# Trematops milleri Williston, 1909 Identified as a Junior Synonym of Acheloma cumminsi Cope, 1882, with a Revision of the Genus

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## ABSTRACT

The Early Permian temnospondyl amphibians *Acheloma cumminsi* Cope, 1882 and *Trematops milleri* Williston, 1909 of the family Trematopsidae prove, upon reexamination of the holotypes, to be indistinguishable. Since the former name has priority, *Trematops milleri* is declared to be a subjective junior synonym of *Acheloma cumminsi*. The family name Trematopsidae is retained.

The generic diagnosis of *Acheloma cumminsi* is revised to emphasize the presence of a slitlike, posteriorly closed otic notch, a supratympanic shelf, an internal naris with an anteroposterior length less than that of the posterior division of the external naris, and a median septum of the vomers that contacts the roof of the antorbital region.

The slitlike, dorsally convex otic notch of *Acheloma cumminsi* is unique among labyrinthodont amphibians. The dimensions of this otic notch suggest that the tympanum, if present, was similarly reduced and could not have been part of an efficient impedance-matching hearing apparatus.

## INTRODUCTION

The family Trematopsidae is a small group of poorly known terrestrially adapted amphibians of the order Temnospondyli collected from North American deposits of Lower Permian age. At present, the family is composed of the two genera *Acheloma* and *Trematops*. A third, *Trematopsis* (= *Trematopsoides* Romer, 1966), erected by Olson (1956) on the basis of a fragmentary skeleton, has been reduced recently to subjective junior synonymy with *Cacops* cf. *C. aspidephorus* by Milner (1985a). *Actiobates peabodyi* Ea-

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ton (1973), a Late Pennsylvanian dissorophoid, has been placed provisionally within the family Trematopsidae by Berman et al. (1985) and Milner (1985a, 1985b). The type and only known specimen of *Actiobates* is thought by the former to exhibit features suggestive of a juvenile and by the latter to possess a combination of primitive dissorophoid and advanced trematopsid features. Eaton (1973) did not comment on the ontogenetic status of *Actiobates* but presumably considered it to be an adult. *Actiobates* is currently being studied by Ms. Eleanor Daly of the Mississippi Museum of Natural Science.

E. D. Cope (1882) first described *Acheloma cumminsi* and placed it within the family Eryopidae. Cope distinguished *Acheloma* from *Eryops* primarily on the basis of a scapulocoracoid with a scapular blade tilted medially and posteriorly at a 30° angle to the coracoid, the apparent absence of otic notches on the skull, and the absence of articular condyles on the humeri.

*Trematops milleri,* also from the Lower Permian red beds of Texas, was initially described by S. W. Williston in 1909. The unique attributes of *Trematops* include an elongate external naris occupying most of the antorbital region and a slitlike, posteriorly closed otic notch. Williston (1910) subsequently erected the monogeneric family Trematopsidae to house this unusual amphibian.

Following the discovery of *Trematops milleri,* the taxonomic position of *Acheloma cumminsi* was reevaluated as part of independent studies of Williston (1916) on the tetrapods of the Permian and Carboniferous of North America and Watson (1919) on the early evolution of amphibians. Although neither author was apparently able to examine firsthand the holotype of *Acheloma,* each considered it to be sufficiently distinct from *Eryops* to warrant its removal from the family Eryopidae. They differed, however, in their final taxonomic conclusions. Williston chose to assign *Acheloma* to the family Trematopsidae, but made this decision with extreme reservations because he was unsure of the true nature of the external naris and otic notch. Watson, on the basis of illustrations of the pectoral girdles of *Acheloma* (Case, 1911),

argued that the unusually acute angle between the scapula and coracoid was merely an artifact of the poor postcranial ossification of the specimen and, thus, did not constitute a valid diagnostic feature. Watson accepted Cope's statement that *Acheloma* lacked otic notches and, recognizing the taxonomic significance of this character, placed *Acheloma* within a new family, the Achelomidae.

It was not until a review of the family Trematopsidae by E. C. Olson in 1941 that the affinities of *Acheloma* were properly established. After a reexamination of the type material, Olson concluded that it possessed the same elongate external naris and slitlike, closed otic notch as *Trematops* and, accordingly, expanded the family Trematopsidae to include *Acheloma.* Olson interpreted the Trematopsidae as carnivores that were closely related to the family Dissorophidae, a morphologically diverse group of terrestrially adapted temnospondyls that occupied a span of time from the Middle Pennsylvanian (Westphalian D) to Upper Permian.

The possible synonymy of *Acheloma* and *Trematops* has not been studied in detail until now. Although expressing some doubt, Williston (1909) accepted Cope's description of *Acheloma* as accurate and concluded that each was a valid genus. Romer (1935) stated that *Trematops* was probably synonymous with *Acheloma* but did not elaborate. Following Olson's review of the family, Romer (1947) apparently reversed his opinion and retained *Acheloma* and *Trematops* as distinct genera, a conclusion unquestioned to the present.

## ABBREVIATIONS

*Institutional*

AMNH      American Museum of Natural History

FMNH UC    Field Museum of Natural History

*Anatomical*

| | | | |
|---|---|---|---|
| a | angular | pp | postparietal |
| d | dentary | prf | prefrontal |
| ect | ectopterygoid | pt | pterygoid |
| f | frontal | q | quadrate |
| in.f. | internarial fenestra | qj | quadratojugal |
| j | jugal | sa | surangular |
| l | lacrimal | sm | septomaxilla |
| m | maxilla | sp | splenial |
| n | nasal | spp | postsplenial |
| p | parietal | sq | squamosal |
| pal | palatine | st | supratemporal |
| pf | postfrontal | t | tabular |
| pm | premaxilla | v | vomer |
| po | postorbital | | |

## REDESCRIPTION OF HOLOTYPES

Descriptive statements given below are limited to those characters that are relevant to the taxonomic reevaluation of the holotypes.

### *Acheloma cumminsi* (AMNH 4205)

Many of the details of cranial morphology, in particular the pattern of skull roof sutures, were unknown to earlier workers because AMNH 4205 had been only partially prepared. Extensive mechanical and chemical preparation allows, for the first time, a critical comparison of the two holotypes.

The holotypic skull of *Acheloma cumminsi* (fig. 1) has suffered significant dorsoventral crushing with a slight increase in width of the temporal region. The majority of the dermal skull elements are preserved. The left tabular, left supratemporal, left postfrontal, and both parietals and postparietals are complete. Accompanying these elements are a partial right supratemporal, right postfrontal, and right tabular. Portions of the right frontal, prefrontal, and nasal that form the dorsal margin of the orbit and posteromedial margin of the external naris are present. The premaxillae, maxillae, lacrimals, and jugals are partially preserved. Neither squamosal is complete; the left, however, is missing only that portion bordering the anterior corner of the otic notch.

The left quadratojugal is complete, although slightly damaged, whereas the right quadratojugal is fragmentary. The left quadrate is complete. Both lower jaws are in place and lack the section beneath the external naris. The dermal sculpturing exhibited by each element consists of a uniform pattern of round pits at the ossification center and slightly oval pits at the periphery. The prominent ridges and protuberances characteristic of many dissorophids (Carroll, 1964; DeMar, 1968; Berman et al., 1981) and commonly found along the margins of the skull table, the cheeks, or the medial rim of the orbit are absent in *Acheloma*. There are no lateral line grooves or pits.

A large internarial fenestra is situated near the tip of the snout, opening below into a small, median, internarial pit. The position of the partial posteromedial rim of the right external naris indicates that the external naris is greatly elongated posteriorly. An elongate external naris is a derived feature found in trematopsids, the dissorophid *Ecolsonia* (Vaughn, 1969; Berman et al., 1985), and *Actiobates* (Eaton, 1973). Medial to the rim of the right external naris is a partial narial flange consisting of a laterally concave sheet of bone projecting down and inwards from the roof of the snout. As preserved, this flange is composed of separate sheets from the nasal and prefrontal that abut against each other with no sign of overlap. Although the narial flange is incomplete anteriorly and posteriorly, the nasal portion probably continued forward underneath the nasal. The prefrontal portion of the flange, curving laterally to follow the rim of the narial opening, probably reached the narrow antorbital bar that separates the orbit and external naris. The height of the narial flange increases posteriorly, reducing the space between the flange and palatal surface. There is, however, no evidence of osseous contact between the preserved portion of the narial flange and palate. The morphology of the narial flange of *Acheloma* conforms with that of the smaller trematopsids as described by Bolt (1974a) and differs significantly from the narial flange of dissorophids (Bolt, 1974a, 1974b).

Dissorophoid amphibians and several other groups of labyrinthodont amphibians and primitive reptiles possess a ventral process
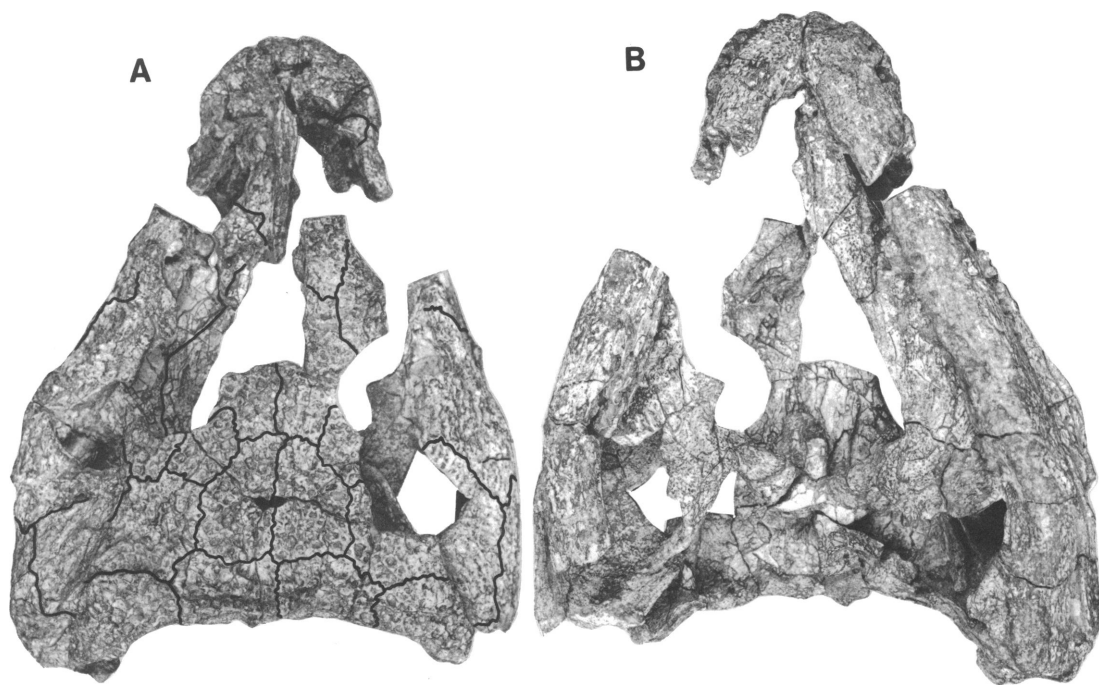
Fig. 1. *Acheloma cumminsi* Cope 1882. Skull of holotype (AMNH 4205) in (A) dorsal view, and (B) ventral view. Scale = 2 cm.

of the prefrontal (VPP) inside the anterior rim of the orbit either in combination with or separate from a lateral exposure of the palatine (LEP) along the suborbital bar (Bolt, 1974b). These features may have evolved primarily as a consequence of the common possession of large orbits and, in the case of labyrinthodonts, palatal fangs beneath the orbit. It cannot be determined if a VPP is present on AMNH 4205 because both orbits are incomplete anteriorly. The suborbital portion of the left orbit is poorly preserved and sutures are difficult to establish. There appears to be no LEP.

The otic notch of *Acheloma cumminsi* is greatly reduced in height and closed posteriorly by a long extension of the tabular that curves gradually down to meet a robust quadrate process. There is no indication of any fusion between the tabular and quadrate processes; instead the tabular process rests along the lateral face of the quadrate process and inserts into a shallow depression at its base.

Posterior closure of the otic notch is also present in the North American dissorophids *Cacops* (Williston, 1910; Bolt, 1977); *Dissorophus* (DeMar, 1968); *Longiscitula* (DeMar, 1966); *Ecolsonia* (Berman et al., 1985); and the Russian dissorophids *Kamacops, Iratusaurus* (Gubin, 1980), and *Zygosaurus* (Efremov, 1940). The manner of otic closure in these dissorophids differs, however, from that of *Acheloma*. When the dissorophid skull is viewed laterally, the tabular process is bent down sharply at an approximate right angle to the dorsal edge of the skull table and fused to the quadrate process, thus enclosing a large, triangular otic notch.

The dorsal surface of the left quadrate process of AMNH 4205 is unfinished bone indicating a probable cartilaginous continuation. A deep groove that extends dorsally and medially along the posteromedial surface of the tabular process and ends in a shallow, oval depression may have received the cartilaginous portion of the quadrate process.

The unsculptured ventral border of the otic notch, formed by the squamosal and quadratojugal, is highly convex. The quadratojugal sheathes the quadrate lateral and posterior to the quadrate process.

A pronounced supratympanic shelf overhangs the otic notch. Medial to this shelf, a vertical supratympanic flange projects down into the notch space. Dermal sculpturing is absent from the ventral surface of the supratympanic shelf and the supratympanic flange. The squamosal lacks the semilunar curvature found on most dissorophids (DeMar, 1968). The sutures delineating the right supratemporal can be traced from the skull roof to the underside of the shelf but disappear before reaching the supratympanic flange. Along the posterior edge of the skull table is a well-developed groove lacking sculpture and a posteroventrally oriented sharp ridge that probably served for the insertion of craniocervical muscles. This ridge is more pronounced at the common suture of the postparietals above the foramen magnum and along the hornlike tabular processes.

A significant portion of the palate of AMNH 4205 is preserved; sutures, unfortunately, cannot be established with confidence. The interpterygoid vacuities are smaller than in dissorophids and the pterygoids probably reached the vomers, a primitive condition for dissorophoids. Anteriorly, the vomers are deflected dorsomedially to form a deep internarial pit. Posterior to the internarial pit, each vomer has a median sheet of bone that probably contacts the roof of the snout. These two vertical sheets of bone, separated only by a slight gap, form a structure here referred to as a median vomerine septum. The median vomerine septum extends posteriorly beyond the rim of the interpterygoid vacuities perhaps to contact the sphenethmoid. Olson (1941) described a similar structure on an isolated snout of a large trematopsid.

The internal naris is situated directly below the posterior expansion of the external naris. The anteroposterior length of the internal naris is considerably less than that of the expansion of the external naris. In contrast, the posterior margins of the internal and external nares of smaller trematopsids and the dissorophid *Ecolsonia* are equal. A large, rect-angular septomaxilla, its damaged posterior edge raised slightly, is situated within the right external naris of AMNH 4205 along the anterolateral rim of the internal naris.

Fragments of a partial braincase, recognized for the first time, are present on AMNH 4205 and consist of the left exoccipital, most of the left opisthotic, portions of the body of the parasphenoid, the base of the cultriform process, both basipterygoid processes, and a small section of sphenethmoid immediately anterior to the right basipterygoid process. The morphology of the braincase of *Acheloma* follows in most details the expected rhachitome pattern (Sawin, 1941; Romer and Witter, 1942; Berman et al., 1981). The left paroccipital process is present but incomplete anteriorly. Its ventral surface is slightly concave. There is a deep, transverse groove along the posteroventral edge of the paroccipital process continuing onto the occipital process of the tabular and the posteromedial surface of the tabular. A craniocervical muscle may have inserted along this groove. The circular fenestra ovalis has a diameter of about 5 mm. The parasphenoid portion of the basipterygoid process is fused to the pterygoid, preventing any movement between palate and braincase.

The dentition of *Acheloma* consists of approximately 9 premaxillary teeth, 23 to 26 maxillary teeth, and the expected paired palatal fangs on the vomer, palatine, and ectopterygoid. The second to last premaxillary tooth, located below the anterior division of the external naris, is greatly enlarged. The nature of the maxillary teeth beneath the external naris is unknown because this region is not preserved.

The postcranial skeleton consists of a string of 22 articulated presacral vertebrae past the atlas–axis complex, ribs associated with the first six vertebrae, both scapulocoracoids, and both humeri. A radius and ulna described by Case (1911) but not mentioned by Cope (1882) are not among the holotypic material and may be specimens that Case mistakenly included with the holotype. The vertebrae are rhachitomous in design resembling those of *Eryops* (Moulton, 1974). The ribs are short, flat, and expanded distally. Both scapulocoracoids suffer from poor ossification and preservation. The portion of the coracoid below
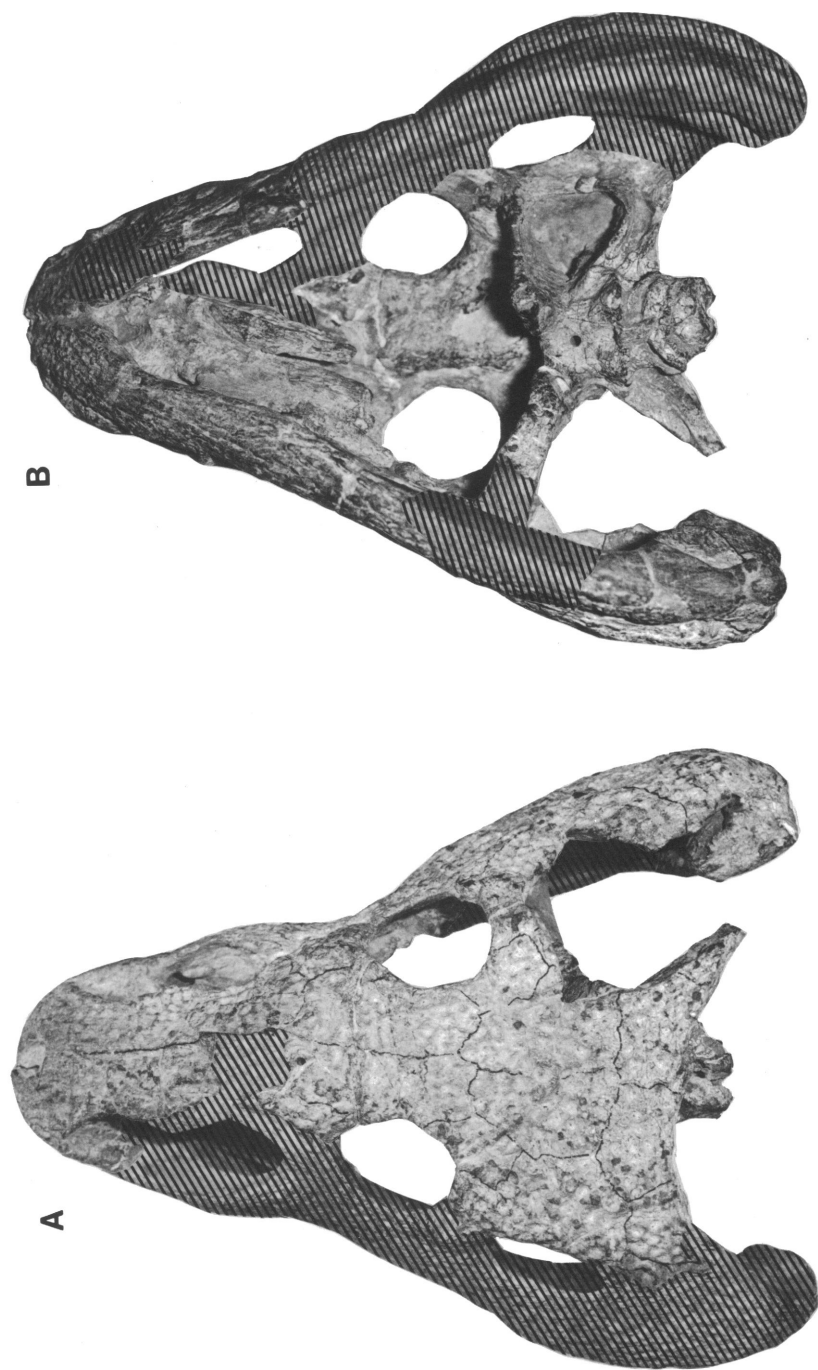
Fig. 2. *Trematops milleri* Williston 1909. Skull of holotype (FMNH UC 640) in (**A**) dorsal view, and (**B**) ventral view. Hatched areas represent missing portions occupied by plaster. Scale = 2 cm.

the supraglenoid foramen is missing and the scapular blade is incomplete distally due to imperfect ossification and loss of most of the anterior region. Proximal and distal articular facets of the humeri are absent, further evidence of poor postcranial ossification. A large perforation of the entepicondyle of the right humerus, interpreted by Cope (1882) as an entepicondylar foramen, was reinterpreted by Case (1911) and Olson (1941) as postmortem damage. The absence of a corresponding hole on the left humerus leaves little doubt that it is not a natural feature.

### *Trematops milleri* (FMNH UC 640)

The skull (fig. 2) is missing the entire left side below the orbit and portions of the right side. Most of the skull table is preserved but the dorsal rim of the right otic notch, including nearly the entire tabular and supratemporal and small portions of the parietal and postparietal, are lost. Only a small portion of the contributions of the squamosal and quadratojugal to the smooth ventral margin of the right otic notch are present. Dermal sculpturing is uniform and the skull lacks lateral line grooves or pits.

A large internarial fenestra is present at the tip of the snout. The fenestra presumably opened ventrally into an internarial pit; the lower jaws, unfortunately, completely cover that region of the palate.

The external naris of *Trematops* is elongate and oval in outline. A spur from the nasal partially divides the narial opening into a circular anterior portion and a slightly larger oval posterior portion. This spur probably marks the boundary between the true external naris near the tip of the snout and the derived posterior expansion. Williston (1909) observed a flattened or concave bone in the right naris which he interpreted as turbinated bone. This bone is probably the septomaxilla (contra Olson, 1941). Unfortunately, little can be said of the narial flange beyond confirmation of its presence.

It is uncertain whether or not FMNH UC 640 possesses an LEP along the ventral rim of the orbit or a VPP inside the anterior rim of the orbit. Bolt (1974b) noted the possible presence of a rectangular piece of bone ventral and anterior to the right orbit which he interpreted as an LEP that had been excluded from the orbit by the contact of the jugal and lacrimal. The existence of this rectangular piece of bone cannot be confirmed. Bone is present within the anterior portion of the right orbit but it is heavily fractured and no VPP can be identified.

The rim of smooth, finished bone along the left side of the skull table was correctly interpreted by Williston (1909) as the dorsal margin of a posteriorly closed otic notch. A well-developed supratympanic shelf overhangs the otic notch and a supratympanic flange is situated medially. No sutures are visible on the underside of the shelf or on the flange. The smooth ventral margin of the notch appears to be strongly convex. Neither quadrate process is preserved; a region of broken bone on the dorsal surface of the right quadrate marks the former presence of a quadrate process.

There is a groove along the point of union of the skull roof and occiput, similar to but slightly shallower than the one observed on *Acheloma*. It cannot be determined if the possible recess for the quadrate process found on the tabular of *Acheloma* is present because both tabulars of *Trematops* are broken proximally.

The braincase of *Trematops* resembles that of *Eryops* (Sawin, 1941), *Edops* (Romer and Witter, 1942), and *Platyhystrix* (Berman et al., 1981). As pointed out by Olson (1941), the parasphenoid, thought by Williston (1909) to be absent, is actually present and covers the ventral surface of most of the braincase. The ventral surface of the paroccipital process of *Trematops* is deeply concave with the anterior and posterior edges developed as ventrally projecting flanges. The anterior flange is confluent with the supratympanic flange and the posterior flange, unfortunately incomplete, occupies the position of the deep, posteroventral paroccipital groove observed on *Acheloma*.

Only those portions of the palate anterior to the orbits are present. No sutures are visible. The interpterygoid vacuities are reduced and the inner edge of the palatal shelf is thickened, presumably representing the anterior extension of the pterygoid to the vomers. The pterygoid and the parasphenoid are indistinguishably fused at the basicranial joint.

The combined premaxillary and maxillary dentition of FMNH UC 640, according to Williston (1909), numbers 25 or 26 teeth of which 6 are borne by the premaxilla. This estimate is probably too low because the tooth row is damaged at its anterior and posterior ends. A more accurate tooth count, based on the length of the alveolar ridge and the observed size of preserved teeth, is 9 premaxillary teeth and 23–26 maxillary teeth. The maxilla is swollen laterally beneath the posterior division of the external naris to hold a pair of enlarged teeth. Although the premaxillary teeth are damaged, the base of a single, large tooth is present near the premaxilla–maxilla suture and below the functional narial opening.

According to Olson (1941), each presacral intercentrum of *Trematops milleri* is closed dorsally, presumably by inward curvature and union of the dorsal tips of the intercentra, thus producing a ring of bone to completely surround the notochord. No mention of ring intercentra was made in Williston's (1909) original description. Reexamination of the preserved presacral vertebrae of FMNH UC 640 has failed to reveal any evidence of ring intercentra.

Presacral ribs are short in length throughout the series and expanded proximally and distally, the proximal expansion becoming reduced on the posterior ribs.

The remainder of the postcranial skeleton of *Trematops milleri,* as described by Williston, is similar to *Eryops* and displays a slightly higher level of ossification than that observed in the holotype of *Acheloma cumminsi.*

## COMPARISON AND SYSTEMATIC RESULTS

In his review of the family Trematopsidae, Olson (1941) retained *Acheloma* and *Trematops* as distinct genera because of perceived morphological and stratigraphic differences. Although he was unable to find a locality card with the holotype of *Acheloma,* and Cope (1882) failed to include specific locality data, Olson (1941: 151) concluded that "the nature of preservation, the type of matrix, and the similarity to referred specimens from the Wichita formation suggest that the genotype comes from the Wichita." The holotype of *Trematops milleri* is documented by Willis-

ton (1909) as being from the stratigraphically higher Clear Fork Group. Thus, according to Olson's interpretation, the boundary between the Wichita and Clear Fork groups separates *Acheloma* and *Trematops.* The former genus would presumably be the more primitive of the two because of its lower stratigraphic position. All other specimens were then assigned to either *Acheloma* or *Trematops* principally upon stratigraphic location. Romer (1947) noted locality information placing *Acheloma* in the Clear Fork but considered it to be erroneous and accepted Olson's argument for a Wichita age.

A locality card, yellowed with age and designating the specimen as part of the Cope Collection, was found with the holotype of *Acheloma cumminsi* and may be the source of locality information mentioned by Romer (1947). The specific location given is Coffee Creek, Baylor County, Texas, clearly from the classic Lake Kemp collecting region of the Arroyo Formation and near the locality where *Trematops milleri* was found. If this information is correct, then any theory of stratigraphic separation of *Acheloma* and *Trematops* must be discarded. Regardless of the accuracy of the *A. cumminsi* locality data, stratigraphic position is not, on its own, sufficient to warrant taxonomic separation of specimens; the holotypes must possess demonstrable morphological differences.

Olson (1941, 1970) has provided a list of morphological differences to strengthen his argument of the generic validity of *Acheloma* and *Trematops.* According to Olson, the following features may distinguish *Trematops* from *Acheloma*: (1) the external naris of *Trematops* is farther from the tip of the snout than in *Acheloma*; (2) the posterior tip of the maxilla of *Trematops* lies directly below the anterior corner of the otic notch while the maxilla of *Acheloma* ends anterior to the notch; (3) the nasal of *Trematops* is relatively longer than that of *Acheloma*; (4) the ratio of the length of the frontals to parietals of *Trematops* is smaller than that of *Acheloma*; (5) the squamosal of *Trematops* is relatively smaller than the squamosal of *Acheloma*; (6) the tabular of *Trematops* is relatively larger than the tabular of *Acheloma*; (7) the intercentra of *Trematops* are closed dorsally while the intercentra of *Acheloma* are open dor-

sally; and (8) the scapulocoracoid of *Trematops* displays a more advanced state of ossification than the scapulocoracoid of *Acheloma* and the scapula of *Acheloma* is inflected posteriorly to a much greater extent than the scapula of *Trematops*. Relevant cranial measurements of *A. cumminsi* and *T. milleri* are provided in table 1.

Where it is possible to obtain accurate measurements, comparisons of element size and cranial proportions of *Acheloma cumminsi* and *Trematops milleri* (table 1) reveal no significant differences. Furthermore, a thorough reexamination of the skull of each holotype has failed to uncover any heretofore hidden features that are not held in common, provided the cranial regions in question are preserved and accessible in both skulls. The many similarities between the holotypic skulls that include a slitlike, posteriorly closed otic notch, an expanded external naris with a medially situated narial flange, an enlarged premaxillary tooth, a large internarial fenestra, reduced interpterygoid vacuities, and fused basicranial articulations are strongly suggestive of synonymy.

Olson (1941), in addition to determining the correct familial placement of *Acheloma*, described a number of trematopsid skulls collected within the Lower Permian formations of Texas by field parties from the Harvard Museum of Comparative Zoology and the Walker Museum, University of Chicago in 1934, 1936, and 1937. With the exception of a single skull made a referred specimen of *A. cumminsi*, these skulls were assigned by Olson to *Acheloma* and *Trematops* as new species. However, the cranial differences between this assemblage of trematopsids and *Acheloma* and *Trematops* are far more striking than those between the two genera. Total midline skull length of these trematopsids seldom exceeds half that of *Acheloma* or *Trematops*. The otic notch of the smaller trematopsids is greatly enlarged, angular in outline, and open posteriorly. In this respect, the smaller trematopsids bear a striking resemblance to those small dissorophids with open otic notches (Carroll, 1964). The source of cranial differences 1–6 presented by Olson (1941, 1970) to differentiate *Acheloma* and *Trematops* was undoubtedly the smaller trematopsids because the holotype of *Ache-*

TABLE 1

**Selected Cranial Measurements (in millimeters) and Ratios of *Acheloma cumminsi* (AMNH 4205) and *Trematops milleri* (FMNH UC 640)**

| | Taxon | |
|---|---|---|
| Character | *Acheloma cumminsi* | *Trematops milleri* |
| Total midline skull length (TL) | 155 | 177 |
| Distance from anterior rim of orbit to tip of snout (SN) | 80 | 94 |
| Distance from anterior rim of external naris to tip of snout (SE) | 17 | 16 |
| Length of nasal (NS) | 52 | 59 |
| Length of frontal (FR) | 40 | 50 |
| Length of parietal (PR) | 32 | 43 |
| SN/TL | 0.51 | 0.53 |
| SE/TL | 0.11 | 0.09 |
| NS/TL | 0.34 | 0.33 |
| FR/PR | 1.25 | 1.10 |

*loma* was incompletely prepared and few sutures could be recognized. Combining the morphologically distinct small and large trematopsids in the same genus is justified only if the smaller ones are juveniles of *Acheloma* and *Trematops*. This assumption is implicit in Olson's review and explicit in his recent analysis of a larval trematopsid (Olson, 1985). Reexamination of those small trematopsids described by Olson (1941) and several collected after the publication of his review, indicates that the specimens represent individuals from a wide ontogenetic span. Only the smallest may be convincingly thought of as juveniles; those at the opposite end of the size range display a series of cranial and postcranial features consistent with an adult. Therefore, the inclusion of features found only on the smaller trematopsids in the diagnoses of *Acheloma* and *Trematops* is incorrect.

Far greater emphasis has been placed on the supposedly more distinct postcranial differences 7 and 8. However, these features are based on misinterpretation of the specimens. Ringlike presacral intercentra, as stated above, cannot be established in any of the preserved vertebrae of FMNH UC 640. Even if the intercentra were closed dorsally, recent work on the vertebral column of the classic Early Permian rhachitome *Eryops* (Moulton,

1974) strongly indicates that coossification of the separate cartilage embedded elements or portions of a single element is a size-related condition; larger and presumably older individuals display a greater incidence of coossification than do smaller ones. Dorsally closed intercentra, simulating the "stereospondylous" condition of many Triassic temnospondyls, have been reported in the posterior presacrals and caudals of *Parioxys* (Shawki Moustafa, 1955). The dorsal tips of the presacral intercentra of the dissorophid *Ecolsonia* (Berman et al., 1985) approach each other but do not make contact. Thus, dorsal closure of the intercentra of rhachitomes may be variable both in position within the vertebral column and in the degree of enclosure of the notochord and is of little importance taxonomically.

The scapulocoracoid of *Acheloma cumminsi,* as originally described by Cope (1882) and repeated verbatim by Case (1911), was thought to be highly unusual for labyrinthodonts. An area of poor ossification on the coracoid just below the supraglenoid foramen was interpreted as the glenoid fossa. When this "glenoid fossa" was directed laterally, the scapula was inflected back and over the vertebral column. The angle formed between the scapular blade and the coracoid was, according to this interpretation, considerably more acute than in any other known labyrinthodont. Watson (1919), however, reinterpreted the unusual configuration of the scapulocoracoid as the product of the presumed immaturity of the animal. Olson (1941), although probably aware of Watson's argument, followed Cope's original explanation. As discussed in the previous section, the scapulocoracoids of *A. cumminsi* are incomplete due to poor ossification and preservation. The apparent medial inflection of the scapula is the result of the misidentification of the region of rough bone surface on the coracoid as the glenoid fossa. This surface is in fact an oblique, ventrolaterally facing section through the coracoid and is, therefore, not the glenoid fossa. Slight ventral distortion of the scapula relative to the coracoid, particularly evident in the left scapulocoracoid, has emphasized the apparent inflection. Damage to the anterior edge of the scapular blade is responsible for the observed posterior aspect of the

inflection. Reinterpretation of the morphology of the scapulocoracoid of *A. cumminsi,* in the light of these observations, reveals no significant structural differences between it and the scapulocoracoids of other rhachitomes.

In all observable aspects, no significant morphological differences exist between the holotypes of *Acheloma cumminsi* and *Trematops milleri.* In accordance with the law of priority, *Trematops milleri* Williston, 1909 is deemed to be the subjective junior synonym of *Acheloma cumminsi* Cope, 1882. The family name, following Article 40 (synonymy of the type-genus) of the International Code of Zoological Nomenclature (Ride et al., 1985), remains Trematopsidae, Williston, 1910 (= Achelomidae Watson, 1919).

As a consequence of the above proposed synonymy, the exclusion of the smaller trematopsids, and past misinterpretations of morphology, a revised diagnosis of *Acheloma cumminsi* is presented.

## SYSTEMATICS

### CLASS AMPHIBIA

### ORDER TEMNOSPONDYLI

### SUPERFAMILY DISSOROPHOIDEA BOLT, 1969

### FAMILY TREMATOPSIDAE WILLISTON, 1910

### Genus *Acheloma* Cope, 1882

TYPE SPECIES: *Acheloma cumminsi* Cope, 1882.

REVISED GENERIC DIAGNOSIS: Large trematopsid temnospondyl characterized by the following derived features: a slitlike otic notch closed posteriorly by the contact of a hornlike tabular process and the base of a stout quadrate process; a groove on the posteromedial surface of the tabular; a long, broad shelf overhanging the otic notch; an internal naris with a posterior margin well forward of the posterior margin of the external naris; an ossified median vomerine septum contacting the roof of the snout.

A reconstruction of the skull of *Acheloma* in dorsal and lateral views is given in figure 3. Lack of information regarding the pattern of palatal sutures and precise braincase morphology prevents a reconstruction in ventral view.
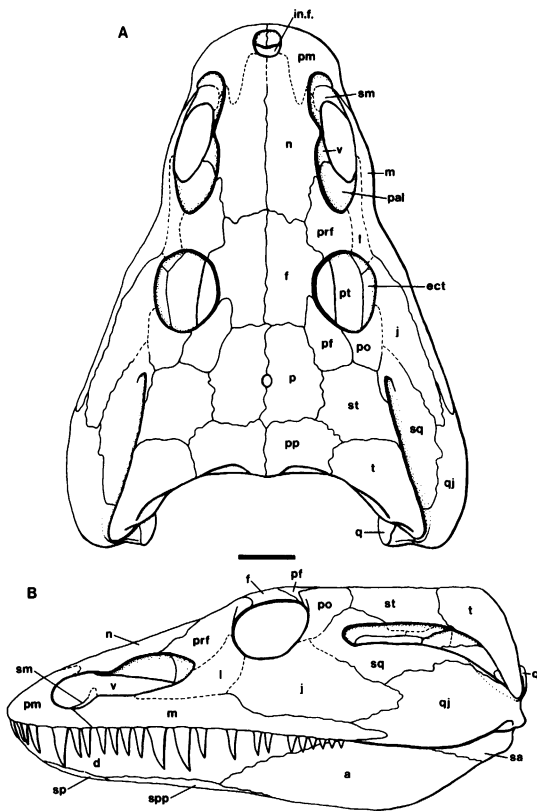
Fig. 3. Reconstruction of skull and mandible of *Acheloma cumminsi* based primarily upon the holotype (AMNH 4205). (A) dorsal view; (B) left lateral view. Scale = 2 cm.

The unique construction of the otic notch of *Acheloma* indicates that the tympanum, if present, was much smaller than that of other dissorophoids (Carroll, 1964; DeMar, 1968; Boy, 1985). Recent work by Clack (1983) on middle ear evolution among tetrapods has shown that the morphology of the stapes is the crucial factor in the interpretation of a temporal embayment. A lightly built, rodlike stapes implies the presence of a tympanum and a middle ear system capable of transmitting a wide range of airborne vibrations to the inner ear. Conversely, a massively built stapes with a large footplate that was unable to move freely within the fenestra ovalis argues against the presence of a tympanum and instead implies either a supportive role for the stapes or that it was capable of receiving only low-frequency air- and waterborne sounds.

Neither holotype possesses a stapes. Olson (1941: fig. 9) described and illustrated the stapes of *Trematops* as a well-ossified and slender rodlike element which would suggest the existence of a tympanum. The shape of the otic notch, however, argues against an impedence-matching hearing system because the vibrational properties of the postulated tympanum would be profoundly different from one with the same surface area but circular in outline. The reduced height of the tympanum would severely dampen vibrations, thereby limiting efficient sound detection to lower frequencies.

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