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Osteology, Function, and Evolution of The Trematopsid (Amphibia: Labyrinthodontia) Nasal Region

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INTRODUCTION

The family Trematopsidae, at present known exclusively from the Lower Permian of North America, departs from the usual labyrinthodont pattern in both morphology and presumed habitat. Like the related dissorophids and doleserpetontids which, with trematopsids, constitute the superfamily Dissorophoidea (Bolt, 1969), the trematopsids are thought to represent an early tetrapod experiment in terrestriality. This view of trematopsid habits has most recently been expressed by Olson (1970), on the basis of extensive collecting experience. Morphologically, trematopsids are probably unique among labyrinthodonts in their possession of a very elongate external naris. This character is also one of the main reasons for separation of trematopsids from the generally similar dissorophids. The various suggestions which have been made regarding the function of this peculiar naris are of doubtful validity. We have only the most general knowledge regarding the position of the nasal capsule and the relationship of the capsule to several septa in the nasal region which were first described by Olson (1941). There has been no attempt to derive the trematopsid narial region from that of more "normal" labyrinthodonts, even the dissorophids. Since the Dissorophoidea may be ancestral to the living Amphibia (Bolt, 1969), information on dissorophoid relationships and biology should be of considerable interest to both paleontologists and herpetologists.

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The comparative study presented below provides data which are relevant to questions of both phylogeny and function. As regards the latter, I will suggest that:

1. The elongate trematopsid external naris reflects the presence of a nasal salt gland, and
2. The elongation of the external naris, and the consequent narrowing of the antorbital bar, required transfer of forces away from the bar. This was achieved by the "nasal flange" characteristic of trematopsids.

As regards phylogeny, I will attempt to show that the characteristic trematopsid narial morphology can be derived from that of dissorophids or *Doleserpeton*, by a series of changes involving little more than posteriad enlargement of the external naris and (perhaps) an increase in the size of some other already-existing, uniquely-dissorophoid structures in the nasal region. The existence of these structures strengthens the case for relationship of dissorophids, trematopsids, and doleserpetontids. At the same time, a multiple origin among dissorophoids of the trematopsid condition appears very possible.

DeMar (1966) described an armored dissorophid, *Longiscitula houghae*, with very elongate external nares like those of trematopsids. Assignment to the Dissorophidae is, I believe, correct. However, examination of the type specimen (FMNH UR 430), the only known skull with preserved nasal region, casts doubt on the condition of the external naris. The region on both sides is severely damaged, and I am unable to trace most sutures in the area or to determine the boundaries of the external naris. It is, therefore, possible that *Longiscitula* did not possess elongate external nares, and is a normal dissorophid in this regard.

Throughout this paper, the term "external naris" refers to the paired laterally-placed openings lying anterior to the orbits and including the external narial openings. Earlier papers describing trematopsids referred to the elongate external naris as a confluent external naris and antorbital vacuity. This terminology doubtless derived from the (inappropriate) comparison of trematopsids with archosaurian reptiles, in which an antorbital vacuity completely separate from the external naris is characteristically present. There is no evidence that any labyrinthodont, including the ancestors of trematopsids, possessed such an antorbital vacuity. This was finally

recognized by the disappearance of all reference to an antorbital vacuity in Romer's (1947) labyrinthodont review.

I am grateful to H. Barghusen, R. DeMar, and J. Hopson for helpful discussion and criticism. I also wish to thank the Museum of Comparative Zoology of Harvard University and the University of Texas Memorial Museum for the loan of specimens. D. Cohn and R. Roesener deserve thanks for preparing illustrations.

The following abbreviations refer to specimen depositories:

FMNH, Field Museum of Natural History, Chicago, Illinois

MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

UT, University of Texas Memorial Museum, Austin, Texas.

A list of abbreviations used in figures is given on p. 28.

SYSTEMATICS AND MATERIALS

The family Trematopsidae presently consists of four genera: *Trematops*, *Acheloma*, *Trematopsis*, and *Ecolsonia*. The latter two are monotypic and represented by very incomplete material. *Trematops* and *Acheloma* each include three species; all but the type species were erected by Olson (1941, 1970). Despite an abundance of specimens of *Trematops* and *Acheloma*, difficulties of preparation and interpretation have combined to keep even these genera relatively poorly known. It seems certain, however, that among the materials already collected there are specimens which cannot easily be fitted into the named species as presently understood. This is pointed out in a previous study (Bolt, MS) dealing with the morphology and function of the labyrinthodont palatine and anterior orbital wall. It is not necessary to repeat here the observations which support that conclusion; others will be given below. Until available material has been more completely prepared, erection of new taxa is justified only for the most obviously different specimens.

These remarks stem from the fact that the description of the trematopsid nasal region given below is (unavoidably) based on a specimen which may represent a new taxon. The specimen (MCZ 1485) is provisionally referred to *Acheloma* sp.; comparison with the types of both *A. whitei* and *A. pricei* shows at least a specific difference, and this seems true also of *A. cummingsi* based mostly on Olson's (1941) description (Bolt, MS). Throughout this paper, the term "A. sp." refers only to MCZ 1485.

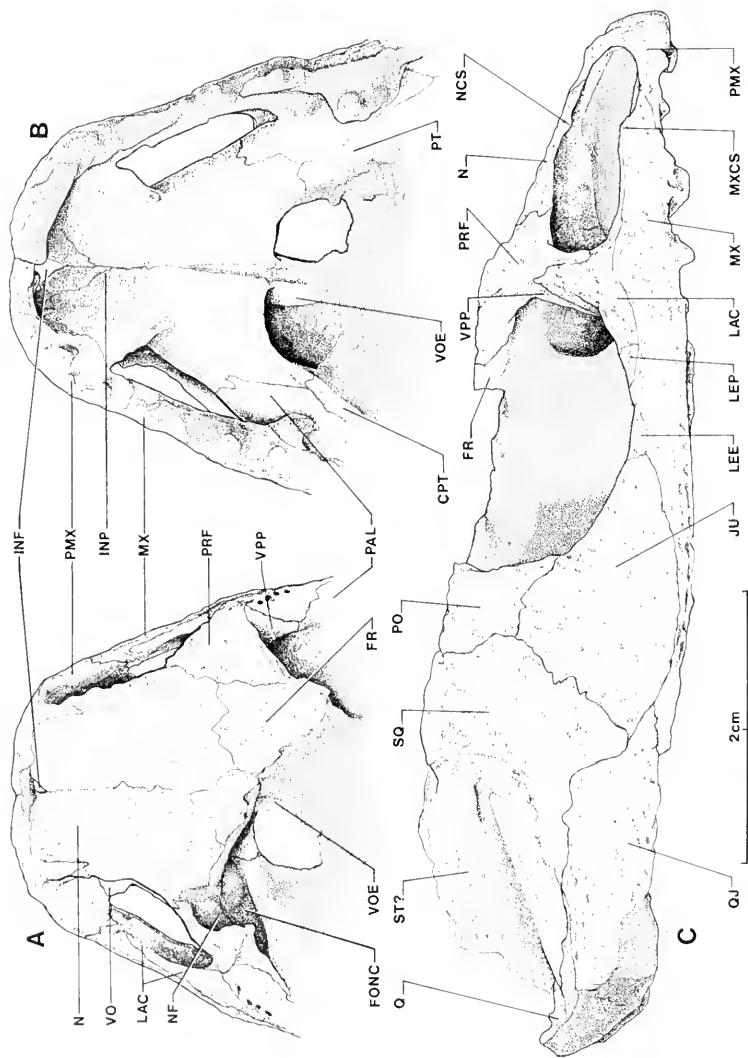


FIG. 1. Skull of *Acheloma* sp., MCZ 1485. Dense, patterned stippling represents areas of matrix. A. Dorsal view of snout; B. Ventral view of snout; C. Right lateral view of skull.

MCZ 1485 was collected in 1936, but is not mentioned in Olson's (1941) review. The specimen was filled with a purplish, friable, fine-grained sandstone. Sutures are generally easily determined. Most of the skull is virtually undistorted, although the dorsal roofing bones behind the level of the anterior orbital walls are missing. All dermal bones of the palate are present, but the pterygoids are slightly displaced mediad; the parasphenoid and attached basisphenoid have been displaced posteriad and rotated. Only the (damaged) right quadrate is present. Part of the braincase is present, but has not yet been completely prepared. No sphenethenoid has been found despite preparation of the interorbital area. The need for support of the fragile bone has precluded complete removal of matrix from the nasal region.

Horizon—Lower Permian; Admiral Formation

Locality.—Archer County, Texas; "Copper Hill School," South of Little Wichita River near Mankins-Archer City Highway.

MORPHOLOGY

External naris and internarial foramen (figs. 1, 2).—The external naris is surrounded by the bones usually seen here in labyrinthodonts (premaxilla, maxilla, lacrimal, and nasal), with the addition of the prefrontal. In typical trematopsid fashion, the opening is partly subdivided into anterior (shorter) and posterior (longer) portions, by a constriction. This characteristic is noted by Olson (1941). Olson figures specimens (for instance, the holotype of *A. pricei*, MCZ 1419) in which constriction is due to the maxilla alone and others (for instance, the holotype of *Trematops milleri*, FMNH UC 640) in which constriction is due only to a ventrolateral projection from the nasal. Examination of the two specimens mentioned, confirms Olson's interpretation. The difference is apparently not generically diagnostic (see Olson's (1941) Figure 2 showing a specimen of *A. cummingsi* with a pronounced projection from the nasal). In *A. sp.* both nasal and maxilla contribute to the constriction, although the nasal projection is little developed.

An internarial foramen (fig. 1A, B) is developed in *A. sp.* much as in other trematopsids. The boundaries shown may or may not exactly correspond to those present in life. Carroll's (1964) study of the dissorophid *Tersomius texensis* demonstrates a small bone in this position; postmortem loss of such a bone would produce a trematopsid-like internarial foramen, and in any given trematopsid

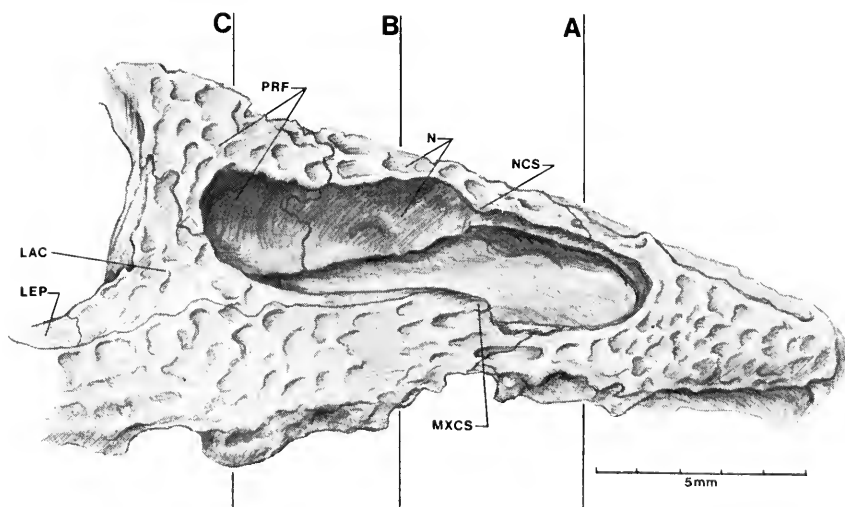


FIG. 2. *Acheloma* sp., MCZ 1485. Snout in right lateral view.

specimen it is likely to be difficult to prove that this did not happen. Thus the internarial foramen can usually not be confidently used as a diagnostic character.

Internal naris and anterior palate (figs. 1, 3).—The internal naris is of normal labyrinthodont appearance, and is surrounded by the usual labyrinthodont bones—maxilla, premaxilla, vomer, and palatine. It is not so elongate as the external naris, although it extends slightly farther posteriorly. The constrictions in the external naris approximately coincide with the anterior border of the internal naris.

As in most dissorophoids, the vomers form a large anterior and medial internarial pit. The internarial foramen opens into the anterior portion of this pit. The anterior vomerine borders could not be completely determined, but the figured condition must be very nearly correct. The medial margins of the vomers are reflected upward within the internarial pit (fig. 3A); Olson (1941) referred to the two reflected areas jointly as the "internasal septum." This terminology may be retained, although the two halves of the "septum" approach one another only dorsally. The internasal septum closely approaches the underside of the skull roof, but it cannot be determined whether there was actual contact. Posterior and lateral to the internarial pit, the vomer (anteriorly) and palatine (posteriorly) bend up along the border of the internal naris at about a 20° angle to the horizontal (fig. 3B, C). This lateral, reflected area of the

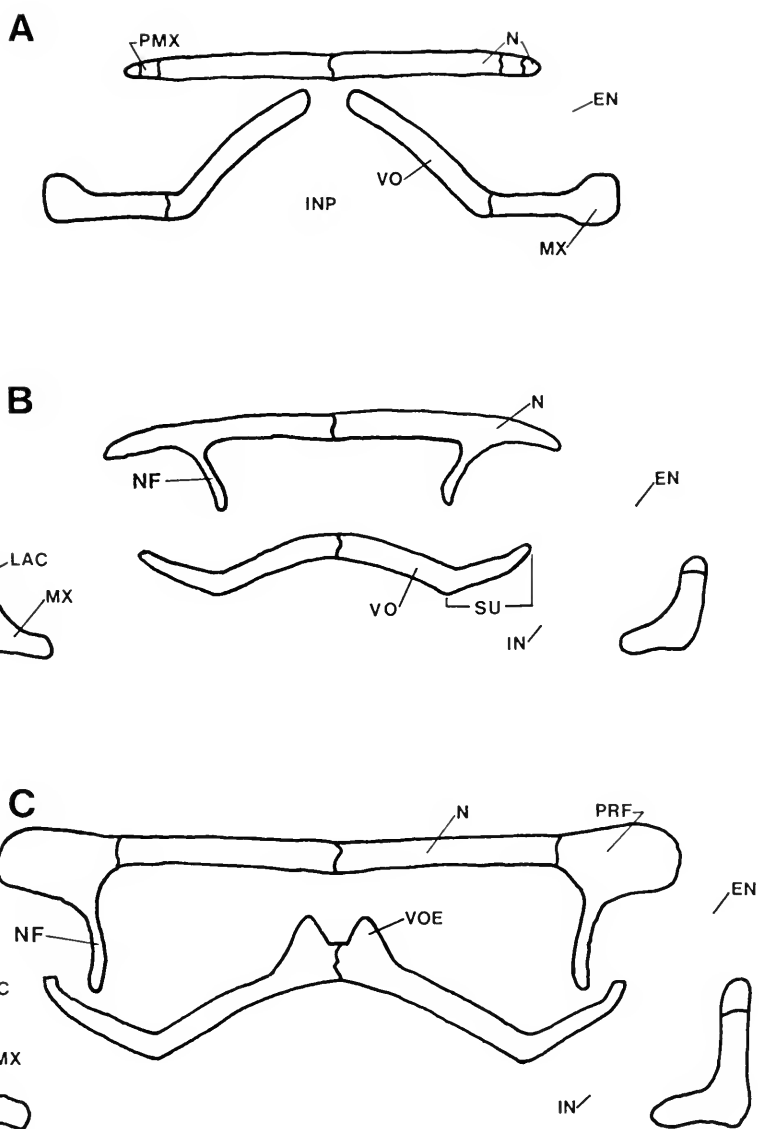


FIG. 3. *Acheloma* sp., MCZ 1485. Schematic cross-sections through snout, at levels indicated in Figure 2. In Figure 3A, the dorsally-reflected portions of the vomers together form the 'internasal septum' (see text). Figure 3B is taken just posterior to the internarial pit. In Figure 3C, SU is present but unlabelled.

vomer and palatine was thought by Olson (1941) to consist of vomer only; Olson considered this area as forming another (unnamed) septum (SU in fig. 3B). This septum disappears at the antero-medial corner of the internal naris, opposite the maxillary constriction of the external naris. In lateral view (figs. 1C, 2) the upturned medial border of the choana is thus masked by the maxillary border of the external naris.

Several additional features of *A. sp.* pertinent to classification may be noted here. The primitive contact of pterygoids with vomers is retained. Although the contact is a narrow one in this instance, trematopsids are the only dissorophoids known to possess it. (Carroll's (1964) Figure 4 shows a close approach to a pterygoid-vomer contact in the primitive dissorophid *Tersomius texensis*. Examination of the specimen (MCZ 1912) on which Carroll based his figure, suggests that the anterior portion of his suture line is a crack. The pterygoid may not even reach the palatine in *T. texensis*, ending instead at or posterior to the ectopterygoid tooth). The interpterygoid vacuities in *A. sp.* are large for a trematopsid, but this is also the case in *Ecolsonia* (Vaughn, 1969). There are three sets of fang-teeth, of varying sizes. Compared to the diameter of an average marginal tooth, the palatine fangs are considerably larger; the ectopterygoid fangs are the same or slightly greater, and the vomerine fangs are apparently the same or smaller. The left vomerine tooth illustrated in Figure 1B may or may not be a small fang. The vomerine fangs might have been removed in preparation. A posterior extension (VOE in fig. 1B) is present on each vomer. Each extension runs forward an undetermined distance into the unprepared area behind the internarial pit. The extensions are not part of the sphenethmoid: on both sides no suture with the vomer is visible. So far as I can determine, this peculiar extension is unique to *A. sp.* among labyrinthodonts. The extension falls well short of the skull roof. The parasphenoidal rostrum could conceivably have lain either dorsal (usual condition in labyrinthodonts) or ventral to the vomerine extensions. Measurement of the preserved portion of the parasphenoidal rostrum shows that it certainly reached as far forward as the vomerine extensions, and perhaps the main portions of the vomers. It is uncertain whether the rostrum made contact with the vomers. There is a vomerine contact in *Ecolsonia* (Vaughn, 1969), with the anterior tip of the parasphenoidal rostrum apparently ventral to the vomers.

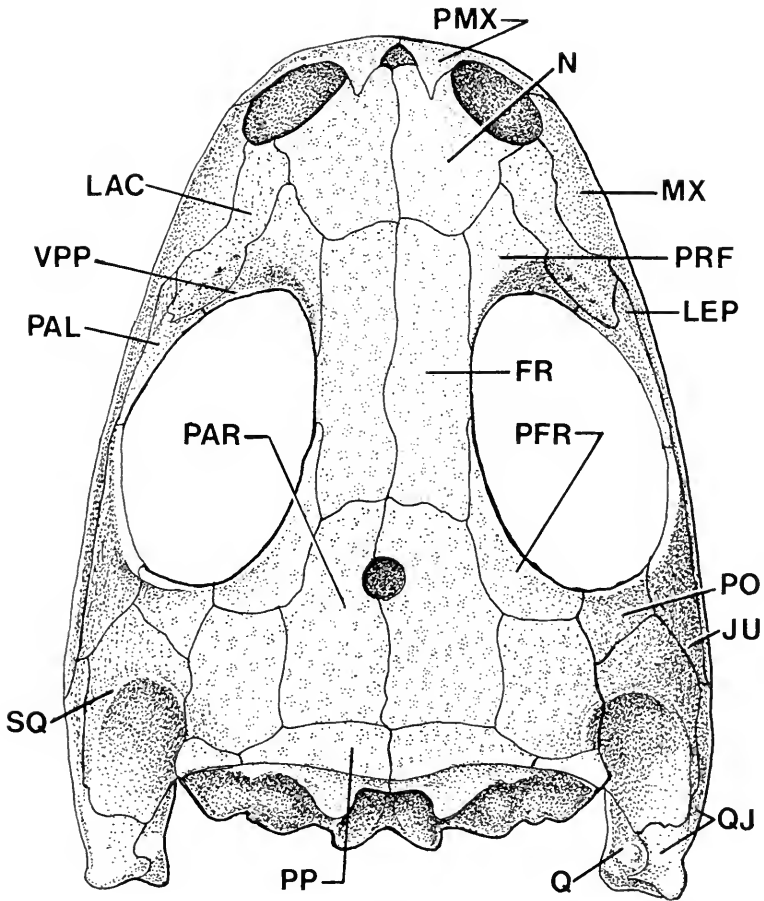


FIG. 4. *Doleserpeton annectens*. Skull in dorsal view. Composite, based on numerous specimens. Skull length approximately 15 mm.

Nasal flange and nasal capsule (figs. 1, 2, 3).—Olson (1941) describes a total of three “septa” in the nasal region. Two of these have been described above; the third, Olson’s “descending septum of the nasal,” is also well-preserved in *A. sp.* As seen in Figures 2 and 3C, the septum is an extension of the nasal anteriorly, and of the prefrontal posteriorly. The septum will hereafter be referred to as the nasal flange, for convenience. The term “nasal septum” is pre-empted by a braincase structure. Besides the nasal and prefrontal, the nasal flange is also formed by an extension from the lacrimal. The lacrimal contribution is small, being restricted to the postero-

ventral portion of the flange. The lacrimal portion of the flange is oriented in a transverse plane, just behind the posterior border of the external naris. The area is thus not visible in lateral view. Here as elsewhere in its course, the nasal flange is oriented approximately vertically. From its posterior end, the nasal flange runs forward and medially at about a 45° angle to the midline. It thus increasingly diverges from the lateral edge of the (unnamed) septum (SU in fig. 3B) formed by the medial margin of the internal naris. Posteriorly, the nasal flange is close to the dorsal surface of the palate (fig. 3C), although apparently nowhere does it make contact with the palate. The separation increases anteriorly, largely due to the decreasing height of the nasal flange. Except for suture lines, the lateral surface of the nasal flange is featureless. Thickness of the flange posteriorly appears less than that of the frontal and nasal, where those bones are broken above the orbits. Over most of its extent, however, thickness of the nasal flange is unknown.

A minimum estimate for the antero-posterior extent of the nasal capsule, is the distance between the anterior border of the external naris and the posterior border of the internal naris. Its posterior extent may be further indicated by a distinct fossa developed in the dorsal surface of the palatine (FONC in fig. 1A). The posterior border of the fossa is formed by a ridge whose posterior face rises gradually from the palatine. The ridge is not as pronounced medially, and disappears at the dorsal suture line between palatine and vomer. The dorsal suture line lies some distance medial to the ventral suture line between these bones; as in *Doleserpeton*, the palatine overlaps the vomer for a considerable distance medial to the internal naris. That face of the palatine ridge which borders the fossa, meets the surface of the palatine at a sharp angle (about 90°). This fact suggests that some soft structure lay against the anterior face of the ridge. The fossa might indicate the posterior limit of the nasal capsule, which as expected would thus be only a short distance behind the posterior border of the internal naris. Although the fossa is limited laterally by the medial margin of the internal naris, this should obviously not be interpreted to mean that the nasal capsule did not extend around the internal naris. The ridges which border the fossa may serve to stiffen the edges of the thin bone. In any case, the fossa and its bordering ridges are not necessarily very accurate indicators of nasal capsule position, especially as regards the medial extent of the capsule. If the fossa is accepted as indicative of nasal

capsule position, the nasal flange must be seen as probably dividing the cavity of the nasal sac into medial and lateral portions. There is another possibility, however, which will be adopted here. The nasal capsule might have been confined to the area lateral to the dermal bone of the nasal flange. Such an arrangement is admittedly unusual among tetrapods, in which the medial walls of the nasal capsules are generally replaced by the midline chondrocranial nasal septum (de Beer, 1937, p. 395). However, according to Jurgens (1971) the primitive condition in both urodeles and anurans is one in which the nasal capsules are separated by an extension of the cavum cranii. This observation is consistent with the suggestion (Bolt, 1969) of a dissorophoid origin for the Lissamphibia although such separated and laterally-placed nasal capsules may have been widespread among labyrinthodonts. The fossa, particularly its posterior part, may indeed have contained cartilage, but this cartilage was not necessarily part of the nasal capsule. The fossa may, for instance, mark the position of a processus maxillaris posterior which was here connected to the pterygoid process of the palatoquadrate cartilage.

FUNCTION AND EVOLUTION OF THE NASAL FLANGE

Function of the nasal flange.—Posteriorly, the nasal flange lies very close to the dorsum of the palate. A small portion of the flange is thus in position to prevent large upward movements of the adjacent palate. However, aside from the lack of bony contact between flange and palate, the orientation and height of the rest of the flange is not such as to indicate that direct palatal support was one of its functions. As indicated above, the flange might have been pushed into the nasal capsule and sac, thus subdividing the latter into medial and lateral components. This was suggested by Olson (1941), who thought that the medial subdivision might house Jacobson's organ. In general, the possible function for such subdivision would be to increase the area of epithelium within the nasal sac, or to physically separate functionally different areas. Ordinarily in lower tetrapods, however, the skeletal support for flanges and ridges within the nasal sac is provided mostly by the cartilaginous nasal capsule. There is no obvious reason why the support of a long extension from the dermal roofing bones should have been required in this case. Similarly, there is no reason to suppose that a gland in the nasal region required support from the flange. The apparent rigidity of the nasal flange renders it unsuitable for participation in movements which

might change the volume of any part of the nasal sac. The flange might have served for the origin of muscles—but there is no other indication of the presence and function of such musculature.

A clue to the possible function of the nasal flange is provided by the extensive fenestration of the trematopsid skull. Between the posterior margin of the orbit and the anterior margin of the external naris, the tooth-bearing maxilla appears to be attached to the skull roof only by the antero-posteriorly narrow antorbital bar composed of lacrimal and prefrontal. Forces acting on the tooth row would be transmitted to the skull roof *via* the antorbital bar, across the frontal-prefrontal and nasal-prefrontal sutures. For convenience, these sutures may be referred to jointly as the frontonasal-prefrontal suture, although the frontal and nasal are actually separate bones in all labyrinthodonts. The trematopsid skull is actually less extensively fenestrated than it appears, however. In *A. sp.*, starting from a point near the ventral end of the antorbital bar, the nasal flange unites the lacrimal and prefrontal to the nasal. The flange in effect forms an extension of the antorbital bar, greatly increasing the bar's anteroposterior extent.

The nasal flange was perhaps useful in shifting some compressive stress from the antorbital bar. At the same time, it seems reasonable to suppose that forces acting on the tooth row sometimes produced dangerously large turning moments about the frontonasal-prefrontal and the prefrontal-lacrimal sutures. The sutures themselves might be endangered, or sufficient rotation about the suture(s) might occur to endanger some bone(s) which could not deform to the extent permitted by the sutures. Possibly such forces could produce dangerous deformation in the narrow suborbital bar and adjacent bone even in the absence of significant rotation around sutures. No decision as to the relative significance of these alternatives is possible in the absence of detailed information on the bending strengths of the sutures and adjacent bones. In either case, failure could be prevented by strengthening the sutures and/or transferring part of the bending stress away from the antorbital bar. The nasal flange appears situated so as to be capable of doing both. A suture-strengthening function of the nasal flange might explain the apparently non-bevelled nature of the frontonasal-prefrontal suture in *A. sp.*

Evolution of the nasal flange.—Even if one accepts the functional suggestions above, the question remains as to why this structure (the nasal flange) was used to meet certain functional requirements. At least part of the explanation may lie in the presumably ante-

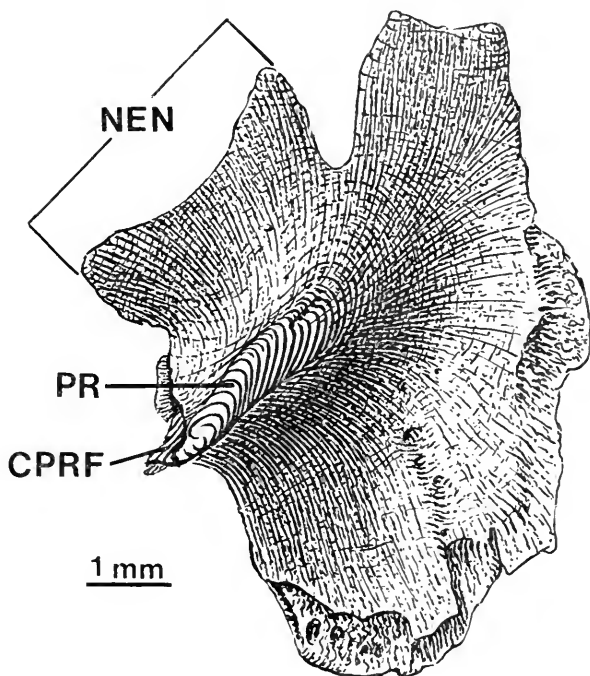


FIG. 5. *Doleserpeton annectens*. Right nasal in ventral view.

cent conditions seen in other dissorophoids. These may be represented by *Doleserpeton annectens* (figs. 4, 5), for which the best material is available.

The nasal region of *A. sp.* can be transformed to closely resemble that of *Doleserpeton annectens*. As discussed below, this is a reversal of the probable direction of change. *D. annectens* represents the primitive dissorophoid condition, *A. sp.* the derived; but since the nasal region of *A. sp.* has just been described, the reversed transformation sequence may be easier to follow. The order in which changes are listed below has no particular significance, as they must have taken place more or less simultaneously. With *A. sp.* as the starting-point then, and *D. annectens* as the goal, the necessary changes are:

1. The snout becomes broader and more rounded.
2. The nasal bones become shorter and broader.
3. The posterior border of each external naris, still formed by the lacrimal, migrates forward. The result of this change, together with (2), is a subcircular, slightly elongate external naris; there is a short

contact of nasal and lacrimal, and the prefrontal is thus excluded from the external naris.

4. The nasal flange decreases in height, i.e., it projects a smaller distance below the skull roof and does not approach the palate so closely.

5. The lacrimal portion of the nasal flange expands anteriorly and dorsally, remaining lateral to the prefrontal portion. The end-point is reached when the lacrimal portion of the nasal flange is approximately coextensive with the prefrontal portion. The two-layered flange thus formed retains contact with a strong, low flange, or process, from the nasal bone to complete the "nasal flange" of *Doleserpeton*.

Some minor alterations in the palate, which need not be detailed, accompanied the listed changes. The picture can be rounded out by the *Doleserpeton* nasal (fig. 5). A strong process projects from the undersurface of the nasal, somewhat posterior to the border of the external naris. A small depression (CPRF in fig. 5) is incised into the antero-lateral terminus of the process; this depression probably marks the contact with the prefrontal portion of the nasal flange.

In *D. annectens* the nasal flange is clearly in a position to brace the prefrontal-lacrimal suture against turning moments. Contact between the flange and the nasal bone indicates a probable role in bracing the nasal-prefrontal and nasal-lacrimal sutures also. The arrangement seen in *D. annectens* might have reduced stress on the frontal-prefrontal suture due to turning moments, but probably not to the extent seen in *A. sp.* Such bracing was not needed in *Doleserpeton*, because of the bevelled nature of that suture and the existence of a larger antorbital bar. The condition of the nasal flange in *A. sp.* (and presumably other trematopsids) then may reflect primarily a change in emphasis, rather than assumption of a new functional role. Considering both the function and morphology of the *Doleserpeton*-type and trematopsid-type nasal flanges, it seems that the latter most likely was derived from the former. (This conclusion does not imply that trematopsids are derived from either *Doleserpeton* or dissorophids—this is quite unlikely on other evidence.)

The nasal flange in dissorophids.—At present, the nasal flange can be demonstrated in only two dissorophid genera. However, with the evidence from trematopsids and *Doleserpeton* this distribution seems sufficient to strongly suggest that the flange is a primitive dissorophid character. A nasal flange is present in *Broiliellus olsoni*, UT 3189-8; this specimen has the same catalog number as the holotype,

but is actually a referred specimen (DeMar, 1967). It is a fragmentary left half of the snout, consisting essentially of the area which in trematopsids I have called the antorbital bar. The specimen is figured in lateral and posterior view in Bolt (MS). It has been prepared to show a well-developed nasal flange. The sutures between contributing bones cannot be made out. The flange is broken off anteriorly, the break passing through the broad-based nasal portion.

Broiliellus is an advanced, armored dissorophid. A primitive, unarmored dissorophid with a probable nasal flange is *Tersomius texensis*. Carroll (1964, p. 172) has described a ridge on the under-surface of the nasal and prefrontal. The exact course of this ridge is uncertain from his description. Carroll's Figure 6C, based on acetate peels of serial sections through MCZ 3236, shows a ridge (unlabelled) which is probably the nasal portion of a nasal flange. Re-examination of the peels of MCZ 3236 shows the flange to be present in sections numbered 21-11. The specimen is too damaged to permit tracing of the nasal flange in detail. However, there is a fairly clear transition from a ridge composed of nasal alone anteriorly, to one composed of prefrontal plus lacrimal posteriorly (section 11). Anteriorly the flange begins somewhat posterior to the external naris, as in *Doleserpeton*. The anterior orbital wall and the adjacent area of the nasal flange are not present in the other specimens sectioned by Carroll—MCZ 3234 and 1694.

The nasal flange in labyrinthodonts in general.—It appears that a nasal flange is not present outside of the Dissorophoidea. This conclusion rests on a very narrow base, as few sufficiently-detailed descriptions of the snout are available. Some examples of well-described labyrinthodonts lacking the flange are: the stereospondyl *Benthosuchus* (Bystrov and Efremov, 1940); the rhachitome *Eryops* (Sawin, 1941); the seymouriamorph *Seymouria* (White, 1939). Absence of the flange in *Eryops* and *Benthosuchus* is unsurprising: both have small orbits and extensive antorbital bars. In the case of *Seymouria*, the relative length of the antorbital bar is closer to that of dissorophoids, but is still significantly greater. The point may be illustrated by a simple comparison: As a rough indicator of head size, we can use the snout-quadrate length (L), measured parallel to the midline. The length of the antorbital bar (BL) can be expressed as the shortest distance between the posterior margin of the external naris and the anterior margin of the orbit. The orbit of *Seymouria* is notched antero-ventrally, and the antorbital bar was measured from the anterior wall of the notch. Measurements are

TABLE 1. Length of antorbital bar (cm.) in *Seymouria* and dissorophids.

See text for explanation.

	L	BL	L/BL
<i>Seymouria baylorensis</i> (FMNH UC 666)	11.2	3.1	3.6
<i>Dissorophus multicinctus</i> (MCZ 2122-1)	14.2	3.3	4.3
<i>Broiliellus texensis</i> (holotype) (FMNH UC 684)	9.5	1.7	5.6

given in Table 1. These two dissorophid genera were chosen because they are represented by relatively complete and undeformed specimens, presumably adult, which are approximately the same size as *Seymouria*.

The comparison with *Seymouria* is particularly interesting, as the lacrimal-prefrontal suture is strongly bevelled as in dissorophids (Bolt, MS). Due to its peculiar palatal construction, however, the lack of a nasal flange in *Seymouria* cannot be ascribed solely to the size of the antorbital bar (cf. Bolt, MS).

FUNCTION AND EVOLUTION OF THE EXTERNAL NARIS

Morphological aspects of the evolution of the trematopsid external naris are fairly clear and straightforward. Functional aspects of the evolution of this unusual naris, however, have remained obscure. The generally-accepted explanation is given by Olson (1941, p. 161), who suggests that the anterior part of the external naris ". . . was concerned primarily with the sense of smell, while the more posterior part functioned principally as an air intake. It has been suggested previously that the posterior part housed a gland of some sort. While this is possible, the structure outlined above makes it seem rather improbable."

The basis for this explanation was the observation that the internal naris lies beneath only the posterior part of the external naris. Olson's conclusion does not follow, however. Inspired air does not necessarily take the shortest possible path between internal and external nares. During its transit of the nasal passages, air may be filtered, humidified, and otherwise modified, while being exposed to various sensory cells. As might be expected, the nasal cavities of living amphibians and reptiles can be quite complicated (cf. Matthes, 1934; Stebbins, 1948; Parsons, 1959, 1970). It is, therefore, reasonable to suppose that the anterior part of the trematopsid external naris served as an air intake. In support of this possibility

is the observation that, by comparison with other labyrinthodonts, this portion occupies the usual area of the external naris. The same conclusion was drawn by Williston (1909), on the basis of comparison with *Eryops*.

The suggestion may then be revived, that the posterior part of the trematopsid external naris housed a gland. A possible candidate is the "glandula nasalis externa." This gland, lying lateral to the nasal sac but opening into it, is widespread in living amphibians (Matthes, 1934). A similar and apparently homologous glandula nasalis externa occurs in most living reptiles, although some (secondarily) lack it (Parsons, 1959). It has recently been discovered that this gland is an important route for salt excretion in some lizards both marine and terrestrial (see Dunson, 1969, for recent review of salt glands in general). According to Dunson (1969, p. 95), "The animals with the greatest secretory capacity seem to be associated with environments and food highest in salt and lowest in water, but this is an impression supported by only limited data."

These characteristics might or might not apply to the environment of the trematopsids. Trematopsids were likely highly terrestrial, and were certainly carnivorous. More detailed description of trematopsid environment and food would be speculative at this time. However, it seems plausible to suggest that the posterior portion of the trematopsid external naris was occupied by a salt gland, possibly homologous with the glandula nasalis externa. Perhaps in the ancestral trematopsids enlargement of the gland was blocked in all directions but laterally. Medial enlargement, for instance, might have adversely affected nasal functioning. This might occur by squeezing the nasal capsule between the gland and the nasal flange. Laterad expansion could occur by enlarging the external naris; at the same time, the nasal flange gradually assumed its trematopsid morphology and function. Dissorophids and *Dole-serpeton* did not necessarily lack salt glands; the varied homologies of reptilian salt glands (Dunson, 1969) indicates the possibility of similar differences in labyrinthodonts. In reptiles, the salt glands compensate for the kidney's inability to produce a hypertonic urine (Schmidt-Nielsen *et al.*, 1963). If the same were true of trematopsids, the elongate external naris might be regarded as an indirect result of this renal characteristic.

The hypothesis outlined above as to the origin of the elongate external naris of trematopsids has phyletic implications. These implications exist regardless of the homologies, and even the nature

(glandular or non-glandular) of the structures involved in posteriad narial expansion. In any labyrinthodont, we need only grant the presence of a nasal flange similar to that of dissorophids and *Dole-serpeton* in both structure and function. Enlargement of any structure lateral to the nasal sac is then likely to produce the trematopsid external naris and nasal flange. Two conclusions follow:

1. Within the Dissorophoidea, similar types of experimentation would likely occur, and lead to similar modifications of the external naris and nasal flange.

2. The elongate external naris, even if accompanied by a trematopsid-type nasal flange, is not a diagnostic character for the family Trematopsidae.

ABBREVIATIONS

CPRF	— Contact area for prefrontal
CPT	— Contact area for pterygoid
EN	— External narial opening
FONC	— Fossa, possibly for nasal capsule
FR	— Frontal
IN	— Internal narial opening
INF	— Internarial foramen
INP	— Internarial pit
JU	— Jugal
LAC	— Lacrimal
LEE	— Laterally-exposed portion of ectopterygoid
LEP	— Laterally-exposed portion of palatine
MX	— Maxilla
MXCS	— Constriction of external narial opening, due to maxilla
N	— Nasal
NCS	— Constriction of external narial opening, due to nasal
NEN	— Area of nasal bordering the external naris
NF	— Nasal flange
PAL	— Palatine
PAR	— Parietal
PFR	— Postfrontal
PMX	— Premaxilla
PO	— Postorbital
PP	— Postparietal
PR	— Process on ventral surface of nasal
PRF	— Prefrontal
PT	— Pterygoid
Q	— Quadrate
QJ	— Quadratojugal
SQ	— Squamosal

- ST — Supratemporal
SU — Unnamed septum
VO — Vomer
VOE — Vomerine extension
VPP — Ventral prefrontal process

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