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A Trematopsid Skull from the Lower Permian, and Analysis of Some Characters of the Dissorophoid (Amphibia: Labyrinthodontia) Otic Notch

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INTRODUCTION

The partial skull (UR 2400) described in this paper came from the Lower Permian Fort Sill locality, Comanche County, Oklahoma. This locality has been described elsewhere (see Gregory et al., 1956; Olson, 1967). Olson's faunal list contains eight genera, of which all but one (*Xenacanthus*) are small tetrapods. This list can be expanded to 11 by the addition of *Basicranodon* (Vaughn, 1958), *Phlegethontia* (McGinnis, 1967), and *Doleserpeton* (Bolt, 1969). As Olson notes, there are certainly a number of undescribed forms in the fauna, but the usually disarticulated condition of materials and dispersal of collections hampers study.

With the exception of *Doleserpeton*, UR 2400 is the first example of even a partial labyrinthodont amphibian skull described from Fort Sill. The specimen is thus important in providing a guide to association of well-preserved but disarticulated labyrinthodont dermal bones from Fort Sill. Excellent preservation of this skull fragment makes it useful in understanding the morphology of other dissorophoid labyrinthodonts, which are mostly known from less well-preserved red-beds specimens. (The superfamily Dissorophoidea was originally composed of Dissorophidae, Doleserpetontidae, and Trematopsidae (Bolt, 1969). Boy (1972) has added the Micromelanerpetontidae and Branchiosauridae, neither of which will be discussed here due to unavailability of material). Finally, UR 2400 is of interest as a possibly new species of trematopsid.

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Abbreviations used in this paper for repositories of specimens are:

AMNH—American Museum of Natural History
MCZ—Museum of Comparative Zoology, Harvard University
UC or UR—Field Museum of Natural History
UT—University of Texas Memorial Museum.

Materials Studied—All are from Lower Permian deposits. A complete list is given in Table 1.

DESCRIPTION OF UR 2400

The roofing bones show well-developed, typically labyrinthodont sculpturing. No attempt has been made to reproduce this sculpturing exactly in the figures. The sculpturing suggests that UR 2400 was not a juvenile (cf. Bystrov, 1935), but gives no information as to maximum adult size. There is no development of bony knobs or ridges on the outer skull table (cranial ornamentation in the sense of Carroll, 1964). Presence or absence of ornamentation in a single specimen is probably of low taxonomic importance, however (cf. DeMar, 1968, on variation in this character). Some, perhaps all, sutures are strongly interdigitated. Small clusters of pyrite crystals (not shown) were scattered over the surface, especially on the outer skull table, but occupied only a small percentage of the total area. Although the pyrite tends to occur along suture lines and obscure short segments of them, virtually all sutures could be accurately determined.

The skull fragment as preserved is shown in Figures 1-3. The tabulars are broken off posteriorly, but the natural borders of tabulars and postparietals have been preserved on the occiput. Several points which are not clear from the figures, or which will be discussed below, merit comment:

1. The bone around the orbits is thickened. This is achieved without producing a very noticeable circumorbital ridge. Thickening is greatest at the level of the postfrontal-postorbital contact.

2. The squamosal bears a thin, transverse process (FSQ in fig. 3) in front of the lamina ascendens of the pterygoid, and presumably made contact with it originally.

3. The postfrontal-postorbital contact is strongly bevelled in the orbital rim, with the postfrontal underlying the postorbital.

4. The lamina ascendens of the pterygoid is preserved on each side, apparently *in situ* as the orientation is identical on both sides.

Each stands vertically and at approximately right angles to the midline. The lamina is paper-thin dorsally, and ends just short of a contact with the skull roof.

5. There is a pronounced thickened area or boss (B in fig. 3) on the ventral surface of each postparietal. Each boss lies just anterior to an occipital flap of the postparietal, of the type which in labyrinthodonts usually covers the upper part of the occipital aspect of the exoccipital. The boss is therefore almost certainly directly dorsal to the exoccipital. Direct contact may have existed between boss and exoccipital; more likely, a supraoccipital or part of the opisthotic (cf. Bolt, 1969) intervened.

6. Just lateral to the boss on the postparietal is a process (partially preserved, and only on the left side) on the tabular. This process (OP in fig. 3), directed ventro-medially, may have made contact with the parocipital process of the opisthotic. There is no other indication on the tabular of a possible opisthotic contact.

7. The otic notch is deep. Its dorsal border is formed by a vertical flange composed of squamosal, supratemporal, and tabular. Such a flange will hereinafter be referred to as the supratympanic flange (SF in figs. 2-4). The squamosal and tabular meet below the supratemporal, excluding it from the ventral margin of the flange. Extending laterally above the flange, the skull table forms what may be called the supratympanic shelf (SS in fig. 3). The shelf is here defined as existing only if there is a supratympanic flange, or at least a semilunar flange on the supratemporal (see below). The shelf is damaged on the right side. The supratemporal extends into the supratympanic flange as a rounded projection. Such a projection of the supratemporal above the otic notch, whether or not associated with a supratympanic flange, is called a semilunar flange (SLF in figs. 2 and 4). The terminology adopted is based on, but different from, that of DeMar (1968). DeMar observed that dissorophids generally have a distinctively-shaped supratympanic flange, which he called a "half-moon-shaped flange" (see fig. 4). The same condition is referred to here as a "supratympanic flange of dissorophid shape." DeMar (1968, p. 1212) noted that ". . . *Trematops* [*milleri*] does have a ventrally directed ridge on the dorsal margin of the otic notch which narrows it from above," but he did not name the flange in *Trematops*.

8. The antero-ventral wall of the otic notch is formed entirely by the squamosal. This part of the notch is roughly cone-shaped with the apex of the cone pointing medially.

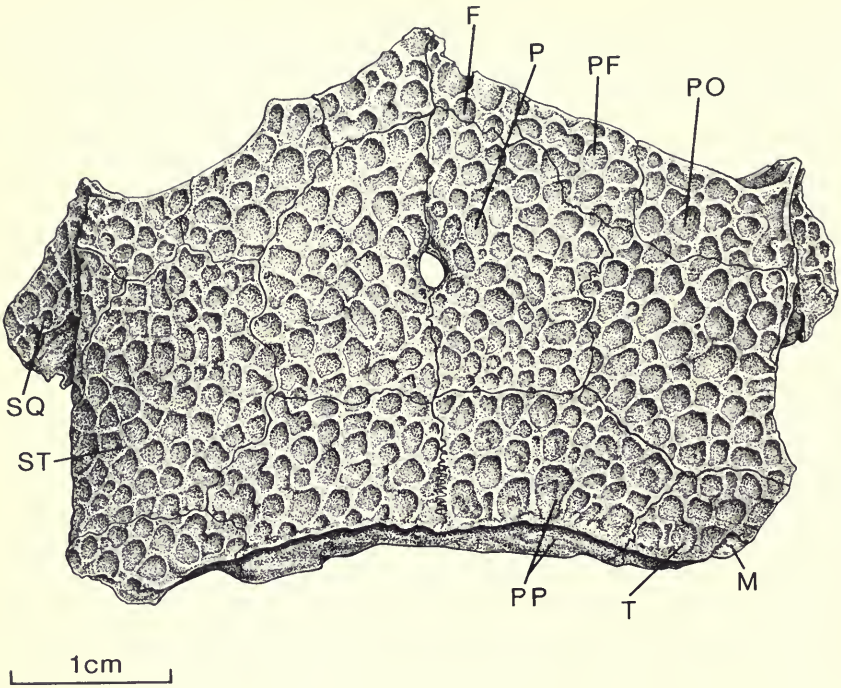


FIG. 1. Dorsal view of partial trematopsid skull, UR 2400. Abbreviations: **F**, frontal; **M**, matrix; **P**, parietal; **PF**, postfrontal; **PO**, postorbital; **PP**, postparietal; **SQ**, squamosal; **ST**, supratemporal; **T**, tabular.

SYSTEMATIC POSITION OF UR 2400

There is little doubt that the specimen is a dissorophoid labyrinthodont. There are no features inconsistent with this conclusion, and it is supported by the presence of a supratympanic flange and by the shape of the squamosal. These features do not indicate a particular position within the Dissorophoidea, however. The affinities of UR 2400 within the Dissorophoidea are examined in more detail below, using quantitative and qualitative characters.

An attempt to distinguish the three families within the Dissorophoidea on the basis of postorbital skull proportions was unsuccessful. The three types of measurements in Table 1 were graphically compared as follows: L_{pb}:L_t, L_{pb}:W, and L_t:W. The three families could not be distinguished from one another nor from UR 2400 on this basis. This is interpreted as strengthening the argument for relationship of UR 2400 to the Dissorophoidea. These proportions are prob-

ably not unique to dissorophoids, however, even though apparently not common among rhachitomes. Text-figures in Moustafa (1955), for instance, suggest that *Parioxys ferricolus* (family Parioxyidae) resembles dissorophoids in the parameters measured for Table 1. *Parioxys* can, of course, easily be distinguished from dissorophoids when other skull proportions are considered.

CHARACTER ANALYSIS

The systematic position of UR 2400 can apparently best be determined by use of qualitative characters. Comparison with other dissorophoids suggests several characters that might usefully be examined (table 1). The states defined for each character will be analyzed below as primitive or derived, as advocated by Hennig (1966). Hennig's method of phylogenetic reconstruction requires that a number of characters be so analyzed. There are presently very few properly analyzed characters available for dissorophoids; thus no phylogenetic reconstruction is given in this paper. Boy's (1972) tentative analysis of sister groups within the Dissorophoidea is interesting but premature.

The advantages and theoretical basis of Hennig's system have been treated in many recent publications (e.g., Brundin, 1966; Nelson, 1970; Cracraft, 1972; Schaeffer et al., 1973), and the arguments pro and con will not be repeated here. However, a note on methodology is necessary: This paper basically follows the practical procedure outlined by Marx and Rabb (1970, 1972). Criteria for determining primitive and derived character states are modified from those presented by Marx and Rabb. Criterion 1 is uniqueness: character states occuring in the "descendent" group (in this case, dissorophoids), but not in the "ancestral" group (see below) are derived. Criterion 2 is relative abundance: character states found in both the "ancestral" and "descendent" groups are primitive.

The superfamily Edopoidea is generally considered ancestral to the Eryopoidea, which in turn appears the most likely group of origin for the Dissorophoidea. Accordingly, the edopoids and eryopoids have been taken as the "primitive" reference groups. In practice, due to the lack of good descriptions of the region under consideration, three reasonably well-described genera will represent the two superfamilies. The Edopoidea are represented by *Edops* (Romer and Witter, 1942) and *Dendrepeton* (Carroll, 1967); the Eryopoidea, by *Eryops* (Sawin, 1941). Addition of a number of less completely described genera would strengthen the analyses only in appearance.

TABLE 1. Cranial measurements (in mm.) of dissorophoids, and states of four characters (see text). Abbreviations: + = present; − = absent; i = intermediate; NA = area is missing or unprepared; est = estimated; D = dissorophid shape; T = trematopsid shape.

	L^1_{pb}	L^2_t	W^3	Character 1: supratympanic flange	Character 2: squamosal-tabular contact	Character 3: semilunar flange of supratemporal	Character 4: supratympanic shelf
UR 2400	11	20	43/39[4]	+; T	+	+	+
Tersomius texensis MCZ 1912	13	19	33	i?	NA	+	-?
Tersomius texensis MCZ 1415	14	18	31	i?	-?	+	-?
Tersomius texensis, holotype, AMNH 4719	8	11	20 (est)	NA; NA	NA	NA	NA
Broiliellus texensis, holotype, UC 684	18	38	58	+; D	+	+	-?
Broiliellus texensis UC 685	17	33	53	+; NA	+	+	−
Broiliellus brevis[5], holotype, MCZ 1424	12	19	38	+; D	+	+	NA
Longiscitula houghae, holotype, UC 430	16	35	54	+; D	+	+	−
Cacops aspidephorus UC 649	22	33	74	+; T?	NA	NA	+
Conjunctio multidens, holotype, UC 673	NA	NA	NA	+; NA	+	+	i
Dissorophus multicinctus MCZ 2122-1	26	48	77	+; D	+	+	−
Dissorophus angustus, holotype, MCZ 1695	12	17	37	+; D	+	+	i
Brevidorsum profundum, holotype, MCZ 3250	12	21	40	+; D	+?	+?	i
Aspidosaurus novomexicanus[6]	−	−	−	+; D	+	+	?
Acheloma sp? MCZ 1485[7]	16	NA	NA	+; T	+?	NA	NA
Acheloma cumminsi UC 481	NA	46	76	+; T	+	+?	i
Acheloma whitei UC 482	16	22	37	+; T?	NA	NA	-?
Trematops willistoni, holotype, UC 1584	14	21	38	+; T	+	+	+

TABLE 1. Cranial measurements (in mm.) of dissorophoids, and states of four characters (see text). Abbreviations: + = present; − = absent; i = intermediate; NA = area is missing or unprepared; est = estimated; D = dissorophid shape; T = trematopsid shape—*Continued.*

	L^1_{pb}	L^2_t	W^3	Character 1: supratympanic flange	Character 2: squamosal-tabular contact	Character 3: semilunar flange of supratemporal	Character 4: supratympanic shelf
Trematops milleri, holotype, UC 640	17 (est)	51	86 (est)	+; T	NA	NA	+
Trematops milleri UC 1760	23	52	84 (est)	+? NA	NA	NA	+?
Doleserpeton annectens, holotype, UR 1308	3	4	4	−	−	+	−

[1] Length of postorbital bar, measured as least distance between orbit and otic notch.
[2] Length of skull table measured in the skull midline from a line tangent to posterior portions of both orbits (if skull is undistorted) to posterior margins of postparietals on skull table.
[3] Width of skull table usually measured as least width of table above the otic notch. In UR 2400 W is measured between points opposite ½ L_t.
[4] The high figure is obtained by measurement as though the supratympanic shelf were present on both sides; the low figure as though the shelf were absent on both sides.
[5] Data obtained from figure in Carroll (1964) as specimen is lost.
[6] Data from figure in Carroll (1964); measurements and character 4 could not be determined with confidence.
[7] For comments on taxonomic status of this specimen, see Bolt (1974).

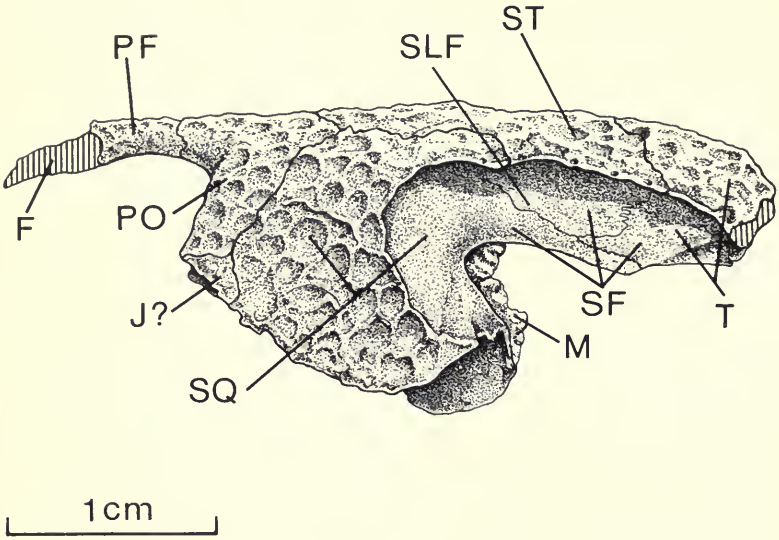


FIG. 2. Lateral view of partial trematopsid skull, UR 2400. Vertical shading indicates broken surfaces. Abbreviations: J?, possible fragment of jugal; SF, supratympanic flange, including part of squamosal, supratemporal, and tabular; SLF, semilunar flange of supratemporal. Other abbreviations as for Figure 1.

The tabulation below includes most North American dissorophoid genera and species. Missing are *Ecolsonia* (Trematopsidae) and *Amphibamus* (Dissorophidae). *Amphibamus* has recently been reviewed by Carroll (1964), but the nature of the material severely limits interpretation of the region around the otic notch. This is unfortunate in view of *Amphibamus'* position as the oldest and generally most primitive dissorophid (Carroll, 1964).

Particularly in the case of *Doleserpeton*, which is small and is also represented by more or less immature specimens, the effects of absolute size and of degree of maturity may be important. This is simply a cautionary note; nothing can be said about these problems at present due to the absence of proven growth series. All specimens are here treated as mature for purposes of analysis.

Character 1: supratympanic flange—Four states: (a) absent; (b) intermediate; (c) present and trematopsid shape; (d) present and dissorophid shape. It must be emphasized that the difference in shape between the flanges of (c) and (d) is due to the presence (fig. 4) or absence (fig. 2) of a semilunar curvature of the squamosal along the ventral border of the supratympanic flange. In UR 2400 (fig. 2), the

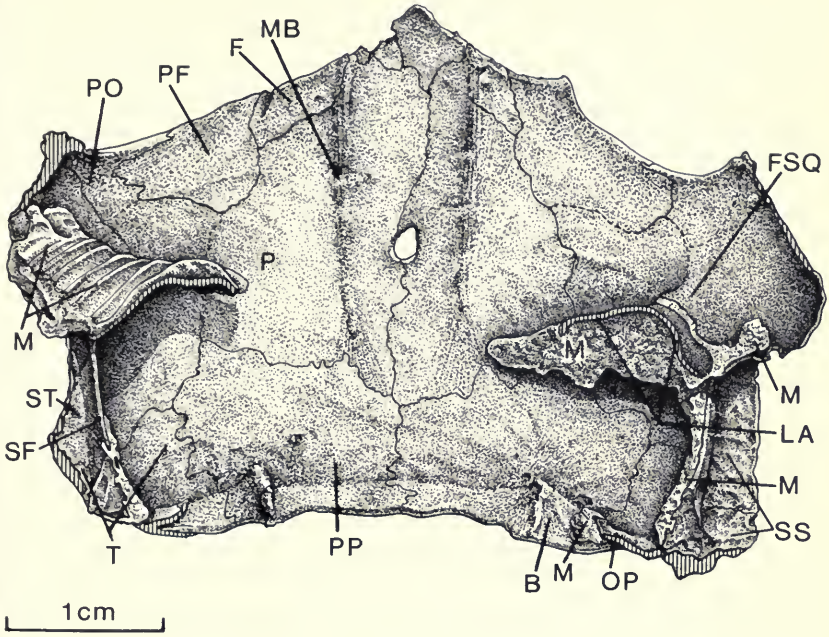
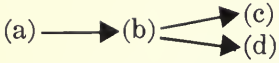


FIG. 3. Ventral view of partial trematopsid skull, UR 2400. Vertical shading indicates broken surfaces. Abbreviations: **B**, boss on postparietal; **FSQ**, flange on squamosal; **LA**, lamina ascendens; **MB**, markings associated with contact between braincase and skull roof; **OP**, process from tabular, presumably for contact with opisthotic; **SF**, supratympanic flange, composed of parts of squamosal, supratemporal, and tabular; **SS**, supratympanic shelf. Other abbreviations as in Figure 1.

flange ends posterior to the squamosal-tabular suture by rising to merge with the undersurface of the tabular. Particularly if the skull table were bent downward, this inflection could be mistaken for a semilunar curvature of dissorophid type. None of the three reference genera shows any sign of developing a supratympanic flange, nor indeed is there any known development of the flange in any other labyrinthodont, as noted also by DeMar (1968). Absence of the flange (a) is therefore primitive; the intermediate condition (b), seen only in the early dissorophid *Tersomius*, is reasonably interpreted as derived. Still more derived are states (c) and (d), but it is presently impossible to determine whether one was derived from the other. The apparently straight ventral edge of the weak flange in *Tersomius* provides some evidence that state (c) may be more primitive than (d), but this is inconclusive. Tentative phylogeny of these states is

thus:



Character 2: squamosal-tabular contact—Two states: (a) absent and (b) present. State (a) applies to species which completely lack the contact. State (b) applies to species in which there is slight contact, or to species with a well-developed contact such as that in UR 2400 (fig. 2). All dissorophoids in which a squamosal-tabular contact is definitely present resemble UR 2400. It is uncertain whether or not contact is present in *Tersomius texensis*. *Longiscitula houghae* is described by DeMar (1966) as possessing state (a), but re-examination shows that state (b) is present. There is definitely a slight contact of squamosal and tabular in *Eryops*, and possibly in *Edops* and *Dendrerpeton* as well. State (b) is thus presumably primitive, state (a) derived.

Character 3: semilunar flange of supratemporal—Two states: (a) absent and (b) present (SLF in figs. 2 and 4). The condition in *Edops* is uncertain; in *Dendrerpeton* and (particularly) *Eryops*, a more or less wedge-shaped flange is present. The available evidence thus suggests that state (b) is primitive, state (a) derived.

Character 4: supratympanic shelf—Three states: (a) absent, (b) intermediate, and (c) present. State (a) applies to specimens with no projecting shelf or ridge, or very slight development of a ridge. This state also applies to specimens (*Dissorophus multicinctus*) in which dermal sculpturing extends downward over the semilunar flange, with no development of a shelf. Apparent absence of the shelf may be secondary and due to breakage. As noted for UR 2400 in Table 1, the loss of a supratympanic shelf by breakage can significantly affect measurement of table width (W). Secondary loss of the shelf can also result in a significant change in shape of the skull table—compare right and left sides of UR 2400 in Figure 1. Skull-table shape is a potentially useful character, but must obviously be used carefully. A specimen lacking the shelf but showing signs of damage in the area is scored (-?); probably most of these were originally state (b). State (b) applies to specimens in which there is no shelf as such, but a distinct ridge of dermally-sculptured bone. State (c) applies to specimens such as UR 2400, where a shelf is present and its undersurface, where visible, is unsculptured.

The semilunar flange of dissorophoids is presumably homologous to the more or less wedge-shaped supratemporal flange seen in the reference genera. Projection of the skull table laterally beyond the

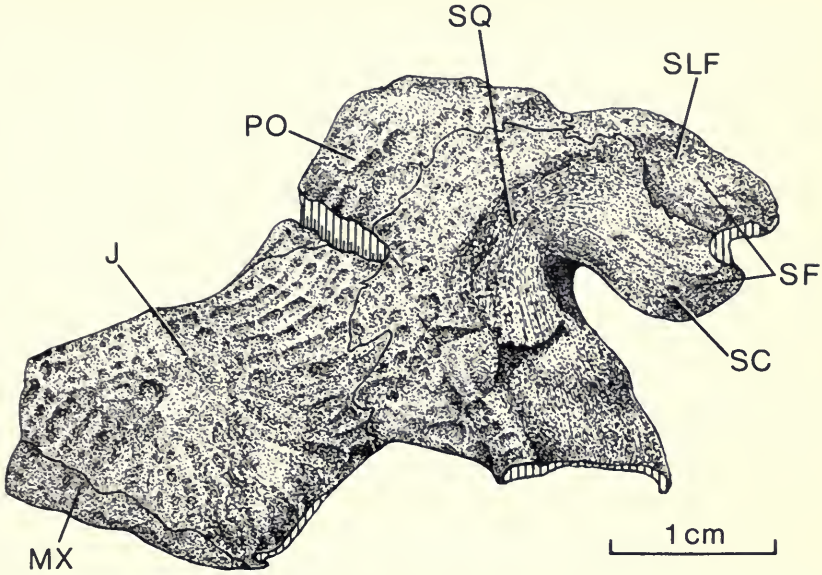


FIG. 4. *Broiliellus olsoni*, UT 3189-8. Left lateral view of part of skull of holotype, to show dissorophid shape of supratympanic flange. Supratympanic flange, including all of tabular portion, is broken off posteriorly; flange is in plane of paper. Vertical shading indicates broken surfaces. Abbreviations: **J**, jugal; **MX**, maxilla; **PO**, postorbital; **SC**, semilunar curvature of squamosal within supratympanic flange; **SF**, supratympanic flange, including parts of squamosal, supratemporal, and tabular (tabular portion is broken off in this specimen); **SLF**, semilunar flange of supratemporal; **SQ**, squamosal.

homologue of the semilunar flange would thus constitute a supratympanic shelf. A supratympanic shelf as thus defined apparently does not occur in the reference genera. Therefore state (a) is primitive; state (b) is reasonably considered derived, and state (c) more derived.

Systematic results—UR 2400 is probably a trematopsid, on the basis of the derived state (c) of character 1: supratympanic flange present and of trematopsid shape. The specimen cannot be definitely assigned to any trematopsid genus. However, in view of the general lack of morphological information on trematopsids, and the small portion of the skull preserved, a new taxon should not be established for this specimen.

State (c) of character 1 apparently serves to define the Trematopsidae as a monophyletic group in Hennig's sense, i.e., a group all members of which share at least one derived character only with each other. This conclusion leaves out of consideration the possibly trematopsid shape of the flange in *Cacops*—the specimen is so poorly preserved in this area as to make determination of character state

very uncertain. DeMar (1968) suggested the presence of the dissorophid shape of supratympanic flange in most dissorophids as a unifying character of the family. This is correct in a sense; however, the absence of this character state in *Tersomius*, and possibly in *Amphibamus* and *Cacops*, precludes using it to formally demonstrate monophyly in Hennig's sense. Similarly, none of the other characters analysed can be used to demonstrate monophyly of the Dissorophoidea or its constituent families. This should not be taken as a denial of monophyly, but simply as a statement that monophyly has not yet been demonstrated. Finally, this analysis suggests that it was incorrect to use the semilunar flange on the supratemporal to show relationship of *Doleserpeton* to dissorophids (Bolt, 1969). The semilunar flange is probably a shared primitive character, and as such should not be employed in phylogenetic analysis.

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