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RHINATREMATIDAE: A NEW FAMILY OF CAECILIANS (AMPHIBIA: GYMNOPHIONA)

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Of the three orders of modern Amphibia, the caecilians (Gymnophiona) are the least known. Prior to 1968, caecilians were thought to be poorly diversified and all species were placed in a single family (Caeciliidae). Largely because of the efforts of Dr. Edward H. Taylor, we now know that caecilians have undergone a much greater evolutionary expansion than was previously believed. Current classification of caecilians is based largely on Taylor's 1968 and 1969a publications, in which three families and many new genera and species were named.

Taylor (1968) placed a group of species which he considered to be the most primitive in the family Ichthyophiidae. This family has a broadly disjunct distribution in the tropics of southeast Asia and northern South America. All ichthyophiids are thought to have an aquatic larval stage and terrestrial, semifossorial adults. The most diverse family, Caeciliidae, is also the most widespread, being found in the tropics of India, Seychelles, Africa, and South and Central America as far north as southern Mexico. Caeciliids are advanced over ichthyophiids, both in morphological organization and mode of life history. In general, caeciliids are more specialized for burrowing than are ichthyophiids. While some caeciliids have larvae, others have direct terrestrial development, and yet others are livebearers. A third family, Typhlonectidae, consists of specialized aquatic forms which are livebearers; they are confined to South America. The fourth and last family, Scolecomorphidae is found only in

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Africa and contains one genus and six species of highly specialized burrowers.

   According to Taylor (1968) there are four ichthyophiid genera: *Ichthyophis* and *Caudacaecilia* in southeast Asia, and *Epicrionops* and *Rhinatrema* in northern South America. The two Asian genera are reasonably well studied morphologically (Peter, 1898; Sarasin and Sarasin, 1887-1890; Taylor, 1969b), but the two South American genera, especially *Rhinatrema,* are rarely collected and have been inadequately studied.

   The diagnostic features given by Taylor (1969a) for the Ichthyophiidae are: 1) prefrontals present, 2) orbitals (post-frontals) present, 3) septomaxillae present, 4) premaxillae and nasals present as separate elements, 5) stapes present, 6) orbitosphenoids not widely exposed on ventral surface of skull, 7) no distinct diastema between prevomerine and palatine teeth, 8) tentacles closer to eyes than to nostrils, 9) primary annuli divided into three or four secondary annuli which externally are indistinguishable from the primaries, 10) scales present, 11) a distinct tail, 12) no spines on penis, and 13) an aquatic larval stage. To this list can be added the presence of distinct pterygoids and foramina in the stapes for passage of the stapedial arteries. Not all of these character states are unique to Taylor's ichthyophiid genera. For example, some caeciliids like-wise have aquatic larvae, and only scolecomorphids are known to lack stapes and have penial spines. Furthermore, the diagnosis of the Ichthyophiidae is based largely on *Ichthyophis* and *Caudacaecilia; Epicrionops* and *Rhinatrema* were not studied in detail by Taylor.

   I have recently studied specimens of *Epicrionops* and *Rhinatrema* by x-raying, dissection, and clearing and staining. Specimens examined were: *Epicrionops*—American Museum of Natural History (AMNH) 1380, 1454, 1457, 17304-6, 42858, 42860-1, 46205, 51262; British Museum of Natural History (BM) 1933.6.24.70; University of Kansas Museum of Natural History (KU) 119397-402; United States National Museum (USNM) 159793, 160355-7, 160359-62, 166414, 166422: *Rhinatrema*—Museé National d'Histoire Naturelle, Paris (MNHN) 585, 1899-101 (one specimen); Rijksmuseum van Natuurlijke Histoire, Leiden (RMNH) 17667. I have also studied numerous specimens of *Ichthyophis* and *Caudacaecilia.* Among caeciliids I have dissected *Caecilia, Dermophis, Geotrypetes, Gymnopis, Hypogeophis, Schistometopum,* and *Uraeotyphlus.* Specimens of

Typhlonectes (Typhlonectidae) and *Scolecomorphus* (Scoleco-morphidae) were also examined in detail. I have drawn freely from the literature, but all observations are original unless otherwise noted.

Epicrionops and *Rhinatrema* lack prefrontals and postfrontals and, therefore, they do not fit Taylor's ichthyophiid diagnosis. Either the familial diagnosis must be expanded to accommodate these two South American genera, or they must stand alone. Reexamination of Taylor's diagnostic characters and study of new characters (see below) show that the Asian and South American genera are similar in the retention of a few of the same ancestral character states, and that they differ widely in many important features. Hence a new family must be constructed for the South American genera.

Rhinatrematidae fam. nov.

Diagnosis.— Tentacle immediately adjacent to or on the eye, eyes visible and in the usual position; mouth terminal; primary and secondary annuli indistinguishable externally, annuli complete and orthoplicate at all levels along body; premaxillae and nasals present as separate bones (Fig. 1); squamosal widely separated from frontal; paired dorsolateral processes on os basale opposing posterior squamosal notches; wide gap between squamosal and parietal for passage of musculus levator mandibulae anterior; cultriform process of parasphenoid portion of os basale prolonged anteriorly separating the relatively short prevomers; sides of parasphenoidal portion of os basale nearly parallel; no basipterygoid processes; os basale not strongly articulated with processus pterygoideus of quadrate; orbito-sphenoids not widely exposed in ventral view; pterygoids present; stapes present, pierced by stapedial artery; quadrate articulates with maxillary portion of maxillopalatine as well as with squamosal; processus retroarticularis relatively short and straight, not strongly curved upwards posteriorly (Fig. 2); ceratohyals fused medially and joined to the similarly fused first ceratobranchials by the first basibranchial (Fig. 3); medially fused ceratobranchials gradually reduced in size posteriorly; three (*Epicrionops*) or two (*Rhinatrema*) ceratobranchials; gap between last ceratobranchial and larynx, with no muscular attachment between larynx and last ceratobranchial; musculus
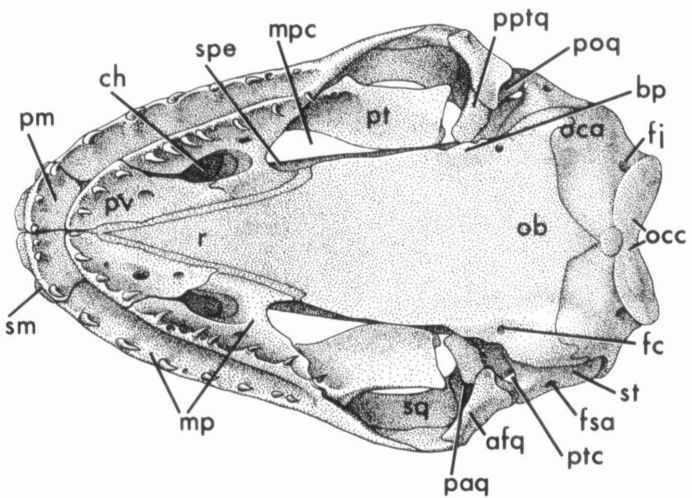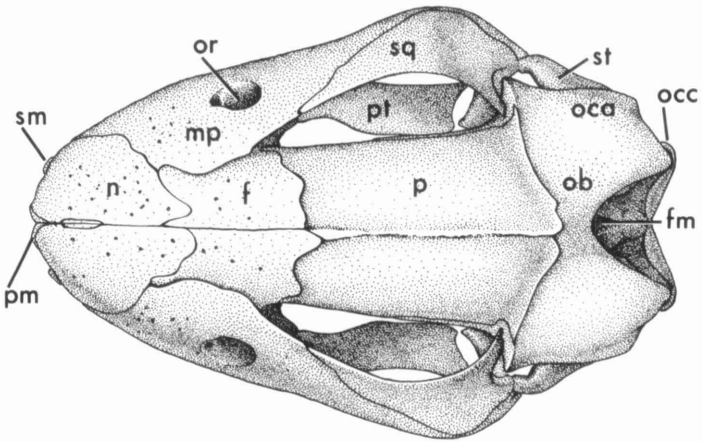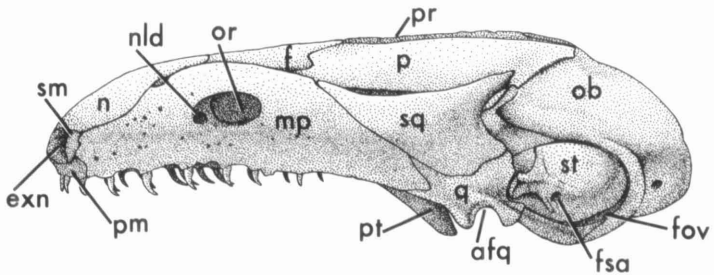
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interhyoideus inserts largely on the retroarticular process with a few anterior fibers inserting on the end of the ceratohyal; musculus interhyoideus posterior small, obliquely oriented in one bundle; musculus subarcualis rectus II and III absent; paired musculus levator mandibulae anterior meet in midline above the interparietal suture; musculus depressor mandibulae fan-shaped, with obliquely oriented anterior fibers and vertically oriented posterior fibers.

*Content.—* Two genera: *Epicrionops* with eight species and *Rhinatrema* with one species.

Etymology.— The family named is derived from the type genus, *Rhinatrema: rhin* (Gr.) meaning nose and *atrema* (Gr.) meaning without holes; referring to the lack of tentacular apertures on the snout.

Distribution.— Northern South America: *Epicrionops* occurs in Columbia, Equador, Perú, and Venezuela; *Rhinatrema* is known from French Guiana and Surinam.

ANALYSIS OF CHARACTERS

General remarks.— The major assumption in any analysis of character states across taxa is that the ancestral and derived states for each character have been accurately identified. However, every directed character state tree has some likelihood of being wrong. The degree of uncertainty varies greatly (but is not measureable) depending on the biological nature of the character, the distribution of its states across extant taxa, and the usefulness of the fossil record in interpreting its evolutionary history. Of all modern groups of vertebrates, caecilians are perhaps the least known biologically and have the poorest fossil

FIG. 1. Lateral, dorsal and ventral views of the skull of *Epicrionops petersi* (USNM 160360). *afq.,* articular facet of quadrate; *bp.,* region of basipterygoid process, not developed as a distinct process in this genus; *ch.,* choana; *exn.,* external naris; *f.,* frontal; *fc.,* carotid foramen; *fi.,* jugular foramen; *fm.,* foramen magnum; *fov.,* foramen ovale; *fsa.,* stapedial artery foramen; *mp.,* maxillopalatine; *mpc.,* medio-palatinal cavity; *n.,* nasal; *nld.,* nasolacrimal duct; *ob.,* os basale; *oca.,* otic capsule; *occ.,* occipital condyle; *or.,* orbit; *p.,* parietal; *paq.,* processus ascendens; *pm.,* premaxilla; *poq.,* processus oticus of quadrate; *pptq.,* processus pterygoideus of quadrate; *pr.,* parietal ridge; *pt.,* pterygoid; *ptc.,* ptero-occipital cavity; *pv.,* prevomer; *q.,* quadrate; *r.,* parasphenoidal rostrum of os basale; *sm.,* septomaxilla; *spe.,* sphenethmoid; *sq.,* squamosal; *st.,* stapes.

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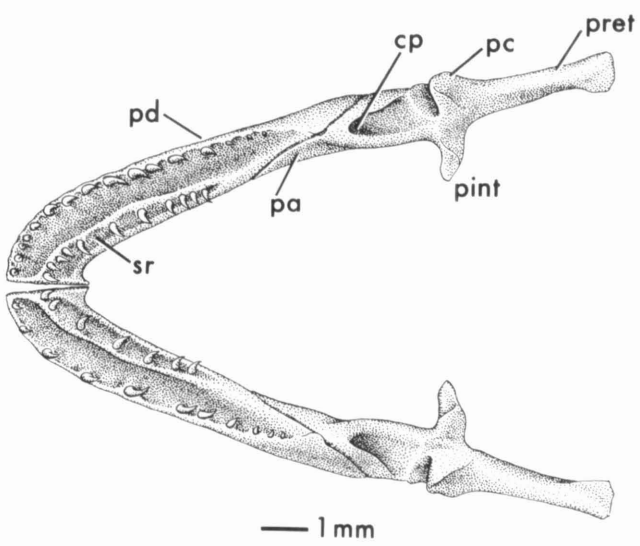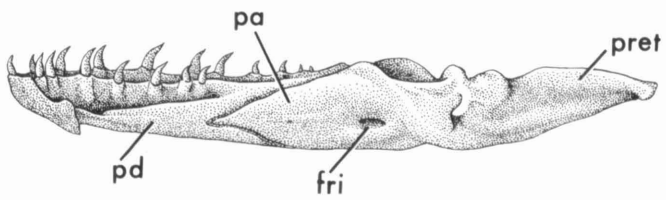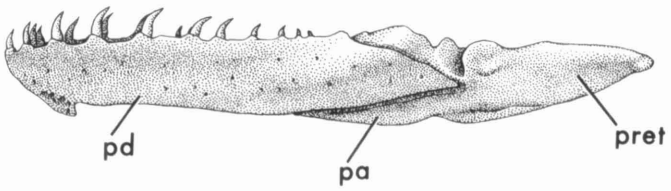
record—a single fossil vertebra is known (Estes and Wake, 1972). Therefore a high degree of uncertainty must accompany any interpretation of the evolution of caecilian characters. I have used the standard criteria (Maslin, 1952) for estimating ancestral versus derived character states and have attempted to categorize every character regardless of the degree of uncertainty associated with it.

Conspicuously missing from this analysis are characters associated with karyology, the vertebral column and non-muscular, soft organ systems. Too little is presently known of these features to justify their inclusion.

Eye-tentacle relationship.— The position of the tentacular aperture varies widely among caecilians, so that often this information is useful only for distinguishing genera or species. However, the opening for the tentacle in *Epicrionops* and *Rhinatrema* is unique when considered in relation to the well-developed eyes. In both genera, the tentacular opening is a small longitudinal slit adjacent to the anterior edge of the eye. In *Epicrionops,* the opening is in contact with the clear tissue covering the eye, and in *Rhinatrema* the opening projects well into the window over the eye. By contrast, the tentacular aperture is far anterior of the eye in *Ichthyophis* and *Caudacaecilia.*

Since the tentacular apparatus is derived from the nasolacrimal duct (Wiedersheim, 1879; Sarasin and Sarasin, 1887-1890) and because the tentacle migrates anteriorly away from the eye during ontogeny in *Ichthyophis, Caudacaecilia,* and probably all other caecilians, it seems likely that the rhinatrematid condition is ancestral to the ichthyophiid condition. However, the possibility that the position of the tentacle near the anterior edge of the eye is a derived paedomorphic trait in rhinatrematids cannot be discounted.

Mouth opening.— The mouth is terminal in rhinatrematids. In ichthyophiids the position of the mouth varies from nearly terminal in many species to distinctly subterminal in others. All

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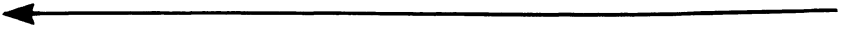
FIG. 2. Lower jaws of *Epicrionops petersi* (USNM 160360); lateral (upper), medial (center), and dorsal (lower) views. *cp.,* canalis primordialis (common opening into the lower jaw for the mandibular artery and the ramus mandibularis externus V received from the Gasserion ganglion); *fri.,* foramen for the exit of the ramulus intermandibularis V; *pa.,* pseudoangular; *pc.,* processus condyloides of the pseudoangular; *pd.,* pseudodentary; *pint.,* processus internus; *pret.,* processus retroarticularis; *sr.,* splenial ridge bearing the splenial teeth.

FIG. 3. Glossal skeleton of caecilians. A— *Epicrionops,* B— *Rhinatrema,* C— *Ichthyophis,* D— *Gymnopis,* E— *Typhlonectes,* and F— *Scolecomorphus.* CH = ceratohyal, BB1 = first basibr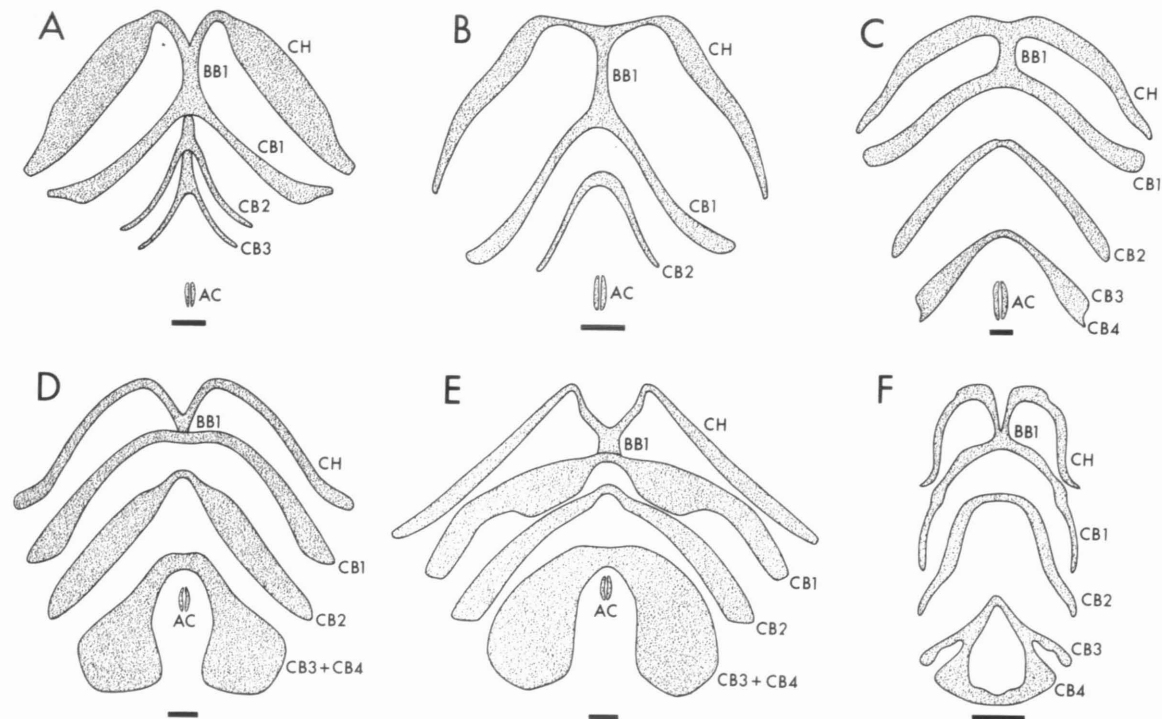anchial, CB1 = first ceratobranchial, CB2 = second ceratobranchial, CB3 = third ceratobranchial, CB4 = fourth ceratobranchial, AC = arytenoid cartilages. *Scolecomorphus* redrawn from Brand (1956). Line = 1 mm.

other caecilians have a boldly projecting snout with the mouth opening well recessed, a condition which reflects a high degree of specialization for burrowing. The recessed mouth and relatively solid skull of the fully aquatic typhlonectids suggest they may have evolved from specialized burrowers rather than from rhinatrematid or ichthyophiid-like forms.

There is no evidence that the rhinatrematid skull, with its labyrinthodont-like terminal mouth, has been secondarily derived. The bony elements of the antorbital region of the skull show no fusions, losses, or evidence of reshaping which might suggest derivation from a skull specialized for burrowing. Therefore the terminal mouth of rhinatrematids is considered to be ancestral; the tendancy towards subterminalization in ichthyophiids is considered to be derived.

Annulation.— Rhinatrematids and ichthyophiids both have complete secondary annuli the full length of the body which are externally indistinguishable from the primary annuli. Dunn (1942) stated that this condition is ancestral to the various manifestations of annuli configuration found in other caecilians such as incomplete secondaries and/or absence of secondaries. Although Dunn did not justify this assertion, it is probably true for at least two reasons. Firstly, in many caecilians (e.g., the caeciliid genus *Microcaecilia*) there is a serial change in annular arrangement along the body. Anteriorly, secondaries are entirely absent, near mid-body the secondaries begin to appear but are incomplete, and posteriorly the secondaries are complete and cannot be differentiated externally from the primaries. Hence, the posterior region of a caecilian such as *Microcaecilia* is rhinatrematid-like in annular configuration. It is well known that evolution often produces more radical changes anteriorly than posteriorly in serially repeated structures (e.g., anthropod appendages). This process, which has been called "cephalization," can usually be detected in the ontogeny of organisms, a fact which offers strong but not compelling evidence that the posterior condition resembles the ancestral condition for serially repeated characters. Secondly, one can argue that complete secondary annuli in rhinatrematids and ichthyophiids is likely to be the ancestral condition because these groups have more other ancestral characters than the remaining families. This is obviously a weak argument, but at least a parsimonious one.

Rhinatrematids and ichthyophiids share the condition of complete secondaries, indistinguishable from primaries. But there

is a fundamental difference between these two families. Rhina-trematids have orthoplicate annuli the full length of the body, whereas ichthyophiids have annuli which curve posteriorly along the mid-ventral line on the anterior one-half to four-fifths of the body. Posteriorly, however, the annuli of ichthyophiids are orthoplicate as in rhinatrematids. By the cephalization argument, the orthoplicate condition of the annuli is considered to be ancestral to the ventrally curved condition.

Taylor (1965) described one ichthyophiid (*Ichthyophis ortho-plicatus*) which he thought had orthoplicate annuli the full length of the body. However, Nussbaum and Gans (1977) showed this to be incorrect.

Scales.— Scales are present in all of the annular folds of rhinatrematids. Some ichthyophiids also have scales in all folds, but both *Ichthyophis* and *Caudacaecilia* have species with no scales in the anterior folds. All other families of caecilians exhibit various degrees of reduction of scales rows; some species have no scales. Scale row reduction usually occurs in the anterior folds so that the posterior folds of a given species are most likely to have scales. In a parallel fashion, scale size may be reduced serially, with no scales found anteriorly, a few minute scales at midbody, and many large scales posteriorly. Such variation in the number and size of scales is functionally related to loss of secondary annuli and reduced prominence of the primary annuli. The rhinatrematid condition is considered to be ancestral to various manifestations of fewer scale rows and smaller scale size by the same arguments given above for loss of secondary annuli.

Tail.— All rhinatrematids and ichthyophiids have distinct tails. With two supposed exceptions, all other genera lack tails. The two exceptions are *Uraeotyphlus* and *Copeotyphlinus* which are currently assigned to the family Caeciliidae (Taylor, 1968). I will show elsewhere (Nussbaum, in preparation) that *Uraeotyphlus* is an ichthyophiid. *Copeotyphlinus* cannot be dealt with since there are no known specimens.

The presence of a tail is the usual condition in vertebrates. Therefore, the universal presence of a tail in rhinatrematids and ichthyophiids is considered to be ancestral to tail loss in the three other families.

Skull morphology.— Separate paired premaxillae and nasals occur in rhinatrematids, ichthyophiids, and scolecomorphids. In all genera of the Caeciliidae and Typhlonectidae so far ex-

amined, the premaxillae and nasals are fused into the paired nasopremaxillae. This fusion of anterior skull elements results in a solid, pointed snout and increased burrowing efficiency. The latter condition is the derived state.

Septomaxillae are present as separate elements in the Rhinatrematidae, Ichthyophiidae, and Scolecomorphidae. These tiny bony elements are either lost or fused to adjacent bones in caeciliids and typhlonectids; loss or fusion are the derived states.

Separate prefrontals are present in ichthyophiids and scolecomorphids, and are missing in rhinatrematids, caeciliids, and typhlonectids. Whether the prefrontal is actually missing or fused to the maxillopalatine in these latter families is unknown for all genera except for the caeciliid genus *Hypogeophis*. Marcus *et al.* (1935) found that the maxillopalatine of *Hypogeophis* represents a fusion of the maxillary, palatine, and lacrimal. Thus, the prefrontal seems to be missing in this genus. The possibility exists, however, that the embryonic lacrimal of these latter authors is in reality the anlage of the prefrontal. Lack of a distinct prefrontal, whether caused by loss or fusion, is a derived condition.

Distinct postfrontals (orbitals of Taylor, 1969b) are present only in ichthyophiids. Their absence in the remaining families may be due either to loss or to fusion to the squamosal. Marcus *et al.* (1935) stated that the postfrontal becomes fused to the squamosal during ontogeny in *Hypogeophis*; the developmental pattern for other genera is unstudied. As with the prefrontal, lack of a distinct postfrontal is thought to be a derived state.

The squamosal and frontal are widely separated in rhinatrematids (Fig. 1) and scolecomorphids. This arrangement is a consequence of the marked zygokrotaphic condition of the skull in these two families. The space which separates the squamosal and frontal forms part of the temporal fossa for the passage of the musculus levator mandibulae anterior (see myology section). In almost all vertebrates, including the primitive stegocephalian amphibians, the squamosal is not in contact with the frontal. Therefore the rhinatrematid-scolecomorphid condition seems to be ancestral to the condition found in all other caecilians, where the squamosal and frontal are juxtaposed. Articulation of the squamosal to the frontal adds solidity to the skull. As with so many characteristics of advanced caecilians, contact of these two elements seems to be correlated with their highly specialized burrowing habit.

The paired dorsolateral processes (Fig. 1) of the os basale which oppose the posterior ends of the squamosals by fitting into notches in the squamosals are unique to the rhinatrematid genera. This juncture affords support to the cheek region when compressional stress is applied to the maxillopalatine-squamosal arcade during burrowing activity. Such support is of obvious advantage to the otherwise weak zygokrotaphic skull of rhinatrematids, and is viewed as a highly specialized derived feature of this family.

Epicrionops and *Rhinatrema* have a wide gap, or temporal fossa, between the squamosal and parietal (Fig. 1). This zygokrotaphic condition does not exist in ichthyophiids where the squamosal and parietal are in contact (stegokrotaphy). In a few skulls of *Ichthyophis,* however, a narrow slit appears between the squamosal and parietal. This slit may result, in part, from loosening during the process of preparing the skull. Even if the narrow slit. is present, the musculus levator mandibulae anterior does not pass through it in ichthyophiids, as is always the case in the large fossa of rhinatrematids. Among those caeciliids examined to date, only *Geotrypetes* is zygokrotaphic. Two typhlonectid genera *Potamotyphlus* and *Typhlonectes,* have zygokrotaphic skulls (Taylor, 1969b; Figs. 12, 13, and 14). In *Geotrypetes* and in the two typhlonectid genera, zygokrotaphy is not as prominent as in the rhinatrematids, and the fronto-squamosal contact is maintained. Zygokrotaphy may be secondarily derived in these forms. Scolecomorphids have a strongly zygokrotaphic skull with no fronto-squamosal articulation.

Some authors (Marcus *et al.,* 1933; Marcus *et al.,* 1935; de Villiers, 1938; Carroll and Currie, 1975) have argued that stegokrotaphy is primitive in caecilians, having been directly inherited from stegocephalian (labyrinthodont) ancestors. Others (Sarasin and Sarasin, 1887-1890; Gaupp, 1895; Peter, 1898; Luther, 1914; Jaekel, 1927; Goodrich, 1930; Werner, 1930; Versluys, 1931; Edgeworth, 1935; de Beer, 1937; Ramaswami, 1941; and Dunn, 1942) have claimed that stegokrotaphy is secondarily derived in caecilians as a correlate of the burrowing mode of existence. I believe there are at least three reasons for favoring the latter hypothesis. Firstly, zygokrotaphy, not stegokrotaphy, characterizes the most primitive (based on other characters) caecilians. Secondly, stegokrotaphy in caecilians differs from primary stegokrotaphy as exemplified by cross-opterygians and labyrinthodonts in a number of ways, including reduction in the number and size of temporal bony elements

and the absence of an otic notch in caecilians. Thirdly, caecilians occupy a burrowing adaptive zone (typhlonectids excepted); it seems logical, therefore, that evolution could have proceeded from zygokrotaphy (weak skulls) to stegokrotaphy (solid skulls), but not the reverse. It appears that the most primitive caecilians with zygokrotaphic (rhinatrematids) or weakly stegokrotaphic (some ichthyophiids) skulls are not highly adapted for burrowing, having been described as "surface cryptic" forms (Ramaswami, 1941). Specialized earth burrowers—mostly caeciliids —are advanced morphologically and have strongly stegokrotaphic skulls.

The prevomers of *Epicrionops* (Fig. 1) and *Rhinatrema* are widely separated posteriorly by the interposition of the cultriform process of the parasphenoid portion of the os basale, which projects further anteriorly in these two genera than in others. In *Ichthyophis* and *Caudacaecilia* the prevomers are in contact for nearly their entire length. This latter condition also characterizes scolecomorphids and most genera of caeciliids and typhlonectids. At present there is little basis for arguing which of these two states, if either, most closely resembles the ancestral condition in caecilians. The latter condition is here considered advanced because close contact of the prevomers lends solidity to these skulls which are otherwise specialized for burrowing.

In the rhinatrematid genera, the prevomers lie entirely anterior of the posterior edges of the choanae, whereas in ichthyophiids, the prevomers extend far posterior of the choanal openings. This character varies considerably across other caecilian genera, but in most the prevomers are larger and project further posteriorly compared to rhinatrematids. Posterior expansion of the prevomers and the resultant stronger articulation of the prevomers with the os basale are consonant with the general theme of increased rigidity of the skull in response to selection for increased burrowing efficiency in advanced caecilians.

The sides of the parasphenoid portion of the os basale are parallel in rhinatrematids, whereas in ichthyophiids and in more advanced families the sides of the parasphenoid region converge anteriorly. Among the most primitive living salamanders (hynobiids, *Andrias, Cryptobranchus, Dicamptodon*) the parallelsided state of the parasphenoid is observed (Tihen, 1958; personal observation). In the earliest fossil urodele in which the palatal structure is well known (*Palaeoproteus klatti,* Eocene)

the parasphenoid is parallel-sided (Herre, 1935; Dechaseaux, 1955). Similarly, parallel-sidedness of the parasphenoid is characteristic of primitive frogs (Estes and Reig, 1973). Because parallel-sidedness occurs in the most primitive genera of the Anura, Caudata and Gymnophiona, I will assume it is the ancestral state.

Taylor (1969a) reported that the orbitosphenoid was clearly visible in ventral view in *Scolecomorphus,* and he considered this condition to be diagnostic of his new family, Scolecomorphidae. In all other genera known to Taylor, the orbitosphenoid was largely or entirely hidden from view dorsal to the parasphenoid region of the os basale. This latter state is characteristic of both the Rhinatrematidae and Ichthyophiidae.

In scolecomorphids, the visibility of the orbitosphenoids results from the narrowness of the parasphenoid region and the oblique rather than vertical orientation of the orbitosphenoids. The scolecomorphid state for this character is derived, based on comparisons to labyrinthodont patterns and to primitive urodeles.

Parker (1941), Parsons and Williams (1963), Taylor (1969b) and Carroll and Currie (1975) stated that a small ectopterygoid occurs in some caecilians. Wiedersheim (1879) illustrated a "postpalatinum (?)" in the proper position for an ectopterygoid in *Siphonops annulatus* and *Hypogeophis rostratus.* However, Gregory *et al.* (1956) wrote that an ectopterygoid does not occur in caecilians. The confused literature results in part from the fact that Parker's (1941) ectopterygoid is the pterygoid of Luther (1914), Marcus *et al.* (1933), and others. Some recent authors have rather uncritically stated that a free ectopterygoid is present in some caecilians as well as a free pterygoid, whereas in reality only a single free bone is present in some species. I have considered it to be the pterygoid.

A distinct pterygoid occurs in both rhinatrematids and ichthyophiids. There is no pterygoid in the Scolecomorphidae (Brand, 1956). In typhlonectids and caeciliids the pterygoid is usually fused to either the maxillopalatine or to the quadrate, but it has been reported as distinct in *Chthonerpeton* (Peters, 1879), *Idiocranium* (Parker, 1936), *Siphonops* and *Caecilia* (Luther, 1914), and *Hypogeophis* (Marcus *et al.,* 1935). There are conflicting reports for these latter genera; it will be necessary to examine series of skulls to resolve this issue. The presence of a distinct pterygoid is ancestral to loss of the pterygoid and to fusion of the pterygoid to adjacent bones.

   Suspensorial region.— A distinct basipterygoid (= basitrabecu-
lar) process is not evident in rhinatrematids. Instead, the basi-
pterygoid region of the os basale is broadly syndesmotically
connected to the pterygoid and to the processus pterygoideus of
the quadrate. In *Epicrionops,* the pterygoid and processus ptery-
goideus meet at an angle and are themselves syndesmotically
joined. In *Rhinatrema* these two elements articulate suturally
into a smooth arch, the medial side of which rides against the
basipterygoid region of the os basale. In these two genera, the
pterygoid serves to prop the maxillopalatine against the side of
the braincase and the quadrate.
   The situation is different in ichthyophiids where a basi-
pterygoid process is present. This latter process is syndesmotic-
ally joined to the processus pterygoideus of the quadrate. The
pterygoid of ichthyophiids is in syndesmotic union with the
processus pterygoideus, but not to the os basale, contrary to the
situation in rhinatrematids.
   According to Brand (1956), the basipterygoid process and the
quadrate are closely articulated in scolecomorphids via a well-
developed processus basalis on the medial face of the quadrate.
Nearly the same arrangement has been reported in two caeciliid
genera: *Hypogeophis* (Marcus *et al.,* 1933) and *Dermophis* (de
Jager, 1939). In the caeciliid genus *Caecilia* this basal articula-
tion shows evidence of nearly complete fusion between the two
processes (de Jager, 1940).
   Both rhinatrematids and ichthyophiids possess kinetic skulls.
As pointed out by de Beer (1937), the widespread condition
among vertebrates in which the basipterygoid process served as
an articular facet against which the pterygoid is free to slide,
indicates that the kinetic bony skull is ancestral to the derived
akinetic condition. Hence, among caecilians, both zygokrotaphy
and kinetism must be considered primitive since there is no
reason to consider either to be secondarily derived. The tend-
ency toward stegokrotaphy and akinetism in advanced caecilians
is correlated with ·increased burrowing efficiency and inde-
pendence of the aquatic environment.
   The pterygoid-os basale syndesmotic connection in rhina-
trematids is similar to the primitive labyrinthodont pattern and
should be viewed as ancestral to the ichthyophiid condition
wherein the pterygoid does not contact the os basale. On the
other hand, lack of a distinct basipterygoid process in adult
rhinatrematids is likely to be derived, whereas its presence in

ichthyophiids, although poorly developed, suggests the ancestral state.

The stapes is present in all caecilians except for scolecomorphids where its absence is a derived feature.

The stapes is pierced by the stapedial artery in rhinatrematids and ichthyophiids. Among caeciliids, only *Boulengerula* (Ramaswami, 1941) and *Hypogeophis* (de Beer, 1937) are reported to have perforate stapes. However, Lawson (1963) did not mention a perforate stapes in *Hypogeophis.* Typhlonectids apparently do not have perforate stapes.

Perforate stapes occur in many genera of gekkonid lizards (Underwood, 1957), and is the usual condition in mammals. Among extinct Amphibia, all primitive labyrinthodonts, including some Embolomeri and Rachitomi in which the stapes is adequately known, have perforate stapes (Goodrich, 1930; Romer, 1947; Lehman, 1955). Among modern amphibians, exclusive of gymnophionans, only one genus of primitive salamanders, *Ranodon,* has perforate stapes (Schmalhausen, 1968). The broad distribution of the perforate state across vertebrate groups, its occurrence in the Labyrinthodontia, and its presence only in primitive genera of Lissamphibia suggests that the perforate stapes is the ancestral condition.

The stapes of rhinatrematids and ichthyophiids is moveably articulated to the processus columellaris (sensu Visser, 1963) of the quadrate, a necessary condition of kinesis in these forms. In advanced burrowing caecilians, which exhibit little or no skull kinesis, the stapes is more firmly articulated to the quadrate. In *Dermophis,* de Jager (1939) reported that the stapes is solidly fused to the quadrate. The loosely articulated state of the stapes and quadrate is here considered to be an ancestral characteristic.

The quadrate articulates with the maxillary portion of the maxillopalatine in *Epicrionops* (Fig. 1) and *Rhinatrema,* a condition which is apparently unique to these two genera among living vertebrates and is, therefore, an important diagnostic feature of the Rhinatrematidae.

In the Labyrinthodontia, there is typically a distinct quadratojugal between the maxilla and the quadrate. In a few genera of labyrinthodonts the posteroventral portion of the jugal is interposed between the maxilla and the quadratojugal; in this case, two bones, jugal and quadratojugal, separate the maxilla and quadrate.

Among the Lissamphibia, the jugal is missing in the Anura,

but the quadratojugal persists in many species and serves to brace the maxilla against the quadrate. There is likewise no jugal in urodeles, but a quadratojugal has been described in the usual position in *Tylototriton,* a primitive salamandrid (Riese, 1891). Among caecilians, the anterior process (processus jugularis of Sarasin and Sarasin, 1887-1890 and Ramaswami, 1941) of the quadrate of *Ichthyophis* was thought by Peter (1898) to be the quadratojugal, now fused to the quadrate. Also, de Villiers (1936) discovered an independent anlage of the developing quadrate in *Hypogeophis* which he homologized with the quadratojugal. Developmental series are not available for either of·the two rhinatrematid genera, but in skulls of adults the anterior process of the quadrate is ņearly distinct, apparently having fused to the quadrate relatively late in ontogeny.

Whether or not the anterior process of the quadrate represents the quadratojugal in rhinatrematids, articulation between the maxillopalatine and quadrate reflects the primitive labyrinthodont pattern. All other caecilians have the derived state in which the bridge between the maxillary portion of the maxillopalatine and the quadrate has been lost.

Lower jaw.— A pronounced postarticular elongation of the lower jaw is diagnostic of the Gymnophiona. In labyrinthodonts, a short retroarticular process was often present on the surangular, apparently for insertion of the jaw opening muscles. The angulare of anurans and urodeles has no discernible retroarticular process.

The processus retroarticularis of the pseudoangular of caecilians serves not only as a lever arm for opening the jaws via the musculus depressor mandibulae, but also as a lever arm for jaw closure (see below). This latter functional relationship is unique to caecilians among modern Amphibia. As I will argue later, the caecilian jaw closure mechanism is highly adapted for a burrowing existence, and perfection of the mechanism can be detected in the transition from primitive to advanced caecilians.

The relatively short and horizontally disposed processus retroarticularis of rhinatrematids (Fig. 2) should be considered ancestral to the longer processes which are curved upwards at about a 45° angle in most other caecilians so far examined. In *Siphonops,* a caeciliid, the condition is intermediate; the processus retroarticularis is relatively short and curved upwards at only a slight angle.

Glossal skeleton.— The larval hyobranchium and meta-

morphosed glossal skeleton are cartilaginous in all caecilians studied to date. Unfortunately there is no information yet available on the structure of the hyobranchium of larval rhina-trematids. The hyobranchium of *Ichthyophis* is known (Müller, 1835; Sarasin and Sarasin, 1887-1890; personal observation), and a brief description of the metamorphosis from hyobranchium to glossal skeleton in this genus is necessary in order to understand the uniqueness of the rhinatrematid glossal skeleton.

The hyobranchium of *Ichthyophis* consists of the ceratohyals, two basibranchials, and four ceratobranchials. At metamorphosis, the second basibranchial is lost and the fourth ceratobranchial fuses to the end of the third ceratobranchial (Fig. 3c). The last ceratobranchial (cb3+4) of ichthyophiids is large, and it lends considerable support to the ventral pharyngeal region. The larynx is enclosed between the posterolaterally directed ends of cb3+4, and is supported by muscles (musculus dilator laryngeus and musculus dorsolaryngeus) which originate on the ends of cb3+4 and insert on the arytenoid cartilages and tracheal wall.

In those caeciliids, scolecomorphids, and typhlonectids studied to date, the glossal skeleton resembles that of ichthyophiids in that the last ceratobranchial is large, appears to incorporate the fourth ceratobranchial (see Brand, 1956 for *Scolecomorphus*; Els, 1963 for *Schistometopum*; and Gehwolf, 1923 for *Hypogeophis*) and encloses the larynx (Fig. 3).

The glossal skeletons of *Epicrionops* (Fig. 3A) and *Rhinatrema* (Fig. 3B) differ from the fundamental plan described above. In these genera there is a gradual reduction in size of the posterior ceratobranchials so that the pharyngeal region receives little support from these cartilages. The larynx is posterior of the glossal skeleton and receives no support from the last cerato-branchial. There is no evidence of a fourth ceratobranchial and, indeed, even the third ceratobranchial is lost in *Rhinatrema*.

The fundamental number of visceral arches in vertebrates appears to be seven. Although a few shark genera have more than seven arches, the trend in vertebrate evolution has been toward fewer visceral arches. The primitive amphibian glossal skeleton is thought to have consisted of arch II (ceratohyal), III (ceratobranchial 1), IV (ceratobranchial 2), V (ceratobranchial 3), and VII (arytenoid cartilages); arch VI (cerato-branchial 4) having been lost (Edgeworth, 1935; Smith, 1960). It is of considerable interest, therefore, that the glossal skeleton of non-rhinatrematid caecilians retains a remnant of the fourth

ceratobranchial. This condition may possibly reflect the true ancestral state for amphibians, contrary to Edgeworth (1935) and Smith (1960), or more probably it is a derived paedomorphic state.

The glossal skeleton of rhinatrematids appears to possess a combination of ancestral and derived character states. Lack of a fourth ceratobranchial is parsimoniously viewed as retention of the ancestral amphibian state, but reduction in size of ceratobranchials two and three (loss of three in *Rhinatrema*) is a derived feature. The independence of the larynx from the glossal skeleton is a consequence of the reduced posterior elements of the glossal skeleton and should be viewed as a derived state.

Myology.— The musculus interhyoideus of rhinatrematids originates on the mid-ventral raphe between the mandibles and inserts anteriorly on the ceratohyal and posteriorly on the processus retroarticularis of the pseudoangular. In ichthyophiids, this muscle inserts entirely in a sheath of connective tissue on the side of the neck dorsal to the musculus interhyoideus posterior, and inserts with its fellow in a mid-ventral raphe. In rhinatrematids the muscle lies largely exposed between the musculus intermandibularis anteriorly and the musculus interhyoideus posterior caudally, whereas in ichthyophiids the musculus interhyoideus is largely covered by the musculus interhyoideus posterior.

Primitively, the musculus interhyoideus inserts on the end of the ceratohyal (Edgeworth, 1935); attachment of the anterior fibers to the ceratohyal in rhinatrematids is therefore viewed as ancestral to loss of this insertion in all other families. Attachment of the posterior fibers to the retroarticular process (rhinatrematids) and connective tissue on the side of the neck (ichthyophiids) are both derived states relative to the presumed gymnophionan ancestor. However, within the Gymnophiona, attachment of the posterior fibers to the processus retroarticularis is likely to be the ancestral state because the primitive position of the muscle places the posterior fibers directly below the retroarticular process and anterior of the neck region. In ichthyophiids, the muscle has been shifted posteriorly (derived position), dorsal to the musculus interhyoideus posterior, and away from the processus retroarticularis. The attachment of the posterior fibers of this muscle is unknown for most other genera, but according to Lawson (1965), they attach to the retroarticular process in the caeciliid, *Hypogeophis*.

The musculus interhyoideus posterior is a fan-shaped muscle which originates in subcutaneous connective tissue at the anterior margin of the musculus obliquus abdominus externus, ventral to the musculus rectus cervicis, and along the anterior margin of the musculus rectus abdominus in both rhinatrematids and ichthyophiids. The muscle passes anteriorly and dorsally to insert in a thick tendon on the processus retroarticularis in both families. In the rhinatrematid genera, the muscle is small, comprises one bundle, and has fibers running obliquely across the neck region. The muscle is much larger in ichthyophiids and is arranged in two bundles: a ventral bundle with oblique fibers as in rhinatrematids, and a dorsal bundle with longitudinally oriented fibers (not found in rhinatrematids). Other families most closely resemble the Ichthyophiidae for this character. In all caecilians, the musculus interhyoideus posterior, along with the levator series, functions to close the jaws. Contrary to Lawson (1965), the longitudinally oriented bundle does not serve to turn the' head. Mobility of the head is effected by the paired musculus rectus capitis superior and the paired musculus intertransversarius capitis inferior.

The arrangement of the musculus interhyoideus posterior in rhinatrematids seems to be an early stage (ancestral) in the evolutionary development of this highly specialized jaw closure mechanism (more derived in ichthyophiids).

The zygokrotaphic skull of rhinatrematids permits great expansion of the levator muscles. In both *Epicrionops* and *Rhinatrema,* the paired musculus levator mandibulae anterior originates largely on the parietal and passes ventrally through the temporal fossa to insert on the pseudoangular bone of the lower jaw. The paired muscles meet in the midline, just above the interparietal suture.

The stegokrotaphic skull of ichthyophiids restricts the mass and length of the musculus levator mandibulae anterior. These two muscles are covered dorsally by the squamosals and hence their points of origin are broadly separated.

Although stegokrotaphy is primitive in amphibians, within Gymnophiona zygokrotaphy is considered to be ancestral and stegokrotaphy is secondarily derived. Therefore, in caecilians expansion of the musculi levatores mandibularum anteriores through the temporal fossae to meet mid-dorsally is the primitive pattern, whereas restriction of these muscles below the squamosals is a derived feature.

The paired musculus depressor mandibulae of rhinatrematids is a broad sheet-like muscle which fans out over the dorsolateral region of the neck. All fibers insert on the processus retro-articularis and serve to open the mouth by depressing the lower jaws. The origin of this muscle is broad, extending from the mid-dorsal fascia of the neck region anteriorly across the parietal ridge and onto the parietal and squamosal. The posterior fibers are vertically oriented, but the anterior fibers run obliquely from their point of origin on top of the head in a caudal and ventral direction to the processus retroarticularis. The result is a single fan-shaped muscle in *Epicrionops,* but in *Rhinatrema* there are two discrete bundles: a posterior bundle with vertically oriented fibers, and an anterior bundle with oblique fibers.

In ichthyophiids, the musculus depressor mandibulae has longitudinally oriented fibers in a single bundle. This arrange-ment is correlated with the elongated, dorsally-curved retro-articular process which occurs in this family. The fibers originate largely on the parietal, but a few originate on the squamosal and the fascia above the musculus dorsalis trunci. From their point of origin, the fibers of this muscle run caudally to insert on the processus retroarticularis which curves up to meet them.

The oblique to vertical orientation of the fibers of the musculus depressor mandibulae in rhinatrematids resembles the ancestral condition, whereas the longitudinal orientation of this muscle in ichthyophiids and the other families is a specialized derived state.

The rhinatrematid genera lack the musculi subarcuales recti II and III, whereas both muscles are present in the Ichthyophiidae. Their absence in rhinatrematids is a consequence of the reduc-tion in size and/or number of posterior glossal skeletal elements, and their loss is a derived state. The condition of these muscles is poorly known in other families, but they are present in the caeciliid genus *Hypogeophis* (Lawson, 1965). According to Edge-worth (1935), the musculus subarcualis rectus II is missing but III is present in *Siphonops,* a caeciliid.

Color.— The basic ground color of rhinatrematids and ichthyophiids—indeed of most caecilians—may be variously de-scribed as lilac-slate, purple-slate, or blue-grey, with a tendency toward lighter shades ventrally and anteriorly. Both ichthyophiid genera have unicolor species and species with lateral yellow or cream-colored stripes. In the Rhinatrematidae, *Epicrionops* has uni-color and striped species, and the monotypic *Rhinatrema* is striped.

The occurrence of unicolor and striped species within genera of both families creates an interesting phylogenetic problem which is not easily solved. If the common ancestor of the two families was unicolor, then stripedness has independently evolved at least four times; if stripedness is ancestral, then stripe loss has occurred at least three times. Parsimony suggests that the rhinatrematid-ichthyophiid ancestor was striped.

The presence of bright yellow lateral stripes in caecilians is a striking feature among these otherwise dully colored amphibians. Therefore the presence of stripes in ichthyophiids and rhinatrematids creates an artificial sense of close relationship which has confused the taxonomy of these forms. Possibly the striped color pattern has been independently retained in both families through at least the entire Cenozoic Era.

Life history pattern.— Primitively, amphibians have an aquatic larval stage in their life cycle. The two ichthyophiid genera have larval stages, as does the rhinatrematid genus *Epicrionops.* The life history of the remaining rhinatrematid genus, *Rhinatrema,* is completely unknown, but the single known species almost certainly has a larval stage. Other families of caecilians have species which exhibit various derived life history patterns such as direct terrestrial development and direct viviparous development.

DISCUSSION

Considering the 38 characters summarized in Table 1, there are 19 states which are unique to the Rhinatrematidae among caecilians. I view this fact as justification for affording familial status to this group.

The Rhinatrematidae and Ichthyophiidae share 11 ancestral character states and no derived states (Tables 1 and 2). Of these 11 shared ancestral states, 9 are also shared with at least one genus of one other family of caecilians. Hence the similarity between Rhinatrematidae and Ichthyophiidae reduces to two uniquely shared ancestral states: complete secondary annuli and a distinct tail. These few similarities are hardly justification for including these South American and Asian genera in a single family.

In the Rhinatrematidae, 30 of 38 characters are judged to be ancestral compared to 19 of 38 in the Ichthyophiidae. It appears, then, that rhinatrematids more closely resemble the

hypothetical common ancestor of all caecilians than does any other extant family.

Whereas rhinatrematids have 19 unique characteristics, ichthyophiids have none, considering the 38 characters of Table 1. This is because ichthyophiids share features with both the primitive rhinatrematids and the more advanced families and are, in my view, transitional between primitive and advanced caecilians.

The hypothetical ancestor of modern caecilians apparently was not a burrower, but rather a secretive surface form hiding by day in the loose litter of forest floors, under surface objects, and in preformed burrows; a life style similar in many ways to cryptic tropical snakes and salamanders (e.g., *Geophis, Oedipina*). This hypothetical ancestor resembled rhinatrematids, having a highly kinetic zygokrotaphic skull with a full complement of bony elements. There was a rather poorly developed tentacle and relatively large eyes. The mouth was terminal and

TABLE 1

SUMMARY OF CHARACTER STATES FOR TWO FAMILIES OF CAECILIANS

Character	Rhinatrematidae	Ichthyophiidae
1. Tentacle position	adjacent to eye[1,2]	forward of eye
2. Mouth position	terminal[1,2]	slightly subterminal
3. Secondary annuli	complete[1]	complete[1]
4. Annular shape	orthoplicate throughout[1,2]	orthoplicate caudally
5. Scales	present throughout[1]	may be reduced in size and number, or absent anteriorly
6. Tail	present[1]	present[1]
7. Premaxilla	distinct[1]	distinct[1]
8. Nasal	distinct[1]	distinct[1]
9. Septomaxilla	distinct[1]	distinct[1]
10. Prefrontal	fused to maxillopalatine or absent	distinct[1]
11. Postfrontal	fused to squamosal or absent	distinct[1]
12. Squamosal-frontal contact	no[1,2]	yes
13. Posterior squamosal notch to receive process of os basale	yes[2]	no[1]
14. Temporal fossa	yes[1]	no
15. Prevomer contact	separated posteriorly[1]	in contact posteriorly
16. Prevomers	short[1]	long
17. Parasphenoid shape	parallel-sided[1,2]	sides converge anteriorly

TABLE 1 (cont.)

Character	Rhinatrematidae	Ichthyophiidae
18. Orbitosphenoid	vertically oriented, does not project laterally to parasphenoid portion of os basale[1]	vertically oriented, does not project laterally to parasphenoid portion of os basale[1]
19. Pterygoid	distinct[1]	distinct[1]
20. Basipterygoid process	absent[2]	present (weakly developed)
21. Pterygoid-os basale contact	yes[1,2]	no
22. Stapes	present[1]	present[1]
23. Stapes-perforated	yes[1]	yes[1]
24. Stapes-quadrate articulation	loose[1]	loose[1]
25. Quadrate-maxillopalatine contact	yes[1,2]	no
26. Processus retroarticularis	short[1,2]	long
27. Processus retroarticularis	straight, horizontal[1,2]	curved dorsally
28. Ceratobranchial 4 of adults	absent[1,2]	present
29. Ceratobranchials 2 and 3	small (cb 3 missing in *Rhinatrema*)	large[1]
30. Larynx position	posterior of glossal skeleton[2]	between ceratobranchials 3 and 4
31. Musculus interhyoideus	inserts on processus retroarticularis[1]	inserts on connective tissue on side of neck
32. Anterior fibers of musculus interhyoideus insert on ceratohyal	yes[1,2]	no
33. Musculus interhyoideus posterior in two bundles	no[1]	yes
34. Musculi levatores mandibularum anteriores exposed dorsally above parietals, meet in midline	yes[1,2]	no
35. Musculus depressor mandibulae with longitudinal fibers	no[1,2]	yes
36. Musculus subarcualis rectus II	absent[2]	present[1]
37. Musculus subarcualis rectus III	absent[2]	present[1]
38. Larval stage	yes[1]	yes[1]

[1] ancestral state

[2] unique to this family among caecilians

TABLE 2

DISTRIBUTION OF CHARACTER STATES

	Rhinatrematidae	Ichthyophiidae
Number of ancestral states	30	19
Number of derived states	8	19
Number of unique states	19	0

the jaws were closed largely through the action of the powerful levator muscles (acting as a third-order lever), although the interhyoideus posterior muscles also helped to close the jaws ʰy pulling down on the modest retroarticular processes, thus effecting a first-order lever. The kinetic action of the lateral skull elements against the braincase was effected by the musculus levator quadrati. Eggs were laid in or beside streams and were perhaps attended by the female parent. A stream-dwelling aquatic larval stage was present.

Some descendants of these hypothetical ancestors evolved toward a more active, burrowing existence, although they never became highly specialized burrowers. The temporal fossae closed, adding solidity to the skull. At the same time the length and mass of the levator muscles were reduced and the lower jaws became recessed. As the mandibles shortened the retroarticular processes lengthened and curved dorsally, and the interhyoideus posterior muscles shifted in part to a longitudinal position and increased in size. The importance of these muscles in jaw closure was increased greatly. Although the skull had evolved towards stegokrotaphy, it remained partially kinetic, and the levator quadrati muscles persisted. The tentacles shifted forward of the eyes and at the same time the eyes were reduced in size and importance as sensory organs. Aquatic larval stages were retained. The foregoing approximately describes the ichthyophiid grade of organization.

Highly specialized burrowers evolved from these ichthyophiid-like ancestors. The skull became an efficient burrowing organ by fusion of the premaxillae and nasals into the nasopremaxillae and by loss of other elements. The skull became strongly stegokrotaphic and weakly kinetic. The lower jaw was greatly recessed, the eyes became vestigal or were lost, and the tentacles migrated even further anteriorly. Correlated with increased burrowing specializations, some forms completely abandoned the

aquatic environment by evolving direct terrestrial development or viviparity. Modern species of the family Caeciliidae characterize this grade of evolutionary development.

Although typhlonectids are fully aquatic, they apparently evolved from specialized burrowers as evidenced by their recessed jaws and jaw musculature, reduced number of skull bones, anteriorly disposed tentacles, vestigial scales and viviparous habit. Although there is a temporal fossa in typhlonectids, its form suggests secondary derivation, perhaps by paedomorphosis. Typhlonectids probably have a more recent common ancestor with caeciliids than with rhinatrematids or ichthyophiids.

The ancestry of scolecomorphids can hardly be guessed at because so little is known of their biology. Although they are highly specialized burrowers they seem remote from the Caeciliidae. Their full complement of skull bones suggests two possibilities: 1) independent derivation from an ichthyophiid-like ancestor, or 2) derivation from an early caeciliid-like ancestor with secondary derivation of independent skull bones and zygokrotaphy by retarded skull development. Although scolecomorphids are strongly zygokrotaphic with no fusion or loss of skull bones, the skull is akinetic, and the levator quadrati muscles and stapes have been lost (de Villiers, 1938). Thus it is apparent that although scolecomorphids are specialized burrowers, their skull is adapted for burrowing in a quite different way compared to caeciliids.

Ideally, taxonomists should consider distributional data only in an a posteriori fashion in determining relatedness. In the present case, it is clear that a distributional anomaly is removed by recognition of the great taxonomic distance between the Rhinatrematidae and Ichthyophiidae. If current concepts of plate tectonics are accurate, these South American and Asian forms have been genetically isolated since at least the beginning of the Cretaceous Period.

SUMMARY

A new family, Rhinatrematidae, has been erected to accommodate the South American gymnophionan genera *Epicrionops* and *Rhinatrema*. These genera were previously placed in the family Ichthyophiidae along with two Oriental genera, *Ichthyophis* and *Caudacaecilia*.

An analysis of 38 characters shows that the rhinatrematid genera differ considerably from the ichthyophiids. There are no shared derived states, and of the 11 shared ancestral states, only two are unique to both families.

Rhinatrematids are considered to be the most primitive of the recent caecilians, while ichthyophiids are thought to be transitional between primitive and advanced forms.

ACKNOWLEDGMENTS

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