from all other members of family in the following features: presence of nodular or papillose dermal sculpturing along lateral borders of skull table and adjoining portions of cheek between orbit and otic notch, on all but a small proximal portion of neural spines and on proximal portions of lateral surfaces of dorsal ribs; neural spines of dorsal vertebrae greatly elongated, flattened from side to side and greatly expanded anteroposteriorly toward their distal ends to form an extensive dorsal sail. The following combination of characters distinguishes the skull from those of other dissorophids: nasal long and narrow with length nearly three times width and equal to over one third the midline length of skull; large parietal extends anteriorly beyond level of posterior margin of orbit; length of postfrontal greater than twice its width and equal to length of supratemporal; dorsal exposure of postorbital nearly equal to length of supratemporal; cheek steeply inclined and meets skull table at nearly right angle; squamosal restricted to cheek; otic notch not closed posteriorly; cultriform process of parasphenoid very narrow.

Platyhystrix rugosus (Case, 1910)

Holotype.—AMNH 4785, a few neural spines of dorsal vertebrae from Cope collection.

Referred specimens.—AMNH 11544, partial axial skeleton, and AMNH 11545, partial skull, almost certainly belonging to a single individual; UCMP 39090 and UCMP 39092, fragments of skull, dorsal vertebrae and ribs.



Fig. 1.—*Platyhystrix rugosus*, photograph of skull AMNH 11545 in dorsal view.

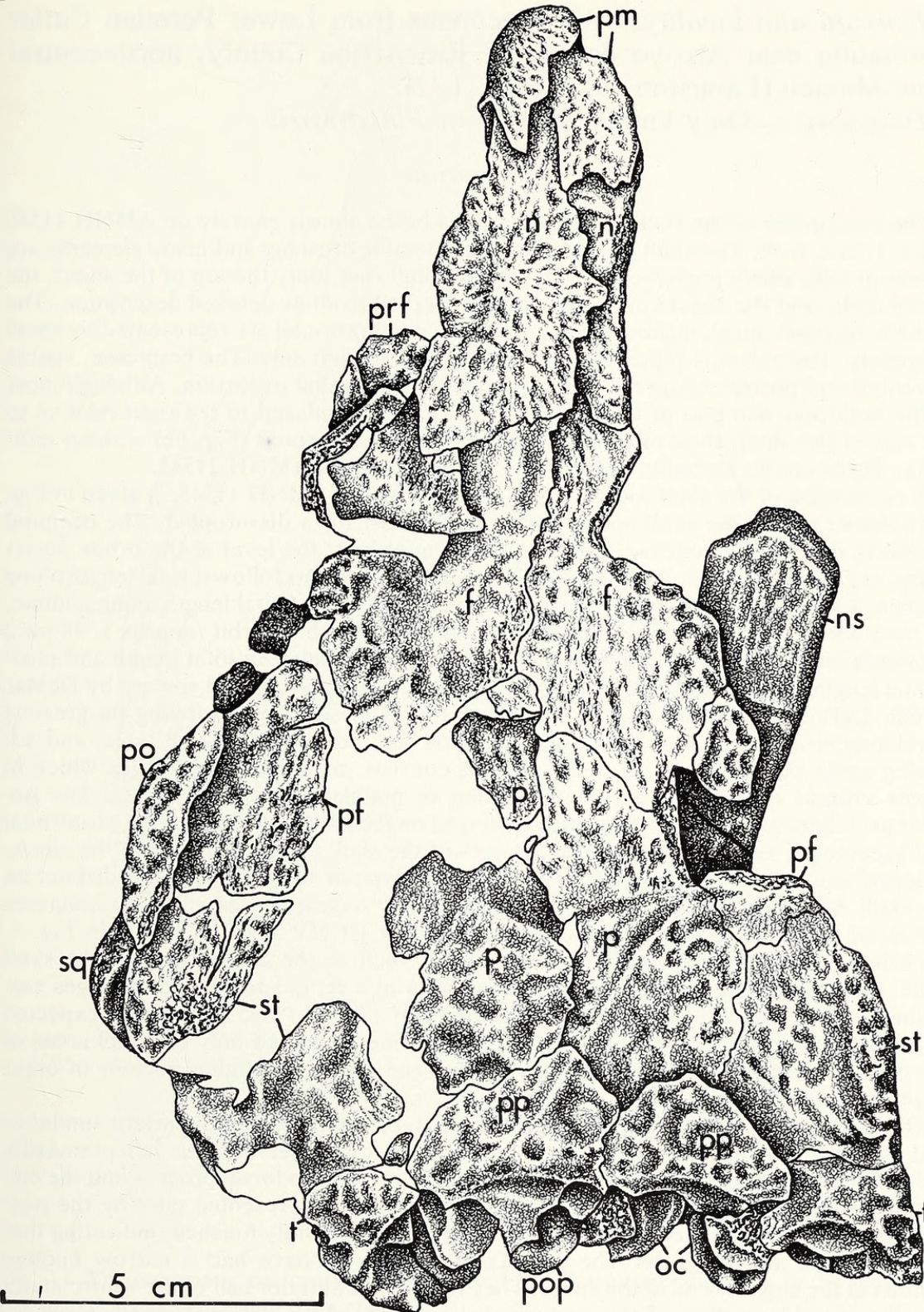


Fig. 2.—*Platyhystrix rugosus* AMNH 11545 as seen in Fig. 1 except that spine fragment (ns) of AMNH 11544 has been joined to spine fragment on ventral surface of skull.

Horizon and locality.—All specimens from Lower Permian Cutler Formation near Arroyo del Agua, Rio Arriba County, north-central New Mexico (Langston 1953, Figs. 1, 2).

Diagnosis.—Only known species of *Platyhystrix*.

Description

The description of the skull of *Platyhystrix* is based almost entirely on AMNH 11545 (Figs. 1, 2, 4, 6–8). The skull has suffered considerable crushing and many elements are absent or only partly preserved. Of the dermal skull roof, only the top of the snout, the dorsal table, and the cheeks are sufficiently preserved to allow detailed description. The maxilla, lacrimal, jugal, quadratojugal, quadrate, and prefrontal are represented by small fragments. The palate is represented by portions of the left side. The braincase, visible in ventral and posterior aspects, exhibits some breakage and distortion. Although most of the braincase and part of the skull table have been displaced to the right relative to the rest of the skull, their original relationships can be restored (Fig. 8b) without difficulty. There are no elements of the mandible preserved in AMNH 11545.

A restoration of the skull roof in dorsal view, based on AMNH 11545, is given in Fig. 3. In dorsal aspect the skull appears long and narrow for a dissorophid. The occipital margin is moderately concave. The cheeks, from at least the level of the orbits posteriorly, are nearly vertical. Pertinent skull measurements are as follows: total length along midline, 190+ mm; preorbital length (approx.), 75 mm; postorbital length along midline, 64 mm; width of skull roof across tabulars, 99 mm; length of orbit (approx.), 48 mm; minimum interorbital width (approx.), 60 mm. The ratio between total length and postorbital length is consistent with those measured for other dissorophid species by DeMar (1968). Dermal sculpturing varies greatly on the skull surface, exhibiting its greatest development along the dorsal half of the orbital rim, edges of the skull table, and adjoining areas of the cheek. In these areas it consists mainly of large ridges which in places support numerous massive, tubercular or nodular-like protuberances. The nodular protuberances are most strongly developed on the lateral surfaces of the postorbital and squamosal, and along the lateral margins of the skull table exposures of the supratemporal and tabular. Because of weathering, this type of sculpturing is less distinct on the skull AMNH 11545 than is on the skull and jaw fragments described by Langston (1953), of which the postorbital-squamosal fragment UCMP 39090 is shown in Fig. 5. On other regions of the skull of AMNH 11545, such as the central area of the skull table, the sculpturing is less nodular and consists of a reticulate pattern of ridges surrounding small pits. The sculpturing on the nasals of AMNH 11545 is finer than expected for a dissorophid skull of such large size. Sculpturing preserved only on small areas of the cheeks is developed to the same extent as seen on corresponding regions of other large dissorophids.

The skull roofing bones of *Platyhystrix* (Figs. 1–3) exhibit a sutural pattern similar to that of other dissorophid genera. Both premaxillae are preserved. The left premaxilla is nearly complete, missing only a small portion of its posterodorsal process and the end of its posterior, marginal ramus. The right premaxilla is represented only by the posterodorsal process; its medial and posterior edges are smoothly finished, indicating that these margins are complete. The premaxillae appear to have had a narrow midline contact at the anterior end of the snout. They formed the anterior half of the ventrolateral and the anterior portion of the dorsomedial margins of the external nares. From its dorsomedial contribution to the narial border the premaxilla tapers slightly as it extends posteriorly to form the broadly forked posterodorsal process. The preserved marginal dentition of the left premaxilla consists of seven teeth, represented mainly by their bases, interspersed with spaces for six more within a length of about 25 mm. Maximum

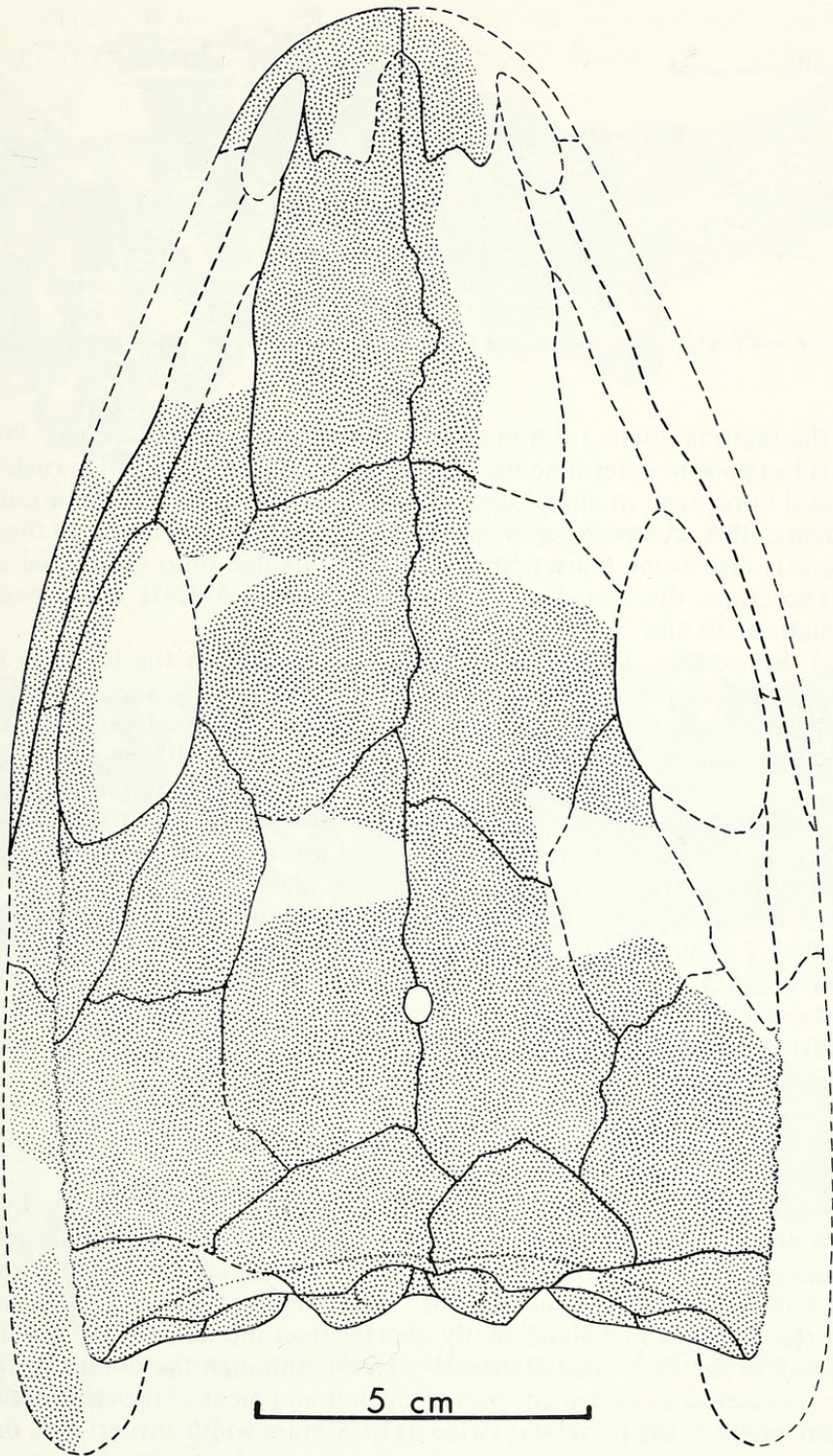


Fig. 3.—Diagrammatic restoration of skull roof of *Platyhystrix rugosus* in dorsal view. Preserved areas represented by shading.

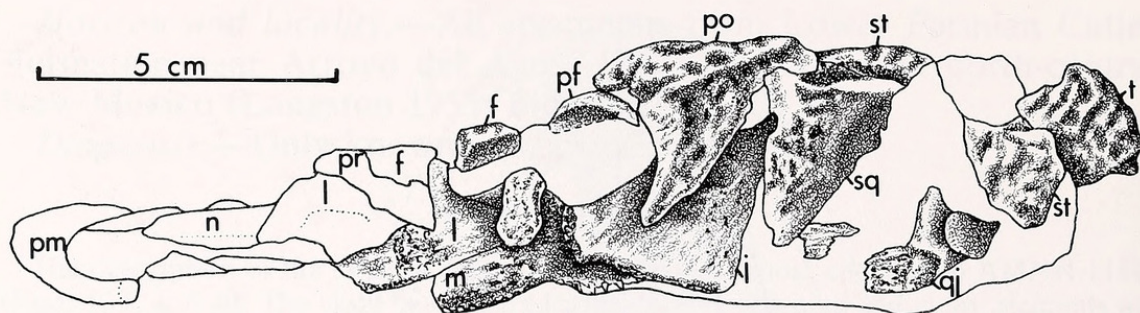


Fig. 4.—*Platyhystrix rugosus*, skull AMNH 11545 in left lateral view.

diameter of the teeth is about 1.5 mm and the length is about 3 to 4 mm. Preservation of the snout is too poor to determine the presence or absence of a median rostral fontanel or an internasal bone seen in some dissorophids (Carroll, 1964). In the absence of any positive evidence, this area of the skull has been restored without either of these features (Fig. 3). There is also some telescoping of the premaxillae onto the dorsal surfaces of the nasals. Therefore, the actual midline skull length of AMNH 11545 exceeded the preserved length of 19 cm.

Portions of the maxilla, lacrimal and jugal can be seen on the left side of AMNH 11545 (Fig. 4). A small part of the maxilla, 4 cm long, is preserved beneath the orbit; its surface is poorly preserved, but appears to have been moderately sculptured. It extends dorsally from the ventral skull margin no more than 10 mm to its suture with the lacrimal. The maxilla bears about 18 teeth, all but three incomplete, in a length of 4 cm. The complete teeth appear to be simple, pointed pegs with a basal width of about 1.3 mm and a length of about 3 mm. The preserved portion of the lacrimal indicates that it was a large element that may have extended far anteriorly to reach the naris as in other dissorophids. The jugal formed the posteroventral margin of the orbit and occupied a large, inverted V-shaped space between the postorbital and squamosal. Although the jugal must have approached closely the ventral margin of the skull, it is unlikely that it overlapped the maxilla to reach the jaw margin as in some dissorophids (Carroll, 1964; DeMar, 1968). As a result of poor preservation it is not known if the palatine was exposed on the skull roof along the ventral margin of the orbit as noted in a number of dissorophids (DeMar, 1968; Bolt, 1974c). A large portion of the left quadratojugal is exposed in medial view (Figs. 6, 7). Its borders are incomplete except where it is sutured to a small fragment of the quadrate (not shown in figures).

Both nasals (Figs. 1–3) are present but only the left is complete. It is a long, narrow element; it is nearly three times as long as wide and represents approximately 35% of the midline length of the skull. The frontals are incomplete, missing the anterolateral corners and portions of the orbital margins. In midline length the frontals are slightly shorter than the parietals and significantly shorter than the nasals. The frontal contributes extensively to the dorsomedial orbital margin. Although the dorsal surfaces of the parietals are weathered and crushed, part of the left and most of the right are preserved. The maximum length of the parietal is twice its maximum width. Anteriorly, the parietals extend well beyond the level of the posterior margins of the orbits. The area where the pineal foramen is usually located has been severely damaged and no part of its border is discernable.

Both the moderate-sized tabulars and large postparietals are wedge-shaped in dorsal view; the tabular-postparietal contact is between their narrow ends. Both bones have well developed, posteroventrally directed occipital flanges, but only the flange of the postparietal contacts of the braincase, suturing to the dorsal process of the exoccipital; a medial occipital flange of the tabular joins the paroccipital process of the opisthotic

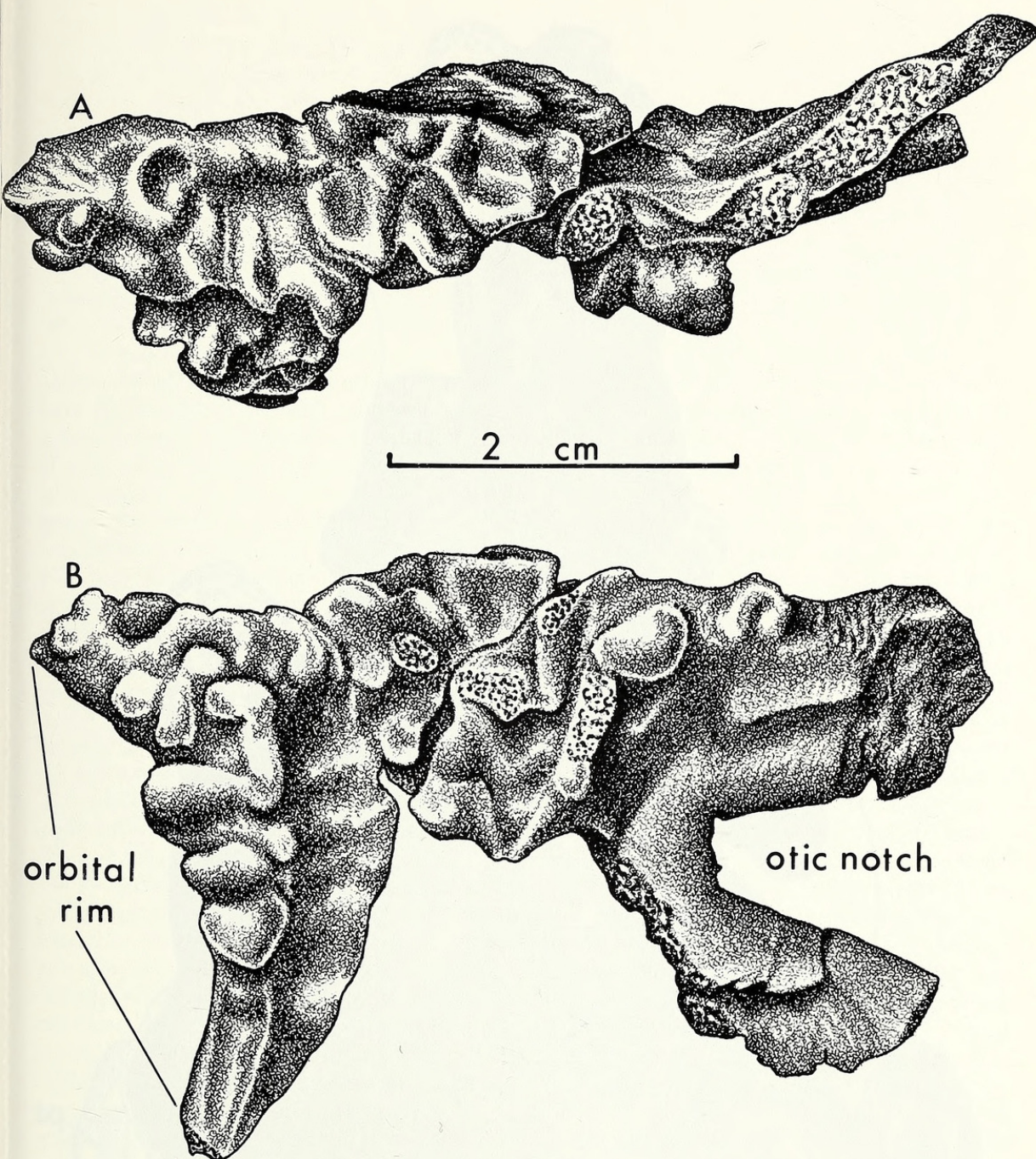


Fig. 5.—*Platyhystrix rugosus*, left postorbital-squamosal UCMP 39090 in (A), dorsal, and (B), lateral views.

(see below). The large supratemporal has a broad contact with the postfrontal and postorbital. The squamosal does not contribute to the skull table, but is restricted to the lateral surface of the skull; this is also indicated in UCMP 39090 (Fig. 5). The postfrontal and postorbital are large, long elements. The postfrontal is restricted to the skull table and it is more than twice as long as wide; it contributes to the posterodorsal margin of the orbit. The postorbital has a long, narrow exposure on the skull table.

From their dorsal exposures along the lateral edge of the skull table the postorbital,



Fig. 6.—*Platyhystrix rugosus*, photograph of skull AMNH 11545 in ventral view.

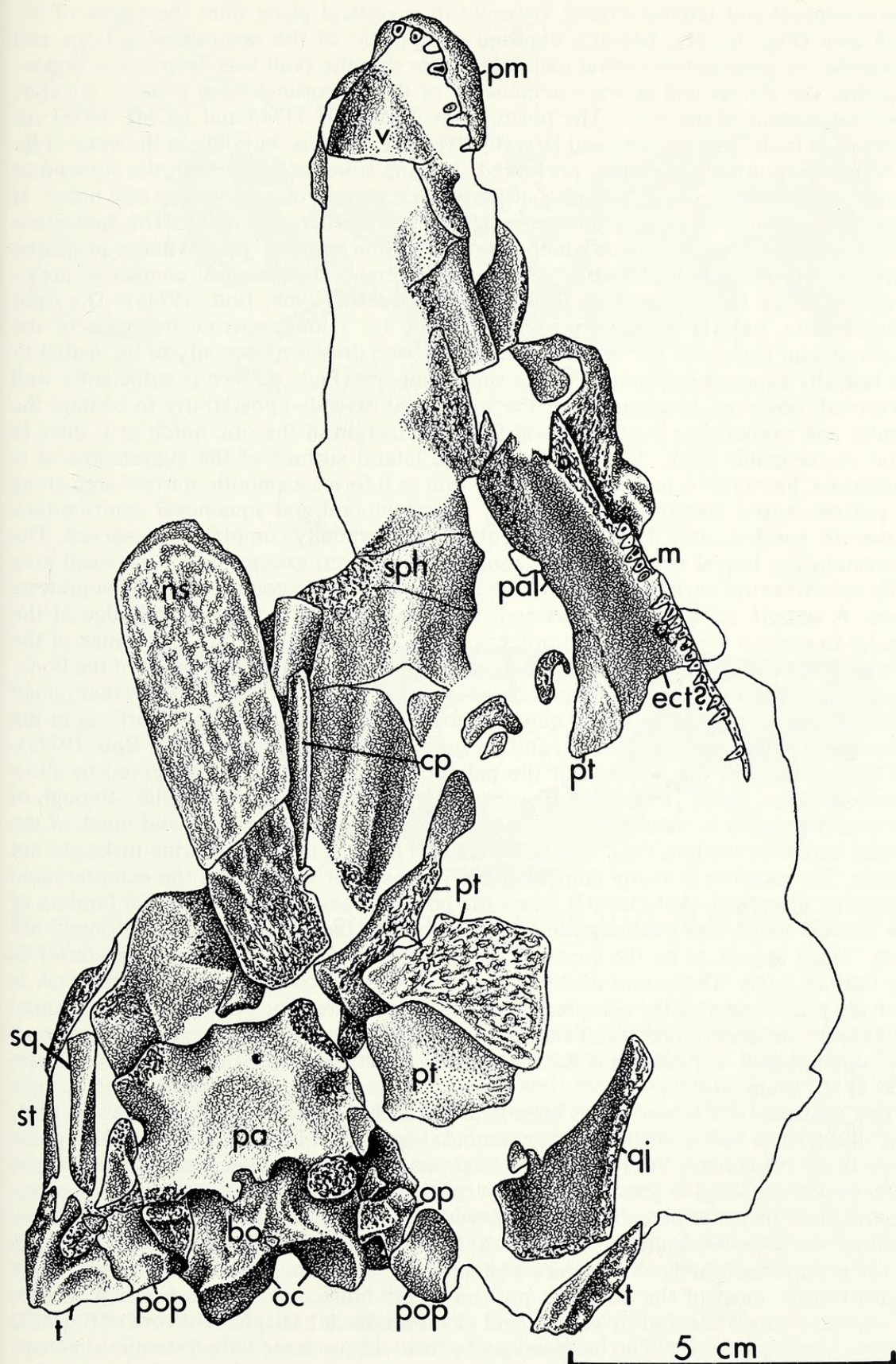


Fig. 7.—*Platyhystrix rugosus* AMNH 11545 as seen in Fig. 6 except that spine fragment (ns) of AMNH 11544 has been joined to spine fragment on ventral surface of skull.

supratemporal and tabular extend ventrally in a vertical plane onto the cheek of the skull roof (Fig. 4). The laterally exposed component of the postorbital is large and triangular; its great anteroventral extent indicates that the skull was deep in this region. Together the dorsal and lateral components of the postorbital form a deep, angular, posterior margin of the orbit. The postorbitals in AMNH 11545 and UCMP 39090 are identical in both their dorsally and laterally exposed portions, but only in the latter (Fig. 5) is the sculpturing completely preserved. Judging from UCMP 39090, the squamosal formed the anterior corner and most of the ventral margin of a very deep otic notch. It is strongly sculptured except for a smooth area that borders the notch. The specimens are too incomplete to determine whether a smooth, thin crescent-shaped flange projected ventrally into the otic notch from near the supratemporal-squamosal contact as previously described for dissorophids (Carroll, 1964; DeMar, 1968; Bolt, 1974b). The right squamosal in AMNH 11545 is represented only by a long, narrow fragment of the posterodorsal margin of the otic notch that has been displaced dorsally to lie medial to the laterally exposed component of the supratemporal (Figs. 6, 7); it is sufficiently well preserved, however, to suggest that the squamosal extended posteriorly to contact the tabular and exclude the supratemporal from the margin of the otic notch as it does in other dissorophids (Bolt, 1974b). Most of the lateral surface of the supratemporal is sculptured; however, it becomes extremely thin as it forms a smooth, narrow area along its posteroventral margin. Of the tabular, supratemporal and squamosal contributions to the otic notches, only those of the tabulars are essentially completely preserved. The subrectangular lateral surface of the tabular is sculptured except for a very small area at its anteroventral corner. Anteriorly the tabular has a wide contact with the supratemporal. A smooth occipital flange extends medially from the posterolateral edge of the tabular to contact the paroccipital process of the opisthotic (Fig. 8). This flange of the tabular also projects a short distance below the level of the lateral exposure of the bone. There is no indication that the tabular developed a ventrally directed process that joined a dorsally directed process of the quadrate to close the otic notch posteriorly as in the dissorophids *Dissorophus*, *Cacops*, and *Longiscitula* (DeMar, 1966a, 1968; Bolt, 1977a).

Only portions of the left side of the palate are sufficiently well preserved to allow comment (Figs. 6, 7). The preserved surfaces are covered by fine denticles. Enough of the vomer remains to indicate that it was long and formed the anterior and much of the medial border of the long (approximately 4.5 cm) internal naris. Vomerine tusks are not visible. The palatine is nearly complete, but its posterior suture with the ectopterygoid cannot be discerned. Anteriorly it forms the posterior and part of the medial borders of the internal naris, and medially the lateral margin of the very large interpterygoid vacuity. What appear to be the bases of two palatine tusks are located just posterior to the internal naris. The extent of the ectopterygoid is difficult to define. A large tusk is partially preserved near the ectopterygoid-maxillary suture. The pterygoid is represented by at least six poorly preserved fragments. What appears to be the palatal portion of the basipterygoid articulation is located slightly anterolateral to the basipterygoid process of the braincase.

The braincase of *Platyhystrix* is in general like that of other rhachitomes (Swain, 1941; Boy, 1971). The well developed parasphenoid (Figs. 6, 7) is exposed in ventral view; its main body is probably fused with the basisphenoid. The narrow, rod-like cultriform process (4.5 cm long) is preserved though broken at several levels with some displacements. Most of the sphenethmoid is exposed in ventral view. It is V-shaped in cross-section with a rounded midline keel which rested on the dorsal surface of the cultriform process. The main body of the parasphenoid is a large, smooth, subrectangular plate that underlies most of the posterior portion of the braincase. The surfaces of the anterolateral corners are slightly convex and cover the thick basisphenoid core of the large basipterygoid processes. The basipterygoid processes are large with flat unfinished surfaces facing anterolaterally. This area is insufficiently preserved to establish whether

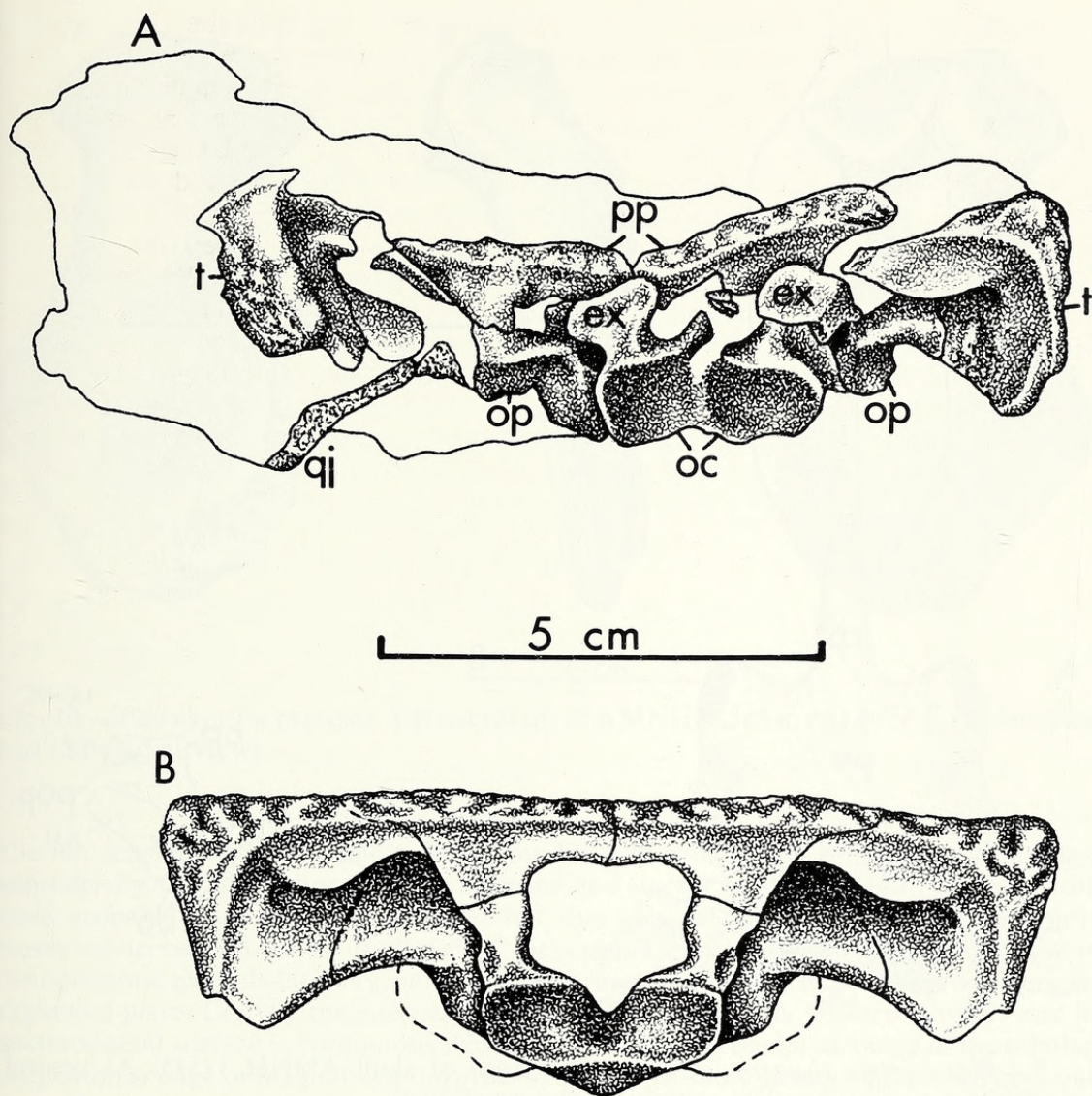


Fig. 8.—*Platyhystrix rugosus*, occiput of skull AMNH 11545. A) as preserved; B) restored.

the joint between the palate and braincase was movable. Posterior to the basiptyergoid processes the lateral margins of the parasphenoid curve dorsally to end as thin, free edges. The posterolateral corners are thickened and ridged slightly to form the cristae ventrolaterales; attached to the left crista is a small, poorly ossified fragment whose identity is uncertain. Medial to the cristae the posterior margin of the parasphenoid is strongly concave on either side of a short, bifurcate stem. The foramina for the internal carotids are clearly visible near the midline between the basiptyergoid processes. The basioccipital and exoccipitals are fused and extend well beyond the posterior margin of the parasphenoid. Although the sutures separating the basioccipital and exoccipitals cannot be defined, it is assumed that the basioccipital forms the narrow, irregular rugose area on the ventral midline.

In posterior view (Fig. 8) the exoccipitals form the lateral portions of the distinctly double occipital condyle; presumably the basioccipital only contributes a narrow ventral wedge between them. The condyle is horizontally oval in outline and the articular surface

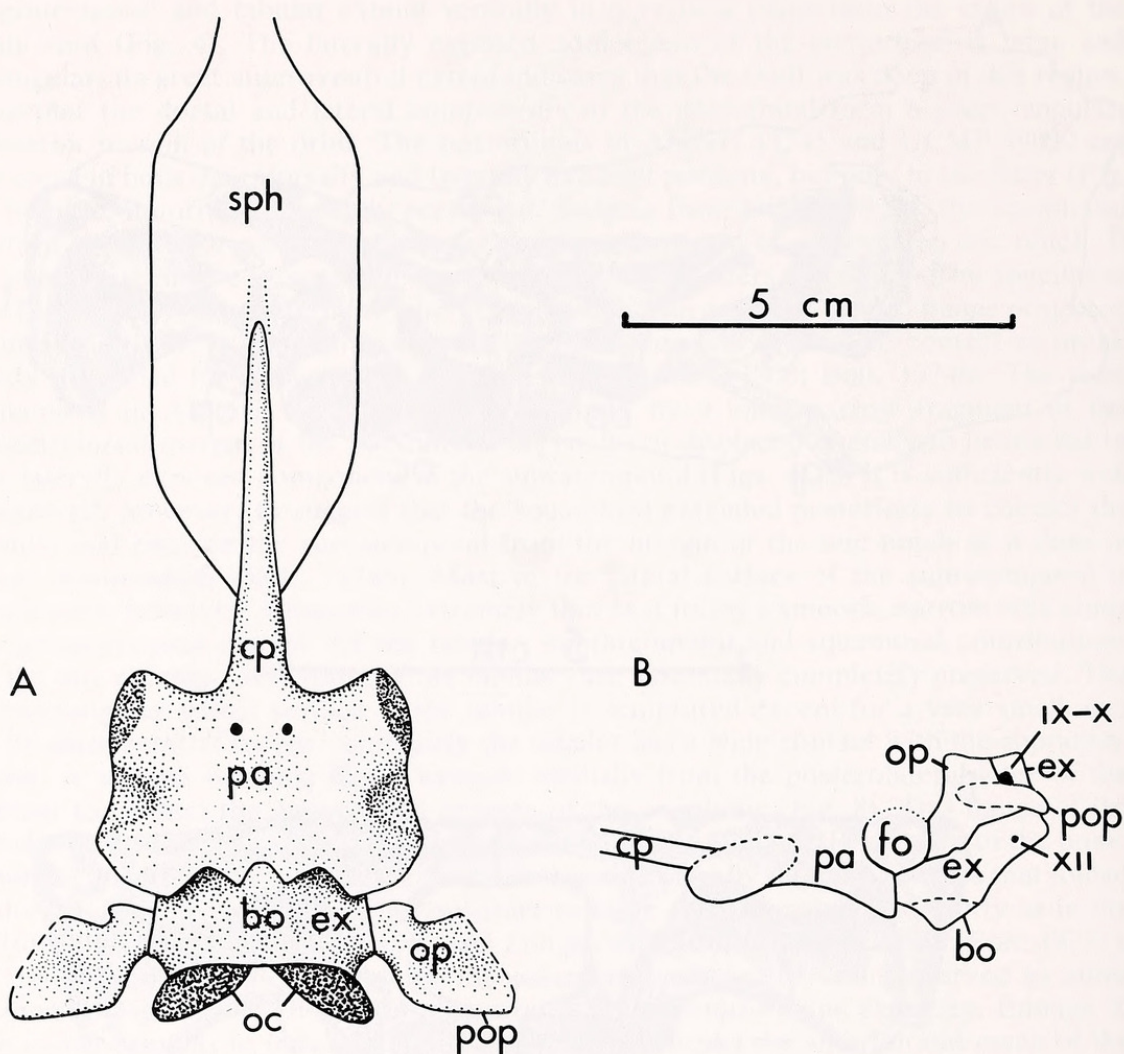


Fig. 9.—*Platyhystrix rugosus*, restored braincase of skull AMNH 11545. A) ventral view; B) diagrammatic outline sketch in left lateral view.

is strongly concave with posteriorly projecting dorsolateral margins. The exoccipitals are separated along the midline of the braincase floor by a narrow channel that was presumably occupied by an unossified portion of the basioccipital. Above the condyles the exoccipitals extend dorsally as stout, slightly waisted processes on either side of the foramen magnum; they do not meet dorsally and there is no trace of an ossified supraoccipital. The large dorsal sutural surfaces of the exoccipitals attached not only to the occipital flanges of the postparietals, but may have also extended a short distance forward beneath the skull table. Small branches of cranial nerve XII (hypoglossal) exit on the lateral surface of the exoccipital just anterior to the condyle rim (Fig. 9). A short distance anterodorsally the exoccipital forms the posterior edge of the large vagus foramen for cranial nerves IX–X. The leading edge of the exoccipital slopes anteroventrally below the vagus foramen. Only the opisthotic portion of the otic region is adequately exposed and preserved for description. This bone forms a stout vertical pillar that extends from near the base of the anterior edge of the exoccipital to the ventral surface of the postparietal near its occipital margin. The opisthotic forms the anterior margin of the vagus foramen and the posterodorsal margin of the large fenestra ovalis.

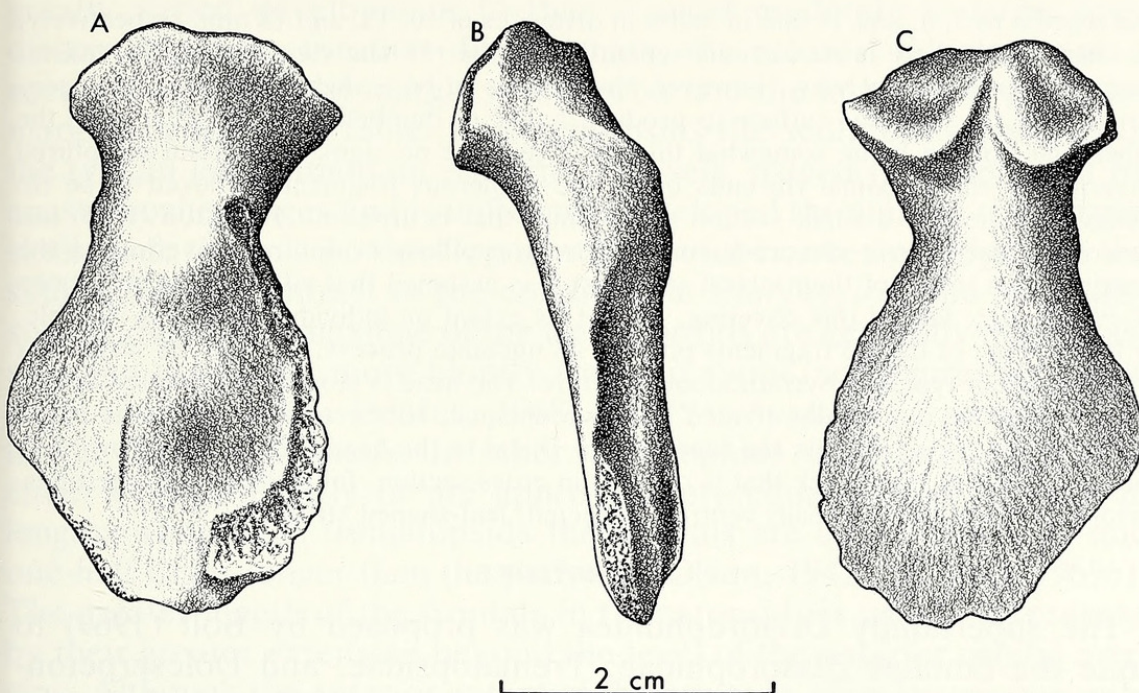


Fig. 10.—*Platyhystrix rugosus*, left sacral rib of AMNH 11544 in (A) lateral, (B) anterior, and (C) medial views.

The left fenestra ovalis is visible; it is bounded posteroventrally by the exoccipital and ventrally by the parasphenoid. The anterior and dorsal borders of the fenestra ovalis were probably formed by the prootic, but this area of the braincase is insufficiently preserved to be certain. At the level of the vagus foramen the paroccipital process of the opisthotic extends laterally and expands abruptly into a nearly flat, anteroposteriorly expanded plate. Distally the paroccipital process slopes steeply posteroventrally and its posterodorsal surface is continuous with that of the medial occipital flange of the tabular; the posterior edge of the paroccipital process extends a short distance posteriorly beyond the posteroventral occipital flanges of the postparietal and tabular. The posttemporal fenestra is bounded by the posteroventral and medial occipital flanges of the tabular and the paroccipital process.

Identifiable elements of the partial axial skeleton AMNH 11544 include the greater parts of five dorsal neural spines, numerous small fragments of other neural spines, two complete intercentra and what may be portions of two additional intercentra, three proximal ends of ribs, numerous fragments of probably unarmored rib shafts, a small section of an armored rib shaft, and a pair of essentially complete sacral ribs. It is estimated that a minimum of seven or eight dorsal neural spines are represented. Vaughn (1971) calculated that fifteen or fewer spines made up almost all of the sail of *Platyhystrix*. In size, structure, variation in shape, and ornamentation the spines of AMNH 11544 conform exactly with those of the *Platyhystrix* specimen described by Langston (1953) and Lewis and Vaughn (1965). In overall size the sail of AMNH 11544 was undoubtedly very close to that indicated by the series of 11 dorsal spines described by Lewis and Vaughn (1965). Except for their slightly smaller size, the two complete intercentra agree with that identified by Langston (1953) as a posterior dorsal. The heads of the three ribs are expanded and triangular in outline with the capitular corner extending a few millimeters beyond the rest of the articular surface to produce a slightly concave proximal margin. The three heads measure 14, 17, and 19 mm in greatest width

and narrow to 5, 8, and 11 mm in width in distances of 10, 15, and 18 mm, respectively. In lateral view there is no obvious separation of the rib heads into capitulum and tuberculum. In proximal view, however, there tends to be a slight anteroposterior constriction of the articular surface to produce a sort of dumbbell-shaped outline with the tubercular portion being somewhat thicker. There are no signs of a lateral sculptured covering on the proximal rib ends or on the numerous fragments believed to be rib shafts, but there is a small section of rib shaft that is armored. Langston (1953) has described *Platyhystrix* ribs as having a heavily papillose sculptured covering on the proximal two thirds of their lateral surfaces. It is assumed that either some of the ribs of *Platyhystrix* lacked this covering, or that its extent on individual ribs was variable, or both. None of the rib fragments possess an uncinat process. The pair of sacral ribs (Fig. 10) are of typical labyrinthodont structure. The head is stoutly constructed and its articular surface is partially divided into two unequal, subcircular portions; the larger surface probably represents the tuberculum. Distal to the head there is a narrowing of the rib to form a short neck that is circular in cross-section, followed by an anteroposterior expansion into a broad, ventrally directed, leaf-shaped structure.

Comparisons

The superfamily Dissorophoidea was proposed by Bolt (1969) to unite the families Dissorophidae, Trematopsidae, and Doleserpetontidae. This grouping was later expanded by Boy (1972) to include two branchiosaur families, the Branchiosauridae and Micromelerpetontidae. Boy envisioned the latter two families as representing secondarily aquatic, at least partially neotenic, divergent lineages of an unknown amphibian stock that rapidly adapted to a terrestrial or riparian habit and differentiated into the other dissorophoid families. The monotypic family Doleserpetontidae Bolt (1969) was erected for the sole reception of the Lower Permian *Doleserpeton annectens*. In a more recent discussion of this species, however, Bolt (1977b) concluded that *D. annectens* is closely related to the Lower Permian dissorophid *Tersomius* and, though specifically distinct from either of the two recognized species of *Tersomius*, it may not be generically distinct. A close relationship between the Dissorophidae and Trematopsidae was first proposed by Olson (1941); Boy's (1972) analysis of the Dissorophoidea also supports this conclusion. This theory of relationship has been especially reinforced by the descriptions of two dissorophids, the Late Pennsylvanian *Actiobates* (Eaton, 1973) and the Early Permian *Longiscitula* (DeMar, 1966a), and a trematopsid, the Early Permian *Ecolsonia* (Vaughn, 1969). Each apparently possesses a combination of cranial features considered characteristic of both families. In noting the close relationship between dissorophids and trematopsids, Eaton (1973) recommended that only one family, Dissorophidae, be recognized to include members of both groups. In light of these observations, it is important to demonstrate that the known skull materials of *Platyhystrix* clearly indicate inclusion of this genus in the Dissorophidae rather than in the closely related Trematopsidae.

The sculpturing of the skull roof of *Platyhystrix* is similar in its

greatly varied development to that of most moderate to large sized dissorophids. As in other dissorophids, the greatest development is seen along the dorsal margin of the orbit and the lateral and posterior margins of the skull table. In trematopsids the sculpturing consists of the typical labyrinthodont pattern of closely spaced pits separated by anastomosing ridges and is uniformly developed throughout the dermal skull roof; there is no development of protuberances or ridges on the skull table. In contrast to the condition in *Platyhystrix* and other dissorophids, the premaxillae of the trematopsids are generally more massive and form a far more bluntly rounded snout (see figures by Olson 1941; Carroll, 1964; DeMar, 1968). In *Platyhystrix* the parietals are longer than the frontals. In other dissorophids the frontals typically either exceed slightly or are approximately equal to the parietals in length, whereas in trematopsids the frontals are as much as one and one-half times longer than the parietals (Olson, 1941; Vaughn, 1969b). The greater length of the frontals in trematopsids is usually expressed by their greater extension beyond the level of the anterior orbital margins. Although the anterior extent of the orbits in *Platyhystrix* can only be estimated, it seems obvious that, as is typical in dissorophids, the frontals did not extend noticeably beyond this level. Probably related to this difference is the generally greater relative preorbital skull length of the trematopsids compared to that of the dissorophids. Measurements made from published illustrations (Olson, 1941; Carroll, 1964; DeMar, 1968; Eaton, 1973) indicate that in the trematopsids the preorbital length ranges from about 44% to 57% (average about 49%) of the skull length (measured along the midline), whereas in the dissorophids the range is about 30% to 45% (average about 39%). The same measurement for *Platyhystrix* is about 38%.

Bolt (1974b, 1977a) has shown that the otic notch regions of trematopsids and dissorophids are similar in most respects, but differences in at least two features can be used here to demonstrate that *Platyhystrix* is a dissorophid. In *Platyhystrix* and other dissorophids the sculpturing of the dorsal skull surface continues onto the cheek above the otic notch, extending over much of the supratemporal and all but a very small area on the anteroventral margin of the tabular. The smooth, narrow border that surrounds most of the otic notch, therefore, pinches out just as it enters the tabular. In the trematopsids, on the other hand, the entire surface of the cheek dorsal to the otic notch is smooth. In addition, the sculptured skull table of trematopsids extends a short distance out from the smooth lateral skull surface dorsal to the otic notch to form a ventrally smooth shelf that Bolt (1974b) refers to as the supratympanic shelf. The supratympanic shelf is poorly developed or absent in dissorophids.

Marginal dentition also offers a way of distinguishing between the

two families. The marginal teeth of trematopsids differ from those of dissorophids in being relatively much larger, often recurved and far less numerous (see figures by Olson, 1941; Carroll, 1964). In his review of the trematopsids Olson (1941) stated that their combined number of maxillary and premaxillary teeth varies considerably, ranging from about 18 to 40 on each side of the skull. The dentitions of the trematopsids *Trematopsis seltini* and *Trematops stonei*, described later by Olson (1956, 1970), also appear to conform to those of other members of the family. Premaxillary-maxillary tooth counts are available for six dissorophid genera (Carroll, 1964; DeMar, 1968) and they range from 45 to 70 or more teeth. Judging from the small preserved portions of the marginal dentition of AMNH 11545, *Platyhystrix* may have had as many as 65 simple, peg-like teeth on either side of the upper jaw. Obviously, these teeth were considerably smaller than those of any trematopsid skull of comparable size. It should also be noted that there are no known cranial features of *Platyhystrix* that are inconsistent with the inclusion of this genus in the Dissorophidae.

As far as the specimens at hand reveal, the skull of *Platyhystrix rugosus* possesses only two derived features that distinguish it from those of all other dissorophids. The most obvious is the presence of the heavy nodular or papillose dermal sculpturing. The skull of *Platyhystrix* also appears distinct because of its large size. Of course, size is of limited use taxonomically; nevertheless, the large size of the skull AMNH 11545, over 19 cm in midline length, is a conspicuous and striking feature that is apparently not unusual for the species. The postorbital-squamosal skull fragment UCMP 39090 suggests a skull size approximately equal to that of AMNH 11545 and the tabular UCMP 39092 is even larger than that of AMNH 11545. Vaughn (1969a) has described a badly weathered dissorophid skull from the Lower Permian Laborcita Formation of New Mexico which he suspected may belong to *Platyhystrix*; he has documented the presence of this genus in that formation with the discovery of a *Platyhystrix* neural spine. The one feature that supports this identification, as noted by Vaughn, is the large size of the skull, measuring 115 mm in width between the maxillary rims at the level of the centers of the orbits. This suggests a skull even larger than AMNH 11545. It should also be mentioned that the above skull sizes are appropriate for the *Platyhystrix* vertebrae described by Langston (1953) and Lewis and Vaughn (1965). The largest previously reported skulls of dissorophid genera are of *Dissorophus*, *Cacops*, and *Longiscitula*, which have maximum midline lengths of 13.7, 12.5 and 12.0 cm respectively; in other dissorophid genera in which this measurement is directly obtainable the range is from 5.0 to just over 9.0 cm (DeMar, 1966a, 1968; Bolt, 1974a). Some of the dissorophids known only from postcranial materials, however, may have

approached *Platyhystrix* in skull size. Comparing relative sizes of post-cranial elements, Bolt (1974a) stated that *Alegeinosaurus* may have been approximately the size of *Cacops*, whereas *Aspidosaurus crucifer*, *A. glascocki*, and *A. apicolis* may have been considerably larger. Olson's (1972) restoration of the dissorophid *Fayella* suggests that the skull may have reached about 17 cm in length.

Apart from size and dermal sculpturing, the skull of *Platyhystrix* differs from those of other dissorophids only on the combined basis of several features. The differences are, however, of sufficient magnitude and number as to make individual comparisons impractical. Instead, an expanded diagnosis that includes both cranial and axial characters is given in the Systematic Paleontology section. Further, many of the differences between the skull of *Platyhystrix* and those of other dissorophids are brought out in the following section.

DISCUSSION

The Dissorophidae are one of the largest Paleozoic amphibian families. Of the 16 or more genera that have been included in this family, only 12 have sufficiently well known skulls to permit comparisons: the Pennsylvanian *Amphibamus* and *Actiobates*; the Permian *Tersomius*, *Brevadorsum*, *Broiliellus*, *Conjunctio*, *Aspidosaurus*, *Longiscitula*, *Dissorophus*, *Cacops* and *Platyhystrix*; the Lower Triassic *Micropholis* (Watson, 1913; Broili and Schroder, 1937; Gregory, 1950; Carroll, 1964; DeMar, 1966a, 1968; Eaton, 1973). Of these genera, a dissorophid assignment of only three has been or can be questioned. Boy (1972) has doubted the otherwise widely accepted view that the unarmored *Amphibamus* is the most primitive member of the Dissorophidae (Gregory, 1950; Carroll, 1964; Bolt, 1979). He regarded *Amphibamus* as the sole member of a separate family, Amphibamidae, having an apomorphic sister-group relationship to the Doleserpetonidae, Dissorophidae, and Trematopsidae. However, almost all of the shared derived characters Boy recognized in *Amphibamus* to support this relationship (relatively short postorbital region, loss of axial ribs and parasphenoidal teeth, perforated stapes) could just as easily be argued to represent paedomorphic, ontogenetic (Bolt, 1979), primitive or convergent conditions. It could also be argued that on the basis of Eaton's (1973) brief description of *Actiobates* there are equally strong morphological grounds for its assignation to the Trematopsidae. Although *Micropholis* has been considered a dissorophid (Romer, 1966; Bolt, 1977), its systematic position within the Dissorophoidea remains problematical. On the basis of rather long lists of comparisons, Boy (1972) presented ample reasons for placing *Micropholis* in its own family, Micropholidae, and viewing it as probably representing a distinct and widely divergent lineage from those comprising the remainder

of the large complex of dissorophoids. Although *Micropholis* may be a dissorophoid, judging from Boy's comments it seems unlikely that it is a dissorophid. Finally, it has been pointed out to us (Baird, personal communication) that, because Carroll (1964) has synonymized *Pelion* with *Amphibamus*, the family name Peliontidae Cope (1875), rather than Dissorophidae Boulenger (1902), should be applied to the grouping being considered here in accordance with the law of priority. Although Peliontidae is the earliest, valid applicable family name, we have chosen to use the far more familiar name Dissorophidae to avoid confusion.

Aside from a few possibly important exceptions, dissorophid cranial anatomy can be characterized as morphologically conservative but distinctive, and as providing few clues for recognizing intrafamilial relationships. On the other hand, vertebral structure, or its so-called "armor," is quite variable and, therefore has been relied on heavily in phylogenetic studies of the dissorophids (Carroll, 1964; DeMar, 1966a, 1968), even though dermal armor is absent or unknown in a few early forms. The tentative phylogeny presented by DeMar (1968), though based mainly on dermal armor, incorporates some cranial and axial skeleton characters, as well as data based on adaptational and paleoecological hypotheses developed by him. Yet, he concluded (DeMar, 1968:1236) that, "Despite the large number of genera and species known for this family, the margin for uncertainty, in evaluating their phylogenetic relationships, is large." Although Carroll (1964) and DeMar (1968) reached different conclusions regarding dissorophid phylogeny, they were in essential agreement in the recognition of primitive and advanced members. Using this aspect of their studies as a framework, a number of features can be cited to indicate that the skull of *Platyhystrix* represents a structural grade of organization between that of the more primitive dissorophids restricted almost entirely to the Pennsylvanian and the earliest Permian (Wolfcampian) and that of the more advanced forms of the later Early Permian (Leonardian). The former group includes *Amphibamus*, *Tersomius*, *Actiobates*, *Breviodorsum*, *Conjunctio*, *Dissorophus angustus*, and *Broiliellus*, whereas the latter group includes *Dissorophus multicinctus*, *Cacops*, and *Longiscitula*. This division, however, is not without some controversial systematic assignments. On the basis of cranial anatomy, placement of *Aspidosaurus* in either of these two groups is difficult, if not impossible. The type species, *A. chiton* (Broili, 1904), although represented by much of the skull and portions of the vertebral column, was not available in recent morphological and taxonomic studies of the dissorophids. The only other species of *Aspidosaurus* known by adequate skull and postcranial materials is *A. novomexicanus*. Langston (1953), however, reassigned the type and two referred specimens to

the genus *Broiliellus*. More recently Carroll (1964) recognized the original generic assignment of the type as valid and made the two specimens referred to *Broiliellus* by Langston the basis of a new genus and species, *Conjunctio multidentis*. Although *Aspidosaurus* is undoubtedly a valid genus, it probably does not include *A. novomexicanus* (DeMar, 1966b). It should also be pointed out that both DeMar (1968) and Bolt (1974a) have questioned Carroll's (1964) erection of *D. angustus*, the former claiming that it is not *Dissorophus* and the latter suspecting that it may represent a growth stage of *D. multicinctus*.

DeMar (1968) noted that the dissorophids show a trend toward increasing depth of the otic notch by backward growth of the lateral margin of the skull table, particularly the tabular. The relatively short otic notch of *Amphibamus*, *Actiobates*, *Tersomius*, and *Conjunctio* distinguishes them from other dissorophids. The advanced condition of a posteriorly closed otic notch has been reported only in *D. multicinctus*, *Cacops*, and *Longiscitula*. Dermal sculpturing is weakly developed only in *Amphibamus* and *Tersomius*, but in *Platyhystrix* it exhibits a development unequaled in any other genus. In its possession of a long, narrow nasal bone *Platyhystrix* can be grouped with *D. multicinctus* and *Longiscitula* in which the length ranges from two and a half to three times the width; in *Amphibamus*, *Actiobates*, *Tersomius*, *Conjunctio*, and *Broiliellus*, on the other hand, the length ranges from slightly greater than to about twice the width. There is also a tendency among the dissorophids toward backward expansion of the postorbital and postfrontal. For example, in *Platyhystrix* and the more advanced later Early Permian forms the portion of the postfrontal posterior to the orbit ranges in length from slightly greater than to nearly twice its width, whereas in the more primitive Pennsylvanian and earliest Permian forms its length ranges from about one half to slightly less than its width. Unfortunately, configurations of the nasal and postfrontal bones are not available for *Cacops* (Case, 1911). The above comparisons indicate that the skull of *Platyhystrix* is structurally advanced over those of essentially contemporaneous (Wolfcampian) dissorophids.

In his study of the Dissorophidae, Carroll (1964) envisioned the vertebral armor as having evolved only once and not until the Early Permian. DeMar (1966b, 1968), on the other hand, has presented a strong case for the development of armor independently in several different lines of dissorophids during the Late Pennsylvanian or Early Permian. Bolt (1974a), however, cautions that many of the differences in armor used by both authors to distinguish genera and species, and to construct phylogenies may actually reflect nothing more than different growth stages. Despite these difficulties, it can still be said that the armor of *Platyhystrix* is sufficiently distinct to preclude its close phy-

logenetic relationship with any of the Permian dissorophids excepting possibly of certain *Aspidosaurus* species (Carroll, 1964; DeMar, 1968). Important here is Vaughn's (1971) description of *Astreptorhachis ohioensis* from the Late Pennsylvanian Conemaugh Group of Ohio, which is based on neural arches and spines having a very *Platyhystrix*-like structure. The apparent relative shortness of the neural spines and the unusual fusion of adjacent neural arches and distal portions of the spines are key features that distinguish *A. ohioensis* from *P. rugosus*. As pointed out by Vaughn, the fusion between adjacent vertebrae is a feature not expected in a Pennsylvanian relative of the Permian *P. rugosus*, yet the similarities in their neural spines make the recognition of a close phylogenetic relationship inescapable, though obviously not a direct ancestor-descendant link. Vaughn (1971) assigned *A. ohioensis* to the Dissorophidae with some reservation because of the uncertain familial status of *P. rugosus* at that time. The evidence presented here that *P. rugosus* possessed a dissorophid skull corroborates this assignment. It can also be concluded, as Vaughn (1971) did, that both species are members of a divergent armored offshoot that separated in the Middle or Late Pennsylvanian from the main evolutionary line or lines that gave rise to the other Early Permian dissorophids. *A. ohioensis* is the only known Pennsylvanian armored dissorophid. The early occurrence of highly specialized armor in the *Platyhystrix*-like dissorophids is consistent with the relatively advanced state of the skull of *P. rugosus*.

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