ANATOMY OF *EOCAECILIA MICROPODIA,* A LIMBED CAECILIAN OF THE EARLY JURASSIC

FARISH A. JENKINS, JR.,[1] DENIS M. WALSH,[2] AND ROBERT L. CARROLL[3]

CONTENTS

Abstract. *Eocaecilia micropodia,* an Early Jurassic caecilian from the Kayenta Formation of northeastern Arizona, is structurally comparable to Recent gymnophionans in numerous aspects but also possesses characters that are primitive or appear to be uniquely derived. The skull of *Eocaecilia* exhibits such distinctively caecilian features as (1) a sulcus along the orbital rim indicating the presence of a tentaculum; (2) an os basale representing consolidation of the supraoccipital, exoccipital, basisphenoid, basioccipital, pleurosphenoid, and parasphenoid elements; (3) an internal naris posterior to the premaxillary–maxillary suture and medial to the tooth rows on the vomer and palatine; (4) enlarged nasal capsules; and (5) an olfactory eminence on the vomer. As in Recent caecilians, the lower jaw comprises a pseudodentary and pseudoangular that are joined along an elongate, oblique suture. The pseudoangular bears a robust internal process and an elongate retroarticular process. The teeth are bicuspid and pedicellate, but are minute in size and are more numerous than in most living caecilians.

Several features of the skull and lower jaw of *Eocaecilia* are unexpectedly divergent from the pattern known in Recent gymnophionans. The apparent

---

[1] Department of Organismic and Evolutionary Biology, and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. E-mail: fjenkins@oeb.harvard.edu.

[2] Department of Philosophy and Institute for the History and Philosophy of Science and Technology, University of Toronto, Toronto, Ontario M5S 1J5, Canada. E-mail: denis.walsh@utoronto.ca.

[3] Redpath Museum, McGill University, Montreal, Quebec H3A 2K6, Canada. E-mail: Robert.carroll@mcgill.ca.

Bull. Mus. Comp. Zool., 158(6): 285–366, August, 2007

fusion of the stapes and quadrate is unique. The obliquely oriented, more or less planar jaw joint would appear to provide little stability, and is thus structurally and functionally unlike that known in any other caecilian. The internal process of the lower jaw is very robust, and projects into the adductor chamber.

Eocaecilia also presents primitive and/or transitional features that might be expected in forms representing an intermediate stage in the development of a specialized life style. The skull retains separate jugal, quadratojugal, postparietal, and ?tabular (or ?supratemporal) bones, elements that in living forms are either co-ossified with adjacent bones or lost. The limb girdles and limbs of *Eocaecilia* are a primitive retention, but the reduction in their relative size would appear to be transitional toward the limbless, gymnophionan condition.

Elongation of the body in *Eocaecilia* is estimated to be comparable to that in primitive extant gymnophionans, but a precise comparison cannot be made because of uncertainty over the number of vertebrae. In general, the postcranial axial skeleton is relatively primitive. Intercentra are present. The parapophyses are not protracted as elongate processes, as in living forms, nor is there a pronounced longitudinal keel on the ventral aspect of centra. In contrast to the atlases of Recent caecilians, an interglenoid tubercle is present. Processes projecting from the internal walls of the neural canal of the atlas and at least the next four postatlantal vertebrae represent attachment points for a suspensory ligament of the spinal cord. Such processes have not been previously reported in living caecilians but are now known to be present in representatives of various families (ichthyophiids, typhlonectids, and caeciliids). Neural spines are absent in the postatlantal and dorsal regions, as in living caecilians. Haemal arches are present in the tail, and distal caudal vertebrae bear posterodorsally recurved neural processes, as in rhinatrematids.

Although our knowledge of caecilian evolution and diversity now extends into the Early Jurassic, *Eocaecilia micropodia* does not provide sufficient evidence to securely recognize the origin of gymnophionans among known Paleozoic amphibians. The discovery of an operculum in *Eocaecilia micropodia* is novel confirmatory evidence that the opercular apparatus is a character shared with other lissamphibians. The absence of a separate operculum in extant gymnophionans may be hypothesized to relate to the loss of the shoulder girdle and the muscular link between the girdle and operculum. Nonetheless, a substantial morphological and temporal gap still intervenes in the identification of caecilian origins. Lissamphibia still remains at best a crown group concept, without a securely rooted stem in the Paleozoic.

INTRODUCTION

Fossil caecilians are sparsely represented in the geological record. Initially known only from an isolated vertebra from the Paleocene of Brazil (Estes and Wake, 1972), subsequent finds—vertebrae from the Paleocene of Bolivia (Rage, 1986) and the Cretaceous of Sudan (Evans et al., 1996; Werner, 1994) and the Miocene of Columbia (Hecht and Laduke, 1997)—offered scant evidence with which to probe the evolutionary history of the group. More recently, Evans and Sigogneau-Russell (2001) described the fragmentary remains of a primitive caecilian, *Rubricacaecilia monbaroni,* from the Lower Cretaceous of Morocco, adding further perspective on the Mesozoic record of caecilians. With fossil caecilians so rare, the discovery of *Eocaecilia micropodia* from the Early Jurassic Kayenta Formation of northeastern Arizona (Jenkins and Walsh, 1993) was particularly significant. This earliest known caecilian, abundantly represented by numerous cranial and postcranial specimens, possesses a number of features, including intercentra and limbs, which are primitive for the order but unknown in living representatives. Our descriptive account documents Early Mesozoic caecilian diversity in terms of characters that are clearly plesiomorphic, as well as features that are autapomorphic for gymnophionans.

In this study, we provide detailed documentation of the skull and postcranial skeleton of *Eocaecilia micropodia,* making anatomical comparisons with major features of Recent caecilians as well as with those few fossil forms that are known. We explore several specializations of *E. micropodia* in a functional context and finally consider the phylogenetic significance of this taxon in relation to current interpretations—and uncertainties—regarding the evolutionary history and relationships of caecilians.

The taxonomic terms “Apoda” and “apodans,” used in reference to extant taxa as a group (cf. Trueb and Cloutier, 1991), is preoccupied (Dubois, 2004; Duellman and Trueb, 1986) and has been abandoned in this account. We follow the suggestion of Frost et al. (2006) that “Gymnophiona”

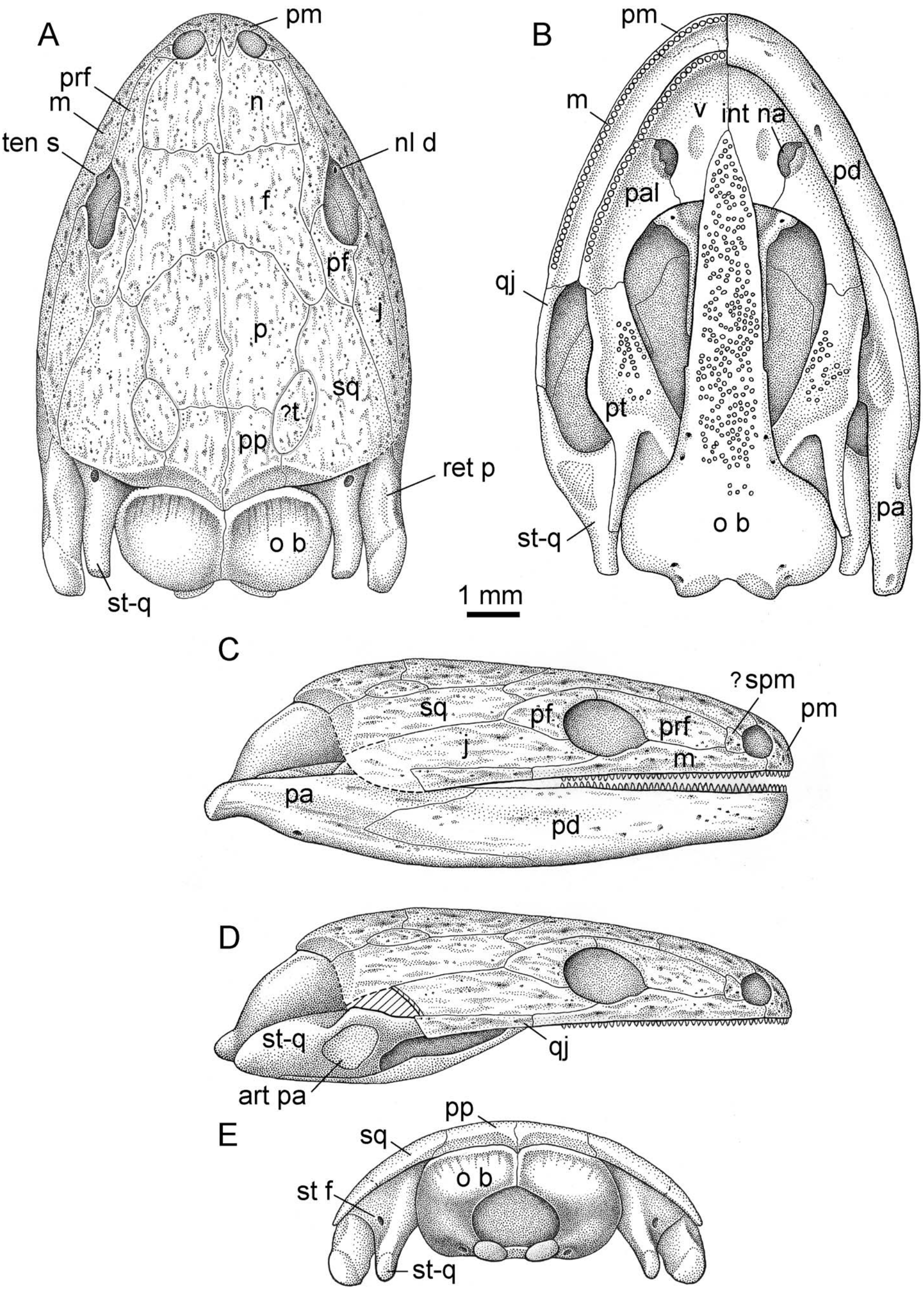


Figure 1. Reconstruction of the skull of *Eocaecilia micropodia* in (A) dorsal, (B) ventral, (C, D) lateral, and (E) occipital views. Major features, including size and general proportions, are based on the type (MNA V8066), but some details have been drawn from other specimens (MCZ 9169, 9015; MNA V8059, 8062). Postmortem compaction of the skulls renders the lateral and occipital views less reliable than the dorsal and ventral reconstructions. In D, the posterior end of the jugal (hatched area) has been truncated to reveal the dorsal margin of the stapes-quadrate.

be restricted to extant, limbless caecilians but do not adopt their proposed systematic reordering in face of incomplete results and ongoing analyses referred to in their work. We employ "caecilian" as an appropriate term for gymnophionans and their fossil relatives.

MATERIALS AND METHODS

Eocaecilia micropodia is represented by 40 specimens. Only two specimens are of more or less complete skulls with articulated lower jaws, but both have been subjected to postmortem compaction and fracturing. Nine specimens represent partial skulls (with or without lower jaws) in various stages of disarticulation, and six specimens are of isolated mandibles. Ten specimens are primarily postcranial: vertebrae, both in isolation and in short, articulated series; disarticulated appendicular elements; or both. The remainder of the collection consists of variably complete associations of cranial and postcranial bones. All of the material derives from a single locality, a quarry at Gold Spring (35°45′35″N, 111°04′51″W), approximately 300 m WSW of Gold Spring, Adeii Eechii Cliffs, Coconino County, Arizona, USA, in the silty facies of the Lower Jurassic Kayenta Formation. The Kayenta fauna, which also includes the anuran *Prosalirus bitis,* is probably at least Pleinsbachian in age if not slightly older (Shubin and Jenkins, 1995; Jenkins and Shubin, 1998). A complete list of the specimens is provided in the Appendix.

The jaw musculature of *Ichthyophis glutinosus* was studied by R.L.C. by frontal and sagittal serial sections and through dissections of preserved specimens prepared by David Dilkes. Bemis et al. (1983) discuss the diverse terminology of caecilian jaw muscles in the literature, reflecting perspectives that varied from morphological description to determination of homology. The present account follows the nomenclature of Lakjer (1926; also employed by Säve-Söderbergh, 1945), who based his identifications on the relationships of muscles to the branches of cranial nerve V, which are readily established in all living amphibian groups. Other descriptions of caecilian jaw muscles have commonly used the terminology of Edgeworth (1935), which differs significantly from that now broadly applied to all groups of terrestrial vertebrates, e.g., Carroll and Holmes (1980) for frogs and salamanders, Rieppel (1980) for squamates, and Bramble (1978) for mammals.

Institutional Abbreviations

FMNH	Field Museum of Natural History, Chicago, Illinois
LSUMZ	Louisiana State University Museum of Zoology, Baton Rouge, Louisiana
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MNA	Museum of Northern Arizona, Flagstaff, Arizona

Abbreviations Used in Figures

Id	dorsal branch of the olfactory tract
Iv	ventral branch of the olfactory tract
II	optic nerve
V	trigeminal nerve
V_1	ophthalmic division of V
V_2	maxillary division of V
V_3	mandibular division of V
VII	facial nerve
AME	adductor mandibulae externus
AMI	adductor mandibulae internus
AMI(pr)	deep head of the adductor mandibulae internus (profundus)
AMI(su)	superficial head of the adductor mandibulae internus (superficialis)
AMP	adductor mandibulae posterior
AMP(lg)	adductor mandibulae posterior longus
art	articular facet
art pa	articular facet for pseudoangular
art pt	articular facet for pterygoid

art pt pal	articulation between pterygoid and palatine
art qu pt	articulating surface for quadrate ramus of pterygoid
art st-q	articular facet for stapes-quadrate
at	atlas
b cul pr	basin on the dorsal surface of the cultriform process
bp	basipterygoid process
c f	foramen for the carotid artery
cor f	coracoid foramen
cul pr	cultriform process
DM	depressor mandibulae
ect	ectopterygoid
ex n	external naris
f	frontal
fb	fibula
fe	femur
f im	intramandibular foramen
f o	fenestra ovalis
g pt m	groove for pterygoideus muscle
gl	glenoid
gr art sph	groove for articulation with the sphenethmoid
gr pt m	groove for pterygoideus muscle
h	humerus
h a	haemal arch
ic	intercentrum
IH	interhyoideus
IHP	interhyoideus posterior
IM	intermandibularis
int na	internal naris
int p	internal process
j	jugal
j f	jugular foramen
lat tr	lateral (labial) tooth row
LQ	levator quadrati
m	maxilla
med t r	medial (lingual) tooth row
m f	mandibular (adductor) fossa
mp	maxillopalatine
mta	metatarsal
n	nasal
nl d	nasolacrimal duct
o b	os basale
o c	otic capsule
o con	occipital condyle
op	operculum
o r	otic ridge for contact with skull roof
orb	orbit
p	parietal
pa	pseudoangular
pal	palatine
p con	processus conchoides
pd	pseudodentary
?pel	possible pelvic element
pf	postfrontal
ph	phalanges
p i p	internal process of pedicle
pl	pleurosphenoid
pm	premaxilla
pp	postparietal
pr	parietal ridge
prf	prefrontal
pt	pterygoid
PT	pterygoideus muscle
q	quadrate
qj	quadratojugal
q r pt	quadrate ramus of the pterygoid
r	rib
rad	radius
ret p	retroarticular process
sc	scapulocoracoid
sph	sphenethmoid
spm	septomaxilla
?spm	possible septomaxilla
sq	squamosal
st	stapes
st f	stapedial foramen
st-q	stapes-quadrate
?t	?tabular
tb	tibia
ten	tentacle
ten o	tentacular opening
ten s	tentacular sulcus
u	ulna
v	vomer
ver	vertebra
ver cd	caudal vertebra(e)
ver d	doral vertebra(e)
ver patl	postatlantal vertebra
v f	vascular foramen
v s	vomerine sulcus

DESCRIPTION

Skull

The skull of *Eocaecilia micropodia* was recognized by Jenkins and Walsh (1993) as sharing a suite of features that are distinctively caecilian, including a well ossified, compact skull roof, a tentacular sulcus, and a large retroarticular process on the lower jaw. The skull appears to have been relatively low, as in most modern caecilians, but all specimens have been dorsoventrally crushed to a variable degree. In dorsal view (Fig. 1A), the most conspicuous feature is the extension of the braincase behind the posterior margin of the skull roof; as a consequence, the jaw articulation is situated in a relatively anterior position (Fig. 1D). The orbits are large compared with those in most Recent caecilians but are small relative to those in Paleozoic tetrapods of similar body size (e.g., gymnarthrids, goniorhynchids, and amphibamids). The mouth, which Jenkins and Walsh (1993) reconstructed as only slightly subterminal, is here reconstructed with essentially no premaxillary overhang, in contrast to the subterminal condition typical of gymnophionans. The skull table and cheek are a continuous bony shield, as in some Recent caecilians.

Evidence of variation in skull size is modest. The length and width of the type (MNA V8066, Figs. 2–4), which is the most complete and least distorted specimen, are 12.7 and 8 mm, respectively. Length was determined in the midline from the tip of the rostrum to a line transversely tangential to the occipital condyles and is equivalent to Lessa and Wake's (1992) measurement 5 in their morphometric study of *Dermophis mexicanus*. Width was determined from the most broadly separated points on the sides of the skull; this measurement approximates but is not exactly equivalent to "skull width at jaw articulation," measurement 3 of Lessa and Wake (1992, appendix 1; incorrectly labeled as "40" on fig. 1). Estimates of other skull lengths and widths are 13.5 and 8.2 mm (MCZ 9169, Fig. 5) and 9.8 and 7.2 mm (MCZ 9015), respectively. The skull of MNA V9346 (Fig. 11) is 14 mm in length but does not permit a reliable measure of width. MNA V8062 (Fig. 8) is too incomplete to provide a direct linear estimate of length, but on the basis of the dimensions of the frontal bone, the skull would appear to have been comparable in size to that of the holotype.

No single specimen shows all elements, but nearly all of the dermal skull can be reconstructed by comparing and compiling structural data from the following specimens: the type specimen, MNA V8066 (Figs. 2–4), a nearly complete skull prepared in dorsal and ventral views; MCZ 9169 (Fig. 5), most of a skull exposed in dorsal view; MCZ 9015 (Fig. 13A, B), a nearly complete skull exposed in dorsal and ventral aspects; MNA V8059 (Fig. 7), exhibiting palate, jaws, both stapes-quadrates, and the underside of the skull roof; MNA V8062 (Fig. 8), a right antorbital region; and MNA V9346 (Fig. 11, a palate and lower jaws in ventral view.

Further study of the material since Jenkins and Walsh's (1993) initial description has resulted in some modifications to the previously interpreted pattern of dermal bones. In some cases, a coating of Glyptal applied to the external surface of the skull roof illuminated narrow, pigmented bands on either side of barely visible sutures. The new findings are the presence of distinct postparietals and ?tabulars/?supratemporals; concrete evidence for the presence of both a postorbital and a postfrontal in the circumorbital series is lacking.

Skull Roof. Almost all of the bones that ancestrally compose the amphibian skull roof are present. In contrast to all Recent caecilians, the skull in *Eocaecilia micropodia* retains the postparietal, jugal, quadratojugal, and ?tabular/?supratemporal; the last three are evident in the type. The sculpturing of the bones indicates that the dermis was firmly adherent to the skull roof, as in Recent taxa.

Postparietals are not readily apparent in the type specimen and were not recognized as distinct elements by Jenkins and Walsh (1993). However, separate postparietals are evident in MCZ 9169 (Fig. 5), in which they are suturally delineated from surrounding bones. Once observed in this specimen, the presence of postparietals in the holotype was detected through an application of the Glyptal technique described above, which revealed the sutural lines separating parietals from postparietals. Similar bands became evident along both sides of the sutures separating parietals and frontals and at the anterior margin of the frontal in the type, but not in other specimens, in which the bones are more coarsely sculptured. In most modern caecilians (e.g., in *Ichthyophis glutinosus,* Fig. 6A), the parietals are longer than the frontals, as would be expected if they incorporated the area that was originally formed by the postparietals. The postparietals exhibit a slightly recessed area of smooth bone surface posteriorly, which was presumably covered by an anterior extension of the dorsal trunk musculature, as is the case in living caecilians.

An irregular, inconsistently shaped bone lies in the position of a tabular or supratemporal in Paleozoic tetrapods. This element, which we tentatively interpret as a ?tabular (Figs. 1, 2, 5, 7), appears to have been relatively loosely articulated with adjacent dermal bones, overlying ventral lappets of the surrounding bones without being suturally interdigitated. In the type (Fig. 2), the right tabular is close to a normal position, but the left has slipped over the left side of the os basale. The left tabular is also displaced posteriorly in MCZ 9169 (Fig. 5). The posterior margin of the tabular is not complete in any specimen, obviating the possibility of determining whether this bone reached the posterior margin of the skull, as is the case in most Paleozoic tetrapods.

The large squamosal, best preserved in MNA V8059 (Fig. 7), forms much of the cheek region. The great width of the squamosal suggests that it probably reached the postparietal, posterior to the tabular. The smooth, thickened medial margin would appear to have abutted the parietal and tabular by a squamous suture in which the adjacent bony margins are reciprocally beveled (rather than by serrate interdigitation). The articular relationship between the squamosal and dermal skull roof in *Eocaecilia micropodia* thus is comparable to that in many stegokrotaphic gymnophionans in which the squamosal is attached to the skull roof by a sutural ligament; the ligament in some taxa is so broad that an apparent "gap" appears on dried skulls. In none of the specimens of *E. micropodia* is the posterolateral portion of the squamosal sufficiently well preserved in dorsal view to determine the configuration of the occipital margin or show the area from which the depressor mandibulae originates in Recent caecilians. The anterior extremity of the squamosal narrows to an acute terminus between the frontal and postfrontal.

In *Eocaecilia micropodia,* the ventral part of the cheek is formed by a large jugal, which extends rostrad to form the posteroventral margin of the orbit, and a long, slender quadratojugal (Figs. 1C, D, 2). In Recent caecilians, a separate quadratojugal is not known to be retained in the adults of any species; thus, the squamosal extends to the inferior margin of the skull. Peter (1898) proposed that the quadratojugal of *Ichthyophis glutinosus* has been incorporated into the quadrate as an anteriorly projecting, laminar process, an interpretation that was adopted by de Villiers (1936) and Visser (1963). In a developmental study of two species of *Epicrionops,* Reiss (1996) identified the "quadratojugal process" as a feature appearing late in ontogeny but presented no evidence for its derivation from a quadratojugal. Studies of *Dermophis mexicanus* by Wake and Hanken (1982) and *Gegeneophis ramaswamii* by Müller et al. (2005) concluded that the quadratojugal is absent. The interpretation of Marcus et al. (1935: 411) that a quadratojugal ("quadratomaxillare") anlagen is

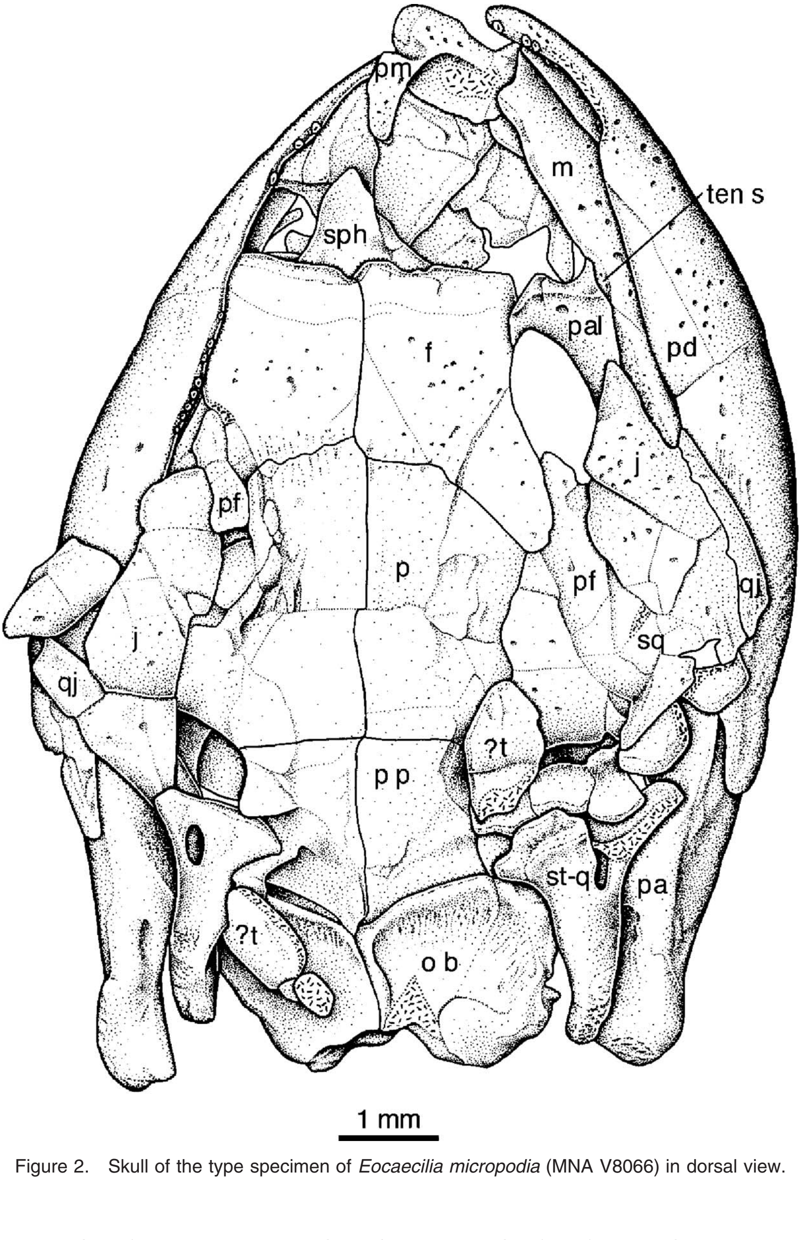


Figure 2. Skull of the type specimen of *Eocaecilia micropodia* (MNA V8066) in dorsal view.

present during development is rendered moot by the observations of Wake and Hanken (1982: 211), who noted several sources of possible error, in addition to the inclusion of different genera in a "single" growth series. Thus, at best, the evidence for the retention of a quadratojugal vestige in living caecilians is equivocal; yet, there is no doubt that a distinct quadratojugal persisted as the posterolateral marginal element of the dermal skull roof until at least the Jurassic.

The large, rectangular nasal, most clearly preserved on the left side of MCZ 9169 (Fig. 5), is incised rostrally at the premaxillary articulation. The nasals are missing

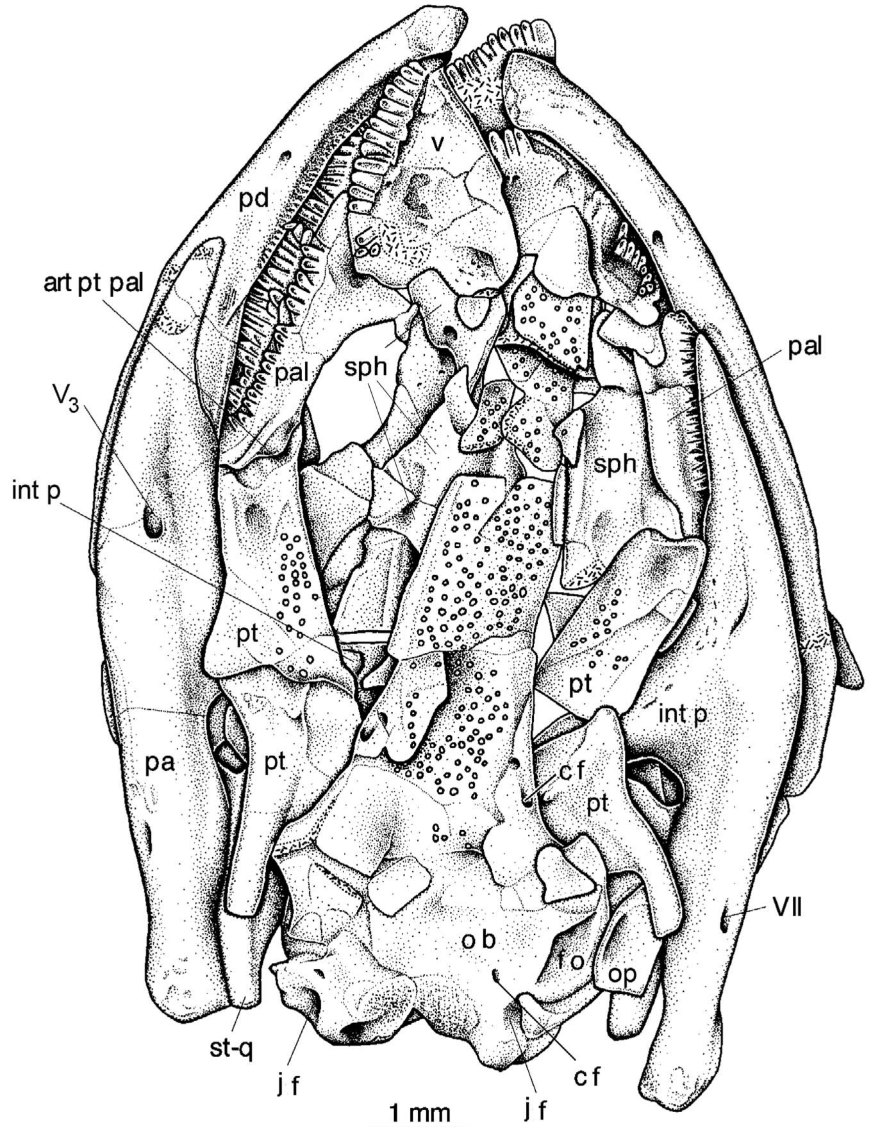


Figure 3. Skull of the type specimen of *Eocaecilia micropodia* (MNA V8066) in ventral view. Both pterygoids (pt) have been broken transversely by postmortem crushing against the adjacent internal process (int p) of the pseudoangular; in life, each internal process projected into the adductor chamber above the level of the pterygoids.

in the type (Fig. 2) and on the right side of MCZ 9169 (Fig. 5), suggestive evidence that they might have been only loosely attached to the frontals.

The long, rectangular prefrontal, best preserved in MNA V8062 (Fig. 8), extends from the midpoint of the dorsal orbital rim to the narial margin. A prefrontal is present in the Ichthyophiidae, Uraeotyphlidae, and Scolecomorphidae, but the bone has been lost or become incorporated into the maxillopalatine in other taxa (Nussbaum and Wilkinson, 1989).

The configuration of the posterior or-

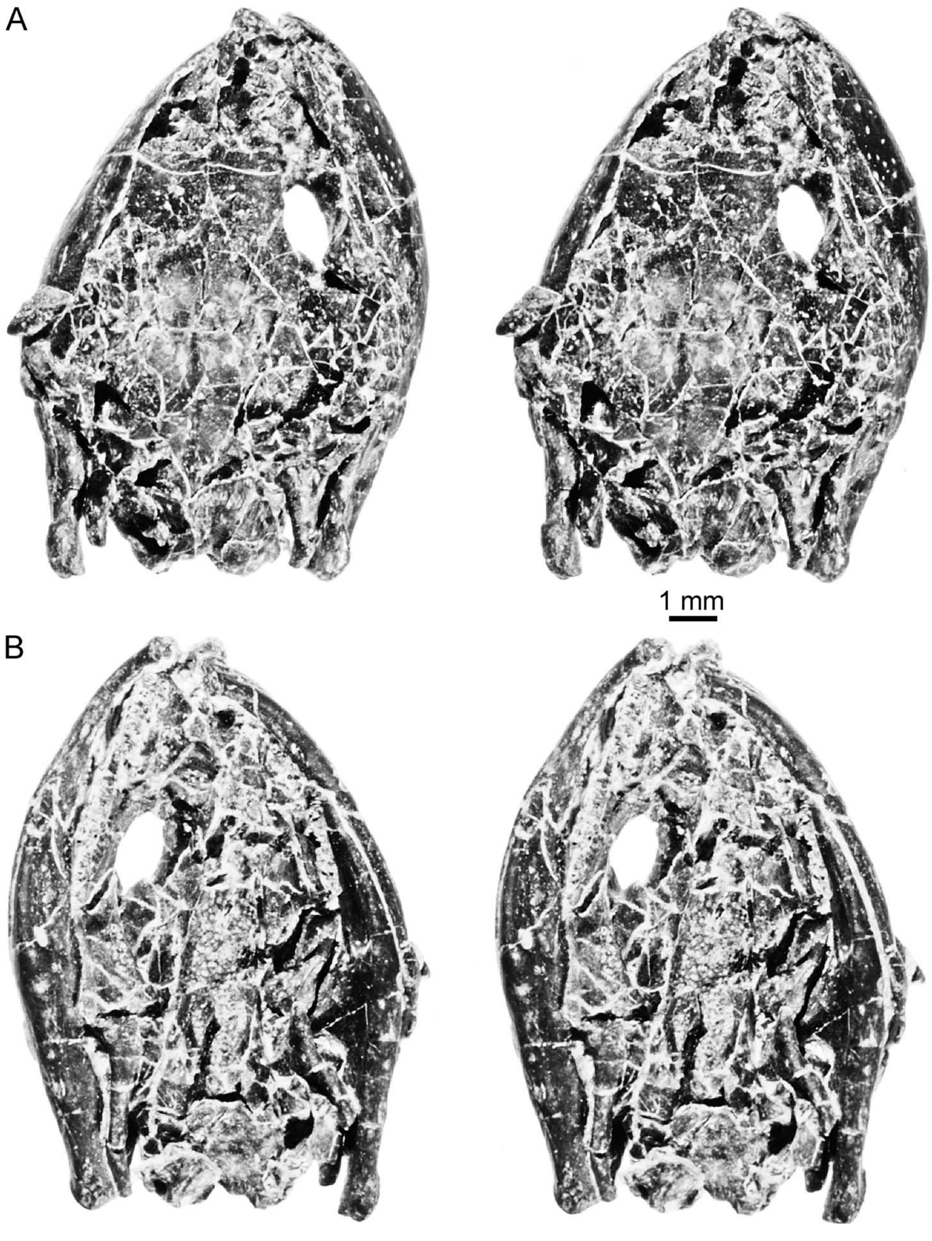


Figure 4. The skull of the type specimen of *Eocaecilia micropodia* (MNA V8066) in (A) dorsal and (B) ventral views (stereophotographs).

bital margin in *Eocaecilia micropodia* is somewhat equivocal because all specimens are to some degree damaged in this area. In most Paleozoic tetrapods two bones—a postfrontal and a postorbital—contribute to the posterior orbital margin. Jenkins and Walsh's reconstruction (1993, fig. 2b) of *E. micropodia* depicted both bones, an interpretation based primarily on the right side of the holotype (Fig. 2) where there

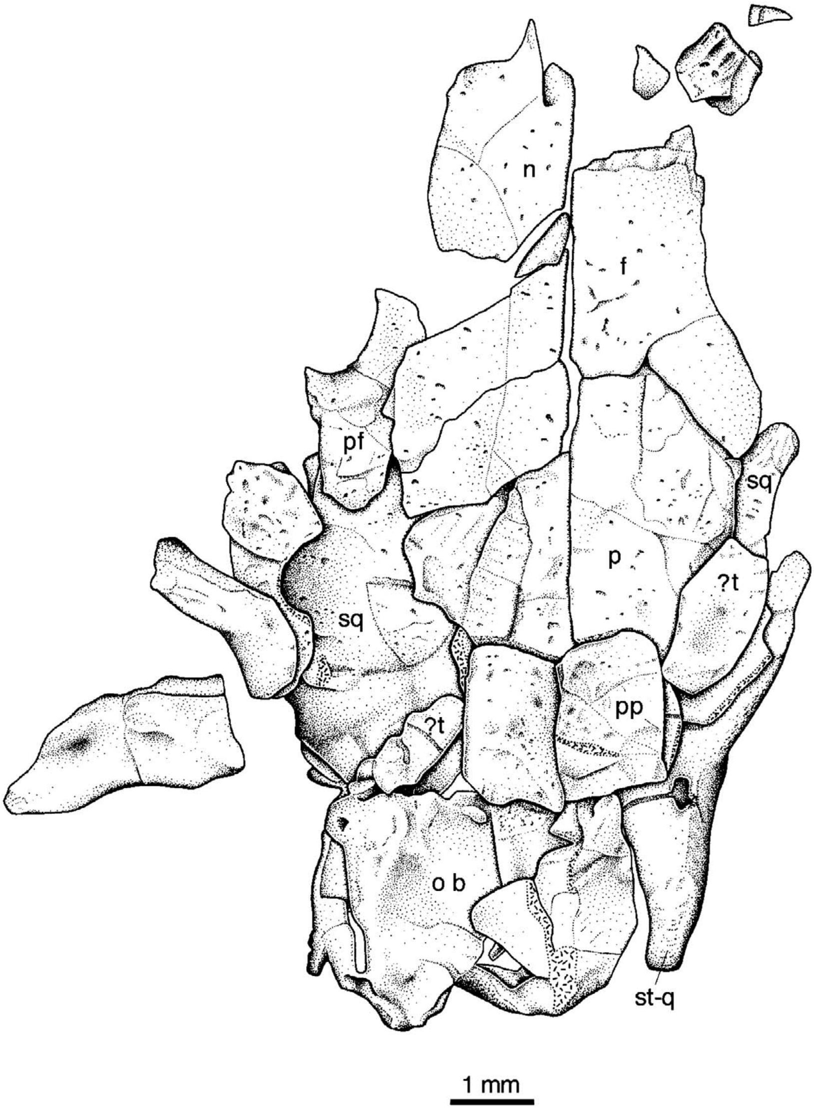


Figure 5. *Eocaecilia micropodia,* dorsal view of the skull of MCZ 9169. Left stapes-quadrate has been removed (see Fig. 20). On the right side, the stapes-quadrate is intact and nearly in its natural position, exposing much of the dorsal and lateral surface. The posterior portion of the bone was removed from the left side so that it can be viewed in all aspects, but the anterior extremity was not complete.

appears to be two elements. Both have been displaced ventrally by crushing, and the adjoining margins are sufficiently obscured that it is not possible to determine definitively whether there are two bones separated suturally or a single element fractured longitudinally. Several other skulls, however, provide evidence that favors the latter interpretation. The left side of MCZ 9169 (Fig. 5) shows only a single bone composing the posterodorsal margin of the orbit. Similarly, but a single element forms the posterodorsal orbital margin in MNA V8059 (Fig. 7); on the left side are

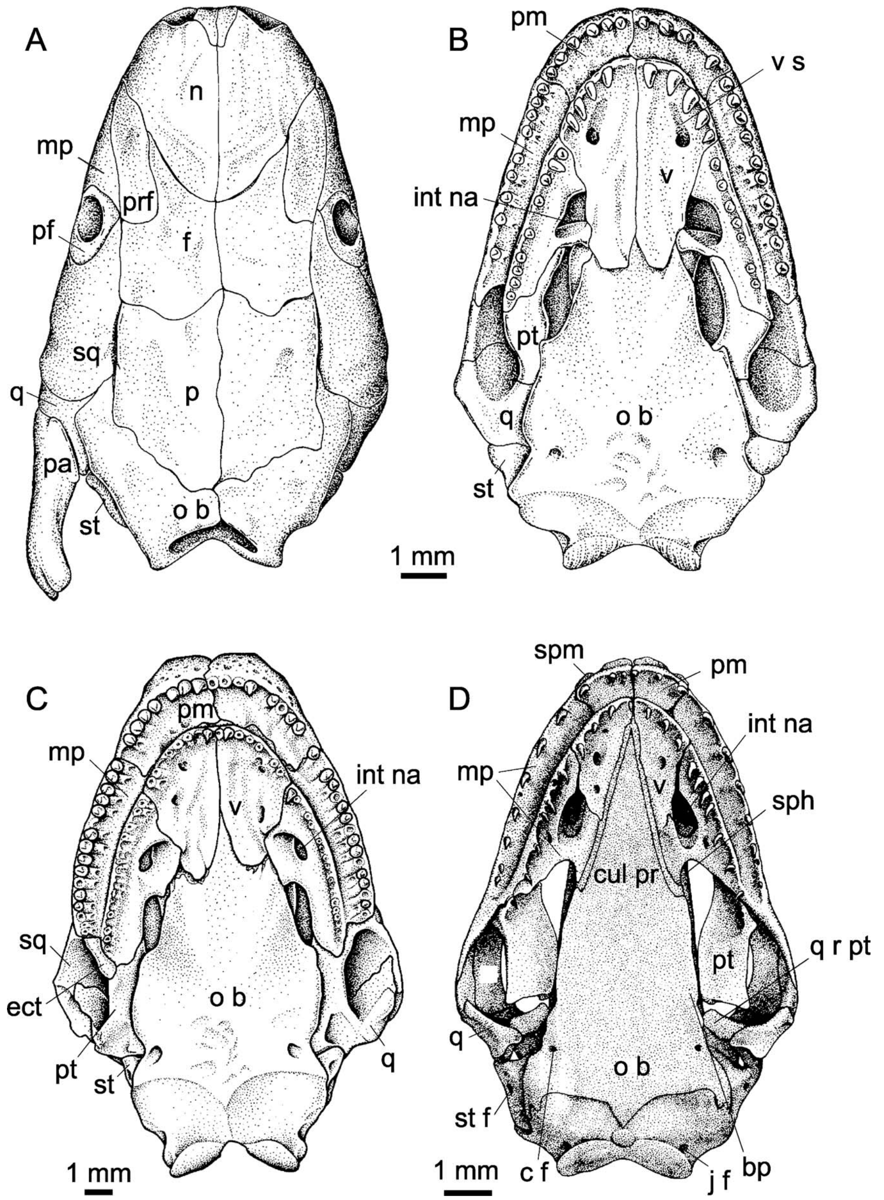


Figure 6. Skull roof and palate of gymnophionans. (A) Skull roof of *Ichthyophis glutinosis.* (B) Palate of *Ichthyophis glutinosis.* (C) Palate of *Gymnopis multiplicata* (FMNH 189131). (D) Palate of *Epicrionops petersi.* Plates A and B drawn are rendered from photographs in Taylor, 1969; plate D is reproduced from Nussbaum (1977, fig. 1).

part of the jugal and a maxillary fragment, and on the right, a sutural contact with the prefrontal is preserved. Cognizant of the limited evidence and the lack of a complete orbital margin, we nonetheless favor the interpretation that *E. micropodia* possessed only a single postfrontal/postorbital element. No living caecilian possesses two elements in this region. Representatives of only two families (Ichthyophiidae, Uraeo-

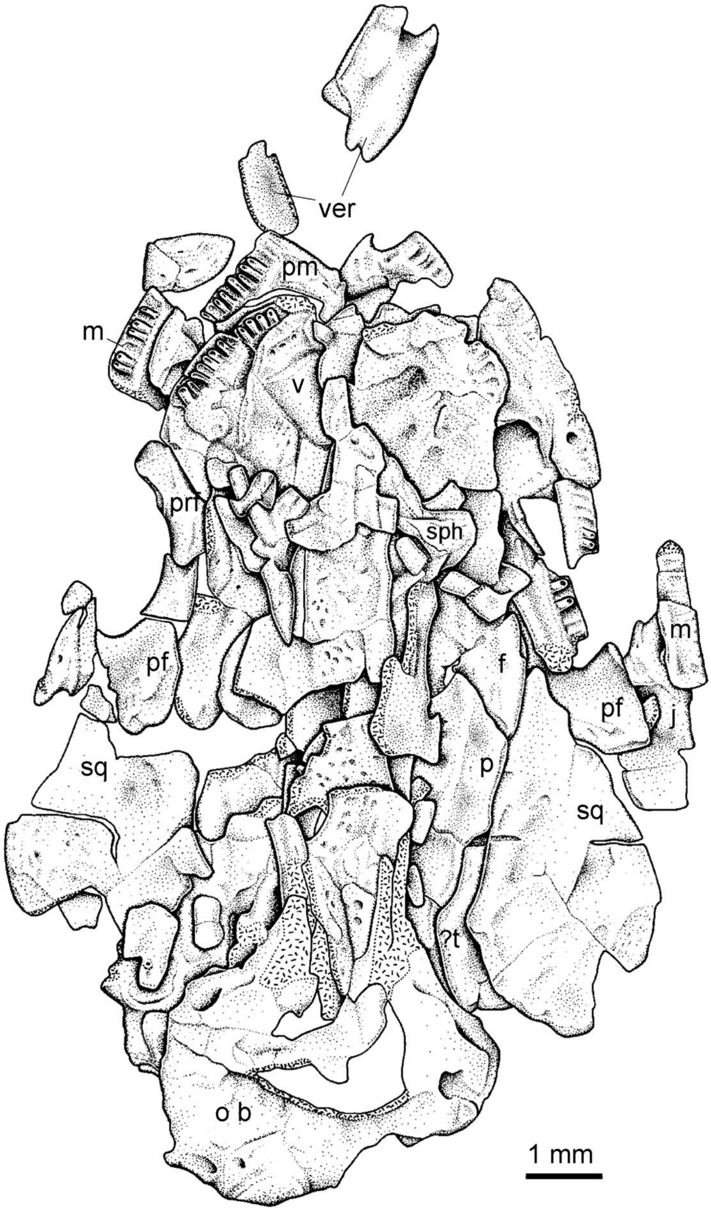


Figure 7. *Eocaecilia micropodia,* MNA V8059, ventral view of the skull roof and palate.

typhlidae) possess a putative postfrontal, which could be distinct or partially or entirely fused to the maxillopalatine (Nussbaum and Wilkinson, 1989). The "postfrontal" of living caecilians is thus a conventional designation for the single ossification that nearly encircles the eye (cf. *Ichthyophis glutinosus,* Fig. 6A; *Uraeotyphlus narayani,* Nussbaum, 1979, fig. 1), occupying the circumorbital margin that in *E. micropodia* is formed by the prefrontal, postfrontal, and jugal bones.

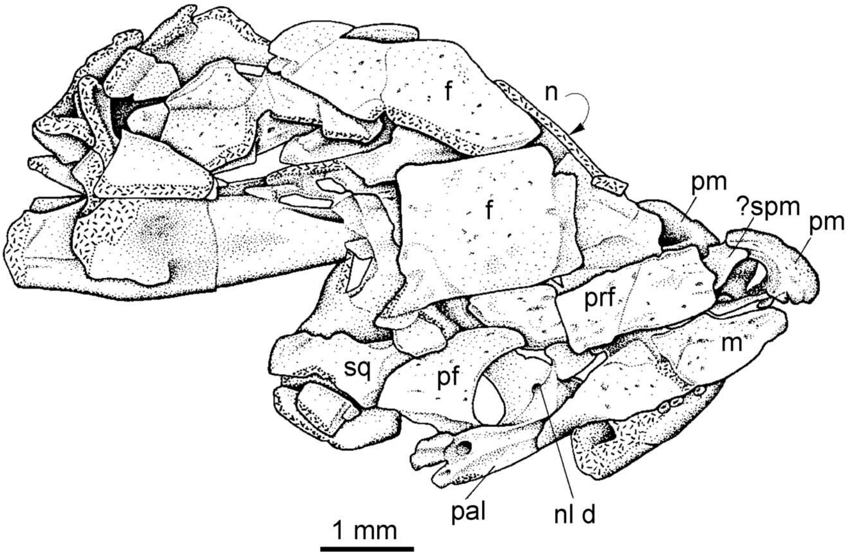


Figure 8. *Eocaecilia micropodia,* MNA V8062, dorsolateral view of a partial skull of which only the anterior part is preserved.

The lacrimal bone presents the most equivocal case for interpretation of any of the skull roof elements. In the only specimen for which the lateral surface of the antorbital region is articulated (MNA V8062, Fig. 8), there appears to be a narrow triangular space between the posterior portion of the prefrontal and maxilla that might have been occupied by a lacrimal. Although a lacrimal is not known in the adult of any Recent caecilian, a separate element in the nasal region of embryonic *Ichthyophis glutinosus* was identified by Peter (1898, fig. 20) as a turbinale (= lacrimal). Similarly, Marcus et al. (1935, fig. 5) identified a lacrimal in their reconstruction of a 68-mm embryo of *Grandisonia alterans* (cf. Wake and Hanken, 1982, table 1). Wake and Hanken (1982), however, found no evidence of a separate lacrimal ossification center in their study of *Dermophis mexicanus*; in view of their cautionary assessment of the evidence presented by Marcus et al. (1935) for multiple ossification centers (including that for the quadratojugal, postparietal, periorbital, ectopterygoid, and interparietal), the fate of the lacrimal in caecilian history must be regarded as unresolved.

The premaxilla, which does not appear to overhang the lower jaw as it does in many Recent caecilians, has a long posterodorsal process that fits into a slot in the nasal and a very narrow extension that occupies a groove along the anterodorsal margin of the maxilla. As is the case for almost all specimens of upper and lower jaws, the crowns of the teeth have disarticulated postmortem from the pedicels; only in the premaxilla of MNA V9346 do a few crowns appear to be preserved in situ. The premaxilla in MNA V8059 (Fig. 7) bears approximately 10–12 tooth positions (10 as actual pedicels and 2 as spaces wide enough to accommodate a pedicel). The pedicels are formed as elongate, narrow tubes that are fused to the inside of the jaw margin. The diameter of premaxillary pedicels was measured with an optical micrometer on specimens in which individual pedicels are well preserved. Four pedicels on MNA V8059 have diameters of 0.10, 0.12, 0.13, and 0.13 mm. One premaxillary pedicel on MNA V9346 has a diameter of 0.14 mm, and an adjacent (disarticulated) tooth crown measures 0.12 mm in basal diameter and 0.22 mm in apicobasal height.

Our present interpretation of the septomaxilla in *Eocaecilia micropodia* differs from that originally proposed (Jenkins and Walsh, 1993, fig. 2b) and is based on a displaced bone in a single specimen (Fig. 8). The bone might have contributed to the posterior margin of the narial opening, as in the case in some extant caecilians. A septomaxilla is present in ichthyophiids, rhinatrematids, uraeotyphlids, and scolecomorphids but is absent as a separate element in typhlonectids and caeciliids (Nussbaum, 1977, 1979; Taylor, 1969; Wake, 2003).

The maxilla is a long, narrow bone that contributes to the anteroventral margin of the orbit for a short distance. The most completely preserved maxilla is on the right side of the type (Fig. 2), but the inferior margin and maxillary teeth are obscured by the overlying, displaced lower jaw. No specimen shows the entire maxillary tooth row. The number of maxillary teeth is probably in the range of 32–39, an estimate based on the length of the maxilla in the type (4.9 mm) and the number of pedicels per millimeter on maxillary fragments of other specimens. Pedicels per millimeter varied from 6.5 on a left anterior maxillary fragment of MNA V9346 to 8 in a right anterior maxillary fragment of MNA V8059 (seven well-preserved maxillary pedicels on the latter specimen range from 0.1 to 0.13 mm in diameter, with a mean of 0.11 mm). Intermediate values of 7.5 were measured from other maxillary fragments (MCZ 1956, MNA V8059, and MNA V8062).

In contrast to Recent caecilians, the maxilla is not fused to the palatine; a suture delineating the adjacent borders of these bones is clearly preserved in MNA V8062 (Fig. 8). The margin of the maxilla that borders the anteroventral rim of the orbit is incised by a shallow, broad sulcus in both the type of *Eocaecilia micropodia* (Fig. 2) and in MCZ 9156 (Figs. 9, 10C). The sulcus is confluent with a comparably smooth depression in the adjacent palatine. We interpret this feature as marking the course of the tentacle as originally proposed by Jenkins and Walsh (1993). Early ontogenetic development of the tentacle in *Dermophis mexicanus* is in close association with the eye, from which various components of the tentacular apparatus are coopted (e.g., the Harderian gland, extraocular muscles and nerves, and lacrimal ducts, among others; Billo and Wake, 1987; Wake, 1992). Although the tentacle in most living caecilians passes through an aperture that is separate from the orbit (Fig. 10A), in rhinatrematids the tentacular opening is not separate (Fig. 10B) but is merely “a small longitudinal slit” along the anterior margin of the orbit (Nussbaum, 1977: 7). In fossil caecilian material, the presence of a tentacular apparatus could only be inferred with certainty if a separate tentacular foramen were present, but the slight depression of the orbital margin in *E. micropodia* (Fig. 10C) is at least consistent with the expected primitive position of this organ.

Sculpturing of the Skull Roof. Most cranial specimens of *Eocaecilia micropodia* possess a shallow rugosity on the superficial surface of the dermal bones comparable to that developed in some larger, extant caecilians (e.g., *Gymnopis* spp.). The skull of the type specimen also exhibits small, scattered foramina (Fig. 2). These foramina, which distribute nerves and nutrient vessels, are most numerous on the bones surrounding the orbit and adjacent to the jaw margins, as in living species (Taylor, 1969), but also occur sporadically on the bones that border the midline of the skull roof.

Palate. The palate of *Eocaecilia micropodia* demonstrates that basic features retained among extant caecilians were acquired by the Jurassic, in contrast to the pattern of dermal bones of the skull, which is only modestly altered from that common among Paleozoic amphibians. A principal feature is a continuous row of teeth that spans each vomer and palatine, paralleling the row on the premaxilla and maxilla (Figs. 1B, 3, 7). The most complete series of pedicels is preserved on the right side of the type (MNA V8066, Fig. 3) where the vomer and palatine each bear approximately 17 teeth. In this series, nine well-preserved palatal pedicels selected for measurement range in diameter from 0.1 to 0.14 mm (mean 0.12 mm) and are comparable in size to those on the maxilla and premaxilla measured from other specimens. On MNA V8059, five pedicels that could be measured range from 0.11 to 0.15 mm in diameter (mean 0.13 mm). A series of 13 pedicels on the vomer of MCZ 9242 (Fig. 12) is the most perfectly preserved palatal row available with which to assess detailed geometry. All the pedicels are slightly oval in cross section, with the labiolingual axis slightly longer than the mesiodistal axis. Labiolingual axes range from 0.14 to 0.18 mm (mean 0.17 mm), whereas mesiodistal axes range from 0.12 to 0.14 mm (mean 0.135 mm). The height of the pedicels ranges from 0.35 to 0.37 mm. Lingual to and between the 11th and 12th pedicel in this series is an inverted tooth crown (circular in cross section, with a diameter of 0.1 mm).

The distance between the premaxillary–maxillary and vomerine–palatine tooth rows varies among extant caecilians, being relatively narrowly separated in species of *Ichthyophis* and well separated in species of *Caecilia* (Taylor, 1969). Direct assessment of this feature in *E. micropodia* is precluded by the fact that, in all specimens with an intact palate, the lower jaws remain in position, concealing the most lateral part of the palate and the premaxillary–maxillary tooth row. However, in view of the close juxtaposition of the tooth rows of the lower jaw, the separation of the palatal and marginal rows was probably only slightly greater (for further analysis, see *Lower jaw*).

The vomers meet anteriorly along a median suture for about half their length. Posteriorly, the medial margins of the vomers are separated by the relatively broad rostral end of the cultriform process of the parasphenoid component of the os basale, which intervenes to complete the bony palate in this area (Fig. 1B). The degree to which the cultriform process is exposed between the recessed medial margins of the vomers in *Eocaecilia micropodia* would appear to be intermediate between the extremes observed in extant caecilians (cf. Trueb, 1993: 275, table 1; Wake, 2003). In the rhinatrematid *Epicrionops petersi* (Fig. 6D), the vomers meet rostrally only along a very short suture; the cultriform process is extensively exposed between them. In ichthyophiids (Fig. 6B) and many other caecilians, by contrast, the vomers are united for nearly their entire length along the median suture. Intraspecific variations can also be substantial, as in *Gymnopis*; in *G. multiplicata* (Taylor, 1969, fig. 34), the vomers are separated for almost their entire length, whereas in *G. multiplicata proxima* (Fig. 6C; see also Taylor, 1969, fig. 35), the vomers are united for more than half their length.

In most Recent caecilians, the vomer is pierced by a large foramen (in some cases two) anteromedial to the internal naris (Taylor, 1969). In *Ichthyophis glutinosus* (Fig. 6B), this opening provides passage for the palatine branch of the facial nerve (VII) and a vein from the snout and dorsal surface of the palate; a rostrocaudally aligned neurovascular sulcus leads to the foramen's palatal opening. In *I. glutinosus,* the vomerine foramen and sulcus on the palatal surface correspond in position to a ridge on the dorsal surface of the vomer; this ridge, the olfactory eminence (Fig. 14A), divides the large nasal sacs into medial and lateral cavities (Badenhorst, 1978, fig. 9; Schmidt and Wake, 1990). Although there are no large vomerine foramina in *Eocaecilia micropodia,* numerous small foramina are variably developed on the bone's palatal surface. A consistent feature is a sulcus on the palatal surface of the vomer, anteromedial to the internal naris.

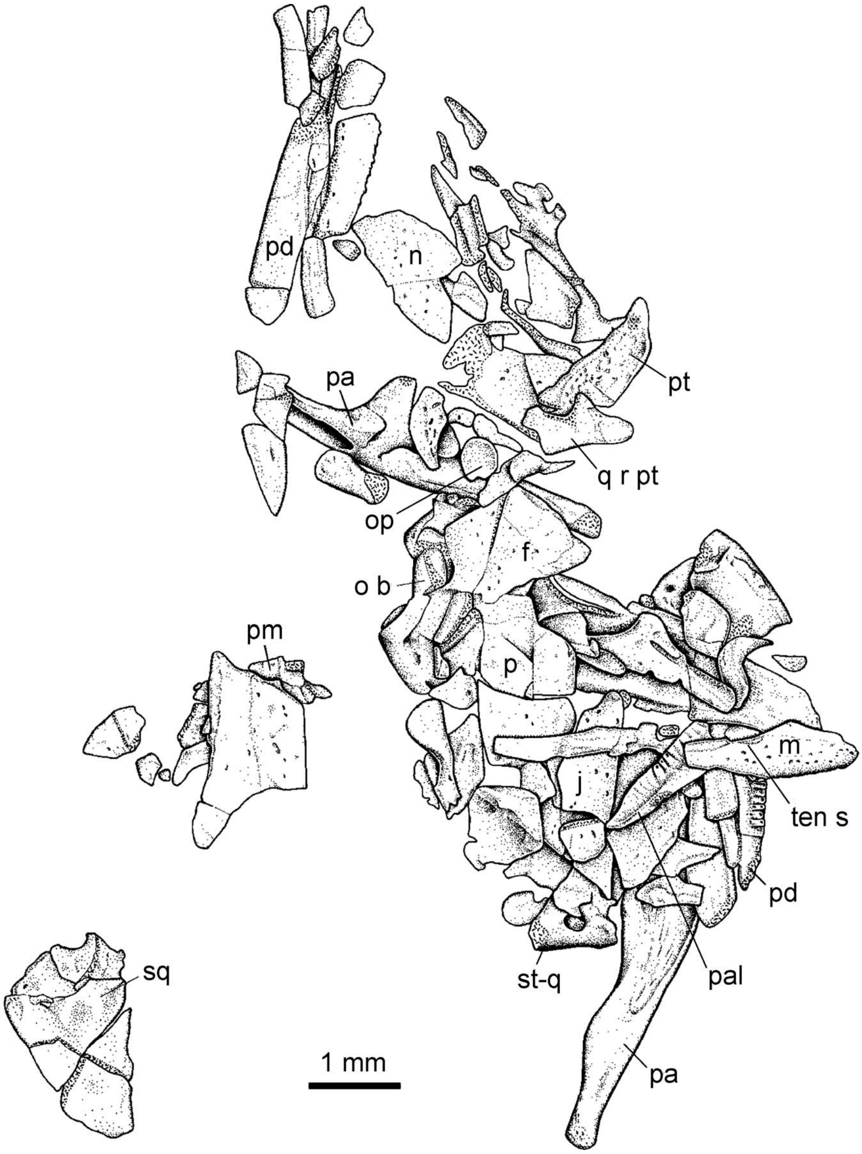


Figure 9. *Eocaecilia micropodia,* MCZ 9156, the disarticulated elements of a skull. For details of the maxilla (m) and tentacular sulcus (ten s), see Figure 10C.

The depression is evident on both vomers of MNA V9346 (v s, Fig. 11) and on the single vomer present in MCZ 9242 (Fig. 12). The corresponding elevation of the dorsal surface of the vomer might possibly represent an olfactory eminence (cf. Fig. 14A).

The internal nares of *Eocaecilia micropodia* open medial to the internal row of teeth, rather than adjacent to the suture between the maxilla and premaxilla as in most Paleozoic tetrapods. Both the vomer and palatine contribute to the margin of the internal naris, a condition that is com-

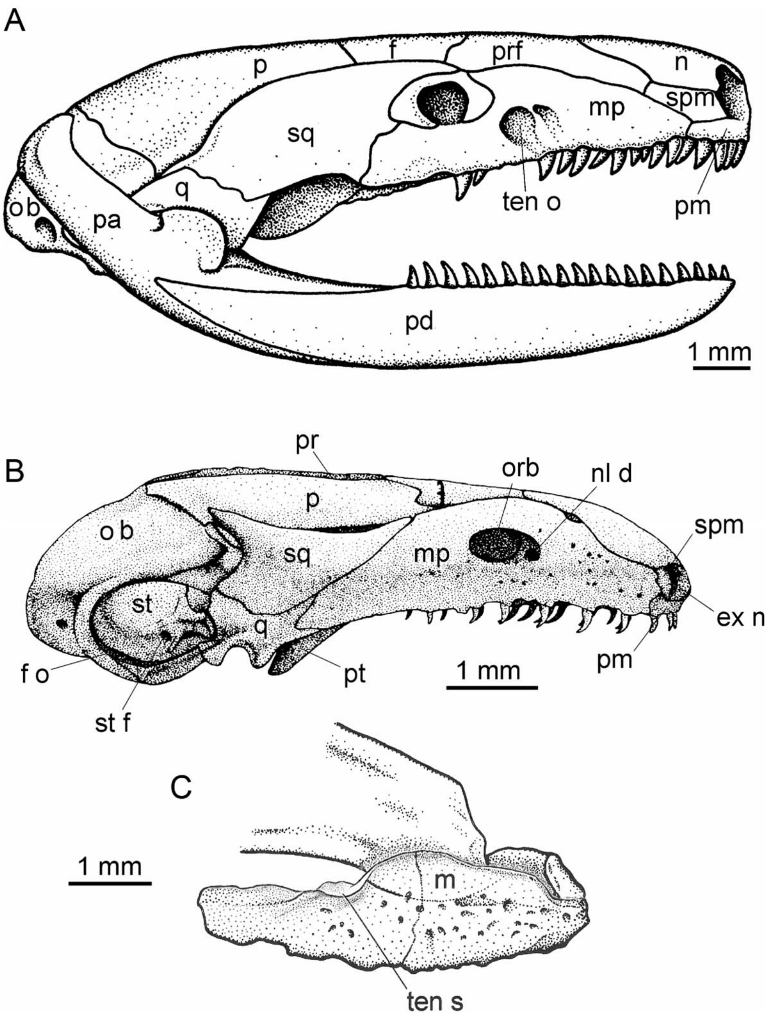


Figure 10. (A) A skull and lower jaw of *Ichthyophis glutinosus* (skull drawn from Taylor, 1969, fig. 2; lower jaw drawn from Sarasin and Sarasin, 1887–1890, pl. 15, fig. 3). (B) Lateral view of the skull of *Epicrionops petersi* (reproduced from Nussbaum, 1977, fig. 1). (C) A right maxilla of *Eocaecilia micropodia* (MCZ 9156) exhibiting a tentacular sulcus (ten s).

mon to representatives of all extant families: rhinatrematids (*Epicrionops,* Nussbaum, 1977, fig. 1), ichthyophiids (*Ichthyophis,* Taylor, 1969, figs. 2–7; Wake, 2003), uraeotyphlids (*Uraeotyphlus,* Nussbaum, 1979, fig. 1; *Uraeotyphlus narayani,* Wake, 2003, fig. 6B), scolecomorphids (*Crotaphatrema, Scolecomorphus,* Nussbaum, 1985, figs. 1, 4; *Scolecomorphus uluguruensis,* Wake, 2003, fig. 6E), caeciliids (*Caecilia, Oscaecila, Herpele,* Taylor, 1969, figs. 17–26, 42; *Oscaecilia ochrocephala,* Wake, 2003, fig. 9H; *Herpele,* Wake, 2003), and typhlonectids (*Typhlonectes, Potamotyphlus,* Taylor, 1969, figs. 12–14; *Typhlonectes natans,* Wilkinson and Nussbaum, 1997, fig. 9C). A few caeciliids exhibit an apparently derived condition in which the internal narial opening is completely surrounded by the palatine (maxillopalatine) (e.g., *Dermophis parviceps, Geotrypetes seraphini,* Taylor, 1969,

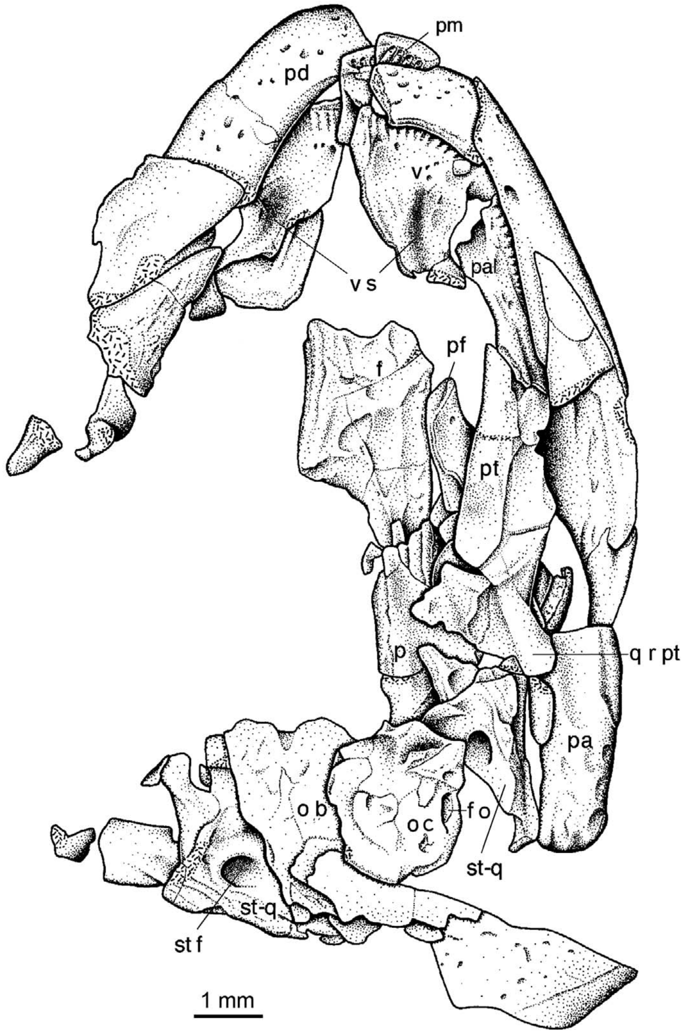


Figure 11. *Eocaecilia micropodia,* MNA V9346, ventral view of the palate, both stapes-quadrates and lower jaws.

figs. 30, 40, 41; *Dermophis mexicanus,* Wake and Hanken, 1982, fig. 2b; *Geotrypetes seraphini,* Wake, 2003, fig. 8E). In other species of *Dermophis,* however, both the vomer and palatine contribute to the narial margin (*D. glandulosus, D. occidentalis,* Taylor, 1969, figs. 31, 32). In various species of *Siphonops,* the internal naris is either variably bordered by the vomer and palatine or completely enclosed by the palatine (Taylor, 1969, figs. 36–39; Wake, 2003).

The pterygoid of *Eocaecilia micropodia* (Figs. 1, 3), together with the palatine and vomer, contributes to the relatively primitive configuration of the palate as a broad plate that laterally borders large interpterygoid vacuities. The articulation between the pterygoid and palatine, which is evident in the holotype where the two bones have partially separated from one another (Fig. 3), appears to have been composed of simple, overlapping surfaces. Both the quadrate ramus and the ascending process of the pterygoid are preserved in MNA V9346 (Fig. 11). The elongate quadrate ramus has an extensive articulation with a sulcus on the inferior surface of the stapesquadrate. In contrast to the condition in Recent caecilians, the quadrate ramus appears to have extended well posterior to the jaw articulation (cf. Figs. 1B, 3). Both the palatal ramus of the pterygoid and the parasphenoid component of the os basale are covered with pedicellate denticles. As reconstructed, the rostrocaudal length of the pterygoid in *Eocaecilia micropodia* is approximately half of the length of the skull, which is longer than in most (if not all) extant caecilians (see Taylor, 1969). Although a separate pterygoid persists in rhinatrematids and ichthyophiids, in typhlonectids and caeciliids the bone is ordinarily fused either to the quadrate or maxillopalatine (Nussbaum, 1977) or, in the case of scolecomorphids, possibly present only as a vestige (*Scolecomorphus vittatus,* Nussbaum, 1985, fig. 4) or lost altogether (*Crotaphatrema bornmuelleri,* Nussbaum, 1985, fig. 1; cf. Brand, 1956, for *Scolecomorphus uluguruensis*).

An ectopterygoid could not be identified in *Eocaecilia.* Nussbaum and Wilkinson (1989: 32) noted that a small "ectopterygoid" [sic] is present in some extant caeciliids. In *Gymnopis multiplicata* (Fig. 6C) and *Grandisonia alternans* (Taylor, 1969, figs. 34, 47), for example, this small bone forms the anteromedial palatal margin of the adductor chamber. Slight disarticulation of most skulls of *E. micropodia* has disrupted the palatal margins of the adductor chamber; in a few more intact specimens, the associated lower jaw is compacted against the region in which an ectopterygoid might be expected. The coronoid eminence, although low, extends anteriorly to approximately the midpoint of the jaw's length; if an ectopterygoid were present, the bone would have probably been much reduced in size so as not to impinge upon the coronoid eminence during jaw closure.

Os Basale. The braincase of *Eocaecilia,* as in all Recent caecilians, is constructed from two components: the os basale posteriorly and the sphenethmoid anteriorly. As in other caecilians, the os basale of *Eocaecilia* is a single bone that has been interpreted to represent a consolidation of ossification across a large area primitively occupied by separate bones (supraoccipital, exoccipitals, basioccipital, basisphenoid, pleurosphenoid, and parasphenoid). This massive element, which incorporates the otic capsules (presumably formed from the fusion of the prootic and opisthotic) as well as posterior elements of the endochondral braincase, is represented by numerous specimens (Figs. 2–5, 7, 11, 12, 15). In the holotype, the maximum width of the os basale, measured across the otic capsules, is estimated to be 3.5 mm; the estimated maximum length of the bone, which includes the cultriform process, is 10.4 mm.

Dorsally, the os basale has a sutural junction with the postparietals and forms a roof over the most posterior portion of the braincase and otic capsules; as in Recent caecilians, a median suture divides the two halves of the braincase above the foramen magnum (cf. Figs. 1, 2; Taylor, 1969). The dorsal surface of each half of the os basale in this region is slightly concave and bears fine, longitudinal striae, features that represent the attachment of epaxial muscles. A low ridge delineates the boundary between the skull's dorsal roof and occipital surface.

A complete occiput is represented only in the holotype, but certain details (such as the size and shape of the foramen magnum and the relative position of the occipital condyles) are distorted or obscured by postmortem compaction. Protuberant occipital condyles are preserved in two specimens (Figs. 13A, B, 15A, B, 16). The facets for the atlas are oval, slightly convex, face medially and slightly ventrally, and appear to have been situated ventral to the foramen magnum. A jugular foramen is present at the base of the occipital condyle (Fig. 3), closely approximating the ar-

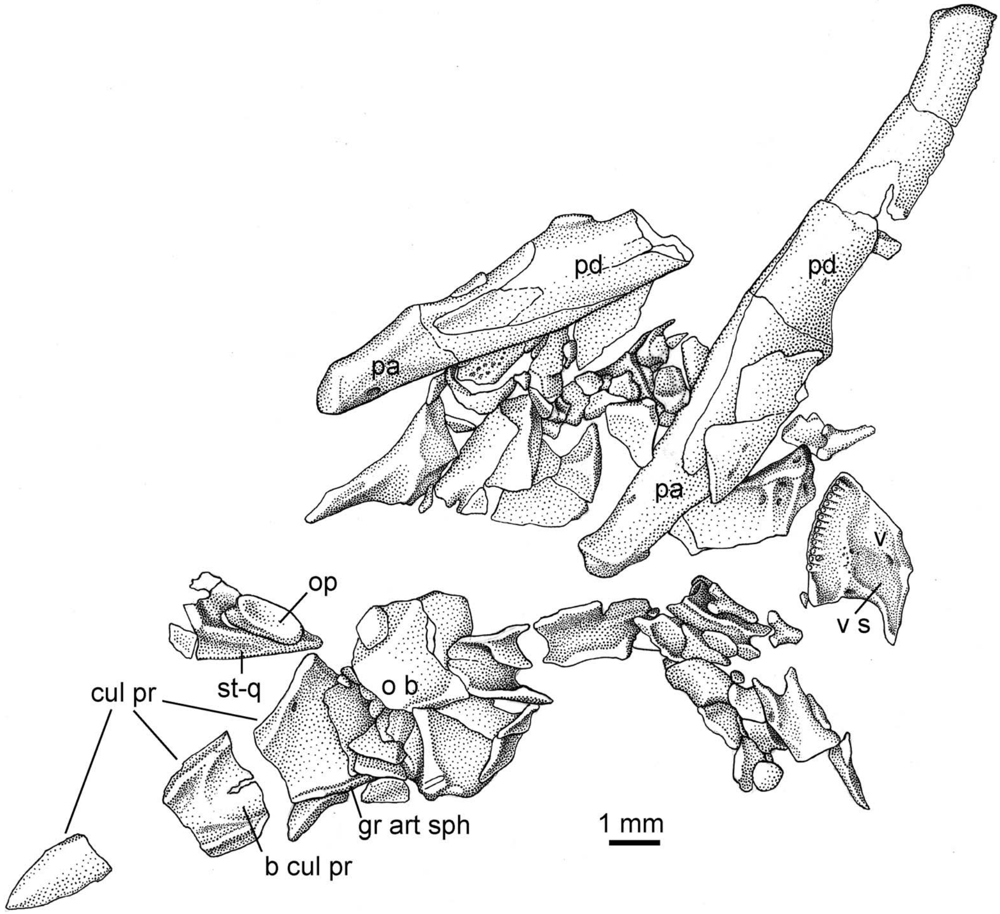
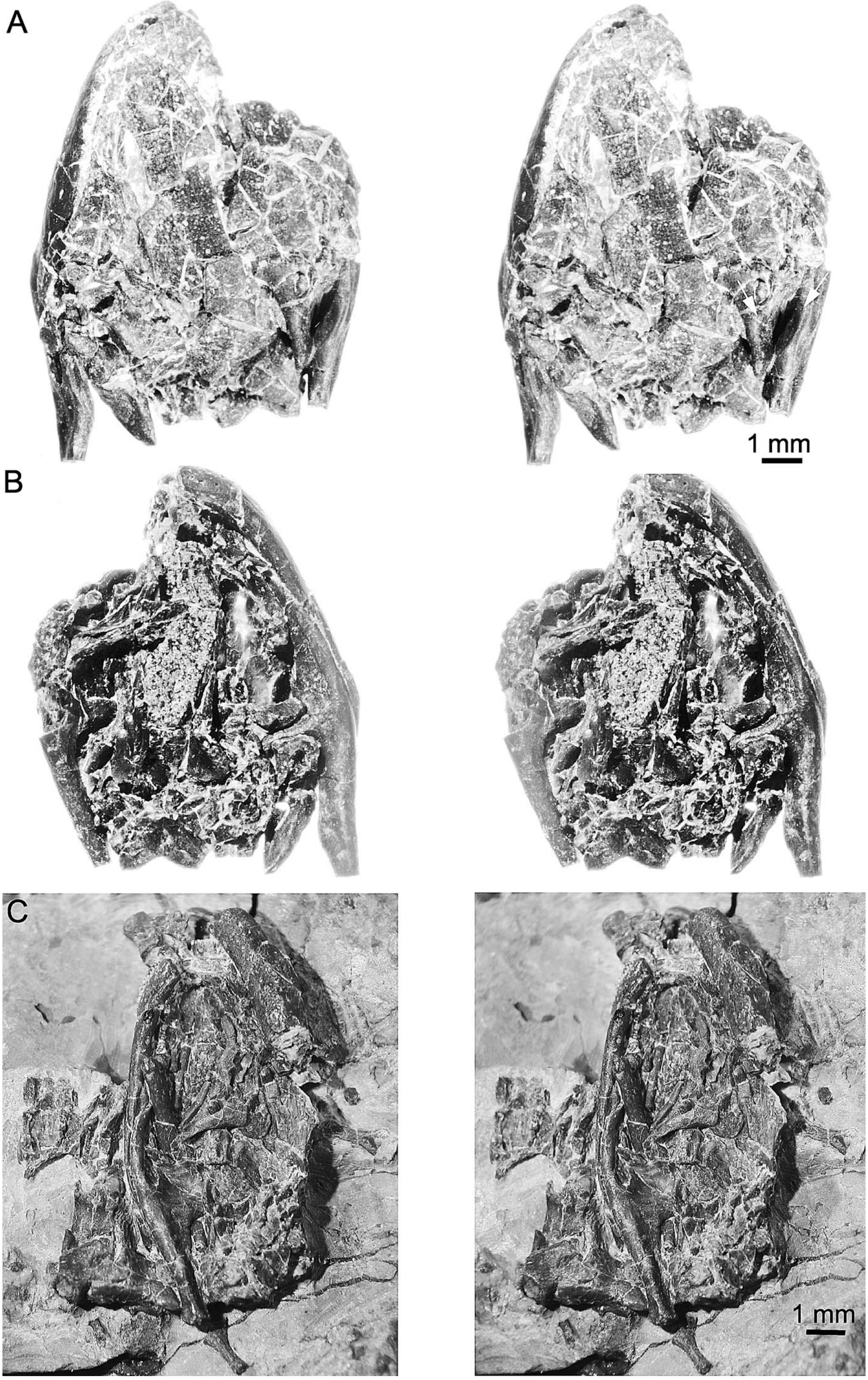


Figure 12. *Eocaecilia micropodia,* MCZ 9242, disarticulated elements of skull.

rangement in most modern forms. Slightly anteroventral to the jugular foramen is a small carotid foramen.

The ventral portion of the os basale incorporates the parasphenoid and is configured accordingly: posteriorly broad in the region of the otic capsules and anteriorly narrow in the region representing the cultriform process (Figs. 1B, 3). At the anterior border of the otic capsule, where the os basale narrows abruptly, one might expect to find a basicranial articulation with the pterygoid (as is common in Recent caecilians, Fig. 18E); no such articulation is discernible in *Eocaecilia* (Figs. 15A, 16, 17). The dorsal surface of the area representing the cultriform process bears a groove adjacent to the lateral margins for the articulation of the sphenethmoid (gr art sph, Fig. 12). The dorsal surface of the os basale is also marked by three depressions. The largest of these extends from the posterior margin of the braincase rostrally to the posterior terminus of the grooves for the sphenethmoid. At the rostral end of the depression is an elevated, hemicircular margin set transversely across the cultriform process that defines a very shallow basin (b cul pr, Fig. 12). Anterior to this depression are two additional shallow fossae, one on each side of the midline.


A
1 mm
B
C
1 mm

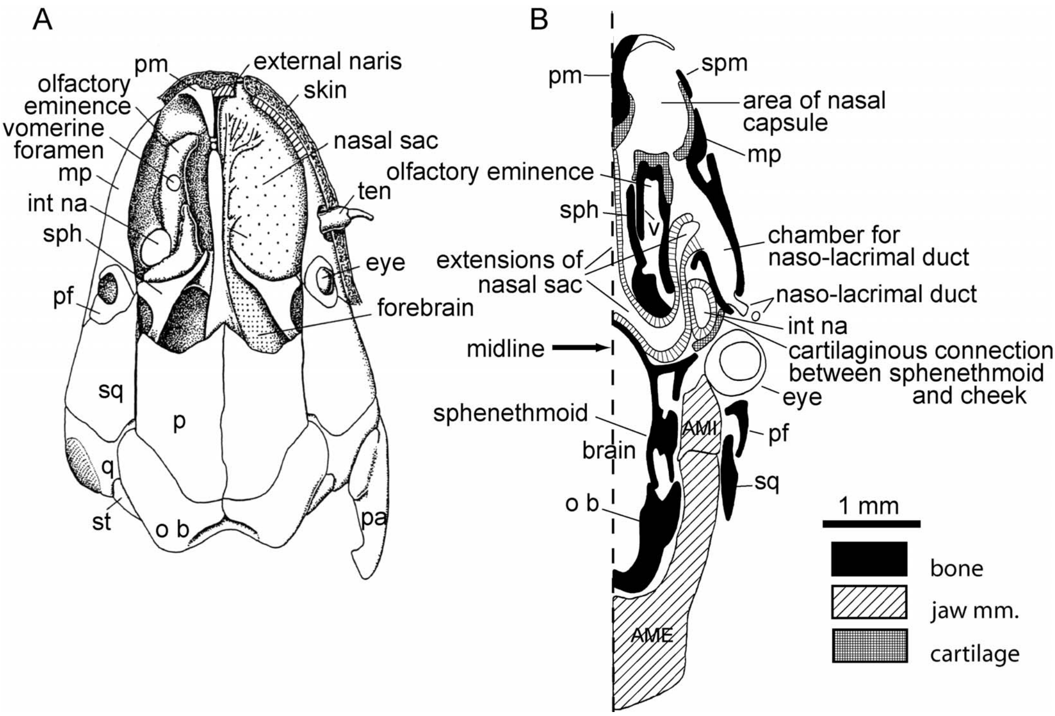


Figure 14. (A) The head of *Ichthyophis glutinosis* (FMNH 121528) in dorsal view, with skin and bones removed to reveal the extent of the nasal apparatus. The openly stippled area on the right side indicates the extent of the entire nasal sac. The finely stippled area indicates the forebrain and dorsal olfactory tract. On the left side, the nasal sac has been removed to expose the dorsal surface of bones underlying the nasal apparatus. (B) The head of *Epicrionops petersi* (LSUMZ 27324) in horizontal section (right side) to show the elaboration of nasal sac contents. The cartilages surrounding the area adjacent to the external nares are comparable in position and relative size to the entire nasal capsule in frogs, salamanders and Paleozoic amphibians.

The lateral aspect of the os basale, and specifically the otic capsule, is appressed to the massive stapes-quadrate; therefore, the structure of the capsule is best revealed by specimens in which the stapes-quadrate is missing or was removed (Figs. 15A–C, 16). An anterolaterally descending ridge marks the line of sutural contact with the skull roof (o r, Fig. 17A). The otic capsule of MNA V8063 is estimated to be approximately 2.0 mm in length and 1.6 mm in height. The lateral face of the otic capsule is dominated by a large fenestra ovalis which, in MNA V8063, is 1.4 mm in length and 0.6 mm in height. In MCZ 9169, the fenestra is irregularly oval in shape (length 1.7 mm; height 0.8 mm). The inferior margin is a gently convex, slightly thickened flange demarcating a narrow boundary between the external and internal surfaces of the capsule. The superior and posterior margins of the fenestra are broadly rounded, and the transition from the external to internal surface is more gradual.

The os basale bears a number of prominent foramina, the largest of which is lo-

---

←

Figure 13. The skull of *Eocaecilia micropodia (*MCZ 9015) in (A) dorsal and (B) ventral views (stereophotographs). The jaw articulation between the stapes-quadrate and pseudoangular (arrows) is shown in the dorsal view. The ventral view reveals the extensive field of pedicels on the cultriform process. (C) A partial skull of *Eocaecilia micropodia* (MCZ 9237) in ventral view (stereophotographs).

cated at the anterior margin of the otic capsule, where the otic and pleurosphenoid regions join. On the basis of the comparable arrangement in modern caecilians (in particular, *Dermophis mexicanus*), this foramen is presumed to convey cranial nerve V (Fig. 15B). A second foramen lies at the anterolateral margin of the otic capsule, slightly ventral and lateral to that for V; elevated on a slight eminence, this foramen is interpreted as the exit of cranial nerve VII (Fig. 15B, C). A third, small foramen opens onto the posterolateral margin of the parasphenoid portion of the os basale and is confluent with a long sulcus on the lateral surface of the parasphenoid; both features are interpreted as representing the passage of the carotid artery (Fig. 15B).

Although the overall configuration of the os basale of *Eocaecilia micropodia* is comparable to that in living caecilians, differences are apparent in a number of details. First, the shape of the cultriform process is distinctive (cf. Figs. 1, 3, 6). Illustrations of the palates of modern caecilians by Taylor (1969) and Wake (2003) reveal a diversity of cultriform process outlines, none of which is especially similar to that of *E. micropodia,* which is elongate (relative to skull length) and narrow. The constricted posterior end of the cultriform process is distinctly demarcated from the broad capsular part of the os basale. Finally, the lateral margins of the process, rather than converging at an acute angle as in many living taxa, remain subparallel for much of their length and converge distinctly only near the apex.

Second, the palatal surface of the cultriform process bears an irregular array of pedicellate teeth (although no specimen preserves a tooth crown in place). The diameters of the pedicel bases on the cultriform process are more variable and, on average, smaller than those found on the jaws. On the type specimen (MNA V8066, Fig. 3), a sample of 14 well-preserved pedicels range from 0.07 to 0.13 mm in diameter; the mean of 0.09 mm is less than the means of 0.11–0.12 mm observed from tooth rows of the upper and lower jaws. On MNA V8071, a sample of eight pedicels on the cultriform process has a mean diameter of 0.1 mm, whereas the estimated diameters of several poorly preserved pedicels on the associated mandible is 0.13 mm.

Third, the condyles and the facets in *Eocaecilia micropodia* are relatively smaller than those of gymnophionans. An index of the relative size of the atlanto-occipital articulation is the bilateral breadth of the condyles (the distance between the lateral margins of the two condylar facets) expressed as a percentage of skull width. The specimen of *E. micropodia* in which the condyles appear undistorted (MCZ 9015, Fig. 13B) reveals their bilateral breadth to be 25% of the skull width. Indices taken from MCZ gymnophionan specimens or the literature reveal a range of values between 33 and 45%: the rhinatrematid *Epicrionops petersi,* 39% (Nussbaum, 1977, fig. 1); the uraeotyplid *Uraeotyphlus narayani,* 41% (Nussbaum, 1979, fig. 1); the typhlonectid *Typhlonectes compressicauda,* 33% (MCZ 24524); the ichthyophiid *Ichthyophis glandulosus,* 34% (MCZ 14003); the scolecomorphid *Scolecomorphus uluguruensis,* 39% (MCZ 12284); and various caeciliids: *Afrocaecilia taitana,* 45% (MCZ 20021); *Dermophis mexicanus,* 38% (MCZ 126357); *Gegeneophis ramaswamii,* 38% (MCZ 29456); *Geotrypetes seraphini,* 42% (MCZ 3424); *Gymnopis multiplicata,* 36% (MCZ 29265); *Oscaecilia ochrocephala,* 40% (MCZ 9591); *Schistometopum gregorii,* 39% (MCZ 20070); and *Siphonops annulatus,* 36% (MCZ 19402).

The articular facets of *E. micropodia* are relatively small as well. In MCZ 9015, the greatest width of a facet (measured along the long axis of the oval) is 0.7 mm, or 10% of the estimated skull width of 7.2 mm compared with values of 15% in *Siphonops annulatus* (MCZ 19405), and 17% in *Gegeneophis ramaswamii* (MCZ 29452)

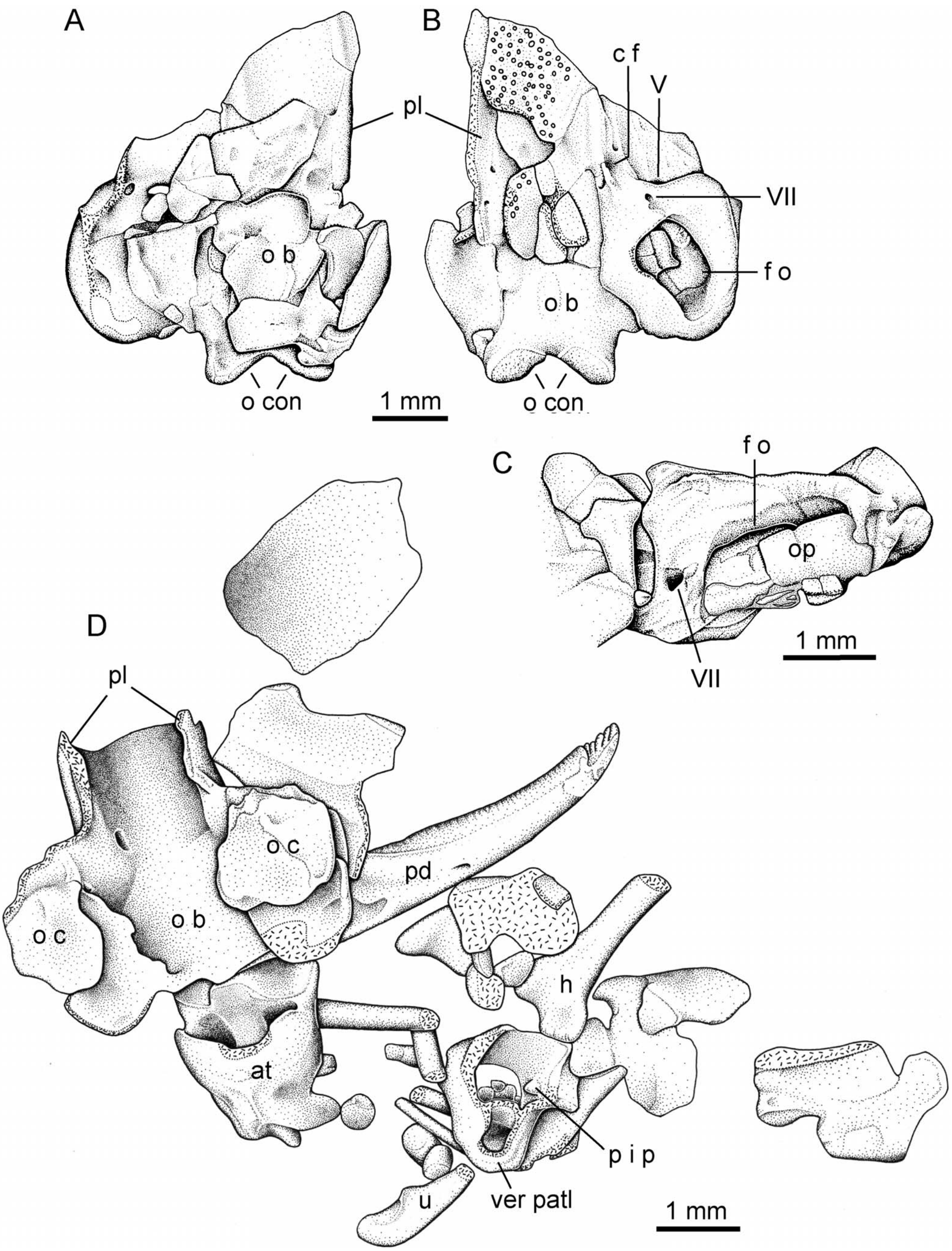


Figure 15. The os basale of *Eocaecilia micropodia* (MNA V8063) in (A) dorsal and (B) ventral views. For stereophotographs of this specimen in ventral view, see Figure 16. (C) An otic capsule (MCZ 9169) in lateral view exhibiting the fenestra ovalis and associated operculum. (D) A partial braincase and the otic capsules in ventral view (MCZ 9167).

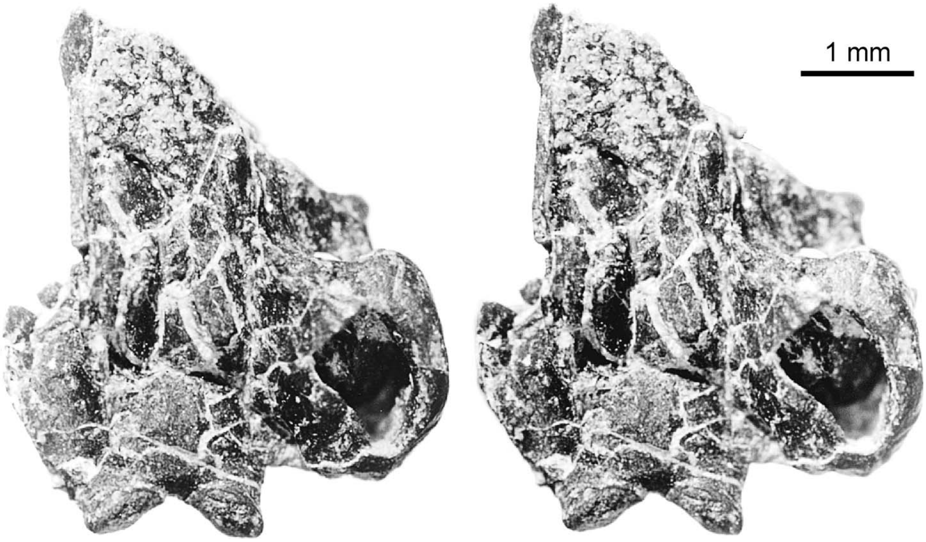


Figure 16. The braincase of *Eocaecilia micropodia* (MNA V8063) in ventral view (stereophotographs). For labeled drawings of this specimen, see Figure 15A, B.

and *Typhlonectes compressicauda* (MCZ 24524).

A fourth difference is that the ventral aspect of the os basale of *Eocaecilia micropodia* lacks any indication on its ventral surface of the attachment of subvertebral cranial depressor musculature, specifically the longus capitis. In many Recent caecilians, a pair of facetlike depressions anterior to the foramen magnum, separated in the median plane by a low ridge, mark this attachment site (cf. Figs. 3, 6B–D). The muscle flexes the skull ventrally, a movement that Bemis et al. (1983) suggested would be employed in both feeding and burrowing.

Pleurosphenoid. Anteromedial to the otic capsule a large pleurosphenoid forms the lateral wall of the braincase, extending anteriorly along the lateral margin of the parasphenoid portion of the os basale toward the sphenethmoid (Fig. 16), as in modern caecilians. The pleurosphenoid does appear to have been fully fused to the parasphenoid (Figs. 15, 16). In MCZ 9167, the pleurosphenoid is approximately 3.4 mm long and 1.9 mm high. The anterior margin of the pleurosphenoid is recessed, and a small gap, estimated to be 1.4 mm in width, separates the anterior margin of this bone from the posterior margin of the sphenethmoid (Fig. 17A). This gap is likely to have accommodated the egress of cranial nerves II, III, and IV.

Sphenethmoid. The sphenethmoid of *Eocaecilia micropodia,* which is not well preserved or visible in its entirety in any one specimen, is reconstructed (Fig. 17) on the basis of the holotype, MNA V8066, and MNA V8059 (Fig. 7). The sphenethmoid appears to conform generally to the pattern in modern caecilians (Fig. 18). In the holotype, the sphenethmoid is estimated to be 3.8 mm in length, or approximately half of the length of the parasphenoid portion of the os basale. This well-ossified, complex element represents the rostral end of the braincase. The posterior half of the sphenethmoid forms the thin lateral walls of the anterior part of the braincase (the walls of the posterior part of the braincase are contributed by the pleurosphenoids, Fig. 17A). The anterior end of the sphenethmoid is a robust, expanded structure that forms the transverse posterior wall of the nasal chambers. As in

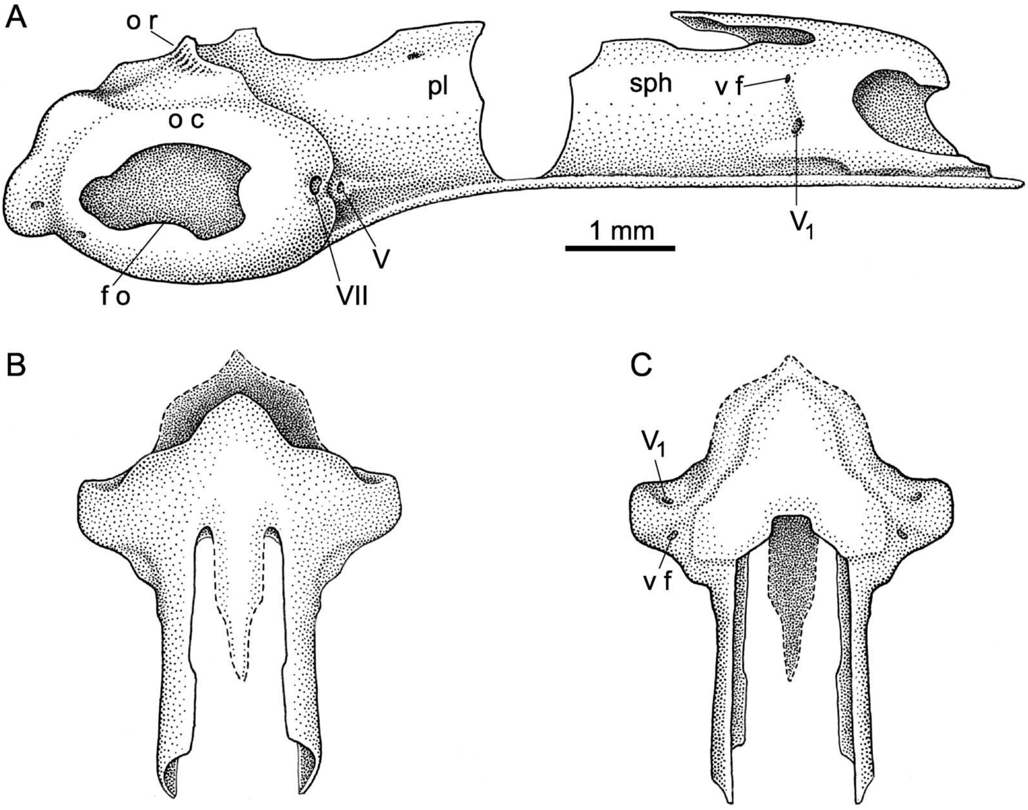


Figure 17. (A) Reconstruction of the braincase in *Eocaecilia micropodia* in lateral view. The reconstruction is based on the holotype (MNA V8066; Figs. 2, 3) and MNA V8059 (Fig. 7). The sphenethmoid (sph) component of the braincase in (B) dorsal and (C) ventral views.

modern taxa, the bone serves a supporting role in the anterior portion of the skull by extending dorsoventrally from the cultriform process of the os basale to the ventral surface of the skull roof. The sphenethmoid is not exposed dorsally as a component of the skull roof, nor is it in most Recent caecilians: rhinatrematids (e.g., *Epicrionops,* Nussbaum, 1977, fig. 1; Wake, 2003, fig. 5A), ichthyophiids (*Ichthyophis* sp., Wake, 2003, fig. 5G), uraeotyphlids (*Uraeotyphlus narayani,* Wake, 2003, fig. 6A), scolecomorphids (*Scolecomorphus uluguruensis,* Wake, 2003, fig. 6D), and typhlonectids (*Typhlonectes compressicauda* and *T. natans,* Wake, 2003, fig. 6G, J; *Potomotyphlus kaupii,* Wilkinson and Nussbaum, 1997, fig. 8B; see also Taylor, 1969; Wiedersheim, 1879). Dorsal exposure of the sphenethmoid does occur in various extant caeciliids in which the bone appears as a median element between the frontals (Taylor, 1969; Wake, 2003). The anterior portion of the sphenethmoid of *E. micropodia* also extends toward the lateral margin of the skull. In *Epicrionops,* the sphenethmoid continues as a cartilaginous posterior wall of the narial passage (Fig. 14B), possibly adding an additional buttress against the compressive forces of burrowing. The same process occurs in *Ichthyophis* (the lamina orbitonasalis of Visser, 1963).

The sphenethmoid in *Eocaecilia micropodia* is pierced by several foramina. One, located on the posterior face of the lateral

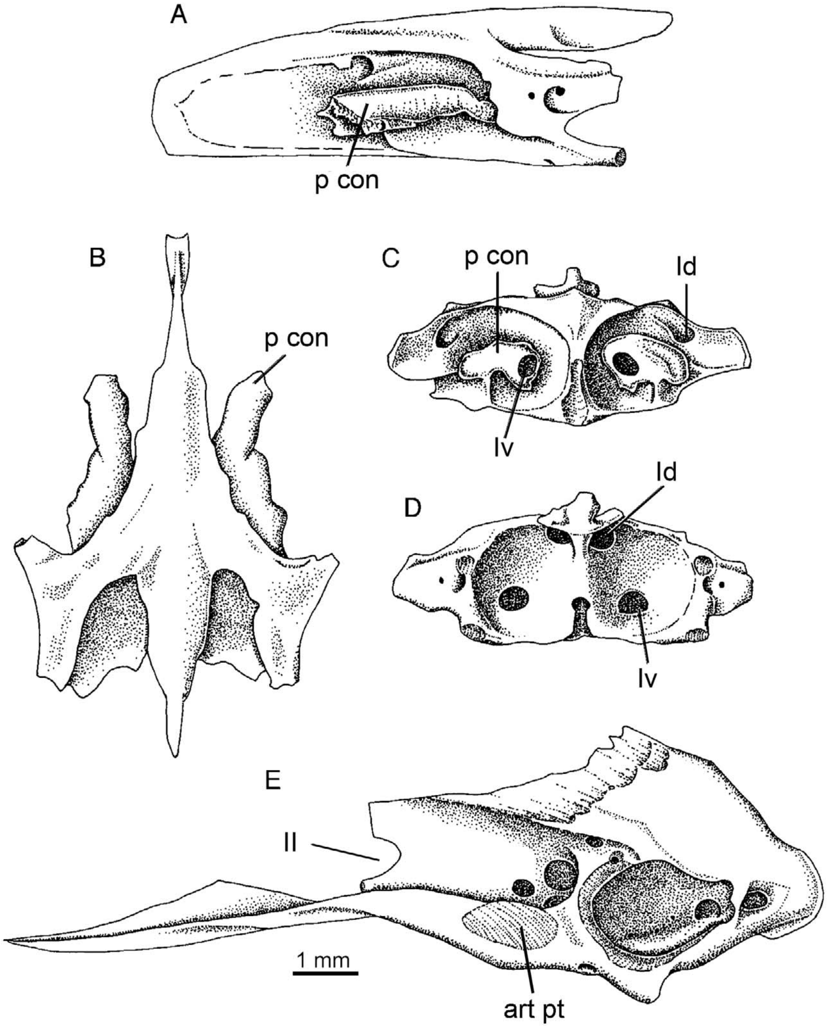


Figure 18. Braincase of *Dermophis mexicanus* based on a specimen described by Wake and Hanken (1982) in the collection of Marvalee H. Wake, Department of Integrative Biology, University of California, Berkeley. Sphenethmoid in (A) left lateral, (B) dorsal, (C) anterior, and (D) posterior views. (E) Os basale in left lateral view.

wing (Figs. 1B, 3; V_1, Fig. 17A, C) is comparable in position to a foramen in Recent taxa (e.g., *Ichthyophis*) that conveys the deep ophthalmic branch of cranial nerve V. Another foramen, visible in both lateral and ventral aspects (v f, Fig. 17A, C), enters the sphenethmoid at a level slightly above the opening for deep ophthalmic branch and is interpreted (by comparison with *Ichthyophis*) to represent a vascular foramen.

Stapes-quadrate. Although the skull and lower jaw of *Eocaecilia micropodia* resemble those of Recent caecilians in many aspects, the structure of the stapes and jaw suspension is unlike that in any other known gymnophionan and, furthermore, appears to have no parallel among other terrestrial vertebrates. There is a single element situated in the stapedial and quadrate region that has characteristics of both bones. As would be expected of a quadrate, the bone is firmly attached to the skull in three areas: posteroventrally to the quadrate ramus of the pterygoid (Fig. 11), dorsally to the back of the skull table (Figs. 1A, C, 2), and anteriorly to the underside of the squamosal (Figs. 5, 19B). Furthermore, the bone bears a distinct facet for articulation with the lower jaw (Figs. 13A, 19B, 20D, 21C). As would be expected of a stapes, the bone is closely associated with the otic capsule and is traversed by a relatively large foramen; the size of the foramen is consistent with a vascular passage (i.e., a stapedial artery, Figs. 2, 11, 19–21) rather than a narrow conduit expected for a nerve (such as the chorda tympani, which traverses the quadrate). The nature of the attachment to the otic capsule, however, is less well defined than in Recent caecilians, in which the thickened edges of the footplate (e.g., in *Dermophis mexicanus,* Fig. 22) articulate with the margins of the fenestra ovalis. This large and complexly shaped single element can be termed a stapes-quadrate, although there is no evidence of sutural fusion in any specimen. Nearly all aspects of the stapes-quadrate can be seen in one or more specimens, yet in no single specimen is the entire bone both complete and fully exposed; integrating a reconstruction (Fig. 21) proved difficult and required certain simplifications to be consistent in all views.

The stapes-quadrate is a large bone (approximately one-third of the skull length) that extends, as a posterior process, behind the dermal skull roof and between the retroarticular process of the lower jaw and the otic region of the os basale (Fig. 2). Although the posterior process of the stapes-quadrate resembles the stem or shaft of a stapes (by analogy with those in Paleozoic tetrapods; cf. Lombard and Bolt, 1988, figs. 3–9), its medial surface lies lateral to the fenestra ovalis and thus occupies a position that would be expected of a footplate. Rather than fitting into the fenestra ovalis, as in modern caecilians (Fig. 10B), the medial surface is large enough to have completely overlapped the margins of the fenestra. However, in the type, which is the least distorted specimen, neither stapes-quadrate lies in intimate contact with the fenestra ovalis (Fig. 3). The presence of an ossicle in this region (see below, *Operculum*) is additional evidence favoring the interpretation that the stapes actually had withdrawn from contact with the otic region (and assumed principally a jaw suspensory function and only secondarily, by bone conduction, an auditory function). The caudal end of the posterior process of the bone is free (i.e., lacks any bony contact). The lateral surface of the distal end of the process is rugose; the rugosity is slightly raised along the dorsolateral margin of the process and could represent evidence of tendinous attachment. The adjacent medial surface of the lower jaw's retroarticular process is also rugose.

A deep, triangular fossa on the anterior surface of the stapes-quadrate (Figs. 20C, 21E), medial to the area of articulation with the lower jaw and dorsolateral to the articulation with the quadrate ramus of the pterygoid, represents an extension of the adductor chamber. The anterodorsal portion of the stapes-quadrate extends rostrad as a narrow lamina (Fig. 21A–D) that contributes to the lateral margin of the adductor chamber. We interpret the rugosity on the dorsal surface of the lamina as an area of attachment to the undersurface of the lower margin of the cheek.

A large stapedial foramen traverses the bone obliquely from dorsolateral to medial surfaces in a ventromedial and somewhat posterior direction (Figs. 2, 11, 19–21). Laterally, the foramen is distinctly oval (the long and short diameters of which measure 0.4 and 0.2 mm in MNA V8066; in MCZ 9169, the diameters are 0.5 and 0.25 mm, respectively); medially, the foramen is nearly circular. The foramen opens onto the concave medial surface of the posterior process in a position slightly rostral to the fenestra ovalis. Rostral to the foramen's dorsolateral opening, an anterodorsal extension of the stapes-quadrate apparently attaches to the underside of the

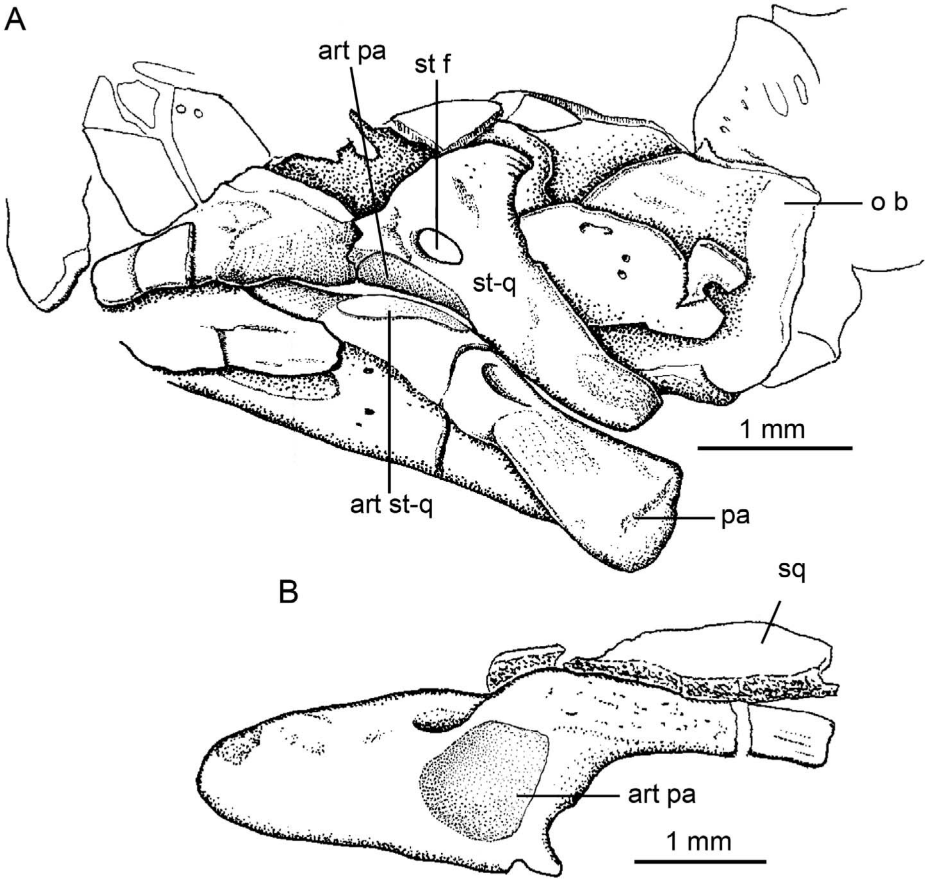


Figure 19. Stapes-quadrates of *Eocaecilia micropodia.* (A) Left side of the type specimen (MNA V8066) in oblique posterolateral view, showing articulation with pseudoangular. (B) Lateral view of right stapes-quadrate of MCZ 9169.

skull roof, near or at the occipital margin (a relationship preserved only in the holotype, Fig. 2).

An approximately oval articular facet is situated at the middle of the lateral surface of the stapes-quadrate (Figs. 19B, 21C). In MCZ 9235, the dimensions of the facet in the anteroposterior and dorsoventral planes are, respectively, 1.1 and 0.8 mm; comparable dimensions are seen in MCZ 9169 (1.1, 0.9 mm). The jaw joint is formed by the apposition of this facet with another on the medial surface of the pseudoangular (Figs. 19A, 24C, 26B; see also Jenkins and Walsh, 1993, fig. 1e). The surfaces of both facets are of "unfinished" bone, evidence of a cartilaginous covering and a synovial joint. The facet on the stapes-quadrate faces principally laterally but is inclined slightly ventrally (Fig. 29A); the relatively flat surface, which exhibits a very shallow anteroposterior concavity, contrasts markedly with the complexly configured quadrate and pseudoangular facets in Recent gymnophionans (Fig. 29B, C). Anterior to this facet is a rounded, transverse bar that forms the posterior margin of the adductor chamber; relative to the lower jaw, the bar is positioned at a point just posterior to the insertion of the adductor muscles. The finished surface of the bone lacks any indication of articular cartilage;

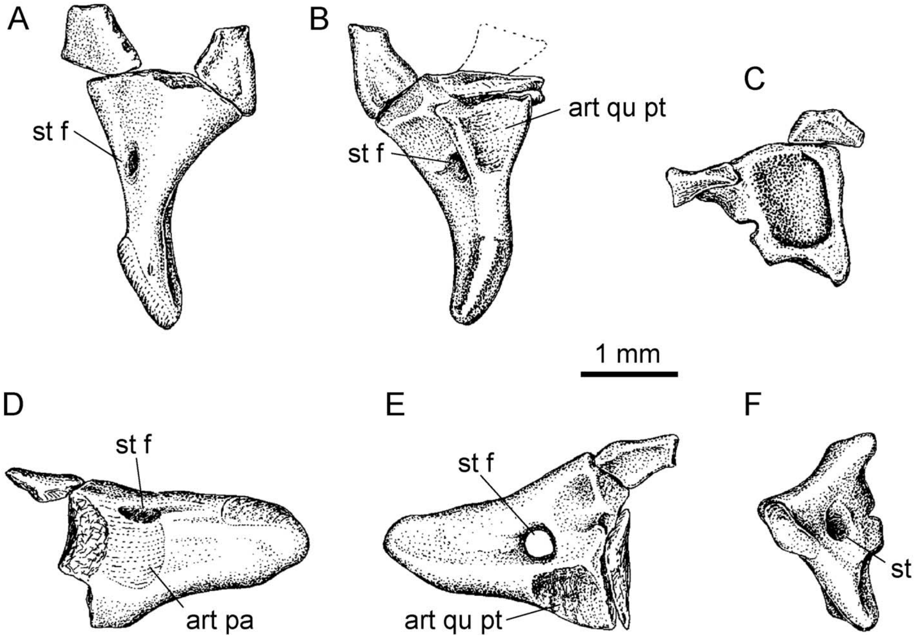


Figure 20. Left stapes-quadrate of *Eocaecilia micropodia,* MCZ 9169. (A) dorsal, (B) ventral, (C) anterior, (D) lateral, (E) medial, (F) posterior views.

therefore, the bar appears not to be a component of the jaw joint.

In most gymnophionans the quadrate and stapes retain separate identities. The apparent fusion of the stapes-quadrate in *Eocaecilia micropodia* represents a more derived condition than that of some Recent caecilians in which the quadrate and stapes are closely abutted and even articulate by means of a synovial joint. In a juvenile *Ichthyophis glutinosus,* for example, de Jager (1939b) described a synovial joint between the stapes and quadrate. Serial sections of adult *Ichthyophis glutinosus* (Fig. 23) and a specimen of *Epicrionops petersi* examined by R.L.C. confirm an extensive contact between the quadrate and stapes. Yet *E. micropodia* is not unique among known caecilians for having completely departed from the ancestral condition of a distinct stapes and quadrate. Scolecomorphids lack stapes as well as foramina ovales (Nussbaum, 1985). Specimens of *Boulengerula boulengeri* were reported by de Villiers (1936, 1938) to variably exhibit a synovial articulation between the stapes and quadrate or partial fusion of the two bones. de Jager (1939a) described an incipient fusion of the stapes and quadrate in *Dermophis mexicanus,* but this condition was not confirmed by Wake and Hanken (1982: 214), who reported that "the stapes is always free of the quadrate. . . ." In *D. mexicanus,* however, the quadrate fuses with the pterygoid (Wake and Hanken, 1982), a condition that Lawson (1963) believed to be present in *Hypogeophis rostratus.*

The massive stapes-quadrate, intimately articulated with the quadrate ramus of the pterygoid and functioning in the jaw articulation, presumably could have transmitted vibrations by bone conductance. Stapes in Recent caecilians serve both auditory and structural roles, linking the braincase (otic capsule) with the cheek (quadrate). Although the modern caecilian stapes is not a component of an impedance matching system, as in amniotes and most frogs, the apparatus does respond to low-

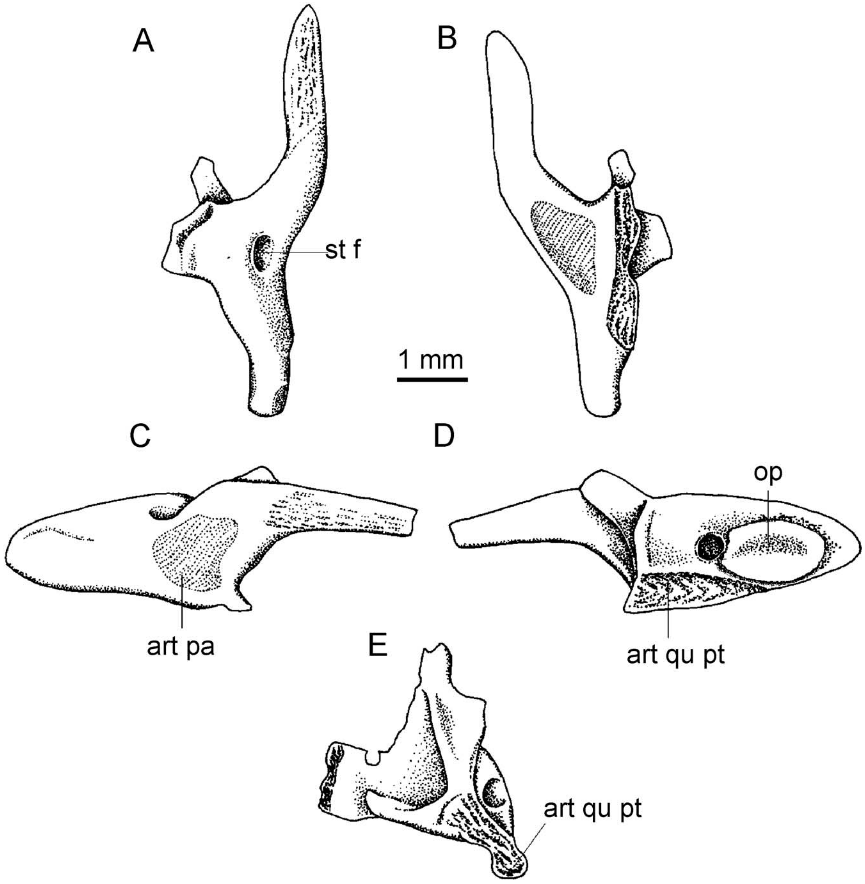


Figure 21. Reconstruction of the right stapes-quadrate of *Eocaecilia micropodia* based on MCZ 9169 and MNA V8066, V9346. (A) dorsal, (B) ventral, (C) lateral, (D) medial, (E) anterior views (E drawn from MNA V8059).

frequency vibrations (Wever, 1975; Wever and Gans, 1976).

Operculum. An ossicle is preserved with several specimens, either in proximity to the fenestra ovalis or stapes-quadrate, or in isolation. In MCZ 9242 (op, Fig. 12) and MNA V8054 (Fig. 25G) the ossicle is a thin, oval plate resting against the stapes-quadrate. The medial surface facing the fenestra ovalis is concave. In both MCZ 9242 (Fig. 12) and the holotype, the edges are thickened, as in the case of gymnophionan stapedial footplates that articulate with the margins of a fenestra ovalis (Fig. 22). In MCZ 9156 (Fig. 9), the ossicle lies against the retroarticular process, close to the jaw articulation. In the holotype (Fig. 3), the ossicle appears to have been turned outward and lies immediately adjacent to the fenestra ovalis. The variable positions in which the ossicle is preserved are evidence that this element was not rigidly attached but presumably was anchored by soft tissue. In MCZ 9169 (Fig. 15C), however, the ossicle was exposed by removal of the stapes and, although fragmented, was found to be closely associated with the fenestra ovalis; the reconstructed shape of the ossicle is an elongate oval that would have occupied most or all of the fenestra ovalis, the margins of which are well preserved.

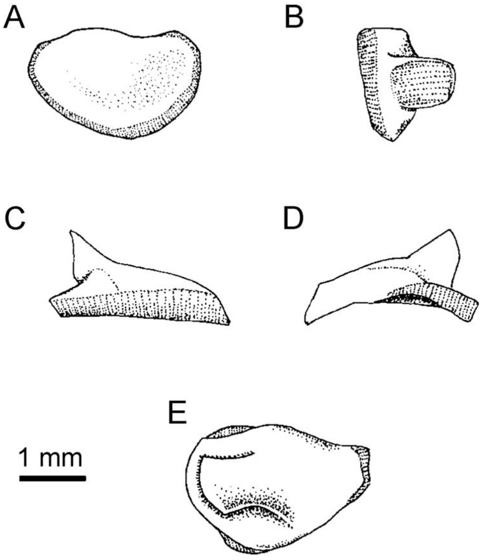


Figure 22. Stapes of the *Dermophis mexicanus* in (A) medial, (B) anterior, (C) ventral, (D) dorsal, and (E) lateral views. Drawn from a specimen described by Wake and Hanken (1982) in the collection of Marvalee H. Wake, Department of Integrative Biology, University of California, Berkeley.

The oval shape and otic association of the ossicle of *Eocaecilia micropodia* are comparable to that found in the opercula of frogs (Wever, 1973) and salamanders (Monath, 1965), and on this evidence, the ossicle can be proposed as a homologous opercular element. Unlike Recent caecilians, *E. micropodia* retained a shoulder girdle to which an opercularis muscle could have attached. No extant caecilian is known to have an operculum. Duellman and Trueb (1986: 387) state that the operculum in caecilians is either absent or fused with the footplate of the stapes and elsewhere (1986: 306) cite Marcus (1935) as suggesting that the operculum in *Hypogeophis* ". . . has been incorporated into the stapedial footplate, as . . . in plethodontid salamanders." However, Marcus actually made no so such claim, having been unable to identify any vestige of an operculum in his developmental study: "Von einem operculum finde ich auch in der Entwicklung keine Spur" (Marcus, 1935: 145). Although Marcus (1935) did suggest that part of the otic capsule is incorporated into the stapedial footplate in *Hypogeophis,* Wake and Hanken's (1982) study of *Dermophis mexicanus* revealed only a single ossification center for the stapes, with no evidence of a separate origin for the footplate. On the basis of the limited evidence available, we conclude that the operculum in Recent gymnophionans has been lost.

An assessment of the possibility that the ear ossicle in *Eocaecilia micropodia* is actually a reduced stapes, rather than an operculum as here interpreted, can only be made with reference to structures in putatively basal gymnophionans (i.e., the rhinatrematids *Epicrionops* and *Rhinatrema*; Nussbaum, 1977, 1979; Wilkinson, 1992, 1996; Wilkinson and Nussbaum, 1996). In these forms, the stapes is a relatively massive bone that fits tightly into the margins of the fenestra ovalis; a rostrally directed stem articulates via a synovial joint with the posterior surface of the quadrate, and a stapedial foramen traverses the base of the stem. Although the stapes-quadrate of *E. micropodia* possesses a stapedial foramen, the bone does not "fit" within the fenestra ovalis. Postmortem distortion obviates the possibility of determining whether the stapes-quadrate contacted or simply lay in close apposition to the otic capsule. Certainly the concave medial surface of the posterior process of the stapes-quadrate exhibits no structural feature that would conform to the fenestral aperture. Two interpretations are therefore possible. First, the ear ossicle of *E. micropodia* is a reduced stapes, and the correspondingly enlarged quadrate has captured the course of the stapedial artery. Alternatively, the ossicle is a true operculum, and the stapes retained the primitive relation to the stapedial artery but lost the primitive seating of a footplate within the fenestra ovalis. We favor the latter interpretation on several grounds. Given the intimate association of stapes and quadrate in numerous extant taxa, the fusion of these two elements is not an altogether

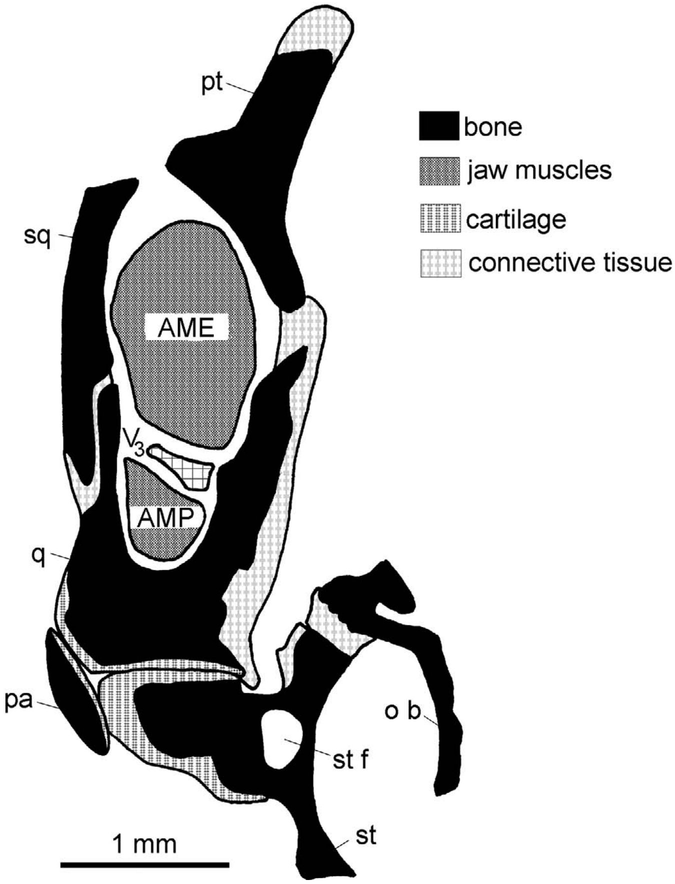


Figure 23. Horizontal section of the quadrate region of *Ichthyophis glutinosus* exhibiting an extensive cartilaginous contact between the stapes and quadrate, with both bones contributing to the facet for the pseudoangular. Based on serial sections in the collection of Marvalee H. Wake, Department of Integrative Biology, University of California, Berkeley.

unexpected specialization. Second, postulating the loss of an arterial foramen from one element and its reappearance in another would require at least some corroborative evidence, of which there is none.

Lower Jaw. Among the most durable of skeletal elements, the lower jaws of *Eocaecilia micropodia* are represented in articulation with several skulls (Figs. 3, 11, 13), as well as by numerous isolated specimens (Figs. 24–26). In contrast, no bones could be recognized as belonging to the hyobranchial apparatus, a not unexpected finding because the hyobranchial apparatus does not ossify in the adults of Recent caecilians.

Eocaecilia micropodia shares with most living caecilians the following unique combination of mandibular features:

The jaw comprises two distinct bones—the pseudodentary and the pseudoangular—which extensively overlap along their medial and lateral surfaces, respectively, and are thus joined along a wide suture that transects the jaw obliquely (Fig. 25C, D). There is no trace of any other separate ossification. The pseudoangular, which incorporates the articular, forms the mandibular articulation with the skull (Figs. 24C, G, 25F, 26B).

A lingual (or splenial) row of pedicellate teeth, which parallels the primary labial row, extends posteriorly from the symphysis to about the midpoint of the labial row (Figs. 24E, 26A). Data presented by Taylor (1968) demonstrate that the lingual row is a highly variable feature among gymnophionans. A row containing 2–20 teeth is present in representatives of three families (rhinatrematids, typhlonectids, and uraeotyphlids) but is altogether absent in scolecomorphids (*Scolecomorphus* spp., *Crotaphatrema bormuelleri*). Of the two genera of ichthyophiids, a lingual row is present in *Ichthyophis* but not developed in *Caudacaecilia.* Among caeciliids, many genera lack lingual teeth (*Boulengerula, Brasilotyphlus, Dermophis, Leutkenotyphlus, Microcaecilia, Mimosiphonops, Parvicaecilia, Pseudosiphonops, Siphonops*) but even more possess them (*Caecilia, Gegeneophis, Geotrypetes, Grandisonia, Gymnopis, Herpele, Hypogeophis, Idiocranium, Indotyphlus, Oscaecilia, Praslinia, Schistometopum, Sylvacaecilia*; for the last genus, see Wake, 1987a).

A well-defined mandibular fossa is developed on the dorsal surface of the pseudoangular for insertion of the adductor musculature (Figs. 24C, 27C). In the depths of the fossa is a foramen (Fig. 27C) whereby V_3 and accompanying vasculature are conveyed into an intramandibular canal. There is no adductor fenestra, as in anurans and salamanders.

The pseudoangular bears a robust internal process that projects dorsomedially (Figs. 24D, 25C, H). The apicobasal height and anteroposterior width (measured across its base) of the internal process is relatively greater, and in some cases substantially greater, than that found in a sample of extant gymnophionans (Table 1). The pseudoangular also bears an elongate, posteriorly projecting retroarticular process that in life likely extended just caudal to the level of the occiput (Figs. 1A, 25D, 26B, 27C). The robustly constructed retroarticular process is slightly less than 20% of the lower jaw length, and thus shorter than those measured from selected extant taxa, which range from 20 to 32% (Table 1). The posterior terminus in a number of specimens is obliquely truncated (Fig. 27D) so as to face posterolaterally, although this geometry is not seen in every specimen (e.g., Fig. 24C). A slightly raised area developed on the terminus extends onto the dorsal aspect of the process (Fig. 24A, C); the area appears to represent a muscle insertion, probably for the interhyoideus posterior. A rugose depression, on some specimens linear (Fig. 25B) but on others irregular (Fig. 24C, G), is situated on the dorsal aspect of the process and might represent the insertion of the depressor mandibulae.

The arrangement of neurovascular foramina is also similar to those in Recent taxa. In *Hypogeophis rostratus* (Lawson, 1963) and other living caecilians, the mandibular branch of cranial nerve V and the mandibular artery and vein pass into the lower jaw via a foramen in the floor of the adductor fossa. A comparable arrangement occurs in *Eocaecilia micropodia,* although two foramina, rather than one, are present (Fig. 24C, G). The neurovascular bundle is distributed to two regions. First, the intramandibular branches of the mandibular vasculature and the ramus intramandibularis of V exit about midway along the medial surface of the jaw through a conspicuous intramandibular foramen. A comparable foramen is present in *Eocaecilia micropodia* (Figs. 24D, 25C, 27B). Second, the external and alveolar branches of both the vasculature and nerve V continue through the ramus toward the symphysis. Small foramina on the medial and lateral surfaces of the symphysial region provide access to surrounding soft tissue; these are evident in *E. micropodia* (Figs. 24A, 27A, B). As in living forms, *E. micropodia* possesses a number of vascular foramina along the trough between the two tooth rows that served the spongy tissue surrounding the tooth rows.

In *Dermophis* and *Gymnopis,* the ramus alveolaris of cranial nerve VII enters the lower jaw through a foramen that lies posterior to the base of the internal process,

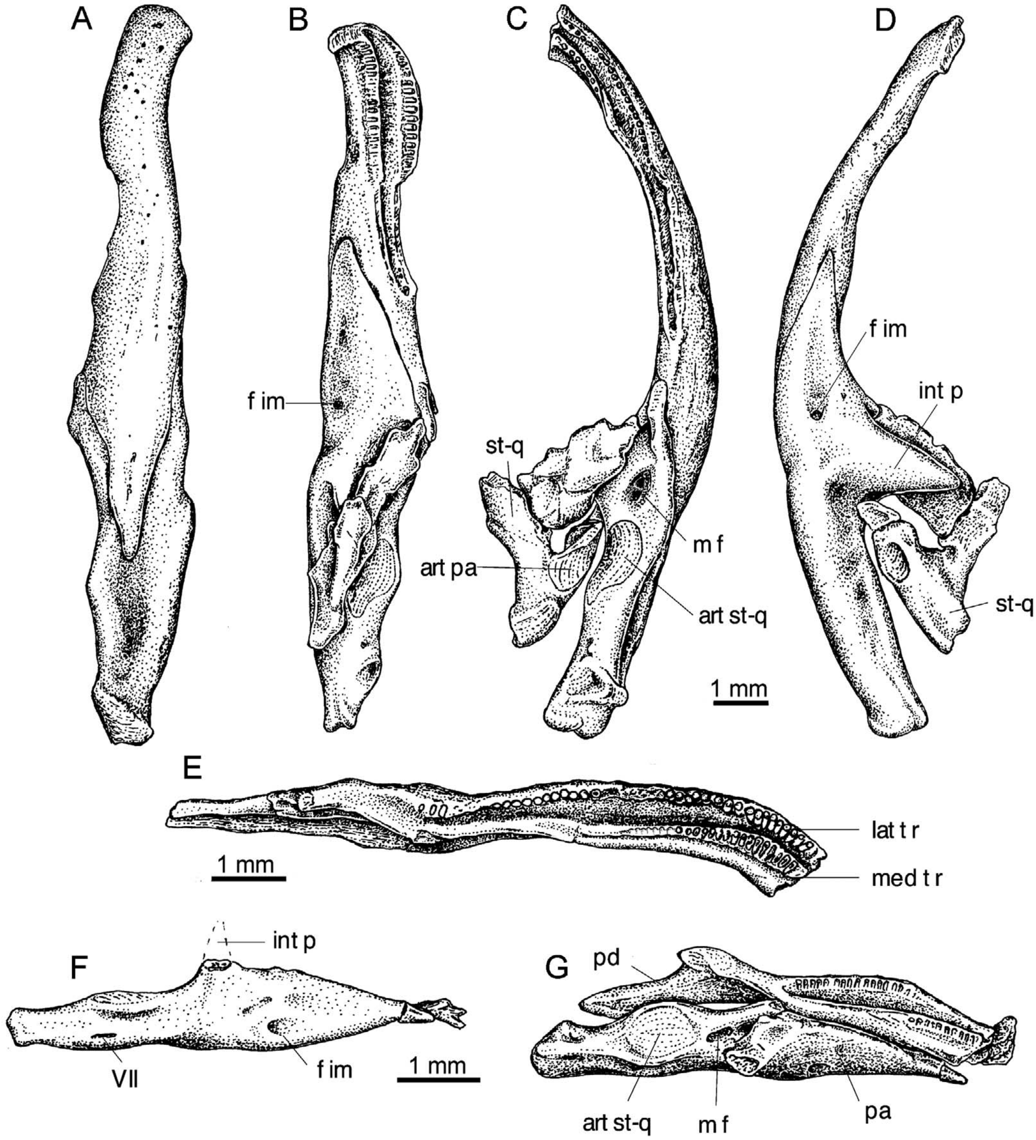


Figure 24. The lower jaws of *Eocaecilia micropodia.* MNA V8070 in (A) lateral, (B) medial, (C) dorsal (see also Fig. 26B), and (D) ventromedial views. In D the jaw is oriented in the plane of the internal process to show the length of the process. (E) A pseudodentary (MCZ 9152) in dorsal view; see also Fig. 26A. (F) A pseudoangular (MNA V8058) in medial view. (G) MNA V8058, a pseudoangular and partial pseudodentary (rostral end missing) in oblique dorsomedial view.

approximately in the transverse plane of the jaw joint (for an illustration of *Hypogeophis rostratus,* see Lawson, 1963, fig. 9a, b). In *Eocaecilia micropodia,* the foramen is comparably positioned relative to the jaw joint but is separated from the internal process which is relatively larger and located in a more rostral position (Figs. 3, 24F, 27A–C). The foramen variably occurs either on the ventral margin of the bone or slightly displaced onto either the medial or lateral surface. In modern

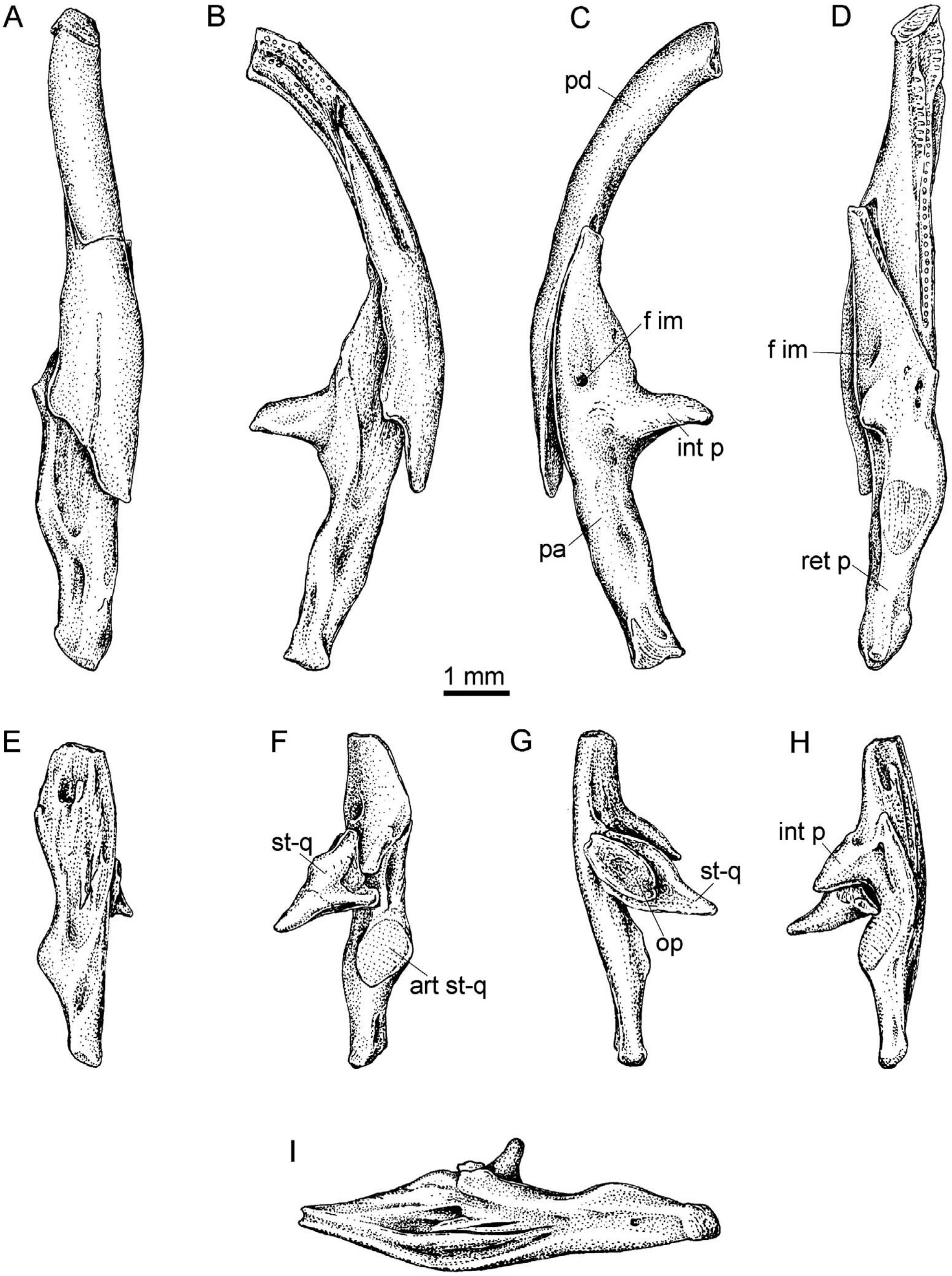


Figure 25. The lower jaws of *Eocaecilia micropodia.* MNA V8068 in (A) lateral, (B) dorsal, (C) ventral, and (D) medial views. MNA V8054, a pseudoangular in (E) medial, (F) dorsomedial, (G) ventral, and (H) dorsal views; the rostral end is oriented upward (as in A–D). (I) MCZ 9158, a pseudoangular in lateral view. (E, I) The extensive interdigitation at the pseudoangular-pseudodentary joint is shown.

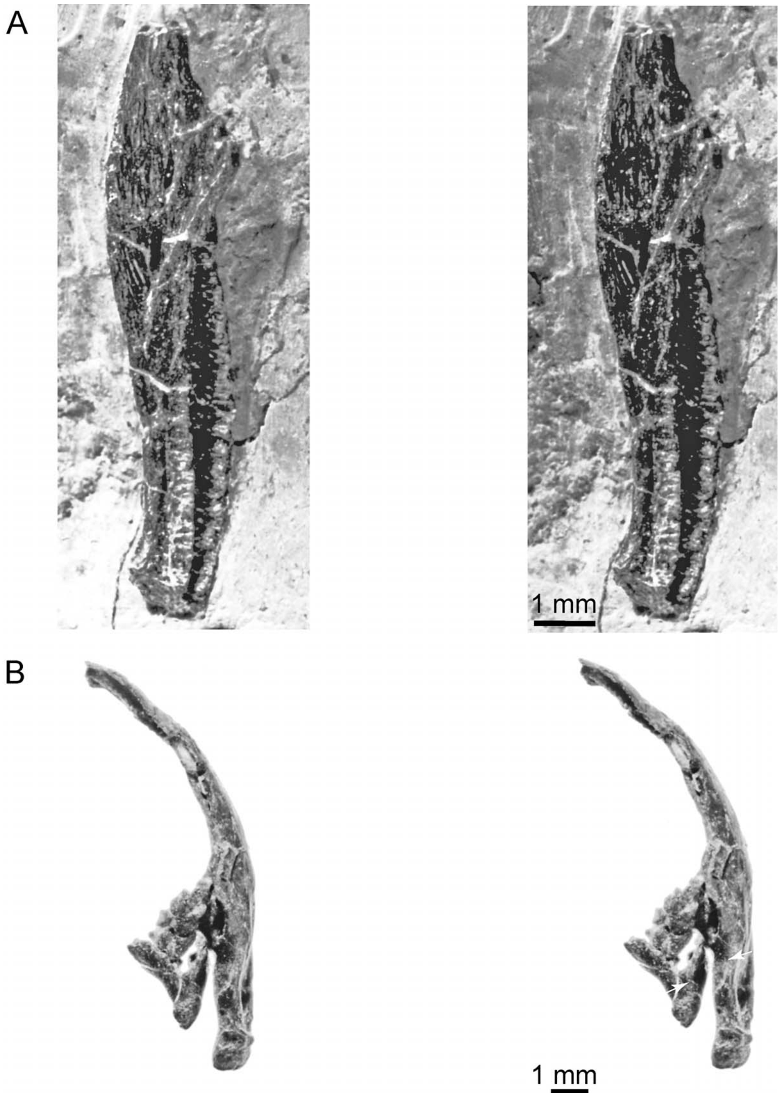


Figure 26. (A) A left pseudodentary of *Eocaecilia micropodia* (MCZ 9152) in medial view. (B) Right lower jaw and stapes-quadrate (MNA V8070) in dorsal view, showing the opposing articular facets of the stapes-quadrate and pseudoangular, here disarticulated and indicated by white arrows, comprising the jaw joint (stereophotographs); see also Fig. 24A–E.

caecilians, the ramus alveolaris of VII joins the ramus alveolaris of the V within the intramandibular canal where they run together toward the symphysis. The comparable arrangement of the intramandibular canal and foramen in *E. micropodia* and living caecilians would seem to indicate similarities in vascular and neural distribution. The intramandibular canal of *E. micropodia* was probably also occupied by a remnant of Meckel's cartilage, which is retained in Recent caecilians.

All of the foregoing characteristics of the lower jaw, considered together, indicate that the overall pattern of caecilian masticatory adaptations had been estab-

Table 1. Relative size of the internal and retroarticular processes of the lower jaw in *Eocaecilia micropodia* and selected taxa of extant gymnophionans. Length of the retroarticular process (C) is the distance from the posterior margin of the articular facet to the posterior terminus of the process. Jaw length (D) was measured from the symphysis to a point midway between the retroarticular processes (i.e., in a sagittal plane)*.

	A Anteroposterior width of the internal process across the base (mm)	B Apicobasal height of the internal process (mm)	C Length of the retroarticular process (mm)	D Anteroposterior length of the jaw (mm)	A/D Relative width of internal process (%)	B/D Relative height of internal process (%)	C/D Relative length of the retroarticular process (%)
Eocaecilia micropodia MNA V8066	2	1.8	2.25	12.7	16	14	18
Eocaecilia micropodia MNA V8068	1.3	1.5	1.8	10.4	13	14	17
Epicrionops petersi USNM 160360†	0.7	1	4	13	5	8	31
Ichthyophis glandulosis MCZ 140003	1.2	0.7	2.6	12.7	9	6	20
Dermophis mexicanus MCZ 12121	1.4	2	4.7	18.4	8	11	26
Gegeneophis ramaswamii MCZ 29460	0.5	0.6	2.35	7.8	6	8	30
Gegneophis ramaswamii MCZ 29458	0.5	0.6	2.3	7.3	7	8	32
Gymnopis multiplicata MCZ 29265	1.3	1.1	5	18.4	7	6	27
Typhlonectes compressicauda MCZ 24524	2	1 e	5.1	20.5	9.8	5	25

* e, Estimated from a damaged specimen.
† Data from Nussbaum (1977, fig. 2).

lished by Early Jurassic times. No evidence appears of derived similarities with the jaws of frogs and salamanders, and yet in several features of mandibular morphology, notably the geometry of the jaw articulation, the large size and dorsomedial orientation of the internal process, and the large number and small size of the pedicellate teeth, *Eocaecilia micropodia* is distinctively different from any living gymnophionan.

The mandibular articular facet in *Eocaecilia micropodia* is set on the dorsomedial aspect of the pseudoangular, positioned posterior to the internal process and the mandibular fossa (Figs. 24C, G, 25D, 26B). The facet is oriented dorsomedially (Fig. 29A). In outline, the articular surface is irregularly oval, with the long axis of the ovoid passing from the facet's posterior, ventromedial margin to the anterior, dorsolateral margin. The surface of the facet exhibits a gentle concavoconvexity; the posterior, ventromedial half of the surface is slightly convex (MCZ 9158; MNA V8054, V8068, V8070), whereas the anterior, dorsolateral half is shallowly concave (MCZ 9158, MNA V8068) or more or less flat (MNA V8054, V8070). In MCZ 9235, the left pseudoangular and stapes-quadrate were preserved together but slightly disarticulated; preparation of the bones from the matrix permitted a comparison on the relative size of apposing facets as measured in planar view. The pseudoangular facet is larger, being 1.5 mm anteroposteriorly and 1 mm dorsoventrally. The analogous dimensions of the stapedial-quadrate facet are 1.1 and 0.8 mm, respectively. Pseudoangular facets preserved on other specimens give comparable anteroposterior and dorsoventral dimensions: 1.8, 1.3 mm (MNA V8070); 1.5, 1.1 mm

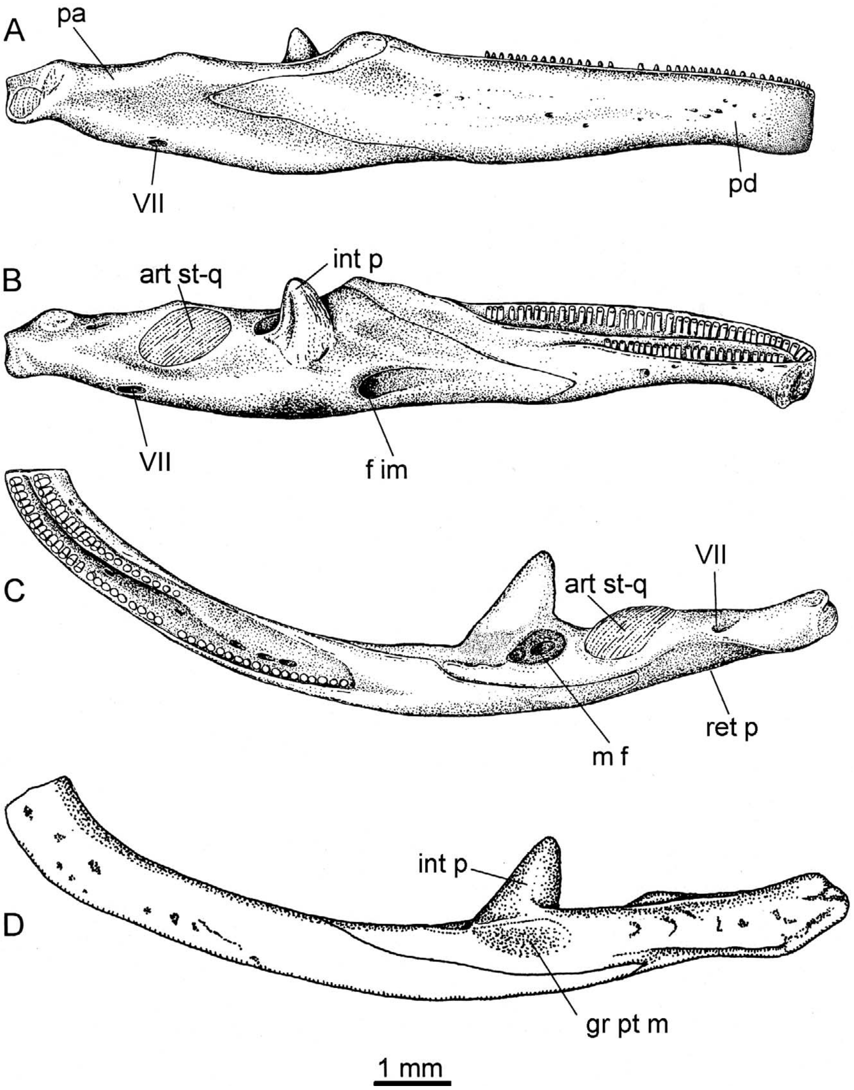


Figure 27. A reconstruction of the lower jaw of *Eocaecilia micropodia* based on the holotype (MNA V8066) and specimens illustrated in Figures 24–26. (A) Lateral, (B) medial, (C) dorsal, and (D) ventral views. The foramen for the ramus alveolaris of VII variably occurs on the lateral (A) and medial (B) aspects of the retroarticular process.

(MNA V8068); 1.4, 1.1 mm (MNA V8054); 1.25, 0.9 mm (MCZ 9158).

The pseudoangular facet would appear to correspond, in position and orientation, with the posterolateral half of the more extensive, U-shaped articular fossa (the processus condyloides of Nussbaum [1977, fig. 2]) that is characteristic of gymnophionans (Fig. 29B, C) and is also present in the Early Cretaceous caecilian *Rubricacaecilia monbaroni* (Evans and Sigogneau-Russell, 2001, fig. 3). However, the posterolateral component of the mandibular facet in Recent caecilians is not only more vertically inclined and more laterally placed than the facet in *E. micropodia*, but faces primarily anteromedially (rather than dorsomedially, as in *E. micropodia*). The

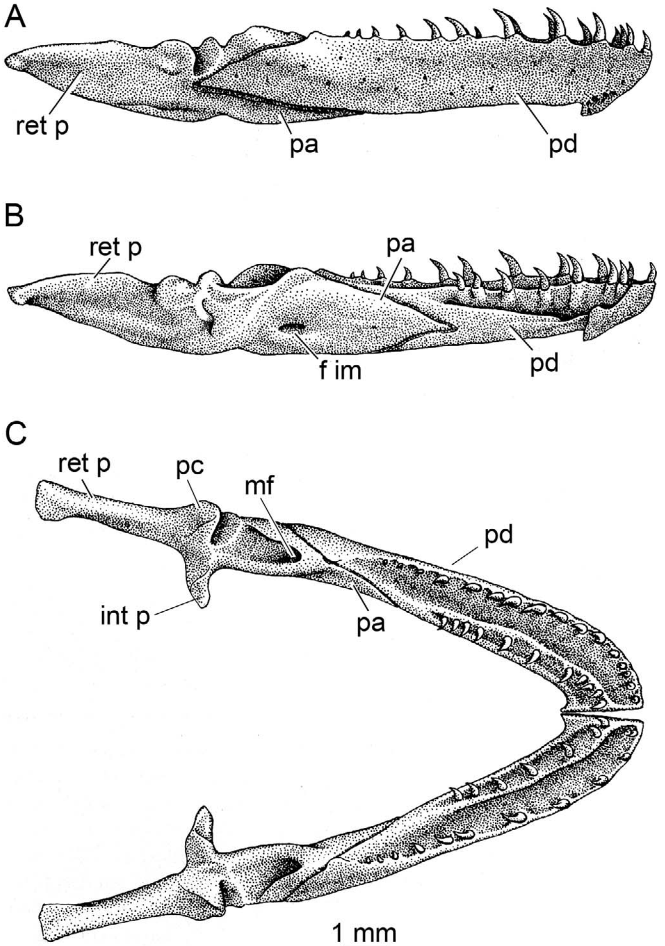


Figure 28. The lower jaw of *Epicrionops petersi* (from Nussbaum, 1977, fig. 2) in (A) lateral, (B) medial, and (C) dorsal views.

primary difference between the configuration of the mandibular facets of modern caecilians and *E. micropodia* is that, in the former, an anteromedial component of the facet is recurved to form a U-shaped fossa, whereas the entire facet in *E. micropodia* is, by comparison, essentially planar.

The internal process of *Eocaecilia micropodia* is notable for its large size. Relative to the length of the lower jaw, the process has greater apicobasal height, as well as greater anteroposterior width across the base, than those in selected representatives of Rhinatrematidae, Ichthyophiidae, Caeciliidae, and Typhlonectidae (Table 1). Only scolecomorphids lack an internal process (Nussbaum, 1985). Furthermore, the process in *Eocaecilia* differs in position, lying approximately at the level of the mandibular fossa for adductor musculature and anterior to the jaw articulation, whereas in Recent taxa, the base of the internal process is typically at the level of the jaw articulation and slightly posterior to the adductor fossa. In all of these features, *E. micropodia* also differs from the Early Cretaceous caecilian *Rubricacaecilia monbaroni,* which Evans and Sig-

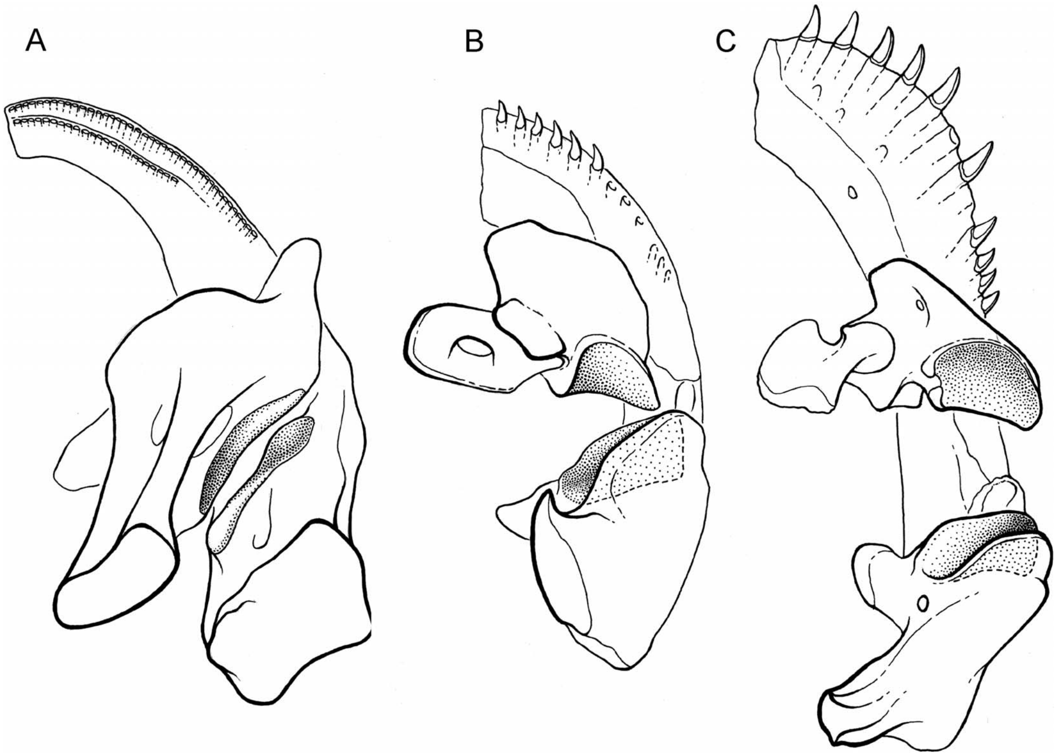


Figure 29. Posterodorsal views of the jaw joints of (A) *Eocaecilia micropodia* (reconstructed primarily from MCZ 9152), (B) *Ichthyophis glandulosus* (MCZ 14003), and (C) *Dermophis mexicanus* (MCZ 12121). In each case, the articular surfaces have been separated to show the geometry of the facets. Not to scale.

ogneau-Russell (2001: 267) noted most closely resembles the condition of rhinatrematids.

In Recent taxa, the relatively short internal process lies below the adductor chamber of the skull and is directed medially, whereas in *E. micropodia,* the elongate internal process must have projected dorsomedially into the adductor chamber, with its distal end extending above the horizontal plane of the quadrate ramus of the pterygoid. The dorsomedial inclination of the internal process is evident in several specimens (Figs. 4B, 13B, C, 25I). The degree of vertical inclination was probably sufficient to ensure that the process did not overlie the quadrate ramus of the pterygoid when the mouth was closed (constraining mouth gape) and thus could be withdrawn from the adductor fossa when the mouth opened. Nonetheless, the proximity of the process to the pterygoid is clearly evidenced by specimens in which the jaws are preserved in articulation with the skull. Typically the pterygoid is broken by compaction across the internal process, an artifact most clearly seen in the type (Fig. 3) and MCZ 9015 (Fig. 13B).

The pseudodentary bears two rows of teeth, as in rhinatrematids, typhlonectids, uraeotyphilds, *Ichthyophis,* and various caeciliids. The pseudodentary teeth of *Eocaecilia micropodia,* all of which are pedicellate, are more numerous than those in almost any modern caecilian, with the exception of *Praslinia cooperi.* In most specimens, the pedicels are closely packed, with a few gaps representing an unoccupied tooth locus or loci. As in most specimens of the upper jaw, no lower jaw crowns are preserved in place, but the diameter of the pedicels is comparable. A sample of 15 well-preserved pedicel bases drawn from MCZ 9152, MNA V8058, and MNA V8068 range in diameter from 0.9 to 0.14 mm, with a mean of 0.11 mm. MCZ 9233 documents a slight size disparity between marginal row pedicels (mean diameter 0.13 mm, $N = 5$) and those of the inner row (mean diameter 0.09 mm, $N = 8$). The left jaw of MCZ 9235, although fractured in two places, possesses 37 pedicels in the marginal row, but if tooth positions are counted where pedicels appear to have been lost, the tooth count is 46; the inner row is not preserved. Contrary to the common practice among caecilian workers, we attempt to count or estimate the total number of tooth positions, although we distinguish between those that are confirmed on the basis of existing pedicels and those estimated from the length of a gap in the dental row. Given the nature of the fossil material, we cannot distinguish between loci which were actually unoccupied and those loci from which a pedicel and tooth crown were lost postmortem. Wake's (1976, 1980b) studies of caecilian dental development demonstrated that not all tooth loci are occupied through successive generations of teeth, but given the nature of the preservation of *E. micropodia,* we can only focus our account on the evidence for the total number of loci.

The jaw that most completely preserves both dental rows (MCZ 9152, Figs. 24E, 26A) has a marginal row bearing at least 40 and possibly as many as 43 tooth positions; 36 pedicels are present, with 4 or more lost postmortem, leaving short gaps in an otherwise continuous tooth row. The lingual (or splenial) row comprises an estimated 22 or 23 positions; only 16 pedicels are preserved in the lingual row, although distally there are vertical grooves in the pseudodentary that are evidence of some 6 or 7 pedicels lost postmortem. The two tooth rows are separated by a deep groove, and another groove is medial to the lingual row. The spacing between the two mandibular rows appears to be narrower than that between the premaxillary–maxillary and vomer–palatine rows. In the best preserved mandibular tooth rows (MCZ 9152, Fig. 26A), the lingual side of the marginal row is separated by 0.25 mm from the labial side of the lingual row; this distance, which was measured at the distal end of the lingual row, narrows further in the symphyseal region. In no skull, however, are the marginal and lingual rows sufficiently exposed and well preserved to permit an accurate measurement of their separation; a rough estimate of 0.6–0.7 mm can be made from MNA V8059 (Fig. 7). Our interpretation is that, with the jaws closed, the two mandibular tooth rows would have been positioned between the upper tooth rows (as is the case in the holotype skull; Fig. 4B).

Comparative Dental Morphology and Tooth Counts. Although tooth crowns are rarely preserved in situ on the pedicels, disarticulated tooth crowns were recovered by micropreparational techniques from several specimens (MCZ 9011, 9015, 9169), either immediately adjacent to the bases of pedicels or in close association with a skull. The crowns, which are conical, bicuspate, and recurved (Fig. 30; Jenkins and Walsh, 1993, fig. 1c, d), resemble those in some Recent gymnophionans (e.g., *Ichthyophis glutinosus, Uraeotyphlus narayani, Hypogeophis rostratus, Geotrypetes seraphini,* cf. Wake and Wurst, 1979, figs. 12–19). However, the teeth are minute in comparison with those of most living caecilians of comparable skull size and could only be examined in detail by scanning electron microscopy (SEM). Ten tooth crowns were successfully extracted from the matrix for this purpose, mounted on SEM discs, and provide a basis for assessing variation in size and structure.

Apicobasal crown heights in this sample range from 0.16 to 0.26 mm, with a mean and standard deviation of 0.22 and 0.03 mm, respectively. The mesiodistal breadths of crown bases (measured from the labial aspect of the tooth, e.g., Fig. 30A) range from 0.09 to 0.13 mm (mean 0.11 mm, SD 0.012). The labiolingual breadths range from 0.08 to 0.14 mm (mean 0.12, SD 0.15). In seven of the 10 crowns, the bases are oval; in six crowns, the linguolabial diameter exceeds the mesiodistal diameter by 8–20%, whereas in one crown, the mesiodistal diameter is 11% longer than the linguolabial. In three specimens, the bases are circular. The small sample also displays a modest amount of variability in the shape of cusps and the lengths of crests. The crests on the apical cusp (or lingual cusp of Wake and Wurst, 1979) can be symmetrically lanceolate (Fig. 30A) or exhibit various degrees of asymmetry that arise from differences in the curvatures of the crests descending from the apical cusp (Fig. 30D, G, I) or in the inclination of the cusp as a whole (cf. Fig. 30A, G). Similarly, the secondary cusp (or labial cusp of Wake and Wurst, 1979) can be asymmetrical or symmetrical in terms of the lengths of the crests (cf. Fig. 30A, D). Although the primary cusp is always inclined lingually, the degree of inclination varies (cf. Fig. 30C, L).

Wilkinson (1991) described variations in the monocuspid tooth crowns of adult typhlonectids that appear to be in part comparable to those observed in the bicuspid teeth of *Eocaecilia micropodia,* despite the fact that the two taxa differ substantially in overall crown structure. In typhlonectids, the mesial and distal flanges descending from the single cusp are symmetrical on anterior teeth, but on posterior teeth, the mesial flange is relatively reduced and, on the posteriormost teeth, could be essentially absent. Wilkinson (1991: 305) also noted that "the curvature of teeth in more posterior loci tends to be skewed, such that these teeth project more posteriorly than they would if their curvature were restricted to a plane perpendicular to the tooth series." Symmetries and asymmetries of crest development, and skewing of the curvature, are evident in *E. micropodia* (Fig. 30). The dental morphology and arrangement of fetal *Typhlonectes compressicaudatus* differ substantially from those of adults (Hraoui-Bloquet and Exbrayat, 1996); the tooth crowns of *E. micropodia,* despite their very small size, are associated with adult specimens with comparably small pedicels and thus appear not to represent an ontogenetically immature stage.

From a study of complete dentitions in two specimens of *Gegeneophis ramaswamii,* Greven (1984) documented considerable variation in the degree of development of the secondary cusps on upper teeth and found that lower teeth were monocuspid. We have no evidence that tooth crown variability in *E. micropodia* attained comparable heterogeneity.

The observation that the conical, bicuspate, recurved teeth of *Eocaecilia micropodia* exhibit only modest variability parallels the conclusion reached by Wake and Wurst (1979: 332) from their morphological study of teeth of selected specimens from four families: Ichthyophiidae, Uraeotyphlidae, Caeciliidae, and Typhlonectidae. In contrast to the marked structural diversity noted by these authors across species, they reported "little variation within species . . . although size of crown and curvature vary slightly with ages and sizes of specimens . . . with larger, more recurved teeth found anteriorly on the jaws, particularly the dentaries . . . teeth are replaced on the jaws throughout the lives of the animals [and] those at particular loci are larger with each replacement."

The number of teeth in *Eocaecilia micropodia* (44–51 in the premaxilla–maxillary row, about 34 in the vomeropalatine, and 40–43 and 22 or 23 in the labial and lingual pseudodentary rows, respectively) is greater than in any known living caecilian, with a single exception. The estimated tooth count in *E. micropodia* is, by necessity, a composite based on the best evidence from multiple specimens and provides no account of the variability that commonly occurs among living caecilians,

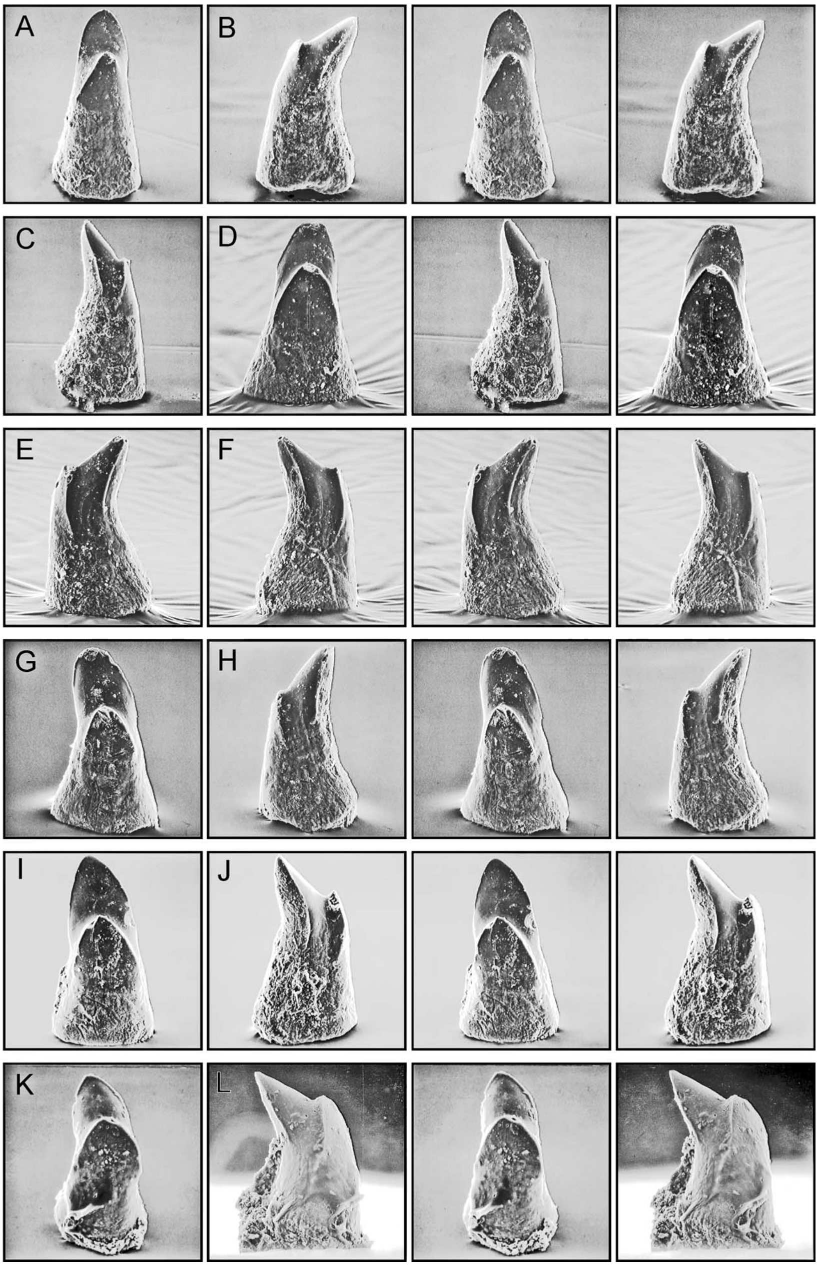


Figure 30. Stereophotographic scanning electron micrographs of tooth crowns of *Eocaecilia micropodia.* Lingual and labial surfaces are identifiable on the basis of crown curvature and relative size of the cusps. The relative tooth positions represented by these isolated crowns cannot be determined, and therefore side views are designated ''mesiodistal,'' with no certainty that the view is anterior (mesial) or posterior (distal). (A) MCZ 9011 in labial view, (B, C) opposite views along the mesiodistal axis; the apicobasal height of the tooth is 0.25 mm. (D–J) Three teeth from MCZ 9169. (D) Labial view and (E, F) opposite views along the mesiodistal axis; the apicobasal height is 0.20 mm. (G) Labial and (H) mesiodistal views; the apicobasal height is 0.24 mm. (I) Labial and (J) mesiodistal views; the apicobasal height is 0.25 mm. MCZ 9015: (K) labial and (L) mesiodistal views; the apicobasal height is 0.16 mm.

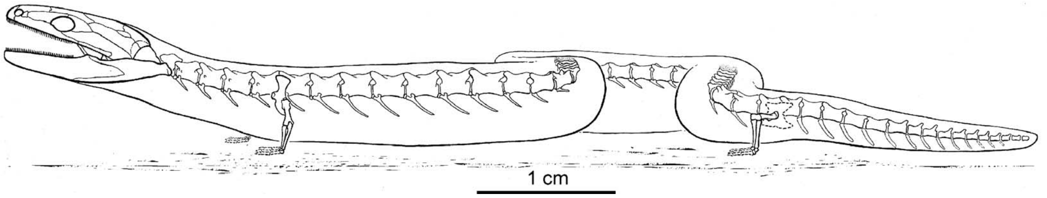


Figure 31. A composite reconstruction of *Eocaecilia micropodia* depicting the relative size of skull, vertebrae, limb girdles and limbs.

where tooth number increases with body size and age. Nonetheless, these uncertainties do not eclipse the fact that *E. micropodia* possesses about twice the number of teeth as most gymnophionans. In a survey of 158 Recent taxa, Taylor (1968) reported 99 species (or 63%) with unilateral tooth counts of 20 or fewer in the premaxilla–maxillary, vomeropalatine, and pseudodentary rows; 136 species (or 86%) have 25 or fewer. At the upper end of the range are the ichthyophiids *Ichthyophis elongatus* and *Caudacaecilia nigroflava,* both with about 30 teeth in the premaxilla–maxillary, vomeropalatine, and pseudodentary rows (Taylor, 1968).

In his original description of the Seychellean species *Praslinia cooperi,* Boulenger (1909: 292–293) noted that "... the teeth are more numerous than in any other known genus of Caeciliids ... [with] 40 to 48 teeth on each side of the upper jaw, and about as many in the outer mandibular series on each side; about 45 inner mandibular teeth altogether." Close examination of Boulenger's illustration (1909, fig. 1b) shows a unilateral count of 47 premaxilla–maxillary teeth, 40 vomeropalatine teeth, and 47 or 48 and 25 or 26 in the labial and lingual pseudodentary rows, respectively. Subsequent authors report comparably high counts; Parker (1941) cited 36–48 premaxilla–maxillary teeth, and Nussbaum and Wilkinson's (1989: 37) diagnosis of this monotypic genus includes "teeth small, uniform in size, more than 50 per row, except for the splenials." No data on the diameter and height are available in the literature; measurements made with an ocular micrometer of the teeth illustrated by Boulenger (1909, fig. 1b) yield a tenuous estimate of an apicobasal height of 0.17 mm, which is in the range observed for *Eocaecilia micropodia* teeth. Thus *P. cooperi* is the only known living caecilian with teeth in equivalent numbers and size as those in *E. micropodia,* and it is therefore regrettable that little is known of the dietary habits of this species; Nussbaum (1984) was unsuccessful in his earlier attempts to collect this apparently rare caecilian but has since reported (personal communication) collecting several specimens.

The Cretaceous caecilian *Rubricacaecilia monbaroni* appears to have had fewer teeth in the lower jaw than *Eocaecilia micropodia*—with 28 in the labial pseudodentary row and only two in the lingual (splenial) row (Evans and Sigogneau-Russell, 2001). Yet, like *E. micropodia,* the teeth of *R. monbaroni* are very small, with a basal diameter of about 0.3 mm (estimated from Evans and Sigogneau-Russell, 2001, fig. 4B). Although the base of the crowns are thus about twice that of *E. micropodia,* both fossil taxa have, by comparison to those of most living caecilians, diminutive dentitions.

Postcranial Skeleton

Overview. Postcranial bones are abundant among the available materials of *Eocaecilia micropodia*; most elements, with the exception of the pelvis, manus, and pes, are represented by multiple specimens. The relative completeness of this assemblage provides a sound basis for a reconstruction that depicts the relative size of the skull, vertebrae, and limbs (Fig. 31).

Although the number of vertebrae cannot be precisely determined on the basis of available material, there is sufficient evidence from several specimens, reviewed below, that the presacral region of *E. micropodia* was elongate, as in modern caecilians. A distinct tail was present, comparable to the postcloacal region of rhinatrematids, ichthyophiids, and uraeotyphlids (Nussbaum, 1977; Nussbaum and Wilkinson, 1989). Relative to the size of the vertebrae, the limb bones and girdles are diminutive.

Postcranial Axial Skeleton

In Recent caecilians, the vertebral column can be most simply described as being composed of an atlas, a large number of trunk vertebrae, and, in taxa in which postcloacal vertebrae occur, caudal vertebrae. The subtly gradational nature of the axial column poses a challenge to distinguishing vertebral regions. In a study of *Hypogeophis rostratus,* Lawson (1963: 271) concluded that "with the exception of the first or atlas . . . , [the vertebrae] are essentially of a uniform structure without regional variation." In contrast, Wake (1980a) identified regional differences in both structure and growth allometry in *Dermophis mexicanus, Ichthyophis glutinosus,* and *Typhlonectes compressicauda* that characterize "cervical," midbody, and posterior vertebrae. Although Taylor (1977) initially suggested that modifications of the anterior four or five vertebrae were sufficiently distinctive to designate them cervicals, Wake (1980a) demonstrated on the basis of the taxa included in her study that the number of distinctive anterior vertebrae is much larger. The first 20 vertebrae typically possess a longitudinal nuchal keel; short, widespread parapophyses; and broad, relatively flat pre- and postzygapophyses; Wake suggested that these "cervical" features are related to stabilizing and elevating the head during burrowing.

Comparison of vertebral regions in *Eocaecilia micropodia* with those of modern caecilians cannot be undertaken with certainty throughout the axial skeleton because no specimen preserves a complete vertebral column. Nonetheless, the atlas is well known, and the identity of the second vertebra (axis) and other vertebrae associated closely with the atlas is secure; these are referred to as postatlantal (PA) vertebrae, rather than cervical (C), for they largely lack those features that characterize the "cervicals" of living caecilians (fide Wake, 1980a). If the precise location of the shoulder girdle along the postatlantal vertebral column were known, a cervical region might be securely identified. The shoulder girdle and forelimb elements in MCZ 9169 (Fig. 35) are disarticulated and not certainly in place with respect to the associated vertebral column. Lacking evidence in any specimen of enlarged ribs on postatlantal vertebrae, which might also indicate the placement of the shoulder girdle, the length of the "cervical" region remains moot. A sacral region is known, as is the caudal series. The fact that the analysis and description of the vertebral column is based on several incomplete specimens removes the possibility of using within-column variations in size as a useful descriptor.

Wake (1970: 33) expressed the opinion that "without fossil evidence, identification of the centrum of modern amphibians [frogs, salamanders, and caecilians] with the pleurocentrum of fossil forms is not warranted." *Eocaecilia micropodia* provides the desired evidence, for caecilians at least, by possessing small, crescentic intercentra. The gymnophione centrum thus appears to represent a pleurocentrum. Intercentra occur in specimens in which the atlas, axis, and other vertebrae of the postatlantal region are preserved in articulation. Intercentra also occur in a specimen interpreted as representing the anterior dorsal region. The absence of intercentra in other series of vertebrae could possibly reflect regional variation, but postmortem loss cannot be ruled out.

Atlas. The atlas, represented in several

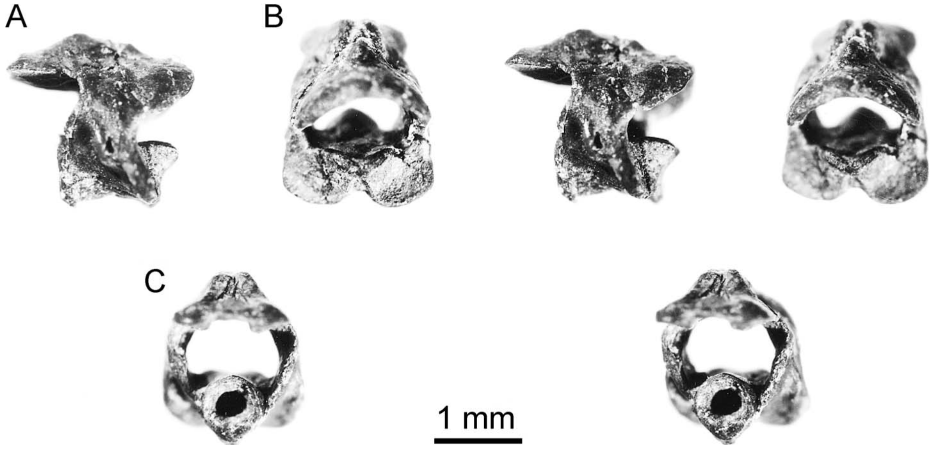


Figure 32. The atlas of *Eocaecilia micropodia* (MCZ 9231) in (A) lateral, (B) anterior, and (C) posterior views (stereophotographs).

specimens (MCZ 9167, 1969, 9171; MNA V8059, V8066), is best preserved in MCZ 9231 (Fig. 32), which serves as the primary basis for the following description. The length of the atlas centrum, excluding the pyramidal interglenoid tubercle that prolongs the floor of the neural canal rostrad (Fig. 32A), is 1.5 mm. An interglenoid tubercle, a feature found in salamanders (Francis, 1934), certain microsaurs (Carroll and Gaskill, 1978, figs. 115, 116), and albanerpetontids (McGowan, 1998), is not known to be present in any Recent gymnophionan (Wake, 1970). The two condylar facets (or cotyles) extend from the ventrolateral aspects of the interglenoid tubercle to the lateral margin of the centrum. The dorsomedial part of each condylar facet thus faces ventrolaterally and the lateral part rostrad (Fig. 32B). The anterior width of the centrum measured across the facets is 1.8 mm. On the ventral surface of the centrum is a distinct notch between the condylar facets; a rounded, median keel occupies the posterior ventral half of the centrum. A small, presumably vascular foramen occurs on the lateral side of the centrum. The posterior end of the centrum (Fig. 32C), excavated by a deep notochordal fossa, is 0.8 mm wide and 0.85 mm high.

No evidence exists of a diapophysis. MCZ 9169 (Fig. 33A) reveals that the head of the first rib articulated with the

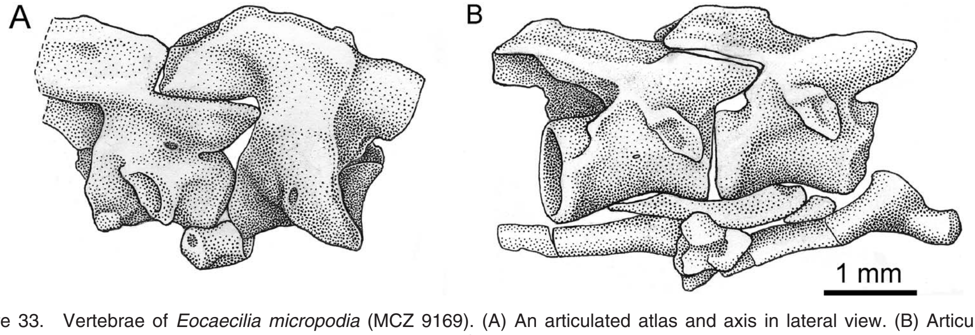


Figure 33. Vertebrae of *Eocaecilia micropodia* (MCZ 9169). (A) An articulated atlas and axis in lateral view. (B) Articulated vertebrae interpreted to be the sixth and seventh vertebrae of the vertebral column, lateral view.

atlantoaxial intercentrum and that the tuberculum articulated with the axial diapophysis. A foramen on the lateral surface of the base of each pedicle is a feature that is also present in other postatlantal vertebrae of *Eocaecilia micropodia.* A comparably situated intravertebral foramen, which communicates with the neural canal, occurs in the atlas in at least some Recent taxa: *Gymnopis multiplicata* (MCZ 29265) and *Dermophis mexicanus, Ichthyophis glutinosus,* and *Typhlonectes compressicauda* (Wake, 1980a). A foramen on the medial wall of the pedicle of the atlas and the following four postatlantal vertebrae in the holotype of *E. micropodia* (MNA V8066, Fig. 34) is evidence of a complete passage through the pedicle; therefore, the canal is most likely an intravertebral foramen for neuronal egress (rather than a vascular channel into the bone). Anteriorly the laminae (i.e., the dorsal roof of the neural arch) extend as an archlike prolongation over the interglenoid tubercle and probably closely approached the margin of the foramen magnum. The anteroposterior length of the arch from the anterior margin of the laminae to the tips of the postzygapophyses is 2.3 mm, or 0.8 mm longer than the length of the centrum. The postzygapophyses, rather than being distinct processes, are united across the midline by a thin lamina of bone. The orientation of the postzygapophysial facets is nearly horizontal; they face only slightly laterally. The central floor of the neural canal is relatively flat, but the laminae composing the roof are distinctly arched; the neural canal is thus hemitubular, in contrast to the condition typical of Recent caecilians in which the neural canal is tubular in cross section (for additional details of the atlantal neural canal, see the description of MNA V8066 below). The atlantal spinous process is represented only by a low tubercle; the spinous process appears to bifurcate posteriorly into a pair of faint ridges that extend posterolaterally onto the postzygapophyses.

The atlas of *Eocaecilia micropodia* resembles the incomplete atlas of *Rubricacaecilia monbaroni* from the Early Cretaceous in the presence of an interglenoid tubercle, the transverse orientation of the condylar facets, and the placement of a conspicuous neural foramen at the base of the pedicle (cf. Fig. 32; Evans and Sigogneau-Russell, 2001, figs. 4, 5A–C). Evans and Sigogneau-Russell (2001: 268, fig. 5A) interpreted the articular surfaces of the condyles in *R. monbaroni* as extending across the midline, implying an unusual condition in which the occipital condyles would be spaced very closely together. In *E. micropodia,* the facets are narrowly separated dorsally, but more widely separated ventrally by a distinct notch (Fig. 32B).

Vertebral Regions. Vertebrae and ribs are associated with many specimens of *Eocaecilia micropodia,* but relatively few are articulated in series (MCZ 9169; MNA V8055, V8062). Although no specimen preserves a complete presacral column, there is sufficient evidence from associated elements (the atlas, pectoral girdle and forelimb, and hindlimb) that five vertebral regions are identifiable: postatlantal, dorsal (including possibly middorsal), posterior dorsal, sacral, and caudal. With the exception of the caudal series, regional variations in structure are subtle.

Postatlantal Region. The holotype of *Eocaecilia micropodia* (MNA V8066, Fig. 34) preserves as an associated series the atlas, axis, and three additional postatlantal vertebrae (PA3–PA5). The vertebrae are damaged and slightly disarticulated postmortem; the left half of the neural arches are missing, probably as the result of the quarrying process. The length of the atlas centrum is 1.5 mm. Other centra are slightly longer; the axis and PA4 are 1.6 mm, and PA5 is 1.7 mm (the length of PA3, as preserved, is 1.5 mm, but this is probably an artifact). Overall vertebral lengths (measured from the rostral extremity of the prezygapophysis to the caudal extremity of the postzygapophysis) could only be estimated on PA2 and PA4 and are in the range of 2.2–2.3 mm.

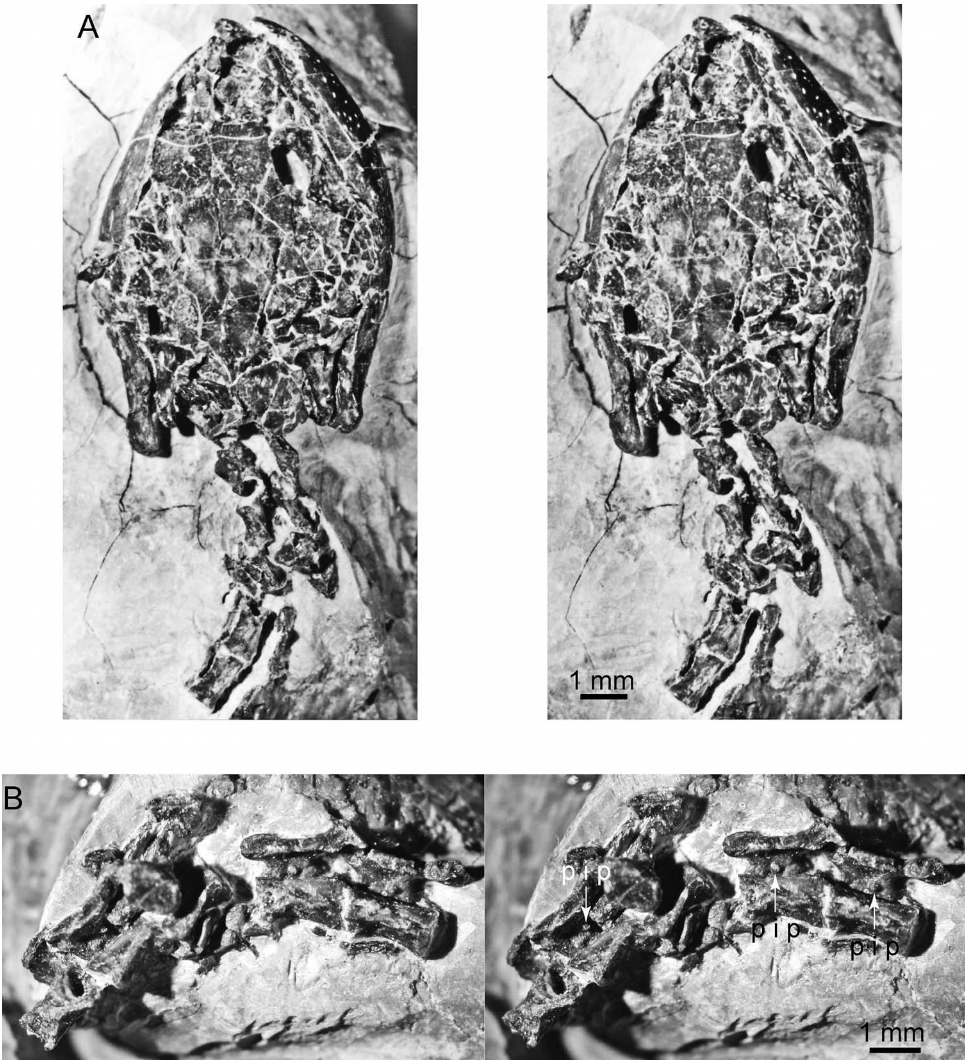


Figure 34. (A) The holotype skull, atlas and associated postatlantal vertebrae of *Eocaecilia micropodia* (MNA V8066) at the completion of the initial stage of preparation and before removing the skull from the matrix. (B) Enlarged view of the vertebrae after detailed preparation; rostral is to the left. The loss of the left half of the neural arches exposes the right pedicles in medial view, which reveals an internal process on the medial surface of each pedicle (p i p, white arrows). Anteroventral to each process is the internal ostium of the intravertebral foramen (stereophotographs).

The loss of the left half of the neural arches of the atlas, axis (PA2), PA4, and PA5 (on PA3 the arch is completely broken away) exposes the internal surface of the neural canal. The medial openings of intravertebral foramina are evident on all pedicles. Bilaterally, along the pedicle–centrum junctions, the floor of the neural canal of the atlas is excavated by a deep, longitudinal sulcus. The rostral end of the sulcus begins at the transverse level of the medial opening of the intravertebral foramen; the sulcus extends caudally to the posterior end of the atlantal centrum. The two sulci together compose about two-thirds of the breadth of the neural canal;

in the midline, the floor of the neural canal is slightly convex, except in the region of the interglenoid tubercle where the surface is slightly concave. Comparable sulci are exhibited on the axis–PA5, although they differ by being transversely narrower and by extending the full length of the pedicle–centrum junction.

The most extraordinary feature of the neural canal is the presence of a bony process that projects medially from the internal surface of each pedicle (Fig. 34B). On the atlas, the process is situated directly posterior to the intravertebral foramen and near the pedicle–centrum junction; the atlas from another specimen shows the same feature (Fig. 15D). On the axis (PA2), the process is likewise posterior to the intravertebral foramen, but both the process and foramen are more dorsally positioned, approximately halfway up the internal face of the pedicle; the process, which is 0.2 mm in length, tapers to an apex and is directed medially and somewhat ventrally. The width of the neural canal of the axis is estimated to be 0.9 mm, but the two processes would reduce the space available for passage of the spinal cord to about 0.5 mm. On PA4 and PA5, the intravertebral foramina lie close to the pedicle–centrum junction, and the processes are situated posterodorsal to the foramina.

Internal processes within the neural canal of anterior vertebrae have not previously been reported in any Recent gymnophionan. A review of atlantal specimens in the MCZ Herpetology collection reveals that comparable processes do occur in some taxa but are apparently not common. Representatives of Ichthyophiidae (*Ichthyophis glandulosus,* MCZ 14003), Typhlonectidae (*Typhlonectes compressicauda,* MCZ 24524), and Scolecomorphidae (*Scolecomorphus kirkii,* MCZ 12234, 27120) exhibit pedicles with smooth internal surfaces. Similarly, a number of caeciliid species are without processes: *Boulengerula boulengeri* (MCZ 12309), *Dermophis mexicanus* (MCZ 12122), *Gegeneophis ramaswamii* (MCZ 29460), *Geotrypetes seraphini* (MCZ 3424), *Gymnopis multiplicata* (MCZ 29265), *Hypogeophis rostratus* (MCZ 48935), and *Oscaecilia ochrocephala* (MCZ 14817). In species of the caeciliid genus *Schistometopum,* however, processes are present. In *S. gregorii* (MCZ 20057, 20070) distinct digital processes are directed anteromedially, whereas in other specimens (MCZ 20055, 20146) the processes are less prominently developed and in some cases are low rugosities. Processes are also present in *S. thomensis* (MCZ 29450). In one specimen of *S. gregorii* (MCZ 20056), dry preservation of soft tissues reveals that the processes are anchor points for a connective tissue suspensory ligament (very likely the pia mater, as in the denticulate ligament) that passes to the ventral surface of the spinal cord. A specimen of the uraeotyphlid *Uraeotyphlus oxyurus* (MCZ 9484) bears low tubercles that are somewhat rugose.

Comparable structures occur in some snakes (e.g., boids, *Python,* Romer, 1956, fig. 129I; *Boa constrictor,* MCZ 13019; colubrids, *Coluber constrictor,* MCZ 160014; and elapids, *Ophiophagus hannah,* MCZ 67054) as a delicate, longitudinal ridge that runs anteroposteriorly along the medial aspect of the pedicle at a level comparable to that of the caecilian process. Illustrations of the atlas of a Cretaceous caecilian, *Rubricacaecilia monbaroni,* and the Recent form *Ichthyophis mindanaoensis* (Evans and Sigogneau-Russell, 2001, fig. 7B, E) might be interpreted to depict similar structures, but in neither case are the features comparable (S. E. Evans, personal communication).

MCZ 9169 preserves an atlas, axis (Fig. 33A), and at least four additional vertebrae in a more or less articulated series. The atlantal centrum is 1.3–1.4 mm in length, very slightly shorter than in MCZ 9231, but otherwise similar to the latter in almost all details, including the presence of both spinal and vascular foramina. The exception is the spinal region. In place of the single, median tuberosity observed in MCZ 9231, the spinous process is a very narrow, low, elongate ridge (the nuchal keel of Recent gymnophionans; Wake, 1980a), flanked on either side by a small tuberosity.

The axial centrum of MCZ 9169, 1.6 mm in length, is separated from the atlas by an intercentrum that bears a posterolaterally directed parapophysis. Although the first rib is missing, the facet for the rib head is round and relatively large (0.4 mm diameter). The posteroventral margin of the axial centrum bears a raised parapophysial demifacet for the second rib (also missing). The axial diapophyses are more massive and project farther from the pedicle than any of the more caudal diapophyses; oval in cross section (diameters 0.7, 0.3 mm), the long axis is oriented obliquely (the caudal end is superior, the rostral end inferior). Above the diapophysis is a foramen, probably serving the same function as that in the atlas, but situated more dorsally on the pedicle. The spinous process, or nuchal keel, is a higher ridge than that on the atlas. A pair of tubercles, comparable to those that flank the spinous process anteriorly on the atlas, are posteriorly positioned on the dorsum of the postzygapophyses. The articulation between the atlas and axis confirms that the midline lamina of bone between the atlantal postzygapophyses intimately overlies the anterior part of the axial neural arch.

The third and fourth postatlantal vertebrae, disarticulated and somewhat displaced, are obscured by fractures and overlying bone fragments. Features that are evident (very low nuchal keel, bony lamina linking the postzygapophyses, orientation of the diapophyses) appear to be comparable to those of the axis. The centra, however, are longer (1.7–1.8 mm). An intercentrum is preserved along the anteroventral margin of PA3. A limb bone with a shaft diameter 0.4 mm and length of over 2 mm is associated with PA4; although the ends are somewhat crushed, the appearance most closely resembles a radius.

Proximal rib fragments associated with a skull (MCZ 9242, Fig. 12) are likely to be derived from the postatlantal region. The capituli and tuberculi, which are well separated, expand toward each terminus and bear a circular facet.

The postatlantal region, reconstructed from MNA V8066 and MCZ 9169, can only be distinguished on the basis of a single feature: spinal nerves traverse foramina through the pedicles on the atlas, axis, and at least the next three vertebrae, whereas on anterior dorsal vertebrae, the egress of spinal nerves appears to have been around the posterior margin of the pedicle. Otherwise, postatlantal vertebrae of MCZ 9169 are structurally gradational with those of the anterior dorsal region. Rostrocaudally, the length of centra increases from 1.4 mm on the atlas to 2.1 mm on the 11th vertebra, the angle of zygapophysial facets shifts from nearly horizontal to about 45°, diapophyses are reduced, and ribs become shorter and more slender, with more closely spaced capituli and tuberculi.

Anterior Dorsal Region. The next two vertebrae in the MCZ 9169 series are articulated and well preserved (Fig. 33B) and are separated from PA4 by a gap of approximately one vertebral length. Two lines of evidence support our interpretation that the gap represents a missing vertebra (or possibly vertebrae), and that the two next vertebrae are probably the sixth and seventh. First, the two vertebrae are lying on their left side, whereas PA4 is lying on its right side, indicating that the continuity of the series has been substantially disrupted. Second, the anterior vertebra of the pair is unlikely to represent PA5 because it lacks a spinal foramen in the pedicle, which is known to be present in PA5 of the holotype.

For purposes of the present description, the pair is designated as the sixth and seventh vertebra (Fig. 33B). The notochordal centra are 1.7–1.8 mm in length, with concave lateral and ventral surfaces. The pedicles are mounted anteriorly on the centrum. Both lack spinal foramina traversing the pedicles. The posterior margins of the pedicles are deeply incised for passage of the spinal nerves; the intervertebral "foramen" is therefore situated over a single centrum, rather than being truly intervertebral. The transition from the condition in which spinal nerves pass through foramina in the pedicles to the condition in which they pass behind the pedicles appears to take place at vertebra 6. Variability of this feature is known in Recent taxa, with the transition occurring between the 15th and 21st vertebra in *Dermophis mexicanus,* and between the fifth and 11th in *Typhlonectes compressicauda* (Wake, 1980a). A small tubercle (anapophysis) along the posterior margin of the pedicle lies in close relation to the prezygapophysis of the following vertebra, and would seem to support the zygapophysis from below. The diapophysial facets are comparable in orientation and dimensions (0.8 and 0.4 mm along the long and short axes, respectively) to those on the axis, but they are not as protuberant. Rib heads in this region appear to have articulated with parapophysial hemifacets developed on the margins of adjoining centra anteroventral to the diapophysis. The postzygapophyses are interconnected by a bony lamina; zygapophysial facets appear to be less horizontally inclined than in more rostral vertebrae. The length of the vertebrae, measured between the tips of the pre- and postzygapophyses, is 2.7 mm. Nuchal keels appear to be low; the spinous process is represented primarily by an elevated area between the dorsal surfaces of the postzygapophyses.

Three ribs preserved on the right side of the sixth and seventh vertebrae appear to be associated with these vertebrae, but they are displaced from their articulations (Fig. 33B). The most anterior rib, which is fractured but complete, measures 3 mm from head to distal tip; the proximal shaft has a diameter of 0.38 mm and the centers of the capitular and tubercular facets are 0.8 mm apart. The successive ribs appear to be slightly more slender, but the proximal ends are unexposed, and the distal ends broken.

An isolated vertebra, lying less than 2 mm away from the atlas axis of the MCZ 9169 series, appears to have characteristics intermediate between the sixth and seventh vertebrae and another articulated series of four vertebrae. The isolated vertebra, tentatively identified as the eighth, has a centrum length of 1.8 mm, a pre- to postzygapophysial length of 2.8 mm, and a smaller diapophysial facet (0.5 and 0.2 mm along the long and short axes, respectively; the long axis is less vertically inclined). The pre- and postzygapophysial facets are inclined with respect to the horizontal by an estimated 20°.

A series of four articulated vertebrae, tentatively identified as the ninth through 12th, is characterized by longer centra (2.1 mm) and very faint nuchal keels, with a slight excrescence between the dorsal surfaces of the postzygapophyses representing the spinous process. Crescentic intercentra are present (anteroposterior thickness, 0.3 mm). The rib heads appear to have articulated with demifacets on adjacent superolateral margins of the ends of the centra. There are no diapophysial processes as such. Rather, tuberculi appear to have articulated in small, circular depressions (0.2 mm diameter) on the side of the pedicle, the centers of which are located 0.5 (on vertebra 11) to 0.6 mm (on vertebra 8) dorsocaudally from the capitular demifacets. Immediately posterior to each depression is a low tuberosity. Other features are comparable to those seen in PA5 and vertebrae 6 and 7, with the exception of the inclination of the zygapophysial facets. Crushing and distortion obviate precise measurement of facet angle, which is estimated to be at least 30° but not more than 45°. The ribs are shorter and more slender than those of more anterior vertebrae, and the capitulum and tuberculum are closer together. Ribs 10 and 11, the most completely preserved in the series, are 2.3 and 2.45 mm long and have proximal shaft diameters of about 0.3 mm; the centers of the capitular and tubercular facets of rib 11 are separated by a distance estimated to be about 0.5 mm.

Two additional isolated vertebrae lie within several centimeters of the anterior dorsal series, but neither is sufficiently well preserved to be informative.

Two centimeters from the anterior dorsal vertebrae described above, a coiled but articulated series of 13 vertebrae is associated with shoulder girdle and forelimb elements (Fig. 35A). The principal features of more anterior dorsal vertebrae are maintained in this series, with only slight changes in proportions. The series can thus reasonably be interpreted as a continuation of the dorsal column, thus representing vertebrae 13 through 25. Measured lengths (in some cases estimated) of 10 centra range from 1.9 to 2.3 mm, with a mean of 2.12 mm, which is comparable to that observed in the anterior dorsal series; variations in length are random along the series and therefore appear to be due to preservational artifact. Total vertebral length, measured from the anterior end of the prezygapophyses to the posterior end of the postzygapophyses, appears to increase slightly. Measured or estimated lengths of seven specimens range from 3 to 3.4 mm, with a mean of 3.2 mm (the greatest overall length that can be measured in the anterior dorsal series is 2.9 mm at vertebra 8). An increase in size of the crescentic intercentra intercalated between the ventral margins of the notochordal centra appears to compensate for the increase in overall vertebral length when the length of the centra remains the same. Intercentra are 0.4–0.5 mm in anteroposterior thickness (versus 0.3 mm in the anterior dorsal region). As in more anterior dorsal vertebrae, the lateral and ventral aspects of the vertebral centra are concave; a faint median crest extends longitudinally along the ventral surface but does not reach the anterior or posterior ends. The orientation of zygapophysial facets in many cases is altered by postmortem plastic deformation; on well-preserved, symmetrical vertebrae, the facets lie at about 30° to horizontal. Spinous processes are absent; a narrow, low median crest extends longitudinally from a slight tuberosity between the bases of the prezygapophyses to a more prominent tuberosity between the postzygapophyses. The ribs associated with the fifth and twelfth vertebra of this series are slightly longer (length 2.65–2.7 mm) than those of more anterior dorsal ribs but are comparable in proximal shaft diameter (ca. 0.3 mm) and in the manner with which they articulate with the centra.

Middorsal Region. In addition to the postatlantal and anterior dorsal vertebrae described above, MCZ 9169 also includes two isolated series of more or less articulated vertebrae (on a separate block of matrix) that lack any direct evidence of axial position. The shorter series of four damaged vertebrae provides little useful information. The longer series represents 18 vertebrae, although the 12th was lost during the quarrying process. The vertebrae are morphologically similar, particularly in rib size and articulation, to those of the anterior dorsal series, with the exception that there is no indication of a median nuchal keel. The lengths of the centra, however, range from 1.9 to 2.0 mm (mean 1.95 mm), which is about 0.25 mm shorter than the lengths of the centra of the last several vertebrae in the anterior dorsal series. If MCZ 9169 comprises a single specimen, the middorsal region is morphologically similar to the anterior dorsal region save for shorter vertebrae and would be comparable to the gradual decrease in centrum and neural arch length in the middorsal and posterior dorsal regions of *Dermophis mexicanus* (Wake, 1980a). Alternatively, the series of 18 could represent the dorsal region of a slightly smaller individual.

Posterior Dorsal, Sacral, and Caudal Vertebrae. Right and left hindlimb elements are closely associated with a series of vertebrae in MNA V8062 (Fig. 36) and thus provide the evidence for identifying posterior dorsal and caudal vertebrae. Var-

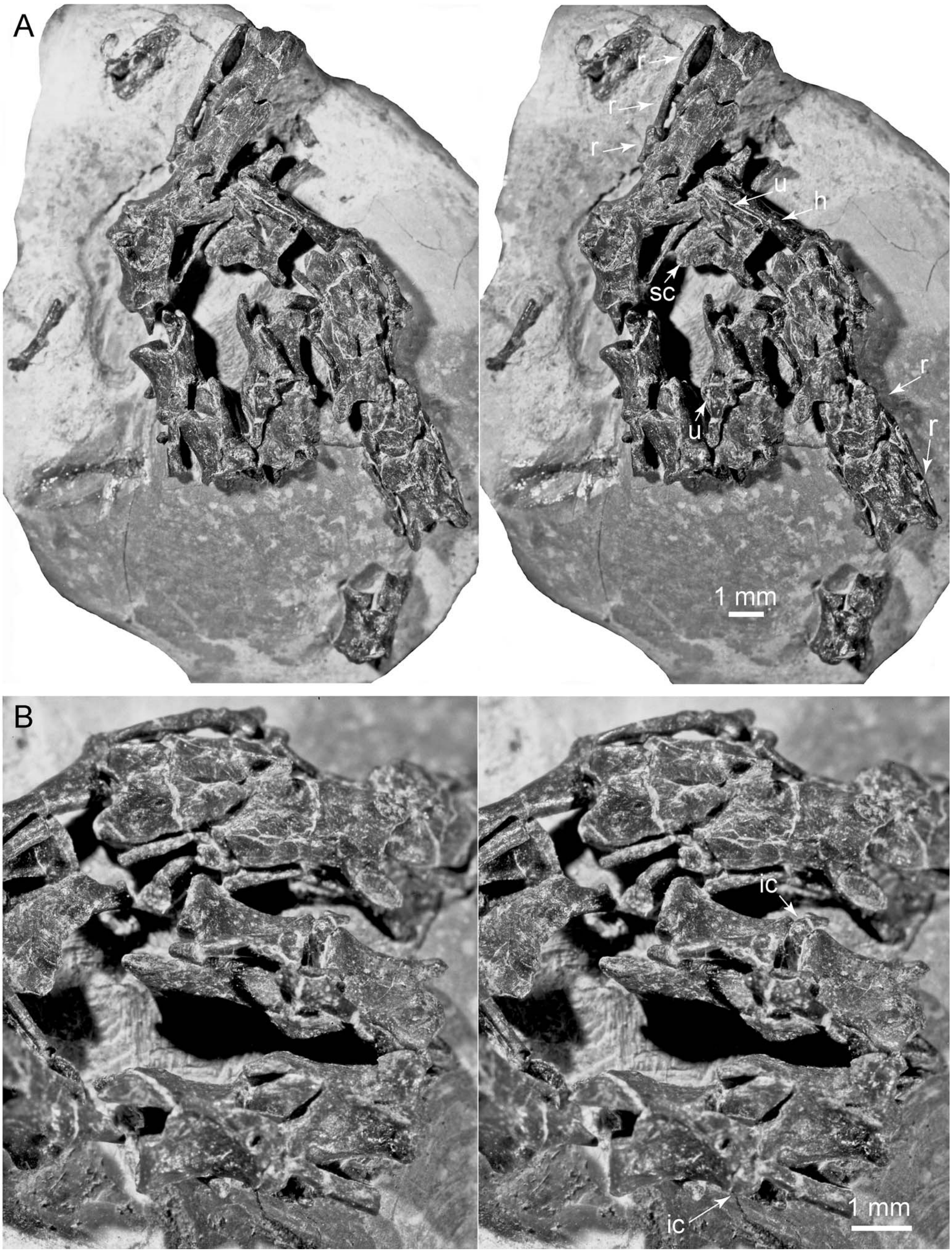


Figure 35. (A) Anterior dorsal vertebrae of *Eocaecilia micropodia* (MCZ 9169) associated with forelimb elements: scapulocoracoid, humerus, and ulna. (B) An enlargement to show the intercentra and details of the vertebrae (stereophotographs).

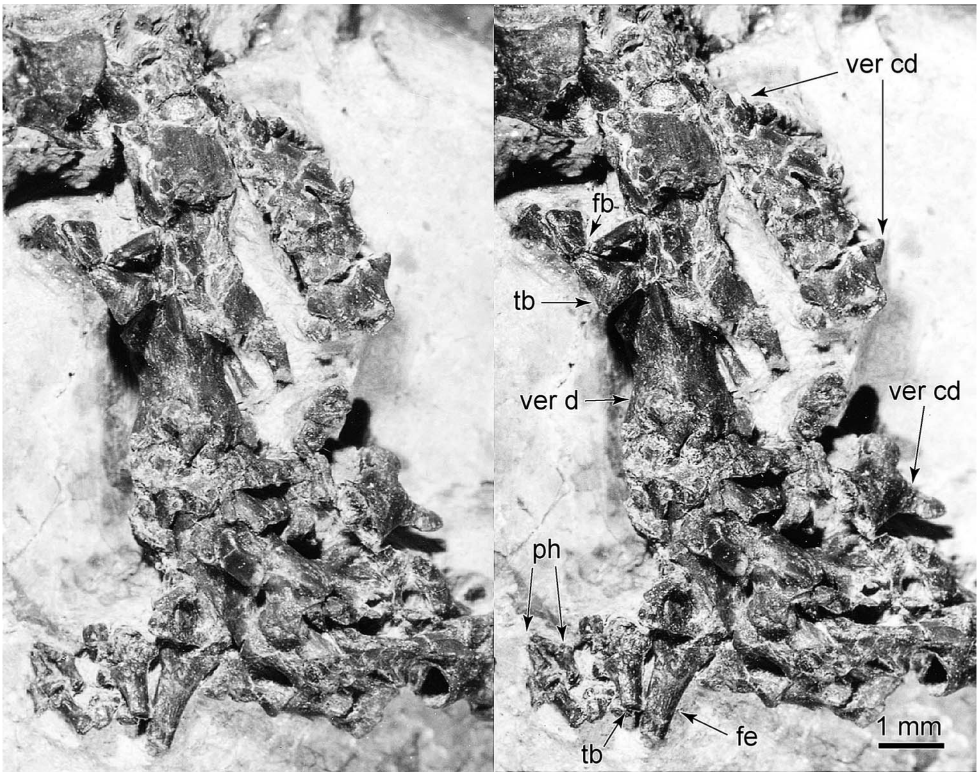


Figure 36. Posterior dorsal and caudal vertebrae, partial femur and ?fibula, and tibia and phalanges of *Eocaecilia micropodia* (MNA V8062; stereophotographs).

iable crushing and distortion of the entire series, however, substantially obscures many structural details. Only one (incomplete) rib is preserved with the posterior dorsals; this slender rib appears comparable to those of other dorsals, with the centers of the tuberculum and capitulum spaced 0.4 mm apart and a shaft diameter of 0.2 mm. The two vertebrae that are immediately adjacent to hindlimb bones are tentatively identified as sacrals. A characteristic sacral feature is the large size of the diapophyses, in contrast to those on posterior dorsal vertebrae that precede them (only four of which are sufficiently preserved to be useful for comparative analysis). In addition to the large size of the tubercular (diapophysial) facets, sacrals appear to differ from posterior dorsal vertebrae in being slightly shorter in overall length and narrower in interzygapophysial width. These features are preserved on the second sacral; the first sacral is largely crushed, and only posterior interzygapophysial width is preserved. Sacral centra are approximately 1.4 mm in length, whereas the centrum of the penultimate posterior dorsal is 1.7 mm; the third vertebra anterior to the penultimate has a centrum length of 1.8 mm. In typical dorsal vertebrae, tubercular facets are flush with the sides of the pedicles; on the putative sacrals, tubercular facets are elevated from the lateral surface of the pedicles and are thus borne on low diapophyses. On two posterior dorsals, the transverse distance between the lateral margins of the postzygapophyses is 1.4 mm, compared with about 1 mm on the two sacrals.

Proximal caudals in MNA V8062 appear

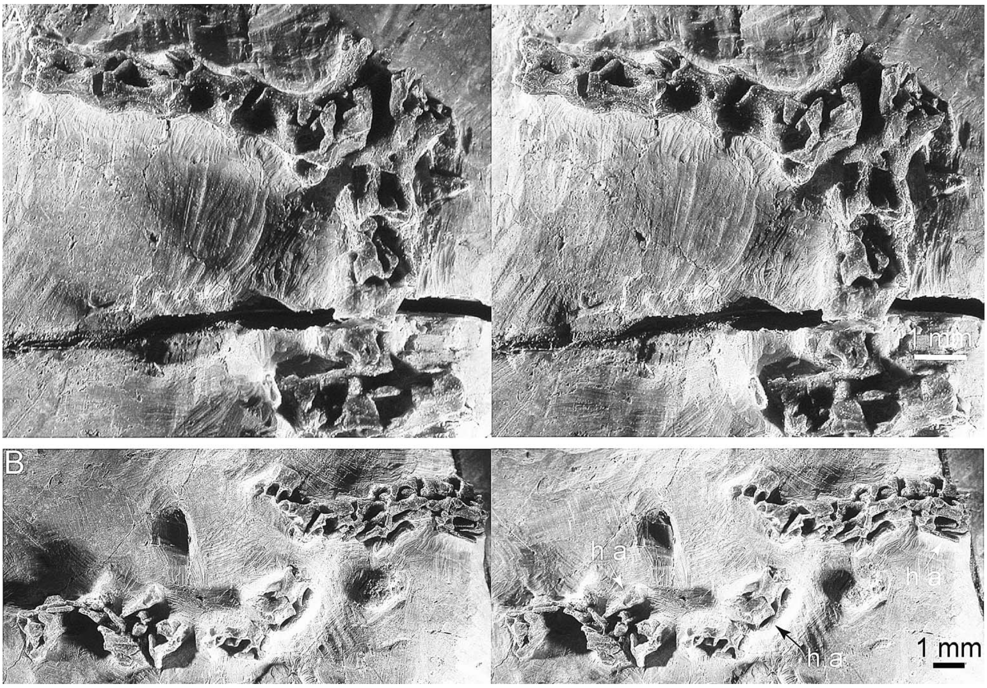


Figure 37. (A) Dorsal vertebrae, (B) caudal vertebrae of *Eocaecilia micropodia* (MNA V8055; stereophotographs).

to have centrum lengths comparable to those of the sacrals (1.4 mm) but have zygapophyses that project dorsally, in contrast to more horizontally inclined processes of dorsal and sacral vertebrae. Distal caudal vertebrae are represented by a single, disarticulated vertebra and an attenuating series of approximately eight vertebrae. The single vertebra has a centrum length of 1.1 mm and bears a prominent, posteriorly recurved, tapering spinous process. The terminal series of vertebrae is very damaged but exhibits a diminishing length gradient of the centra from about 0.7 to 0.4 mm.

MNA V8055 preserves some 30 vertebrae, a number of which occur in articulated series. One series of 12 vertebrae appears to be continuous, although the continuity is disrupted between the sixth and seventh by a disarticulation to a right-angle bend (Fig. 37A). A few slender rib fragments are associated, and the lengths of the centra diminish from about 2 mm anteriorly to 1.55 mm posteriorly; this series appears to represent the dorsal or very possibly posterior dorsal region. Five isolated vertebrae, including two that are articulated, also appear to be dorsals; other isolated vertebrae are too imperfectly preserved to be useful. Caudal vertebrae (Fig. 37B) are represented in a more or less articulated series of 10, with the lengths of the centra diminishing from 1.3 mm on the most anterior to approximately 1 mm on the penultimate. The zygapophyses on the anterior three are small and set close to the midline; distal to the fifth vertebra, zygapophysial articulations are reduced to a simple overlap of a lamina with that of the vertebra behind. Several well-developed haemal arches are associated with this series. The haemals are conventional in structure, tapering from a broad, perforate base (0.6 mm in width) to the distal apex (1.7–1.8 mm in overall length). Among living caecilians, haemal arches are known only in the rhinatrematid *Epicrionops* (Wake, 1987b, 2003, fig. 22A; Carroll et al. 1999, fig. 6A). The last five vertebrae in this series bear a posteriorly recurved, tapering spinous process comparable to those present in the terminal series of caudals in *Epicrionops bicolor* (Wake, 2003, fig. 22A). The caudal series of MNA V8055 is incomplete, however. The terminal vertebrae of *Eocaecilia micropodia,* known only in MNA V8062 (Fig. 36), exhibit recurved processes that decrease in size and are lost altogether as the vertebrae are reduced to tiny cylindrical structures.

Comparative Anatomy of the Vertebral Column. The vertebral column of *Eocaecilia micropodia* differs from those of Recent gymnophionans in the presence of intercentra, an interglenoid tubercle on the atlas, and most notably in the absence of the various elaborate processes that occur in modern forms. Gymnophionans typically possess a longitudinal keel or process along the ventral aspect of the centra, anteriorly projecting parapophysial processes, and postzygapophyses that are interconnected by an extension of the laminae which overlay the following vertebra; neural spines are absent except on anterior vertebrae, where there is a longitudinal nuchal keel. Of these features, *E. micropodia* possesses the postzygapophysial interconnection and overlap, but only the faintest representations of ventral and nuchal keels. With the exception of the postatlantal region, in which there are distinct diapophyses, costal tubercles articulate with facets that are only slightly raised from the surface of the pedicles. The first rib has a capitular articulation on the atlantoaxial intercentrum, but other capituli appear to articulate with pairs of hemifacets developed on adjacent centra, with no elaboration of parapophyses or other processes. Intravertebral neural foramina are present on the atlas and at least the following four vertebrae. Last, the prominent, posterodorsally reflected spinous processes on distal caudal vertebrae of *Eocaecilia* are a feature shared with the rhinatrematid *Epicrionops* (Wake, 2003, fig. 22A).

The vertebral structure of *Eocaecilia micropodia* appears to be generally more primitive than that represented by eight isolated vertebrae of an early Cretaceous caecilian, *Rubricacaecilia monbaroni,* described by Evans and Sigogneau-Russell (2001). *Eocaecilia micropodia* does share certain features with *R. monbaroni*: amphicoelous centra, an increase in centrum length from the postatlantal into the dorsal series, a low nuchal keel on anterior vertebrae, and circular, low diapophyses. However, *E. micropodia* does not exhibit any parapophysial processes or basapophyses, which in *R. monbaroni* would seem to represent an incipient stage in the distinctively gymnophionan elaboration of these structures. Furthermore, the midventral region of the centra in *R. monbaroni* is narrowed to a keellike ridge, of which there is only a faint indication in *E. micropodia.*

Had *Eocaecilia micropodia* attained the distinctively high vertebral counts of modern caecilians? Published estimates of the range of vertebral counts across living taxa vary slightly. Without citing specific taxa, Nussbaum and Naylor (1982) state that vertebral numbers in gymnophionans range from 70 to 283, whereas Wake (1980a) and Duellman and Trueb (1986) cite postatlantal vertebral counts of 95–285. Most recently, Wake (2003) cited 86–285. Taylor's (1968) monograph, however, reports specific counts for individual species; the lowest occur among various specimens of *Epicrionops* (e.g., *E. bicolor subcaudalis,* 75–78; *E. lattivittatus,* 78) and the highest in *Oscaecilia bassleri* (273). Given that vertebral numbers vary intraspecifically (Taylor, 1968), a more precise determination of the range would seem to offer little utility, especially in the context of a comparison with *E. micropodia,* for which a vertebral count can only be estimated. The most complete specimen (MCZ 9169) comprises five series of more or less articulated vertebrae, representing the postatlantal, anterior dorsal, and most probably, dorsal regions. The total number of vertebrae is 49 if several associated but isolated vertebrae are included. MNA V8062 provides an imperfect representation of the sacral and caudal regions. On the assumption that the identification of two sacral vertebrae is correct (these vertebrae are most closely associated with the hindlimb elements), there are at least 13 caudals. A minimum estimate of the total vertebral count in *E. micropodia* is therefore 64. Although the anterior and posterior ends of the column can be enumerated, there is no specimen in which a vertebral series links the fore- and hindlimbs, and thus the count in the dorsal region is uncertain. Our conclusion is that vertebral numbers in *E. micropodia* certainly approached, and very possibly nested within, the lower end of the range of variation known among modern caecilians.

Appendicular Skeleton

Anatomical Location of the Forelimb. As noted above, shoulder girdle and forelimb elements in MCZ 9169 are associated with an articulated series of 13 dorsal vertebrae (Fig. 35A) that likely represent the 13th through 25th vertebrae. The limb bones, although clearly associated, are rather completely disordered (Fig. 38); thus, they provide no definitive evidence that the forelimb was anatomically situated at this point in the dorsal series. The occurrence of an isolated radius lying on PA4 of MCZ 9169 confirms that limb bones were displaced in this specimen. Although the actual position of the girdle and forelimb remains uncertain, the scapulocoracoid is here reconstructed in relation to more anterior dorsal vertebrae (Fig. 31). The occurrence of various shoulder and forelimb elements with numerous cranial specimens (MCZ 9163, 9167, 9171, 9237, 9242; MNA V9056, V8065) is suggestive evidence that the forelimb was positioned closer to the head than the association of MCZ 9169 might imply.

Scapulocoracoid (MCZ 9237, 9238, 9169, 9171; MNA V8056, V8059, V8064, V8065). The two most completely known scapulocoracoids of *Eocaecilia micropodia* (MNA V8056, MCZ 9237, Fig. 39B, C) are 3 mm in height, measured from the dorsal margin of the scapula to the posteroventral margin of the coracoid. The scapular blade is narrowly constricted at its midpoint, which is oval in cross section (Fig. 39). Dorsally, the blade is expanded and ends as a convex margin of trabecular bone indicative of its continuity with a suprascapular cartilage (Fig. 39A). The base of the scapula bears an oval glenoidal facet that faces posteroventrally and slightly laterally (Fig. 38) and an anteriorly directed process that is incised ventrally. The margin of the anterior process, like the dorsal margin of the scapular blade, appears to have been continued in cartilage; thus, the incisure was probably enclosed to form a coracoid foramen. The suture between the scapula and coracoid is preserved as a faint lineation that passes from the incisure across the glenoid. The coracoid bears an approximately circular, dorsolaterally facing glenoidal facet (Fig. 38); the remainder of the coracoid is an approximately rectangular plate of very thin bone and is preserved, in crushed condition, in only two specimens (Fig. 40). The scapular and coracoidal ends of the glenoid facet, which have very different orientations, are connected by a narrow, intermediate part of the glenoid that turns a spiral from one end to the other. The spiral configuration of the glenoid in *E. micropodia* is thus similar to the pattern common among Paleozoic tetrapods. Ventral to the anterior half of the glenoid is a circular fossa of unknown function. A fossa in a similar position occurs in a few microsaurs (e.g., *Asaphestra,* Carroll and Gaskill, 1978: 173–174, fig. 8C; *Batropetes,* Carroll, 1991: 238, fig. 6A), but there is no compelling evidence that these features are strictly comparable.

Humerus (MCZ 9163, 9166, 9167, 9171, 9237, 9238; MNA V8056, V8068). Complete humeri vary in length from 4.25 mm (MCZ 9169) to 4.4 mm (MCZ 9163, Fig. 41). The bulbous head extends from the

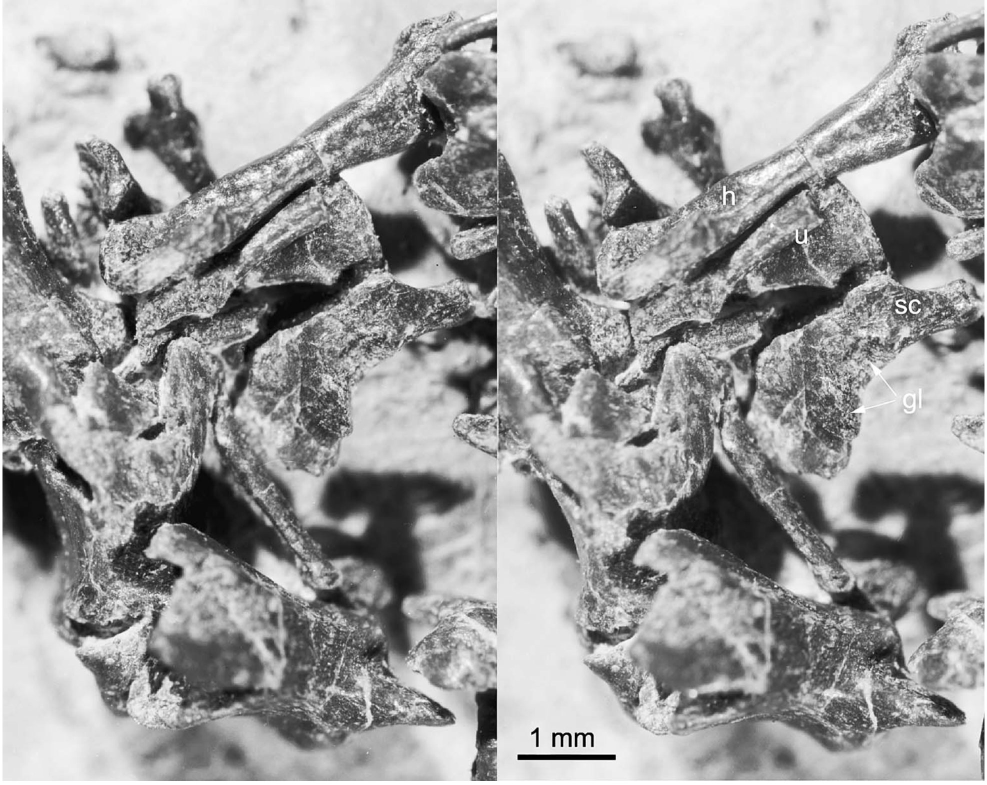


Figure 38. Forelimb elements of *Eocaecilia micropodia* (MCZ 9169), an enlargement of Figure 35A to show details of the scapulocoracoid, glenoid, humerus, and partial ulna. The upper and lower arrows indicating the glenoid (gl) point, respectively, to the scapular and coracoidal components of the glenoid facet (stereophotographs).

dorsolateral to the ventromedial surfaces of the proximal end in a spiral pattern common among Paleozoic amphibians (Fig. 42A–D; also present in MCZ 9166). The deltopectoral crest in an apparently undistorted humerus is reflected ventrally (Fig. 38) and is continuous with a low ridge that extends proximally. A small tuberosity on the dorsomedial side of the proximal diaphysis (Fig. 42C, D) is comparable in position to that in some microsaurs (e.g., *Cardiocephalus, Pantylus, Ricnodon,* Carroll and Gaskill, 1978, figs. 122A, B, 123D). In Recent *Salamandra,* a similar tuberosity serves as the site of insertion of subscapular musculature (Francis, 1934). Complete humeri (Figs. 38, 41) exhibit a simple shaft that is approximately circular in cross section. The distal end of the humerus bears a bulbous, hemispheroidal capitulum for the proximal radius and a broad but distinct trochlea for the proximal ulna (Fig. 42E; see also MCZ 9169, 9172). The ectepicondyle is represented only as a low ridge. The entepicondyle, in contrast, is a relatively robust protuberance that is prolonged distally; there is no entepicondylar foramen. Along the margin of the proximal border of the capitulum, the diaphysis is incised with a deep, hemicircular sulcus that presumably accommodated the radius in its most flexed position. MNA V8056 includes an associated distal humerus and a proximal radius and ulna that lie in nearly articulated position.

Radius (MCZ 9242, 9169; MNA V8056). A radius presumptively associated with an

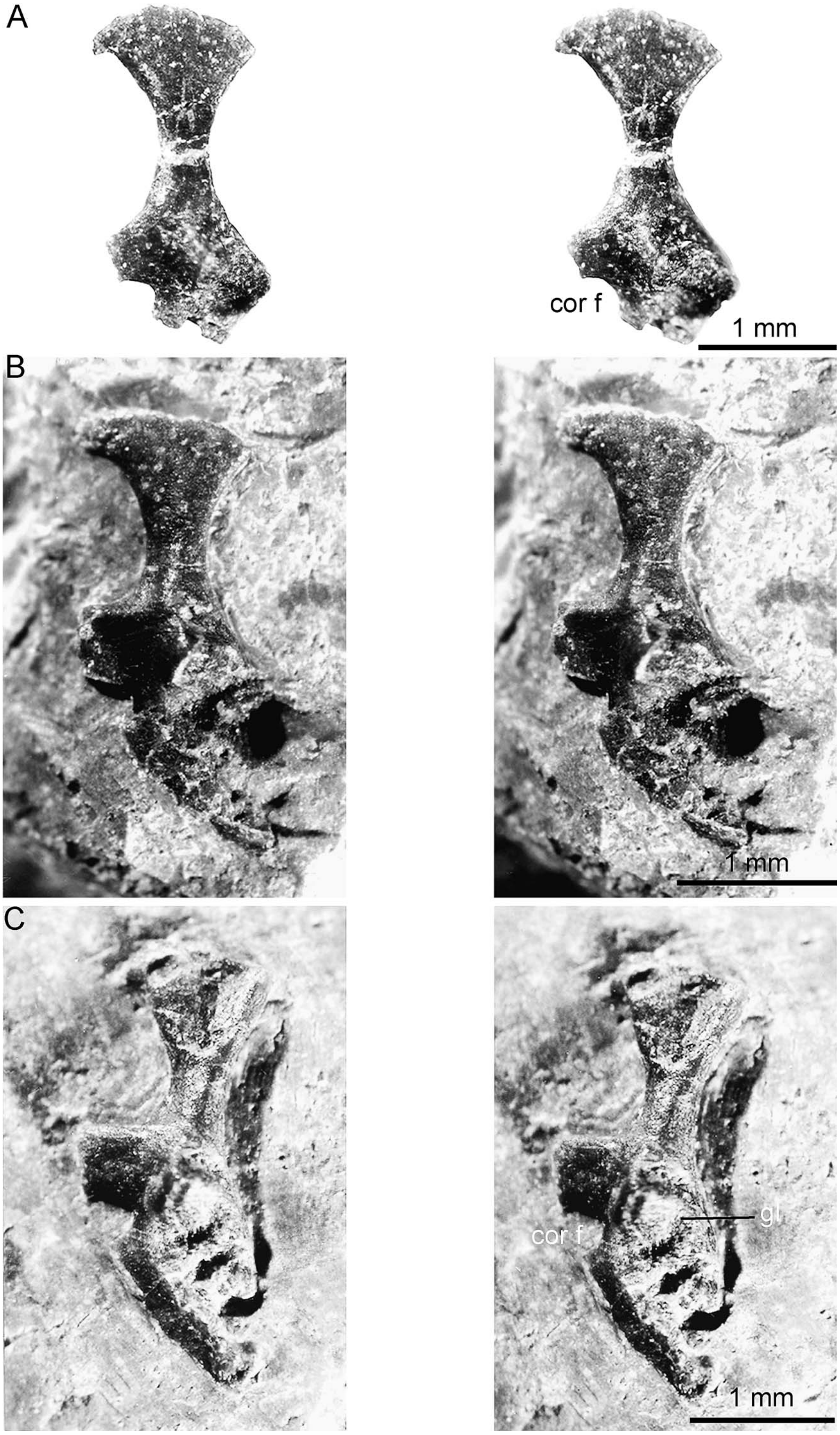


Figure 39. Left scapulocoracoids of *Eocaecilia micropodia* in lateral view: (A) MCZ 9238, (B) MNA V8056, (C) MCZ 9237. The coracoids are incomplete in all three specimens (stereophotographs).

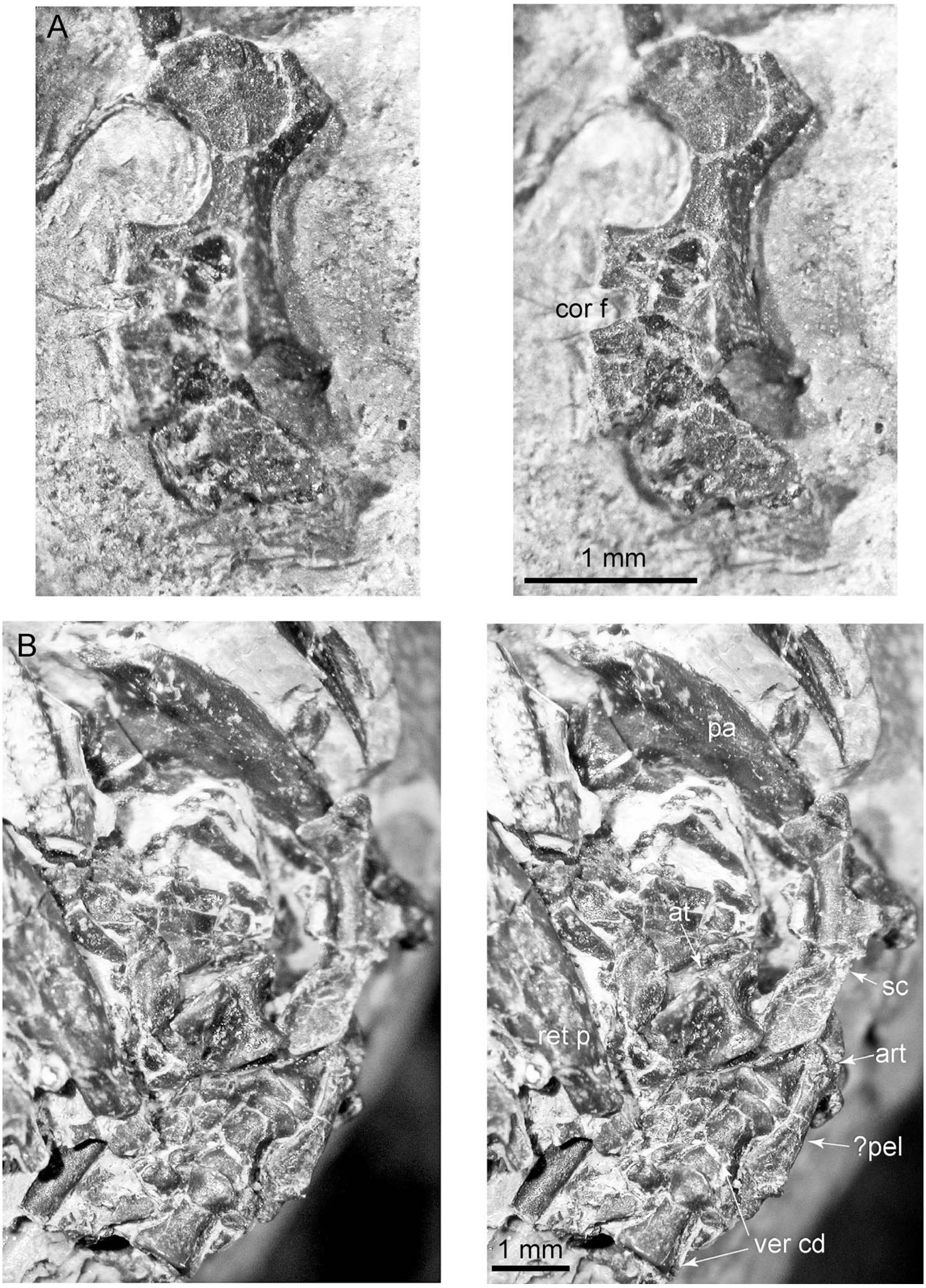


Figure 40. Scapulocoracoids of *Eocaecilia micropodia* with complete, although crushed, coracoids. (A) A left scapulocoracoid in lateral view (MNA V8064); the glenoid region has been damaged postmortem. (B) A left scapulocoracoid (in a medial view) and associated skeletal elements in MCZ 9171 (stereophotographs).

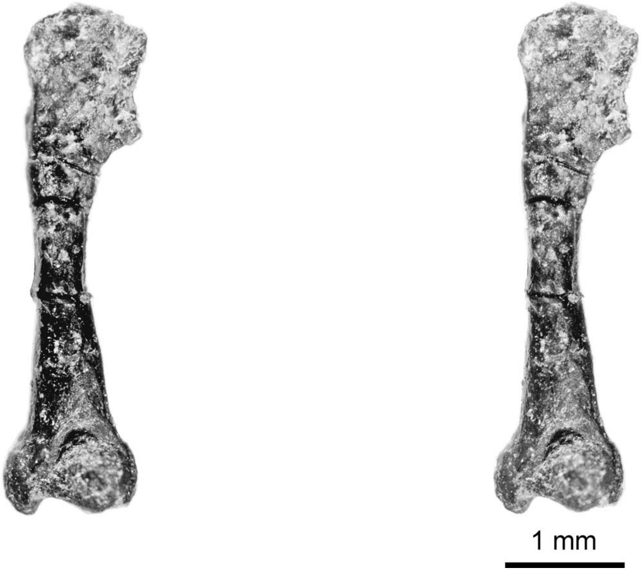


Figure 41. A complete left humerus of *Eocaecilia micropodia* (MCZ 9163) in ventral view. The specimen has been slightly crushed, with the deltopectoral crest deflected from the normal ventral orientation (stereophotographs).

ulna (MCZ 9242, Fig. 43A) is 2.16 mm in overall length. The surface of the proximal facet is set at an angle of about 20° to a plane normal to the shaft. The length of the radius measured from the most distal margin of the articular facet is 1.9 mm. Diaphyseal width narrows at midshaft to 0.39 mm, with the proximal end of the radius being more expanded than the distal end. The smaller distal articular facet is oval in outline and is set almost perpendicular to the shaft.

Ulna (MCZ 9163, 9167, 9169, 9238, 9242; MNA V8054, V8065). Complete ulnae vary in length from 2.1 mm (MCZ 9163) to 2.2 mm (MNA V8065, MCZ 9242). The proximal articular facet is asymmetrically biplanar, with the larger of the two demifacets being on the radial side (Fig. 43B). The olecranon process is short but distinct. The ulna is relatively broad, both mediolaterally and anteroposteriorly at its proximal end, and tapers to its narrowest point at midshaft. The distal end is only slightly expanded and bears a circular articular facet set perpendicularly to the shaft.

Manus. Although various mesopodial, metapodial, and phalangeal elements are associated with several disarticulated specimens of *Eocaecilia micropodia,* none can be confidently attributed to the manus.

Pelvis. No pelvic elements can be positively identified. MCZ 9171 is a disaggregated assemblage that includes jaws, an atlas, a scapulocoracoid, and several caudal vertebrae (Fig. 40B). Adjacent to the caudal vertebrae is a bladelike bone that is not comparable to any other known skeletal element in *Eocaecilia.* The bone (?pel, Fig. 40B) widens at one end, is narrower in the middle, and bears a concave articular facet, as well as a margin that is broken, at the other end, inviting speculation that the facet could be acetabular. The bladelike, rather than platelike, nature of the element is suggestive of an ilium, but in view of the lack of any comparative data on the pelvis of primitive caecilians, such an inference is entirely conjectural. Some crushed bone associated with the hindlimbs of MNA V8062 (Fig. 36) might represent a pelvis, but the state of preservation is uninformative.

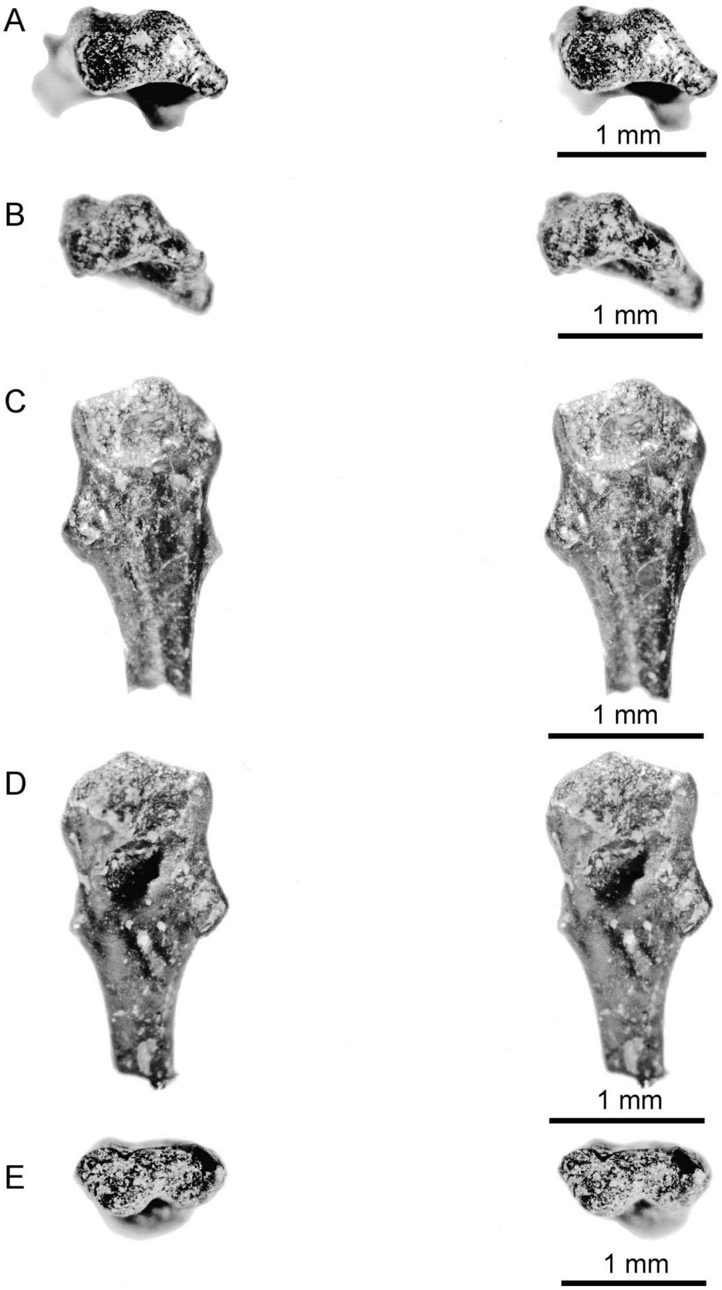


Figure 42. The humeral articular surfaces of *Eocaecilia micropodia.* (A) A left humeral head in proximal view (MCZ 9171). (B) A left humeral head in proximal view and in slightly lateral aspect (MCZ 9237). (C) Dorsal and (D) ventral views of a left proximal humerus (MCZ 9171). (E) A left distal humerus (MCZ 9237) in end view (stereophotographs).

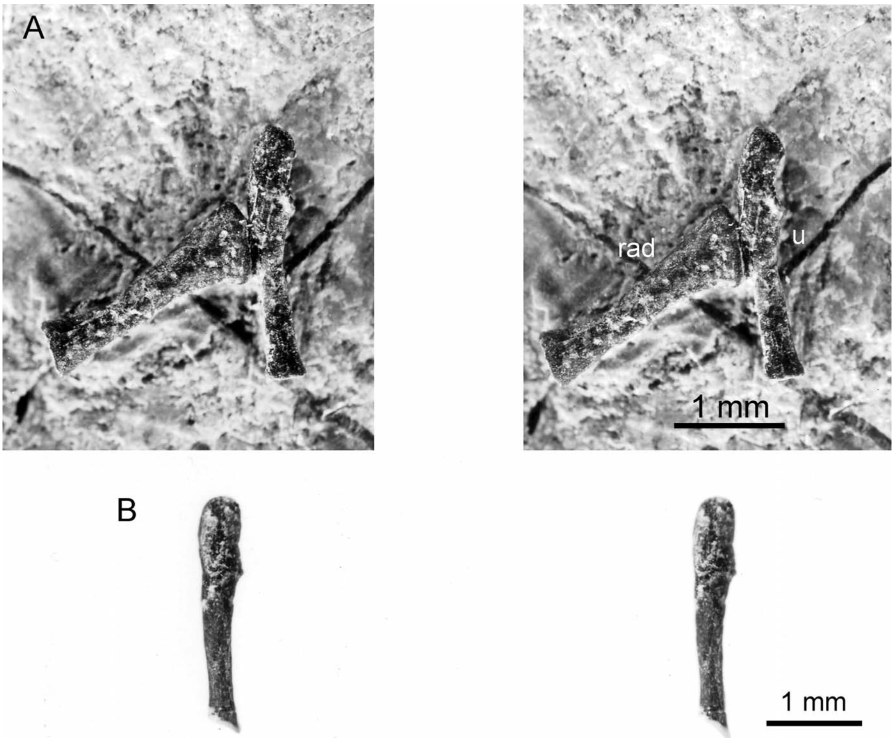


Figure 43. The antebrachial bones of *Eocaecilia micropodia.* (A) A presumptively associated left radius and ulna (MCZ 9242). (B) Proximal left ulna (MCZ 9238) in anterior view (stereophotographs).

Femur (MNA V8055, V8062). A complete left femur (Fig. 44) is 4.4 mm in length and has a midshaft width of 0.4 mm. The bulbous, approximately oval femoral head is oriented primarily dorsoventrally but is slightly skewed, such that the dorsal half is more anteriorly situated than the ventral half. On the medial and lateral sides of the head are shallow depressions, comparable to the foveae of some salamanders that represent the attachments of acetabular ligaments from the pubis and ilium (Francis, 1934, pl. V, fig. 32). A prominent, triangular trochanter is situated on the medioventral side of the proximal shaft. The expanded distal end, which is somewhat damaged (estimated width 1 mm), bears two condyles separated by an intercondylar groove. The lateral condyle is wider and more protuberant and possesses a larger radius of curvature than the medial condyle (Fig. 44C). The lateral epicondylar region is distinctly convex and facetlike, features that probably represent the articular surface for the fibula (Fig. 44B). In overall proportions and, specifically, in the configuration of the femoral head, the foveae, and the trochanter, the femur of *Eocaecilia micropodia* is similar to that in certain modern salamanders (for a comparative illustration, see Jenkins and Walsh, 1993, fig. 1h, i). The femoral head distinctly differs from those of microsaurs and other Paleozoic amphibians, which are anteroposteriorly elongate.

Tibia (MCZ 9237; MNA V8055, V8062). A complete tibia associated with MNA V8062 (Fig. 36) is 2.1 mm in length with a midshaft diameter of 0.4 mm; the tibia associated with MNA V8055 (Fig. 45B) is 1.85 mm in length. The transversely expanded proximal end bears a slightly con-

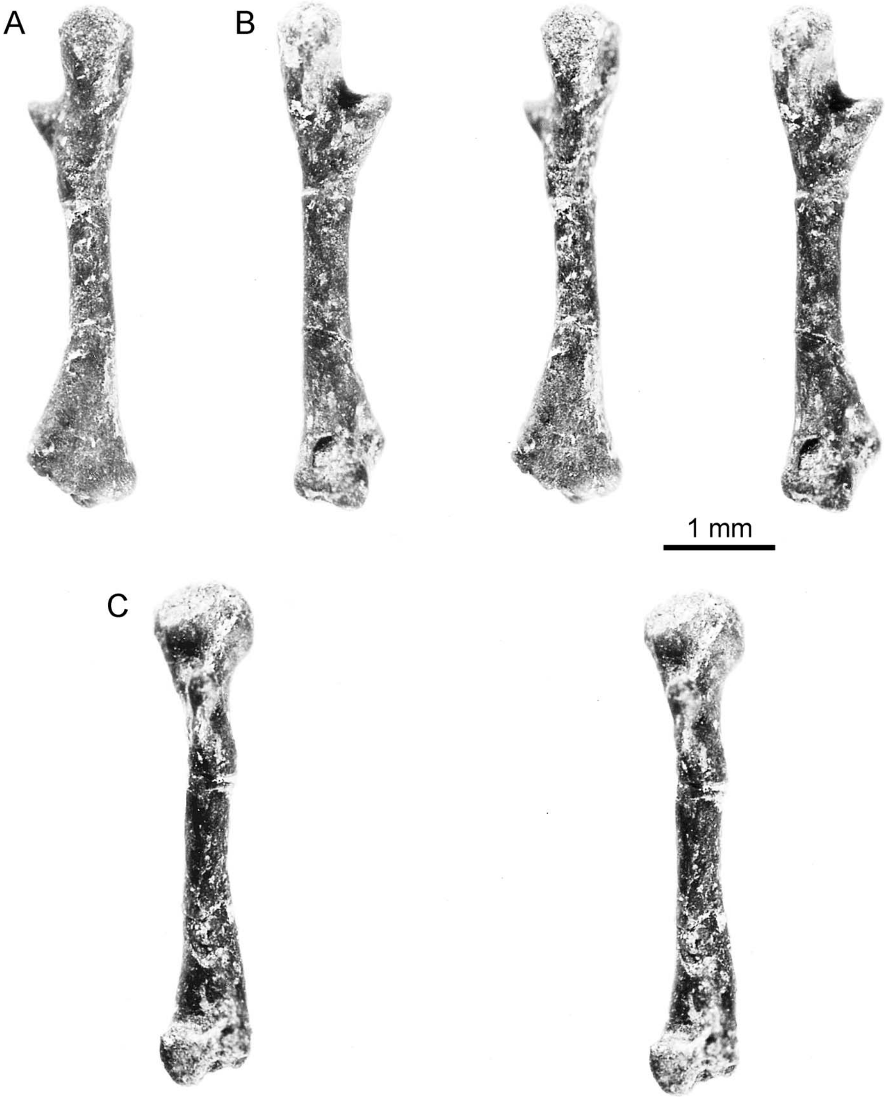


Figure 44. A complete left femur of *Eocaecilia micropodia* (MNA V8062) in (A) dorsal, (B) ventrolateral, and (C) ventral views (stereophotographs).

vex articular facet that accommodates both femoral condyles; the anterior edge of the facet slopes anteriorly and is bordered by a raised lip. A slightly raised area on the proximal, anterior surface of the shaft appears to represent a cnemial tuberosity (Fig. 45A). The distal articular facet is circular in outline and convex.

Fibula (MCZ 9237; MNA V8055, V8062). Fibular lengths range from 1.9 mm (MCZ 9237) to 2.1 mm (MNA V8055); midshaft diameter of the former is 0.3 mm. In both specimens, the fibula appears to have been preserved in an articular relationship with the tibia (Fig. 45). In both cases, the proximal articular facet, the plane of which is set at an angle of about 45° to the shaft, lies proximal to the

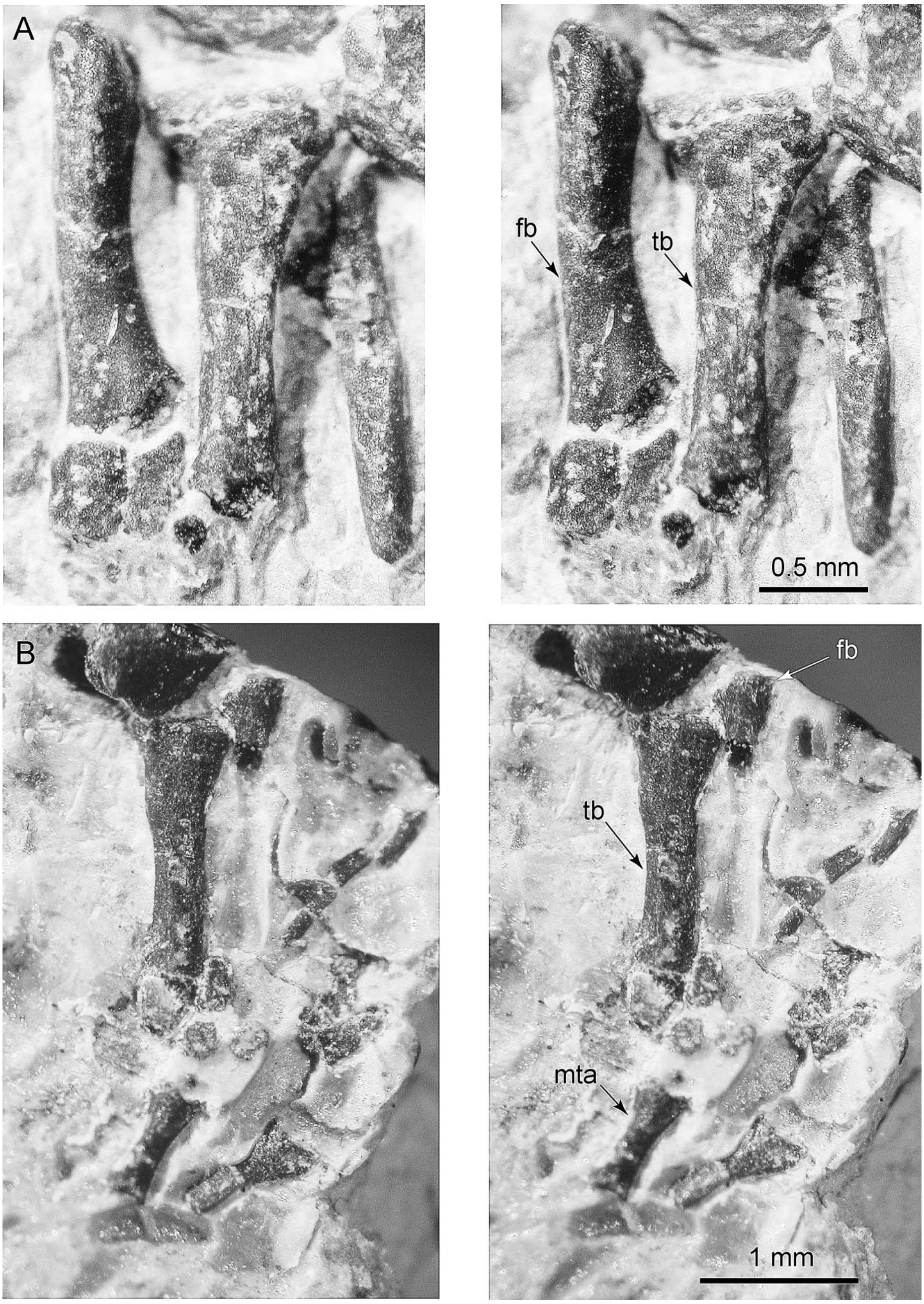


Figure 45. A tibia, fibula, and incomplete tarsus of *Eocaecilia micropodia.* (A) Anterior view of a right tibia and fibula (MCZ 9237) preserved in normal anatomical position, associated with the distal end of the femur (above) and three tarsals (below). (B) A presumptively right tibia in posterior view (MNA V8055). The specimen includes a distal fragment of the associated femur, a proximal fibula preserved in normal anatomical position (the remainder of the fibula, lost during excavation, is represented by a matrix mold), four tarsals, and several metatarsals (stereophotographs).

end of the tibia, evidence that the fibula articulated with the lateral epicondylar region of the femur. The fibular diaphysis is bowed laterally. Distally, the expanded end of the fibula terminates well short of the distal end of the tibia and bears two facets for contact with a fibulare and intermedium.

Pes (MCZ 9237; MNA V8055, V8056, V8062, V8073). MCZ 9237 and MNA V8055, taken together, demonstrate that the proximal tarsal row comprised a tibiale, intermedium, and fibulare (Fig. 45A, B). A partial pes associated with MNA V8062 (Fig. 36) shows that at least some digits possessed three phalangeal bones; the most proximal phalanx of the presumptively middle digit has a length of 0.89 mm and an estimated midshaft diameter of 0.25 mm. It is likely that *Eocaecilia micropodia* possessed only three digits because of the occurrence in several specimens (MNA V8056, V8062, V8073) of triads of phalanges.

DISCUSSION

Jaw Mechanics. Eocaecilia micropodia already possessed many of the major skeletal features of the jaw apparatus that are retained in Recent gymnophionans (e.g., prominent retroarticular process, pseudoangular and pseudodentary, internal process of the pseudoangular, mandibular fossa in close proximity to the jaw joint). These structural similarities invite the inference that the basic pattern of jaw muscles known from living gymnophionans had been developed as well.

Bemis et al. (1983) described various aspects of the feeding apparatus in *Dermophis mexicanus* (skull, lower jaw and articulation, teeth, hyobranchial apparatus, oral cavity and tongue, and jaw muscles) and confirmed the mechanics of the jaw through electromyography. Jaw closure is achieved not only by conventional action of the adductors, but through a gular muscle, the interhyoideus posterior, that acts to lower the retroarticular process (Fig. 46A; cf. Nussbaum, 1977). Jaw opening is accomplished by the depressor mandibulae, which passes from the back of the skull to an insertion on the retroarticular process. Nussbaum (1983) described the relative size of individual jaw muscles in representatives of four families (Rhinatrematidae, Ichthyophiidae, Caeciliidae, and Scolecomorphidae) and presented an analysis of the uniquely caecilian feeding apparatus.

To provide a more specific basis for interpreting the jaw mechanics of *Eocaecilia,* we review here additional details of the cranial muscles in an extant caecilian, *Ichthyophis glutinosus,* which was selected for this purpose as a relatively basal taxon. *Ichthyophis glutinosus* resembles other gymnophionans, with the exception of rhinatrematids, in the relatively large size of the interhyoideus posterior and the relative reduction of the adductors (Nussbaum, 1983, fig. 2). The retention of pre- and postfrontals in ichthyophiids is a primitive feature; they are lost or fused in most other gymnophionans. The derivation of the family Ichthyophiidae as being close to the base of the crown group gymnophionans is supported by morphological (Nussbaum, 1979) as well as molecular data (Hedges et al., 1993; San Mauro et al., 2004).

Four divisions of the adductor mandibulae can be recognized: adductor mandibulae externus, adductor mandibulae internus, adductor mandibulae posterior (which includes a levator quadrati), and pterygoideus (Fig. 46B–E). The first three are oriented essentially vertically and can be recognized primarily on the basis of their separation by branches of the trigeminal nerve.

The adductor mandibulae externus (AME) is the largest and most superficial in position, lying lateral to the maxillary branch of the trigeminal nerve (Fig. 46B). Originating on the ventral surface of the skull roof, the muscle converges ventrally to insert on a small area of the pseudoangular that includes the mandibular fossa.

The adductor mandibulae posterior

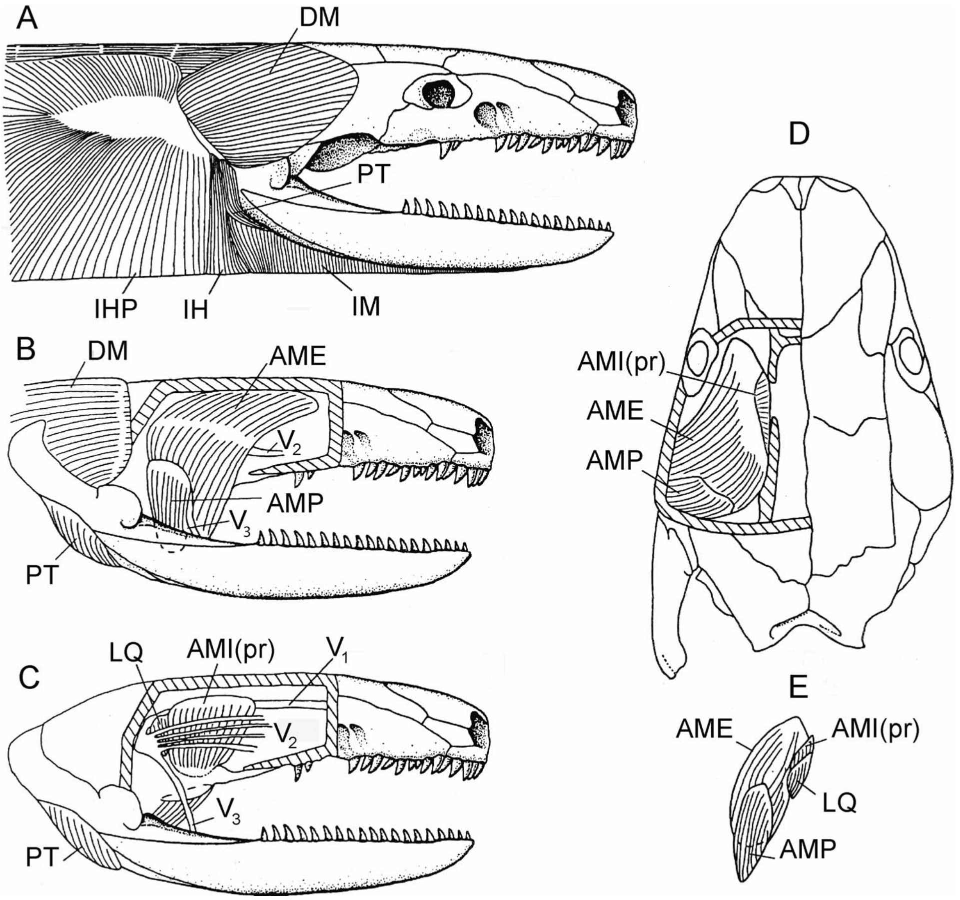


Figure 46. The jaw muscles in *Ichthyophis glutinosus.* (A) Lateral view of superficial muscles. (B, C) Lateral view of deep muscles, with the cranial vault resected (oblique hatching) to show origins within the adductor fossa. The muscles in plate B lie lateral to those in plate C. (D) Dorsal view of the adductor muscles with the cranial roof resected. (E) Isolated adductor muscles in posterior view.

(AMP) occupies the most posterior portion of the adductor chamber and is separated from the AME by V_3 (Fig. 46B, D). The AMP originates from two areas of the quadrate: the lateral surface of the pterygoid ramus and the medial surface of the palatine ramus. The insertion is within the mandibular fossa of the pseudoangular, which also transmits the mandibular ramus of V_3 and the mandibular artery.

In the upper portion of the adductor chamber, the adductor mandibulae internus (AMI) is separated from the AME by branches of V_2, and more ventrally, by connective tissue (Fig. 46C). The AMI originates somewhat ventral to the AME, from a more medial position on the underside of the skull roof. Most of the AMI joins the AME to share the same insertion in the mandibular fossa. A slip of the AMI (the levator quadrati, Fig. 46E), which arises from a more inferior position within the adductor chamber, is separated from the AMI by a large blood vessel accompanying the deep branch of V_1 and connective tissue. The slip converges to its attachment in a pit at the top of the pterygoid ramus of the quadrate.

In contrast to the other adductors, the pterygoideus is oriented more horizontally and is directed posteroventrally from its origin along the anterior margin of the adductor fossa. The muscle divides, with one part inserting on the anterior margin of the internal process of the mandible and the other extending across the ventral aspect of the retroarticular processes to insert on its lateral surface (Fig. 46C). The two divisions are separated by a robust ligament that connects the internal process and the pterygoid.

The interhyoideus posterior (IHP, Fig. 46A) is a large, fan-shaped muscle that arises from the dorsal and lateral aspects of the neck, and the ventral aspect of the gular and "cervical" regions. The fibers converge to insert on the retroarticular process.

A general assessment of the function of some of these muscles can be made from their fiber orientation, relative size, and mechanical advantage (lever arm length) with respect to the jaw joint. The three adductors (AME, AMP, and AMI) insert on the mandible in close proximity to the jaw joint and thus have less mechanical advantage than does the interhyoideus posterior that attaches to the long lever arm of the retroarticular process. Furthermore, the origin of the adductors is confined to a relatively small, enclosed adductor fossa, a common condition among extant gymnophionans (Fig. 6B, C); the adductor fossa in rhinatrematids is larger (Fig. 6D).

The diverging fiber directions of the interhyoideus posterior are evidence of multiple functions. Recruitment of the superior, dorsally directed fibers would raise the retroarticular process and thus initiate jaw opening. Conversely, the bulk of the muscle, with fibers directed ventrally or posteroventrally, would act to depress the retroarticular process and thus contribute to the uniquely caecilian jaw closure mechanism.

The contribution of the pterygoideus is less clear and could involve differential recruitment of its two divisions during the masticatory cycle. The oblique orientation of the division of the pterygoideus that inserts on the internal process likely contributes to jaw closure (a conventional function for the pterygoideus among tetrapods). The other division, which passes below the internal process of the pseudoangular and wraps around the ventral aspect of the retroarticular process, is of uncertain function. In some mandibles of *Eocaecilia micropodia,* a groove on the ventral aspect of the jaw below the internal process records the passage of this part of the muscle to the retroarticular process (Fig. 27D). The line of action of this part of the pterygoideus passes across the jaw joint (Fig. 46C); therefore, the fibers possess no lever arm for either jaw opening or closing. Two possibilities remain. This division could produce an anterodorsally directed compressive effect on the jaw joint. Such an action could contribute to joint stability and, in particular, serve as an antagonist to the posteroventrally directed force of the interhyoideus posterior during jaw closure. A second possibility is that this part of the pterygoideus everts (by longitudinal lateral rotation) the jaw upon opening; the depressor mandibulae would effect inversion upon jaw closing.

The similarities between *Eocaecilia micropodia* and Recent caecilians notwithstanding, the configuration of the stapes-quadrate, jaw joint, and internal process of the pseudoangular in *E. micropodia* is evidence of a divergence in masticatory mechanics. The geometric complexity of the articular surfaces borne by the quadrate and pseudoangular in gymnophionans (Fig. 29B, C), which provides structural stability, contrasts to the nearly vertically oriented, planar facets of *E. micropodia* (Fig. 29A). Unlike the modern caecilian jaw joint, in which the quadrate facets fit securely between condylar processes of the pseudoangular, no interlocking mechanism is present in *E. micropodia,* where the joint possesses no mechanical impediment to anteroposterior or dorsoventral translation. The dimensional differences in the quadrate and pseudoangular facets are small, however. The evidence that pseudoangular facets are about 45% longer along an anteroposterior axis than facets on the stapes-quadrate supports an interpretation of slight protrusion upon jaw opening and retraction upon closing. The dentition of *E. micropodia*—with teeth that are numerous but very small—would seem suitable for apprehending only the smallest of prey, and propalinal jaw movements could well have been employed in ingestion. With a jaw joint of little intrinsic stability, the large size and dorsomedial orientation of the internal process might reflect the employment of the pterygoideus as a jaw protractor. The fusion of the stapes-quadrate and the unusual orientation of the jaw joint might represent a specialization to withstand the medially compressive forces generated by the interhyoideus posterior. In extant caecilians, the same medially compressive forces would be resisted by the obliquity of the complex interlocking of the quadrate and pseudoangular facets.

The Habitus of Eocaecilia micropodia. With the exception of aquatic species, gymnophionans are capable burrowers. Several anatomical features of *Eocaecilia micropodia* provide a basis for evaluating the degree to which this Early Jurassic caecilian can represent a stage in the evolution of gymnophionan fossoriality. In a review of tetrapod limblessness, Gans (1975) observed that the majority of limbless forms are shelterers or burrowers, the exception being snakes (although uropeltids among Serpentes are true burrowers). Lizards in which the limbs are reduced to various degrees (e.g., scincids, anguids, cordylids) are not effective burrowers but are principally shelterers in crevice-rich environments. Gans suggested that a universal correlate of limblessness is body elongation and that "limb reduction followed, and was probably produced by, selective pressure established after bodily elongation had occurred" (Gans, 1975: 465). However, in a review of limb reduction in squamates, Greer (1991: 167–171) noted that 22 of the 53 extant lineages that exhibit various degrees of limb reduction are not patently elongate, although he agreed that ". . . a gross reduction in the number of limb bones is always associated with an elongate body." Our estimate of the vertebral count in *E. micropodia* is suggestive of body elongation but does not demonstrate the feature unequivocally. The evidence that *E. micropodia* had undergone some reduction of the appendicular skeleton, however, is unambiguous (Jenkins and Walsh, 1993, table 1; Fig. 31). In addition to the retention of limbs, *E. micropodia* had not yet attained other characteristics that are likely to be related to the fossorial habits of gymnophionans. The mouth is not obviously subterminal as in gymnophionans. The orbits, although proportionately smaller than is typical for Paleozoic amphibians, are larger than those in gymnophionans in which the eyes are much reduced and in some taxa covered by bone. The atlanto-occipital joint of *E. micropodia* is relatively small compared with those of gymnophionans in which the robustness of the joint is integral to a burrowing style that employs head and "neck" movements.

We conclude that limited evidence favors the interpretation that *Eocaecilia micropodia* was probably not a burrower with the capabilities of Recent gymnophionans. The reduction in overall limb size and the apparent loss of two digits are features shared with various squamates that are either poor burrowers or sand swimmers or that shelter themselves in crevices and other cramped niches, such as dense vegetation (Gans, 1975). If this analogy is appropriate, then we might envision the habitus of these Early Jurassic caecilians as presenting substrate parameters sufficiently dense or spatially constraining that limb reduction was selectively advantageous. Thus, *E. micropodia* plausibly represents a stage in the evolution of gymnophionan burrowing but was probably not fossorial *per se.* The correlate of such a supposition is that the relatively small head size, specializations of the masticatory apparatus, and other cranial features that characterize both *E. micropodia* and Recent gymnophionans and which are commonly assumed to be associated with the fossorial habits of gymnophionans, in fact arose during a stage in caecilian evolution before their entry into the subterranean world.

Zygokrotaphy and Stegokrotaphy. A persistently problematic issue in caecilian evolution is whether an open (zygokrotaphic) or closed (stegokrotaphic) skull roof in the temporal region is the primitive condition. Numerous studies, including those of DeBeer (1937), Goodrich (1930), Parsons and Williams (1963), and Wake and Hanken (1982), have supported the now prevalent view (reviewed by Wake, 2003) that one of the cranial specializations in living gymnophionans is secondary closure of the temporal fenestra, a derived condition most likely related to fossoriality. Bemis et al. (1983), in a functional study of feeding in *Dermophis mexicanus,* took no position on whether stegokrotaphy is primitive or derived. They suggested that the reduction in skull size that accompanied the development of burrowing habits places a constraint on the size of the adductor chamber and that the interhyoideus posterior/retroarticular process functions as a compensatory mechanism. Nussbaum (1983) observed that this novel mechanism is least well developed in rhinatrematids, which are relatively basal gymnophionans in which heads of the adductor mandibulae are exposed by a temporal fenestra. The temporal fenestrae of rhinatrematids and the inferred, secondarily closed fenestrae of more derived groups would thus be a feature shared with frogs and salamanders. The discovery of stegokrotaphy in an Early Jurassic caecilian, which is patently primitive in many cranial and postcranial characters, revived the alternative possibility that zygokrotaphy could be derived (Jenkins and Walsh, 1993). We reconsider this problem in light of this study.

Nussbaum (1983) presented four plausible lines of evidence in support of his interpretation that stegokrotaphy is secondary in caecilians. First, there are no temporal bones between the squamosal and parietal in living caecilians, whether they be zygo- or stegokrotaphic; he regarded their loss as more likely the result of temporal fenestration (displaced by expanded adductor muscles) than by in situ fusion. Alternatively, we note that fusion of adjacent cranial bones is known to have occurred extensively in caecilians (Wake, 2003; Wake and Hanken, 1982).

Second, Nussbaum (1983) noted that the arrangement of postorbital bones in stegokrotaphic caecilians differs from that in labyrinthodonts and considered this difference as evidence that a solid temporal region has been secondarily reconstructed. However, the architecture of the cranial vault in *Eocaecilia* is now known to include such elements as a postparietal, jugal, quadratojugal, and tabular (or supratemporal), all in comparable positions to those in the primitive tetrapod pattern.

Third, Nussbaum (1977, 1983) pointed out that the skulls of rhinatrematids (which are zygokrotaphic) and ichthyophiids (in which zygokrotaphy is incipiently developed) are primitive in the greatest number of features. Furthermore, the highly derived skulls of most caeciliids are stegokrotaphic, an exception being *Geotrypetes* (Wake, 2003). Alternatively, we note that the putatively primitive rhinatrematid, *Epicrionops,* exhibits a number of derived cranial features; these include loss of the pre- and postfrontals, encirclement of the orbital margin by the maxillopalatine, and specialization of the articulation between the squamosal and the lateral margin of the os basale. More primitive character states of these features are found in Ichthyophiidae and Uraeotyphlidae. Stegokrotaphy in *Eocaecilia* is associated with numerous primitive features of the skull and postcranial skeleton.

Finally, Nussbaum (1983: 551) suggested that the incomplete development of the interhyoideus jaw closure mechanism in

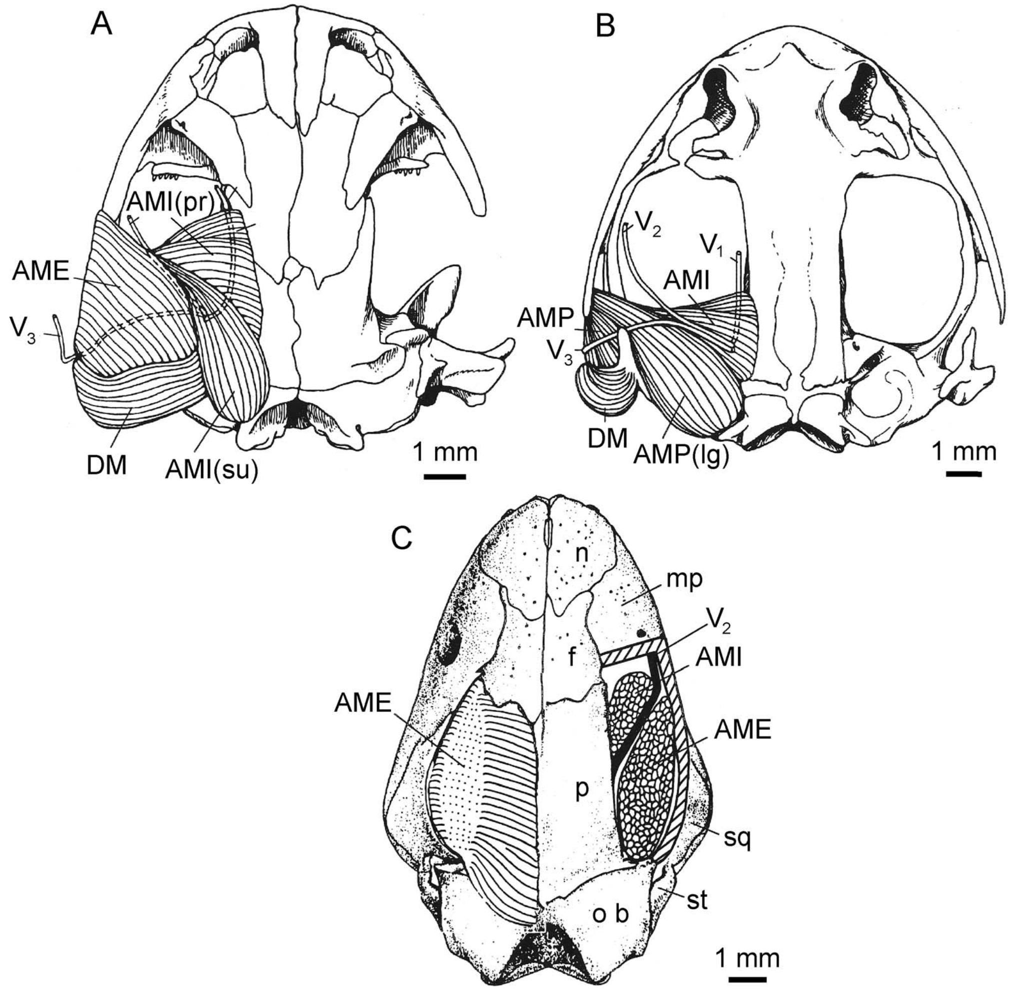


Figure 47. Dorsal view of adductor muscles in (A) a salamander, *Ambystoma maculatum*; (B) a frog, *Ascaphus truei*; and (C) a caecilian, *Epicrionops petersi*. A and B from Carroll and Holmes (1980, fig. 18); C reconstructed from sections (LSUMZ 27324).

rhinatrematids engendered a compensatory enlargement of "... the ancestral component [that] dominates by expansion of the *mam* [musculus adductor mandibulae] through a temporal fossa." Alternatively, we raise the possibility that rhinatrematids (and, to a lesser extent, other caecilians with incipient zygokrotaphy) might exhibit a secondary reduction of the contribution of the interhyoideus posterior to jaw closure and a commensurate increase in the size of the adductors.

Carroll and Holmes (1980) cited differences between frogs and salamanders in the arrangement of the adductor muscles in the temporal fenestra as evidence that the fenestrae themselves were independently derived. This comparison may now be extended to include a caecilian. The dominant muscle at the level of the temporal fenestra in salamanders is the external adductor (Fig. 47A), which is associated with loss of ossification between the maxilla and jaw suspension (Carroll and Holmes, 1980), whereas in frogs, the largest muscle is the posterior adductor (Fig.

47B). In *Epicrionops,* the dominant muscle is the external adductor (Fig. 47C). In each of these groups, different divisions of adductor mandibulae extend posteriorly over the back of the skull table and otic capsule: the long head of the posterior adductor in frogs, the superficial head of the internal adductor in salamanders, and the external adductor in *Epicrionops.* The divergent patterns of the occupation of the temporal opening in these three taxa might support the interpretation that the evolution of the openings occurred separately in the three groups. Alternatively, the relative size and positioning of the adductor divisions could reflect divergences in muscle function that developed subsequent to fenestration.

At present there is no certain basis for making a definitive decision on stegokrotaphy versus zygokrotaphy in caecilian phylogeny. That the stegokrotaphic condition is primitive for amphibians is undeniable—as is the fact that temporal fenestration and other modifications of the skull roof are known to have developed in other groups (e.g., Paleozoic lysorophid amphibians). The lingering questions are whether fenestration in caecilians had already been initiated in the common ancestor of lissamphibians, or whether the condition was acquired subsequently in the ancestors of some living caecilians. *Eocaecilia micropodia,* which is primitive in many aspects of the cranial and postcranial skeleton, supports the latter possibility.

Eocaecilia *as a Stage in Caecilian Phylogeny.* We concur with the phylogenetic hypotheses of Evans and Sigogneau-Russell (2001, fig. 8) and Trueb and Cloutier (1991, fig. 9) that *Eocaecilia micropodia* is a basal caecilian that lies outside the crown group Gymnophiona. This Jurassic form nonetheless has significant implications for our understanding of a previously unknown stage in caecilian evolution and diversity. *Eocaecilia micropodia* shares with extant gymnophionans such a substantial array of shared derived characters that there can be little doubt that the evolutionary transition to gymnophionans had largely taken place prior to the Early Jurassic. The most distinctive gymnophionan features of *Eocaecilia* are: a sulcus along the anteroinferior margin of the orbital rim that could be interpreted as a tentacular sulcus; an os basale representing consolidation of the supraoccipital, exoccipitals, basioccipital, basisphenoid, pleurosphenoid, and parasphenoid elements; an internal naris posterior to the premaxillary–maxillary suture and medial to the tooth rows on the vomer and palatine; enlarged nasal capsules that lie between the sphenethmoid and rostral margin of the skull; an olfactory eminence on the vomer; a lower jaw comprising a pseudodentary and pseudoangular that meet along an elongate, oblique suture; and an internal process of the pseudoangular. Internal processes of the pedicles, which serve to anchor tissue suspending the spinal cord, were first discovered in *E. micropodia* and subsequently found in some gymnophione taxa. On the basis of limited evidence, *Eocaecilia* appears to exhibit an elongation of the body comparable to that in primitive extant gymnophionans, but a detailed comparison cannot be made because of uncertainty over the precise number of vertebrae.

In contrast to the foregoing gymnophionan synapomorphies, *Eocaecilia* also presents primitive or transitional features, or both, that might be expected in forms representing a transition to a highly specialized life style. The retention of jugal, quadratojugal, ?tabular, and postparietal bones is primitive. The presence of intercentra and limbs is also primitive, but the reduction in the relative size of the limbs would appear to be transitional toward the gymnophionan condition.

The discovery of an operculum in *Eocaecilia micropodia* is novel confirmatory evidence that the opercular apparatus is a synapomorphy of Lissamphibia. The apparent absence of an operculum in extant gymnophionans (at least as a separate element) is best explained by the related loss of the shoulder girdle and muscular link between the girdle and operculum. The accessory ear ossicle described by Carroll and Gaskill (1978: 163, fig. 113) in *Rhynchonkos* and other microsaurs is consistently suspended above the stem of the stapes; in shape and position this ossicle appears to differ from the operculum of *Eocaecilia,* which is oval and, in one specimen at least, is preserved in close association with the fenestra ovalis. In contrast to the operculum, the presence of pedicellate teeth in a Jurassic caecilian is entirely expected. This dental specialization, once widely recognized as a lissamphibian synapomorphy, is now known to occur in two Paleozoic amphibians—*Doleserpeton* (Bolt, 1969, 1991) and *Apateon* (Schoch and Carroll, 2003)—which have been interpreted to be sister taxa of frogs and salamanders, respectively.

With an admixture of primitive, transitional, and demonstrably gymnophionan features, *Eocaecilia* appears even more chimeric in possessing an array of specializations that, on present knowledge, are autapomorphic. Many of these features present a perplexing challenge to functional interpretation, for no structural comparability is to be found among living or potentially antecedent forms. The internal process of the lower jaw is very robust, and projects into the adductor chamber. The obliquely oriented, more or less planar jaw joint would appear to provide little stability, and is thus structurally and functionally unlike that known in any other caecilian. The stapes-quadrate is also unique.

Although our knowledge of caecilian evolution and diversity now extends into the Early Jurassic, *Eocaecilia micropodia* does not provide sufficient evidence to securely recognize the origin of gymnophionans among known Paleozoic amphibians, or even contribute substantially to the unresolved issue of liassamphibian monophyly. Carroll and Currie (1975) proposed microsaurs as possible caecilian ancestors, but their hypothesis has been criticized by Bolt (1991), among others, and is not widely accepted. Nonetheless, the third author of this monograph persists in this viewpoint (Carroll, 2000: 1410), from which the remaining authors must demur. We therefore address the list of putative synapomorphies that have been proposed as uniting *Eocaecilia* and the tuditanomorph microsaur *Rhynchonkos* [*Goniorhynchus*], many of which have already been critiqued by Bolt (1991).

1. "far anterior jaw articulation." The relative position of the jaw articulation in the reconstructed skulls of *Rhynchonkos* (Carroll, 2000, fig. 2A, B; Carroll and Gaskill, 1978, figs. 63, 64) is not certainly comparably displaced as in *Eocaecilia.* The central issue is the position of the jaw joint relative to the occiput. To the degree that the central third of the occiput is protracted posteriorly relative to the two lateral thirds, the jaw joint will seem anteriorly displaced. The senior author examined the original material of *Rhynchonkos stovalli* (FMNH-UR 1039 and 1040), and both specimens are deformed and crushed (as shown in Carroll and Gaskill, 1978, figs. 63A, 64, top row), particularly in the occipital region. Not surprisingly, Carroll and Gaskill's two reconstructions (1978, figs. 63B, 64, bottom row) are slightly different. Thus, with the reliability of the reconstructions uncertain, the relative position of the jaw joint in *Rhynchonkos* is moot.

2. "conspicuous retroarticular process." Without attempting to define conspicuous as a quantifiable morphological term, we note that the retroarticular process of *Rhynchonkos* is short (estimated at 5–6% of jaw length) relative to that in *Eocaecilia* (17–18% of jaw length). Retroarticular processes occur widely throughout temnospondyls and are not uniquely shared by *Rhynchonkos* and *Eocaecilia.* In addition to *Rhynchonkos,* retroarticular processes in microsaurs are also found in ostodolepids and some gymnarthrids (Carroll and Gaskill, 1978).

3. "loss of intertemporal and supratemporal." This character has previously been

criticized by Bolt (1991) who pointed out that absence of the intertemporal and supratemporal does not constitute a unique synapomorphy with any of the lissamphibian orders. "The intertemporal is absent in numerous fossil amphibian groups, and the absence of both intertemporal and supratemporal is shared at least with advanced aistopods, lysorophoids and adelogyrinids . . ." (Bolt, 1991: 208–209).

4. "medial rows of teeth on the palate and lower jaw." Bolt (1991: 209) observed that "Many fossil amphibians have a row of palatal teeth disposed like that of *Rhynchonkos*—this character has evolved independently a number of times, on almost any hypothesis of amphibian relationships." As Bolt (1991: 210) further pointed out, *Rhynchonkos* is hardly unique in the possession of an internal row of mandibular teeth, which occurs in various temnospondyls (Jupp and Warren, 1986), including *Colosteus* (Hook, 1983).

5. "closely integrated posterior portion of the braincase." Without attempting to define close integration, we note that Bolt (1991: 209) previously rejected Carroll and Currie's (1975: 237) use of the character of "an extensive pleurosphenoid [that] joins the otico-occipital portion of the braincase with the sphenethmoid." Lateral ossification of the braincase between the otic capsules and sphenethmoid is not unique to microsaurs.

6. "closure of the region anterior to the opening of the Vth nerve." Enclosure of the exit of the trigeminal nerve by a bony pleurosphenoid is simply an expression of the degree of ossification of the braincase and is not uniquely shared by *Rhynchonkos* and caecilians.

7. "holospondylous centra." Holospondylous vertebrae are characteristic of lissamphibians and lepospondyls generally and are not shared just with microsaurs. The general trend of vertebral evolution among Paleozoic amphibians was a reduction of one of two circumnotochordal elements (intercentrum, pleurocentrum) in favor of establishing the other as the dominant, or sole, element.

8. "double occipital condyle." Paired occipital condyles occur in many derived temnospondyls and other lissamphibian groups and are not uniquely shared by *Rhynchonkos* (and microsaurs) and *Eocaecilia* (and gymnophionans).

9. "elongation of the [vertebral] column" and

10. "reduction of limbs." Lengthening of the body through an increase in vertebral number has occurred repeatedly and independently in amphibian evolution—salamanders, lepospondyls, and aistopods being several examples. Likewise, limb reduction or loss has developed convergently in various aquatic or burrowing amphibians. Both characters denote a general resemblance, but neither is uniquely shared by *Rhynchonkos* (and microsaurs) and *Eocaecilia* (and gymnophionans).

11. "a more general similarity is small size." Small size is indeed a general similarity, but diminutive taxa are found across many amphibian groups. Size is more likely a consequence of convergence and provides no persuasive indicator of relationship between microsaurs and *Eocaecilia.*

We thus conclude, with our third author dissenting, that on available evidence, *Eocaecilia* and gymnophionans have no demonstrable relationship to Microsauria. The authors do concur that a substantial morphological and temporal gap still intervenes in the identification of the origins of caecilians, and in fact we might not even be in possession, among all the Paleozoic taxa now known, of the fossil record of caecilian origins. Although Bolt and Lombard (1985; see also Lombard and Bolt, 1988) have produced the most credible evidence yet of an anuran relationship to temnospondyls, and Schoch and Carroll (2003) have identified developmental similarities between branchiosaurids and salamanders, the concept of Lissamphibia still remains at best a crown group taxon, without a securely rooted stem in the Paleozoic.

ACKNOWLEDGMENTS

Paleontological exploration of the Kayenta Formation on lands of the Navajo Nation was made possible through permission of the Navajo Tribal Council and the Coal Mine Mesa Chapter. The discovery of the microvertebrate quarry at Gold Springs is directly attributable to the prospecting and collecting talents of the late William R. Downs, with the assistance of James Kirkland. The senior author acknowledges with warm thanks W. W. Amaral, J. Attridge, the late W. R. Downs, H. E. Jenkins III, J. Kirkland, S. Madsen, D. K. McClearn, R. J. O'Hara, T. B. Rowe, C. R. Schaff, N. H. Shubin, K. K. Smith, and H.-D. Sues for their important participation in fieldwork. The Museum of Northern Arizona, Flagstaff, offered substantial logistical support to the Kayenta project.

The extensive collection of specimens of *Eocaecilia micropodia* was deftly prepared by William W. Amaral, Manager of the Preparation Laboratory in the Museum of Comparative Zoology. We thank E. Selig and R. Pinto for electron microscopy and A. H. Coleman, C. Kenaley, and A. Holmes for stereophotography. Drawings of cranial material were originally drafted by D. Dilkes. Most of the line drawings are the admirable work of the late P. Gaskill (Redpath Museum, McGill) who also undertook preliminary reconstructions of the skull. Figures 1, 17, 29, 31, and 33 were skillfully executed by L. Laszlo Meszoly (MCZ, Harvard). J. P. O. Rosado of the Herpetology Department, Museum of Comparative Zoology, kindly made available skeletal specimens of gymnophionans.

R.L.C. warmly thanks Marvalee H. Wake for providing access to her collection of caecilian materials (skeletal, serial sectioned, and cleared and stained), and for sharing her knowledge and advice during his sabbatical visit to the University of California, Berkeley. The curators of the Field Museum of Natural History and at Michigan State University were generous in providing additional caecilians for examination and dissection. R.L.C. also thanks E. Roman and M.-A. Lacey for processing various figures and other editorial assistance.

We are the grateful beneficiaries of detailed reviews and thoughtful advice from major authorities in the field of herpetology. We warmly thank Professor Susan E. Evans (University College London) for providing an array of helpful guidance on many comparative anatomical points; Professor Ronald A. Nussbaum (University of Michigan) for insightful suggestions on interpreting *Eocaecilia,* particularly on the issue of fossorialism, and for permission to reproduce a number of his published illustrations; and Professor Marvalee H. Wake (University of California, Berkley) for generously sharing her knowledge of caecilian biology and the literature in this field. F.A.J.Jr. is grateful to David C. Blackburn for numerous spirited discussions of matters herpetological, and especially for pointing out the existence of vertebral structures in certain snakes that are comparable to the internal processes of the pedicles in *Eocaecilia micropodia.* Our work was supported by grants from the National Science Foundation and National Geographic Society (F.A.J.Jr.); the Bedford Fund for Zoological Research, King's College, Cambridge (D.M.W.); and the Natural Sciences and Engineering Research Council of Canada (R.L.C.).

APPENDIX:
A List of *Eocaecilia micropodia* Specimens

SPECIMENS ACCESSIONED IN THE MUSEUM OF COMPARATIVE ZOOLOGY

MCZ 9011	anterior two-thirds of skull and jaws
MCZ 9015	crushed skull and jaws; a second skull crushed and disarticulated, including tooth crowns
MCZ 9095	disarticulated jaws, fragmentary vertebrae
MCZ 9152	left lower jaw, vertebra
MCZ 9156	crushed and disarticulated skull
MCZ 9158	right lower jaw mounted on SEM disc, partial left lower jaw, and ?skull fragments
MCZ 9163	crushed skull and jaw, vertebrae and

	various limb bones including complete humerus (mounted on SEM disc) and ulna
MCZ 9166	incomplete mandibles and postcranial bones; proximal humerus mounted on SEM disc
MCZ 9167	partial skull roof with otic region, atlas, partial lower jaw, distal humerus, proximal ulna
MCZ 9169	block A: articulated vertebral series with shoulder girdle and forelimb elements, prepared and mounted on an SEM disc; block B: disarticulated vertebral series including caudals; blocks C, D: articulated vertebral series with crushed skull and jaws; isolated teeth mounted on SEM discs
MCZ 9171	proximal humerus, partial jaws, atlas, vertebrae, scapulocoracoid, and crushed, disarticulated skull
MCZ 9173	fragmentary vertebra
MCZ 9231	atlas and other fragmentary vertebrae, partial jaw
MCZ 9233	disarticulated jaws
MCZ 9235	crushed, disarticulated skull with stapes-quadrate, jaw, and vertebrae
MCZ 9237	crushed skull and mandible, humeri, scapulocoracoid, ?ulna, and associated tibia and fibula with two tarsals
MCZ 9238	scapulocoracoid, ulna, and proximal humerus mounted on SEM disc; vertebrae
MCZ 9241	fragmentary jaw and vertebrae
MCZ 9242	disarticulated skull and jaws, isolated pterygoid, vertebrae, and associated radius and ulna mounted on SEM disc

SPECIMENS ACCESSIONED IN THE MUSEUM OF NORTHERN ARIZONA

MNA V8053	left lower jaw and vertebra
MNA V8054	vertebrae, stapes-quadrate, fragmentary right jaw, and ulna; posterior part of jaw and stapes-quadrate prepared
MNA V8055	several series of vertebrae on different blocks: an articulated posterior dorsal series and an incomplete caudal series; tibia, tarsals, metatarsals
MNA V8056	incomplete skull and jaws, scapulocoracoid on SEM disc, distal humerus, proximal radius and ulna, and fragmentary pedal elements
MNA V8057	vertebrae and ribs
MNA V8058	partial lower jaw
MNA V8059	incomplete skull and jaws with associated postcranial bones
MNA V8060	disarticulated skull and jaws and vertebrae
MNA V8062	articulated posterior dorsal vertebrae, ?sacrals, and caudal vertebrae, crushed skull and jaws, hindlimb elements including phalanges; right femur mounted on SEM disc
MNA V8063	otic capsule with braincase
MNA V8064	vertebrae, right scapulocoracoid (in medial view)
MNA V8065	partial skull roof with otic region, atlas, partial lower jaw, distal humerus, proximal ulna, and partial scapulocoracoid
MNA V8066	[holotype] skull and jaws with associated atlas and postatlantal vertebrae
MNA V8067	articulated vertebral series
MNA V8068	mandible and distal humerus
MNA V8069	vertebrae
MNA V8070	disarticulated skull, mandible, and stapes
MNA V0871	fragmentary skull showing palate, side of os basale, and ethmoid portion of braincase; vertebrae
MNA V8072	fragmentary lower jaw and stapes
MNA V8073	vertebrae and limb elements, including fragmentary pedal bones
MNA V9346	incomplete skull and jaws originally associated with MNA V8059

LITERATURE CITED

Badenhorst, A. 1978. The development and the phylogeny of the organ of Jacobson and the tentacular apparatus of *Ichthyophis glutinosus* (Linné). Annale Universiteit van Stellenbosch, Serie A2, **1:** 1–26.

Bemis, W. E., K. Schwenk, and M. H. Wake. 1983. Morphology and function of the feeding apparatus in *Dermophis mexicanus* (Amphibia: Gymnophiona). Zoological Journal of the Linnean Society, **77:** 75–96.

Billo, R., and M. H. Wake. 1987. Tentacle development in *Dermophis mexicanus* (Amphibia, Gymnophiona) with an hypothesis of tentacle origin. Journal of Morphology, **192:** 101–111.

Bolt, J. R. 1969. Lissamphibian origins: possible protolissamphibian from the Lower Permian of Oklahoma. Science, **166:** 888–891.

———. 1991. Lissamphibian origins, pp. 194–222. *In* H.-P. Schultze and L. Trueb (eds.), Origins of the Higher Groups of Tetrapods: Controversy and Consensus. Ithaca, New York: Cornell University Press.

Bolt, J. R., and R. E. Lombard. 1985. Evolution of the amphibian tympanic ear and the origin of frogs. Biological Journal of the Linnean Society, **24:** 83–99.

Boulenger, G. A. 1909. A list of the freshwater fishes, batrachians, and reptiles obtained by Mr. J. Stanley Gardiner's expedition to the Indian Ocean. Transactions of the Linnean Society of London, Second Series, **12:** 291–300.

Bramble, D. M. 1978. Origin of the mammalian feeding complex: models and mechanisms. Paleobiology, **4:** 271–301.

Brand, D. J. 1956. The cranial morphology of *Scolecomorphus uluguruensis* (Barbour and Loveridge). Annals of the University of Stellenbosch, Section A, **32:** 1–25.

CARROLL, R. L. 1991. *Batropetes* from the Lower Permian of Europe—a microsaur, not a reptile. Journal of Vertebrate Paleontology, **11:** 229–242.

———. 2000. *Eocaecilia* and the origin of caecilians, pp. 1402–1411. *In* H. Heatwole and R. L. Carroll (eds.), Amphibian Biology. Vol. 4. Palaeontology, The Evolutionary History of Amphibians. Chipping Norton, United Kingdom: Surrey Beatty & Sons.

CARROLL, R. L., AND P. J. CURRIE. 1975. Microsaurs as possible apodan ancestors. Zoological Journal of the Linnean Society, **57:** 229–247.

CARROLL, R. L., AND P. GASKILL. 1978. The Order Microsauria. Memoirs of the American Philosophical Society, **126:** 1–211.

CARROLL, R. L., AND R. HOLMES. 1980. The skull and jaw musculature as guides to the ancestry of salamanders. Zoological Journal of the Linnean Society, **68:** 1–40.

CARROLL, R. L., A. KUNTZ, AND K. ALBRIGHT. 1999. Vertebral development and amphibian evolution. Evolution & Development, **1:** 36–48.

DE BEER, G. R. 1937. The Development of the Vertebrate Skull. Oxford, United Kingdom: Clarendon Press. xxiii + 552 pp.

DE JAGER, E. F. J. 1939a. Contributions to the cranial anatomy of the Gymnophiona. Further points regarding the cranial anatomy of the genus *Dermophis.* Anatomischer Anzeiger, **88:** 193–222.

———. 1939b. The Gymnophione quadrate and its processes, with special reference to the processus ascendens in a juvenile *Ichthyophis glutinosus.* Anatomischer Anzeiger, **88:** 223–232.

DE VILLIERS, C. G. S. 1936. Some aspects of the amphibian suspensorium, with special reference to the paraquadrate and quadratomaxillary. Anatomischer Anzeiger, **81:** 225–247.

———. 1938. A comparison of some cranial features of the East African Gymnophiones *Boulengerula boulengeri,* Tornier and *Scolecomorphus uluguruensis* Boulenger. Anatomischer Anzeiger, **86:** 1–26.

DUBOIS, A. 2004. The higher nomenclature of recent amphibians. Alytes, International Journal of Batrachology, **22:** 1–14.

DUELLMAN, W. E., AND L. TRUEB. 1986. Biology of Amphibians. New York: McGraw-Hill Book Company. xvii + 670 pp.

EDGEWORTH, F. H. 1935. The Cranial Muscles of Vertebrates. Cambridge: Cambridge University Press, United Kingdom. viii + 493 pp.

ESTES, R., AND M. H. WAKE. 1972. The first fossil record of caecilian amphibians. Nature, **239:** 228–231.

EVANS, S. E., A. R. MILNER, AND C. WERNER. 1996. Sirenid salamanders and a gymnophionan amphibian from the Cretaceous of the Sudan. Palaeontology, **39:** 77–95.

EVANS, S. E., AND D. SIGOGNEAU-RUSSELL. 2001. A stem-group caecilian (Lissamphibia: Gymnophiona) from the Lower Cretaceous of North Africa. Palaeontology, **44:** 259–273.

FRANCIS, E. T. B. 1934. The Anatomy of the Salamander. Oxford, United Kingdom: Clarendon Press. xxxi + 381 pp.

FROST, D. R., T. GRANT, J. FAIVOVICH, R. H. BAIN, A. HAAS, C. F. B. HADDAD, R. O. DE SÁ, A. CHANNING, M. WILKINSON, S. C. DONNELLAN, C. J. RAXWORTHY, J. A. CAMPBELL, B. L. BLOTTO, P. MOLER, R. C. DREWES, R. A NUSSBAUM, J. D. LYNCH, D. M. GREEN, AND W. C. WHEELER. 2006. The amphibian tree of life. Bulletin of the American Museum of Natural History, **297:** 1–370.

GANS, C. 1975. Tetrapod limblessness: evolution and functional corollaries. American Zoologist, **15:** 455–467.

GOODRICH, E. S. 1930. Studies on the Structure and Development of Vertebrates. London: MacMillan and Company. xxx + 837 pp.

GREER, A. E. 1991. Limb reduction in squamates: identification of the lineages and discussion of the trends. Journal of Herpetology, **25:** 166–173.

GREVEN, H. 1984. The dentition of *Gegeneophis ramaswamii* Taylor, 1964 (Amphibia, Gymnophiona), with comments on monocuspid teeth in the Amphibia. Zeitschrift für zoologische Systematik und Evolutionsforschung, **22:** 342–348.

HECHT, M. K., AND T. C. LADUKE. 1997. Limbless tetrapods, pp. 95–99. *In* R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), Vertebrate Paleontology in the Neotropics, The Miocene Fauna of La Venta, Colombia. Washington, DC: Smithsonian Institution Press.

HEDGES, S. B., R. A. NUSSBAUM, AND L. R. MAXSON. 1993. Caecilian phylogeny and biogeography inferred from mitochondrial DNA sequences of the 12S rRNA and 16S rRNA genes (Amphibia: Gymnophiona). Herpetological Monographs, **7:** 64–76.

HOOK, R. W. 1983. *Colosteus scutellatus* (Newberry): a primitive temnospondyl amphibian from the Middle Pennsylvanian of Linton, Ohio. American Museum of Natural History Novitates, **2770:** 1–41.

HRAOUI-BLOQUET, S., AND J.-M. EXBRAYAT. 1996. Les dents de *Typhlonectes compressicaudus* (Amphibia, Gymnophiona) au cours du développement. Annales des Sciences naturelles, Zoologie, Paris, 13^e Série, **17:** 11–23.

JENKINS, F. A., JR., AND N. H. SHUBIN. 1998. *Prosalirus bitis* and the anuran caudopelvic mechanism. Journal of Vertebrate Paleontology, **18:** 495–510.

JENKINS, F. A., JR., AND D. M. WALSH. 1993. An Early Jurassic caecilian with limbs. Nature, **365:** 246–250.

JUPP, R., AND A. A. WARREN. 1986. The mandibles of the Triassic temnospondyl amphibians. Alcheringa, **10:** 99–124.

LAKJER, T. 1926. Studien über die Trigeminus—Versorgte Kaumuskulatur der Sauropsiden. Kopenhagen: C. A. Reitzel. 154 pp.

LAWSON, R. 1963. The anatomy of *Hypogeophis rostratus* Cuvier (Amphibia: Apoda or Gymnophiona). Part I, the skin and skeleton. Proceedings of the University of Durham Philosophical Society, Series A (Science), **13:** 254–273.

LESSA, E. P., AND M. H. WAKE. 1992. Morphometric analysis of the skull of *Dermophis mexicanus* (Amphibia: Gymnophiona). Zoological Journal of the Linnean Society, **106:** 1–15.

LOMBARD, R. E., AND J. R. BOLT. 1988. Evolution of the stapes in Paleozoic tetrapods: conservative and radical hypotheses, pp. 37–67. *In* B. Fritzsch, M. J. Ryan, W. Wilczynski, T. E. Hetherington, and W. Walkowiak (eds.), The Evolution of the Amphibian Auditory System. New York: John Wiley & Sons.

MARCUS, H. 1935. Zur Entstehung der Stapesplatte bei Hypogeophis. Anatomischer Anzeiger, 80: 142–146.

MARCUS, H., E. STIMMELMAYR, AND G. PORSCH. 1935. Die Ossifikation des *Hypogeophis*schädels. Beitrag zur Kenntnis der Gymnophionen XXV. Morphologisches Jahrbuch, **76:** 375–420.

MCGOWAN, G. J. 1998. The development and function of the atlanto-axial joint in albanerpetontid amphibians. Journal of Herpetology, **32:** 116–122.

MILNER, A. R. 1993. The Paleozoic relatives of lissamphibians. Herpetological Monographs, **7:** 8–27.

MONATH, T. 1965. The opercular apparatus of salamanders. Journal of Morphology, **116:** 149–170.

MÜLLER, H., O. V. OOMMEN, AND P. BARTSCH. 2005. Skeletal development of the direct-developing caecilian *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae). Zoomorphology, **124:** 171–188.

NUSSBAUM, R. A. 1977. Rhinatrematidae: a new family of caecilians (Amphibia: Gymnophiona). Occasional Papers of the Museum of Zoology, University of Michigan, **682:** 1–30.

———. 1979. The taxonomic status of the caecilian genus *Uraeotyphlus* Peters. Occasional Papers of the Museum of Zoology, University of Michigan, **687:** 1–20.

———. 1983. The evolution of a unique dual jaw-closing mechanism in caecilians (Amphibia: Gymnophiona) and its bearing on caecilian ancestry. Journal of Zoology, London, **199:** 545–554.

———. 1984. Amphibians of the Seychelles, pp. 379–415. *In* D. R. Stoddart (ed.), Biogeography and Ecology of the Seychelles Islands. The Hague: Dr. W. Junk Publishers.

———. 1985. Systematics of caecilians (Amphibia: Gymnophiona) of the Family Scolecomorphidae. Occasional Papers of the Museum of Zoology, University of Michigan, **713:** 1–49.

NUSSBAUM, R. A., AND B. G. NAYLOR. 1982. Variation in the trunk musculature of caecilians (Amphibia: Gymnophiona). Journal of Zoology, London, **198:** 383–398.

NUSSBAUM, R. A., AND M. WILKINSON. 1989. On the classification and phylogeny of caecilians (Amphibia: Gymnophiona), a critical review. Herpetological Monographs, **3:** 1–42.

PARKER, H. W. 1941. The caecilians of the Seychelles. The Annals and Magazine of Natural History, series 11, **12:** 1–17.

PARSONS, T. S., AND E. E. WILLIAMS. 1963. The relationships of the modern Amphibia: a re-examination. Quarterly Review of Biology, **38:** 26–53.

PETER, K. 1898. Die Entwicklung und funktionelle Gestaltung des Schädels von *Ichthyophis glutinosus.* Morphologisches Jahrbuch, **25:** 555–628.

RAGE, J.-C. 1986. Le plus ancien Amphibien apode (Gymnophiona) fossile. Remarques sur la répartition et l'histoire paléobiogéographique des Gymnophiones. Centre Researche Académie des Sciences, Paris, **302**(serie II, 16)**:** 1033–1036.

REISS, J. 1996. Palatal metamorphosis in basal caecilians (Amphibia: Gymnophiona) as evidence for lissamphibian monophyly. Journal of Herpetology, **30:** 27–39.

RIEPPEL, O. 1980. The phylogeny of anguinomorph lizards. Denkschriften der Schweizerischen Naturforschenden Gesellschaft, **94:** 1–86.

ROMER, A. S. 1956. Osteology of the Reptiles. Chicago: University of Chicago Press. xxi + 772 pp.

SAN MAURO, D., J. GOWER, O. V. OOMMEN, M. WILKINSON, AND R. ZARDOYA. 2004. Phylogeny of caecilian amphibians (Gymnophiona) based on complete mitochondrial genomes and nuclear RAG1. Molecular Phylogenetics and Evolution, **33:** 413–427.

SARASIN, P., AND F. SARASIN. 1887–1890. Ergebnisse naturwissenschaftlicher forschungen auf Ceylon in den Jahren 1884–1886. Vol. 2. Zur Entwicklungsgeschichte und Anatomie der ceylonesischen Blindwühle, *Ichthyophis glutinosus,* L. Wiesbaden, Germany: C. W. Kreidel's Verlag. 252 pp.

SÄVE-SÖDERBERGH, G. 1945. Notes on the trigeminal musculature in non-mammalian tetrapods. Nova Acta Regiae Societatis Scientiarum Upsaliensis, Series 4, **13:** 1–59.

SCHMIDT, A., AND M. H. WAKE. 1990. Olfactory and vomeronasal systems of caecilians (Amphibia: Gymnophiona). Journal of Morphology, **205:** 255–268.

SCHOCH, R. R., AND R. L. CARROLL. 2003. Ontogenetic evidence for the Paleozoic ancestry of salamanders. Evolution and Development, **5:** 314–324.

SHUBIN, N. H., AND F. A. JENKINS, JR. 1995. An Early Jurassic jumping frog. Nature, **377:** 49–52.

TAYLOR, E. H. 1968. The Caecilians of the World, A Taxonomic Review. Lawrence: The University of Kansas Press. viii + 848 pp.

———. 1969. Skulls of Gymnophiona and their significance in the taxonomy of the group. The University of Kansas Science Bulletin, **48:** 585–687.

Trueb, L. 1993. Patterns of cranial diversity among the Lissamphibia, pp. 255–343. *In* J. Hanken and B. K. Hall (eds.), The Skull. Vol. 2. Patterns of Structural and Systematic Diversity. Chicago: Chicago University Press.

Trueb, L., and R. Cloutier. 1991. A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli), pp. 223–313. *In* H.-P. Schultze and L. Trueb (eds.), Origins of the Higher Groups of Tetrapods: Controversy and Consensus. Ithaca, New York: Cornell University Press.

Visser, M. H. C. 1963. The cranial morphology of *Ichthyophis glutinosus* (Linné) and *Ichthyophis monochrous* (Bleeker). Annale Universiteit van Stellenbosch, Serie A, **38:** 67–102.

Wake, D. B. 1970. Aspects of vertebral evolution in the modern Amphiba. Forma et Functio, **3:** 33–60.

Wake, M. H. 1976. The development and replacement of teeth in viviparous caecilians. Journal of Morphology, **148:** 33–64.

———. 1980a. Morphometrics of the skeleton of *Dermophis mexicanus* (Amphibia: Gymnophiona). Part I. The vertebrae, with comparisons to other species. Journal of Morphology, **165:** 117–130.

———. 1980b. Fetal tooth development and adult replacement in *Dermophis mexicanus* (Amphibia: Gymnophiona): fields versus clones. Journal of Morphology, **166:** 203–216.

———. 1987a. A new genus of African caecilian (Amphibia: Gymnophiona). Journal of Herpetology, **21:** 6–15.

———. 1987b. Haemal arches in amphibians: a problem in homology and phylogeny. American Zoologist, **27:** 33A.

———. 1992. "Regressive" evolution of special sensory organs in caecilians (Amphbia: Gymnophiona): opportunity for morphological innovation. Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere, **122:** 325–329.

———. 2003. The osteology of caecilians, pp. 1809–1876. *In* H. Heatwole and M. Davies (eds.), Amphibian Biology. Vol. 5. Osteology. Chipping Norton, United Kingdom: Surrey Beatty & Sons.

Wake, M. H., and J. Hanken. 1982. Development of the skull of *Dermophis mexicanus* (Amphibia: Gymnophiona), with comments on skull kinesis and amphibian relationships. Journal of Morphology, **173:** 203–223.

Wake, M. H., and G. Z. Wurst. 1979. Tooth crown morphology in caecilians (Amphibia: Gymnophiona). Journal of Morphology, **159:** 331–341.

Werner, C. 1994. Der erste Nachweis von Gymnophionen (Amphibia) in der Kreide (Wadi-Milk-Formation, Sudan). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1994:** 633–640.

Wever, E. G. 1973. The ear and hearing in the frog, *Rana pipiens.* Journal of Morphology, **141:** 461–477.

———. 1975. The caecilian ear. Journal of Experimental Zoology, **191:** 63–71.

Wever, E. G., and C. Gans. 1976. The caecilian ear: further observations. Proceedings of the National Academy of Sciences U.S.A., **73:** 3744–3746.

Wiedersheim, R. 1879. Die Anatomie der Gymnophionen. Jena: Gustav Fischer Verlag. vii + 100 pp.

Wilkinson, M. 1991. Adult tooth crown morphology in the Typhlonectidae (Amphibia: Gymnophiona): a reinterpretation of variation and its significance. Zeitschrift für zoologische Systematik und Evolutionsforschung, **29:** 304–311.

———. 1992. The phylogenetic position of the Rhinatrematidae (Amphibia: Gymnophiona): evidence from the larval lateral line system. Amphibia-Reptilia, **13:** 74–79.

———. 1996. The heart and aortic arches of rhinatrematid caecilians (Amphibia: Gymnophiona). Zoological Journal of the Linnean Society, **118:** 135–150.

Wilkinson, M., and R. A. Nussbaum. 1996. On the phylogenetic position of the Uraeotyphlidae (Amphibia: Gymnophiona). Copeia, **1996:** 550–562.

———. 1997. Comparative morphology and evolution of the lungless caecilian *Atretochoana eiselti* (Taylor) (Amphibia: Gymnophiona: Typhlonectidae). Biological Journal of the Linnean Society, **62:** 39–109.