



Palatal Metamorphosis in Basal Caecilians (Amphibia: Gymnophiona) as Evidence for Lissamphibian Monophyly

John Reiss

Journal of Herpetology, Vol. 30, No. 1. (Mar., 1996), pp. 27-39.

Stable URL:

<http://links.jstor.org/sici?sici=0022-1511%28199603%2930%3A1%3C27%3APMIBC%28%3E2.0.CO%3B2-3>

Journal of Herpetology is currently published by Society for the Study of Amphibians and Reptiles.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ssar.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

erra de Juárez, vicinity of Metates (MZFC 2254); 48.3 km (by road) NE Llano de las Flores, 1640 m, km 103 along Oaxaca-Tuxtepec road (UMMZ 130955); Sierra Mixe, Totontepec, 1768 m (UTA 14538-41, 18232-39); Sierra Mixe, 4.2 km S Totontepec (UTA 14542-44); Sierra Mixe, 2 km W Totontepec, 1950 m (MZFC 5300-03, 5325).

Anolis salvini.—Guatemala: No further data (BMNH 1946.9.8.19, formerly 83.5.24.42, holotype).

Anolis schiedii.—Unknown (ZMB 526, holotype). México. No further data (USNM 12091). Veracruz: 3 km

(by air) ENE Coscomatepec, at junction of Río Japapa and México Federal Hwy 125, 1340-1400 m (MZFC 5096-5106, 5108); about 2 km (by air) SW Banderillas (ca. 8 km by air NNW Xalapa), Rancho El Alamo, 1500 m (MZFC 5141-44); Mirador (USNM 46653); Las Minas, 1400 m (USNM 148949-50); El Esquilón (between Banderillas and Jilotepec) (MZFC 5479); 6.0 km (by road) NE Coscomatepec on México Hwy 125, near km 28 (UTA 18230).

Anolis villai.—Nicaragua. Great Corn Island (KU 159646, holotype; 159647-59, paratypes).

Journal of Herpetology, Vol. 30, No. 1, pp. 27-39, 1996
Copyright 1996 Society for the Study of Amphibians and Reptiles

Palatal Metamorphosis in Basal Caecilians (Amphibia: Gymnophiona) as Evidence for Lissamphibian Monophyly

JOHN REISS¹

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, USA

ABSTRACT.—The morphology of the bony palate in larval and metamorphosed *Epicrionops bicolor* Boulenger and *E. petersi* Taylor (Rhinatrematidae) was studied to assess the extent of palatal change at metamorphosis. In larvae the maxilla is short; it abuts the dorsolateral process of the palatine at mid-choanal level. The pterygoid is long and straight; it runs anteromedially, close to the lateral edge of the parasphenoid. At metamorphosis the maxilla fuses with the palatine. The maxillary part of the maxillopalatine expands dorsally and caudally, surrounding the orbit and lacrimal ducts and completing the lateral border of the subtemporal fenestra. The anterior part of the pterygoid shifts laterally, broadening the interpterygoid vacuity, and separates from the posterior part of the pterygoid. The quadrate develops a rostrally directed quadratojugal process, overlapped by the maxilla and squamosal. A review of the literature shows that a similar pattern of palatal metamorphosis (except for the division of the pterygoid) is seen in other caecilian genera with free-living larvae: *Ichthyophis* (Ichthyophiidae), *Grandisonia* (Caeciliidae), and probably *Uraeotyphlus* (Uraeotyphlidae) and *Sylvacaecilia* (Caeciliidae). This implies that the shared pattern is plesiomorphic for caecilians. Features of palatal metamorphosis shared among caecilians, salamanders, and frogs support the hypothesis of lissamphibian monophyly.

Extant amphibians comprise three distinct, monophyletic groups: frogs (Anura), salamanders (Caudata), and caecilians (Gymnophiona) (Duellman and Trueb, 1986; Milner, 1988; Cannatella and Hillis, 1993). The relationship of each group to the others, and of these to fossil taxa, has been much debated. However, an emerging consensus—based on both morphological and molecular evidence—supports the hypothesis first explicitly proposed by Parsons and Williams (1962, 1963; see also Gadow, 1901;

Parker, 1956; Szarski, 1962): that the extant groups are a monophyletic unit, the Lissamphibia (e.g., Milner, 1988, 1993; Bolt, 1991; Trueb and Cloutier, 1991; Cannatella and Hillis, 1993; Hedges and Maxson, 1993). Since basal members of all three modern groups have a biphasic life cycle with a discrete metamorphosis from the larval to the juvenile form (Duellman and Trueb, 1986), we might expect to find common character transformations retained in the metamorphosis of each group. Such shared character transformations could serve as additional lissamphibian synapomorphies (cf. de Queiroz, 1985).

Both frogs and salamanders undergo profound changes in skull structure at metamorphosis, especially in the palate and the hyo-

¹ Present Address: Department of Molecular and Cellular Biology, University of Arizona, Tucson, Arizona 85721, USA.

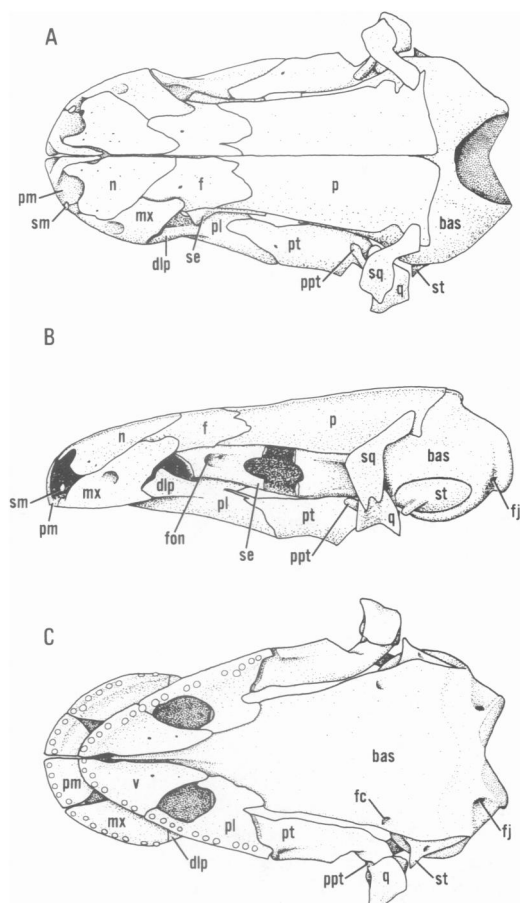


FIG. 1. Osteocranium of an advanced larva of *Epicrionops bicolor* (LSUMZ 27267). A, dorsal view; B, lateral view; C, ventral view. The scale bar is 1 mm.

branchial apparatus (reviewed by Reiss, 1993; Rose and Reiss, 1993). By contrast, the extent of cranial change at metamorphosis in caecilians is not well characterized. Data on metamorphic changes in skull structure are useful because skeletal characters can be compared between extant and fossil taxa. Changes in the bony palate are especially relevant to lissamphibian monophyly, since no non-lissamphibian is known to have had any significant metamorphic remodelling in this region (see below).

To determine the extent of palatal metamorphosis in caecilians, I examined embryonic, larval, and adult specimens of two species in the New World genus *Epicrionops* (Rhinatremaidae). Rhinatrematids are generally considered the sister group of all other living caecilians (Nussbaum, 1977; Duellman and Trueb, 1986; Hedges et al., 1993). Larval specimens of the

Old World genus *Ichthyophis* (Ichthyophiidae) were also available for comparison.

MATERIALS AND METHODS

The larval and adult specimens examined (see Appendix 1) had been previously prepared by M. H. Wake of the University of California, Berkeley (Hetherington and Wake, 1979; Wake, 1989). Both cleared-and-stained and sectioned material was available. All drawings of these specimens were made with the aid of a camera lucida. The late stage embryo of *E. petersi* came from the same clutch described and figured by Noble (1927, fig. 5). The head was decalcified in 5% nitric acid in 70% ethanol, embedded in Paraplast® (Monoject Scientific), sectioned transversely at 10 μ m, and stained with hematoxylin and eosin (Humason, 1979). Bone staining was poor in this specimen, either due to the original fixation or the decalcification. Nonetheless, the outlines of the dermal bones could generally be determined from the surrounding ring of osteoblasts. A graphical reconstruction of the anterior palate was prepared after the method of Pusey (1939).

The only mid-metamorphic specimen of *Epicrionops* available was already completely adult in all palatal characters except tooth count. Metamorphic changes are thus inferred from differences between larvae and adults. The two species examined do not appear to differ in palatal structure, and thus are treated together.

RESULTS

In the following description, the structure of each bone is given in sequence for: (1) large larvae (160–165 mm TL), since these are of greatest interest for comparison with the adult condition; (2) smaller larvae and the embryo (when there are significant differences); (3) adults. The adult palate has been described and figured previously by Nussbaum (1977); my interpretation differs from his only with respect to the pterygoid.

Premaxilla.—In large larvae the premaxilla has dental (alveolar), palatal, and facial (ascending) processes (Figs. 1, 3D, pm). The premaxilla connects syndesmotically to the maxilla, vomer, and nasal capsule, and is sutured to the nasal. The premaxilla serves as a floor and medial wall for the anterior end of the nasal sac. The only change in adults is increased ossification, with the palatal process more closely joined to that of the maxilla (Fig. 2D).

Maxilla.—In large larvae the maxilla has dental, palatal, and facial processes (Fig. 1, mx). The facial process overlies the nasal tectum and the lateral edge of the frontal; it is sutured to the nasal and the dorsolateral process of the palatine. The main ramus of the maxillary nerve

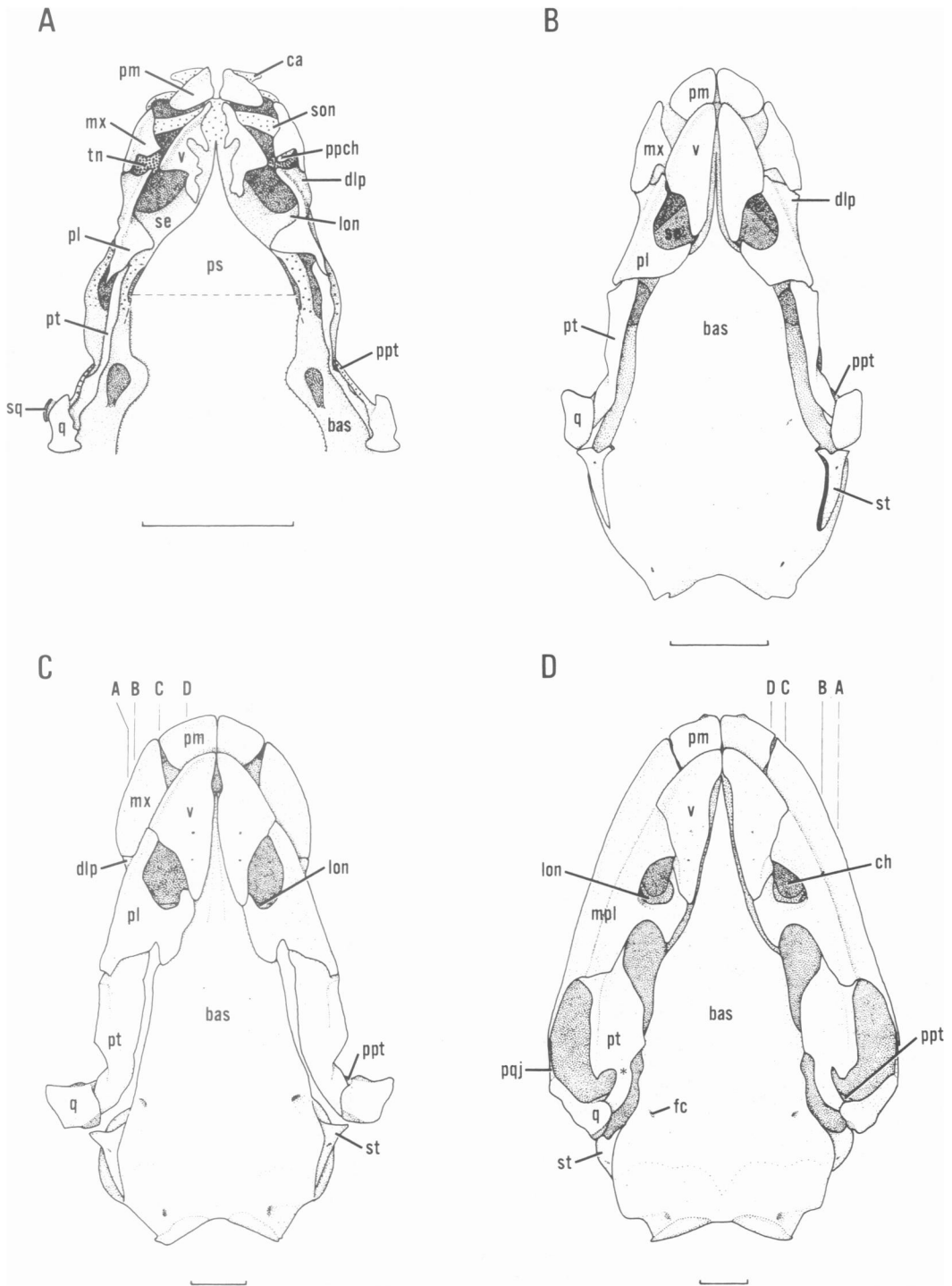


FIG. 2. Developmental series of *Epicrionops* palates, ventral view. Teeth omitted. A, *E. petersi*, late embryo, graphic reconstruction (AMNH 1454). Coarse stipple indicates cartilage. B, *E. bicolor*, young larva (LSUMZ 27293). C, *E. bicolor*, large larva (LSUMZ 27267). Small letters A-D indicate level of sections in Fig. 3. D, *E. bicolor*, adult (LSUMZ 27266). The asterisk indicates the region where the pterygoid has usually divided into anterior and posterior parts. Small letters A-D indicate level of sections in Fig. 4. All scale bars are 1 mm.

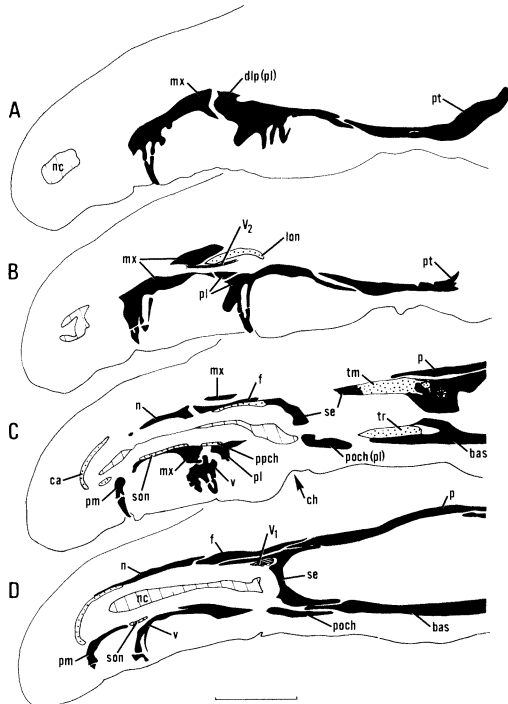


FIG. 3. A-D. Parasagittal sections through the snout of a large larva of *Epicrionops bicolor* (LSUMZ 27254), from lateral to medial. Anterior is to the left. The approximate level of the sections is shown in Fig. 2C. Black indicates bone, stippling cartilage. The scale bar is 1 mm.

runs forward in the angle between palatal and facial processes of the maxilla (Fig. 3B, V_2); the large foramen in the facial process transmits a branch of this nerve (probably including lateral line components). The palatal process of the maxilla is sutured to the base of the dorsolateral process of the palatine. This suture is reinforced ventrally by the lateral angle of the vomer, and dorsally by a caudomedially directed part of the solum nasi, the prechoanal process (Fig. 3C, ppch; this is the "ectochoanal cartilage" of Ramaswami, 1941 and Visser, 1963). In smaller larvae (Fig. 2B) and the embryo (Fig. 2A) the facial process of the maxilla has a notch in its anterior border, rather than the foramen seen later.

In adults the maxilla is fused to the palatine, forming the compound maxillopalatine seen in all adult caecilians (Figs. 2D, 4, mpl). I will treat the part of the maxillopalatine lateral and dorsal to the base of the inner tooth row as the "maxillary part" (cf. Sarasin and Sarasin, 1887-1890), but the dorsolateral process of the larval palatine may also contribute to this region (compare Figs. 3 and 4). Caudal extensions of the palatal, dental, and facial processes of the maxilla now

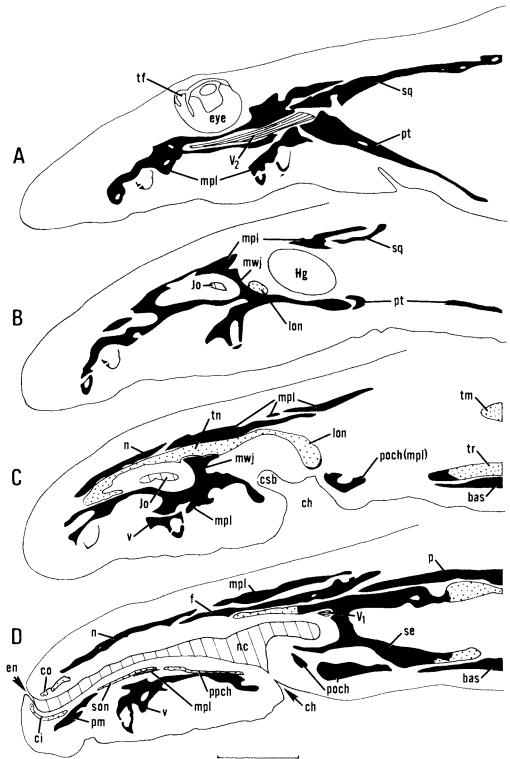


FIG. 4. A-D. Parasagittal sections through the snout of an adult *Epicrionops petersi* (LSUMZ 27312), from lateral to medial. Anterior is to the left. The approximate level of the sections is shown in Fig. 2D. Black indicates bone, stippling cartilage. The scale bar is 1 mm.

reach back around the subtemporal fenestra to the lateral surface of the quadrate (Fig. 2D). The facial process has also extended markedly dorsad, surrounding the orbit. A new bony lamina connecting the facial and palatal processes forms an anterior wall for the orbit (Fig. 5A, aow). The ventral part of this wall lies in the region occupied by the dorsolateral process of the palatine in larvae.

A chamber for Jacobson's organ has developed in the maxillopalatine (Figs. 4B, C, 5, Jo; see Schmidt and Wake, 1990). This chamber opens anteromedially; its medial wall is a vertical lamina of bone connecting the palatal and facial processes, parallel but medial to the inner tooth row (Figs. 4B, C, 5, mwj). The chamber is closed caudally by the anterior orbital wall, which is pierced by a common foramen for the two lacrimal (tentacle) ducts (Fig. 5, 1d). The anterior orbital wall of *Epicrionops* and the medial wall of the tentacular groove or canal in other caecilians have identical relations to the

tentacle, lacrimal ducts, and Jacobson's organ, and are clearly homologous structures. In *Ichthyophis* there is a small chamber for the tip of Jacobson's organ in the inner side of this wall, with relations similar to those of the much larger chamber in *Epicrionops* (Sarasin and Sarasin, 1887-1890, Pl. XVI, Fig. 25; Visser, 1963, Fig. 4).

The main branch of the maxillary nerve is now enclosed in a canal (Fig. 4A, V_2). This canal begins at a foramen in the caudal border of the maxillopalatine, runs anteriorly through the floor of the orbit, passes ventrolaterally to the chamber for Jacobson's organ, and ramifies into smaller canals that exit the maxillopalatine at several points along its lateral and anterior sides (Figs. 4B, C, 5A).

Palatine.—In large larvae the palatine (Figs. 1, 3, pl) has dental and palatal (postchoanal) processes, as well as a prominent dorsolateral process abutting the caudal end of the maxilla (Figs. 1, 3A, dlp). The dorsolateral process has distinct facial and palatal surfaces: the facial surface is coplanar with the facial process of the maxilla; the palatal surface continues anteromedially as a narrow shelf anterior to the base of the dental process (Fig. 3B). The dorsolateral process is a unique feature of larval caecilians; it forms the posteroventral wall of the nasal cavity, and its crest runs along the lateral edge of the lamina orbitonasalis.

The palatine is similar in smaller larvae, but the dorsolateral process is more prominent and forms a distinct lateral articulation with the maxilla (Fig. 2B). On one side of a 66 mm TL *E. bicolor* (Fig. 2B) and both sides of a 101 mm TL *E. petersi* the postchoanal process curves anteriorly around the choana but does not extend caudally along the edge of the parasphenoid. The dorsolateral process of the palatine is even more prominent in the embryo (Fig. 2A). In transverse section this process is a thin lamina, which curves dorsolaterally below the caudal end of the nasal sac. Distinct facial and palatal surfaces have not yet formed. The postchoanal process is short and triangular, and does not extend toward the vomer.

The "palatine part" of the adult maxillopalatine has the same general configuration as the larval palatine, though its shape has changed significantly (Fig. 2D); the fate of the larval dorsolateral process is uncertain (see above). A bony rim has formed around the choana (Fig. 4C, D), completed anteromedially by the vomer. The postchoanal process no longer overlaps the basal.

Pterygoid.—In large larvae the pterygoid is a strap-like bone (Fig. 1, pt) extending parallel to the edge of the basal from the quadrate to the caudal end of the palatine. The rostral end of the pterygoid lies in a shallow fossa on the dor-

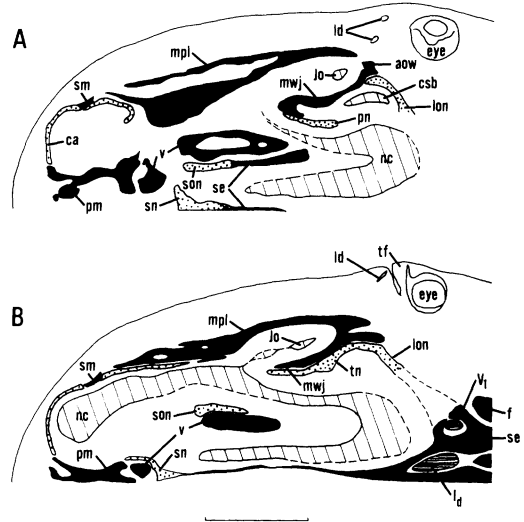


FIG. 5. A, B. Frontal sections through the snout of an adult *E. petersi* (LSUMZ 27312). Anterior is to the left, the midline is at the bottom. A is more ventral than B. Note the tentacle fold just anterior to the eye and the lacrimal ducts passing inwards toward Jacobson's organ (they connect just ventral to section A). Black indicates bone, stippling cartilage. The scale bar is 1 mm.

sal side of the palatine (Fig. 3A, B). Laterally, a ventral ridge adjoins the dental process of the palatine, but it does not bear teeth. More caudally, the lateral edge is flared slightly as a pterygoid flange, serving as the site of origin for the m. levator mandibulae posterior (cf. Bemis et al., 1982). The medial edge of the pterygoid is connected syndesmotically to the lateral edge of the basal; there is no other basal articulation. The pterygoid has three distinct connections to the quadrate: (1) a long dorsal process extends up the anteromedial side of the quadrate; (2) a shallow groove on the dorsal surface houses the pterygoid process of the quadrate; (3) a large lateral process is enclosed in a fossa in the articular head of the quadrate (Fig. 6B).

The pterygoid is relatively narrower in smaller larvae, and the pterygoid flange is only weakly indicated (Fig. 2B); the lateral process is already present (Fig. 6A). The pterygoid is even narrower in the embryo (Fig. 2A). The dorsal process is already well developed, but there is no lateral process.

The pterygoid of adults usually is separated into distinct anterior and posterior parts, connected only by a ligament (see Nussbaum, 1977, fig. 1, redrawn as fig. 13-10 of Duellman and Trueb, 1986). However in one specimen, a 231 mm TL *E. bicolor*, the anterior and posterior pterygoid are synostotically joined (Fig. 2D); this specimen shows no other differences from the

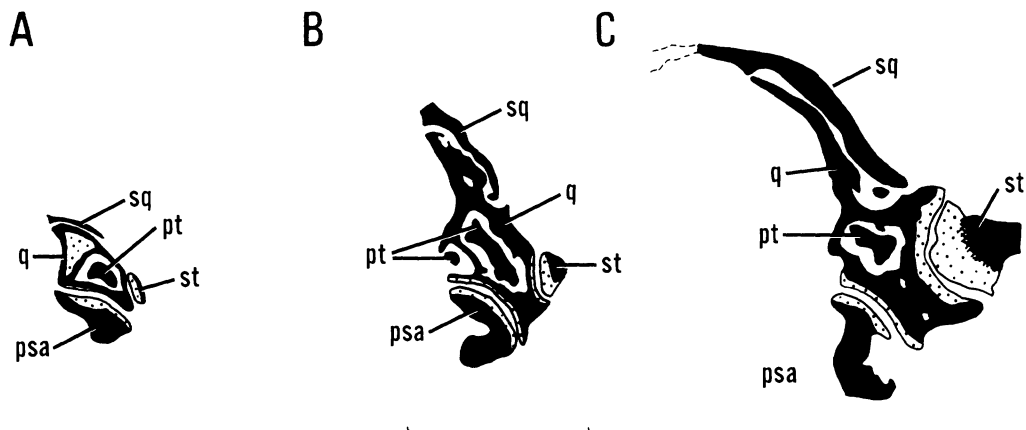


FIG. 6. Parasagittal sections through the pterygo-quadrate articulation. Anterior is to the left. Note the lateral process of the pterygoid, lodged in a cavity in the quadrate. A, 89 mm TL larva. B, 161 mm TL larva. C, 221 mm TL adult. A and B, *Epicrionops bicolor*, C, *E. petersi*. Black indicates bone, stippling cartilage. Scale bar is 1 mm.

typical condition. The anterior pterygoid now runs anterolaterally, rather than anteromedially, so that the interpterygoid vacuity is much wider than in larvae. The anterior pterygoid is syndesmoticly joined to the expanded squamosal dorsolaterally (Fig. 4A, sq), while its posterolateral corner bears the greatly expanded pterygoid flange. The posterior pterygoid appears in ventral view as a small process extending from the quadrate toward the basal process of the basal bone. Nussbaum (1977, fig. 1) labelled the posterior pterygoid the "processus pterygoideus of quadrate," but in section it is clear that this bone is the disconnected rear end of the pterygoid: the posterior pterygoid retains both dorsal and lateral processes (Fig. 6C), and the true pterygoid process is still present along its dorsal surface.

Quadrate.—In large larvae the quadrate body (ossified articular and otic processes of the palatoquadrate) extends dorsally and somewhat anteromedially from the jaw joint, ending beneath the bend of the squamosal (Fig. 1, q). The quadrate is shaped like a truncated pyramid, and bears articular facets for the pseudoangular ventrally, and for the stapes caudally; both joints are synovial (Fig. 6B). Some cartilage is also present at the dorsal end of the otic process. As noted above, the articular process is hollow, with a medial cavity filled by the lateral process of the pterygoid (Fig. 6B). A short, ossified pterygoid process projects anteromedially from the quadrate body (Fig. 1, ppt). The quadrate is attached to the rest of the skull by means of: (1) the pterygoid; (2) the squamosal (bound by ligament to the otic capsule); and (3) the stapes, the footplate of which is partially fused to the otic capsule anteriorly (the processus columello-trabecularis of Visser, 1963).

In smaller larvae (Fig. 2B) the quadrate is less heavily ossified. A large cavity in the articular process is already present, and is enclosed caudally by intramembranous bone, rostrally by perichondrally ossified cartilage (Fig. 6A). The pterygoid process is completely ossified in the smallest sectioned larva examined. The jaw joint is relatively further forward with respect to the long axis of the skull than in larger larvae, but has the same position with respect to the otic capsule and carotid foramen. In the embryo (Fig. 2A) the cavity in the articular process of the quadrate has not yet formed. The relatively long pterygoid process lies along the dorsolateral edge of the pterygoid; its anterior two thirds are cartilaginous throughout, while its caudal third is perichondrally ossified in continuity with the quadrate.

In adults the quadrate is ossified throughout, except for the articular surfaces. A new platelike anterior extension is present in front of the jaw joint, overlapped by the expanded maxillopalatine and squamosal laterally (Fig. 2D, pqj). This extension is the processus jugularis of Sarasin and Sarasin (1887–1890) and Ramaswami (1941), but is better called the quadratojugal process (following the homology proposed by Peter, 1898, and Visser, 1963). As in larvae, there is a cavity for the lateral process of the pterygoid in the medial surface of the quadrate (Fig. 6C). The pterygoid process is very short; it runs anteromedially along the lateral edge of the posterior pterygoid. The articular facet for the lower jaw is now much more elongate in ventral view (cf. Fig. 2C and D). There is no shift in the position of the jaw joint with respect to the longitudinal axis of the skull.

Vomer.—The vomer of large larvae is a relatively simple bone, composed primarily of den-

tal and palatal processes (Fig. 1, v). The palatal process of the vomer meets the palatine medial to the choana. Rostrally, the vomer has a narrow ascending process that extends up along the anterior end of the nasal septum, just behind the facial process of the premaxilla.

The vomer of adults retains the same shape as the larval bone when seen in ventral view, but no longer overlaps the basal (Fig. 2D). Dorsally, the adult vomer has developed a longitudinal ridge, extending from the flange along the medial border of the choana (see above) to the rostral end of the bone. The dorsal edge of this ridge bends medially, and lies against a dorsal extension of the solum nasi (Fig. 5A, son). Together, they make a canal for the nerve formed by the maxillary branch of the trigeminal and palatine branch of the facial (cf. Norris and Hughes, 1918; Ramaswami, 1941; Visser, 1963). More rostrally, the solum nasi extends laterad over the top of the vomerine ridge (Fig. 5B). The combined ridge formed by the solar and vomerine ridges partially divides the main nasal cavity into lateral and medial cavities (Schmidt and Wake, 1990). At the most rostral tip of the vomer, the ascending process still extends up behind the premaxilla (Fig. 5).

Basal.—The compound basal bone has already formed in large larvae (Fig. 1, bas). Anteriorly, the basal is composed of the parasphenoid rostrum, lying ventral to the sphenethmoid (Fig. 3D). The parasphenoid rostrum has a broad, flat keel. The lateral edge of the keel is bound to the medial edge of the vomer. Posteriorly, the parasphenoid is fused indistinguishably to the co-ossified pleurosphenoid, otic capsule, and occiput. The basal is separated from the sphenethmoid by a short unossified region of the taenia marginalis (orbital cartilage) and trabecula, above and below the optic foramen (Fig. 3C, tm, tr).

Behind the optic foramen the ventral margin of the basal spreads laterally, beyond the wall of the braincase, forming a progressively wider subocular shelf, which continues as the otic shelf on the anterior face of the otic capsule. The entire subocular shelf is syndesmoticly bound to the medial edge of the pterygoid; a slight lateral bulge in the shelf where it most closely approaches the pterygoid appears to represent the basal process. The carotid foramen lies at the level of the jaw joint; the foramen opens into a canal running medially in the angle between the otic shelf and the anteroventral face of the otic capsule.

The basal has already formed in the smallest sectioned larva, an 89 mm TL *E. bicolor*, and is as completely ossified as in the larger larvae (Fig. 2B). I could not determine the condition in the embryo with certainty, but the para-

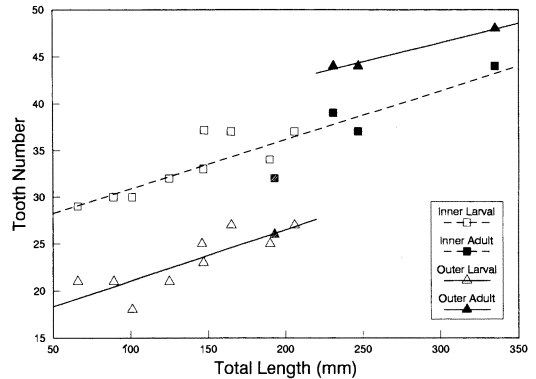


FIG. 7. Total number of teeth in outer (premaxillary-maxillary) and inner (vomerine-palatine) tooth rows of *Epicrionops* plotted against total length. The late metamorphic specimen is indicated by cross-hatching; the small teeth at the back of the outer row were not included in the count.

sphenoid appeared to be distinct from the neurocranial part of the basal (Fig. 2A).

The adult basal differs little from that of larvae (Fig. 2D), though the keel of the parasphenoid rostrum is remodelled in association with the apparent lateral shift of the vomer and palatine. Some hypertrophic cartilage is present in the region of the basal process in the sectioned specimen, confirming that the subocular shelf in this region is a projection of the chondrocranium, and not merely a laterally expanded parasphenoid.

Tooth Number.—Palatal teeth of larvae and adults are arranged in two rows. The outer row is borne by the premaxilla and maxilla, the inner row by the vomer and palatine (Fig. 1C). Total tooth number in the inner row increases steadily with total length, whereas there is a jump in the number of teeth in the outer row associated with metamorphosis (Fig. 7), as one would expect from the caudal extension of the maxilla. The presence of a number of small teeth at the back of the outer row in the late metamorphic specimen of *E. petersi* suggests that the additional teeth are merely added to the existing complement.

DISCUSSION

The basic pattern of palatal metamorphosis in *Epicrionops* is as follows: The maxilla fuses with the palatine to form a compound maxillopalatine. The maxillary part of this bone extends caudally around the subtemporal fenestra to meet the quadrate, surrounds the orbit, and encloses the lacrimal ducts of that side in a foramen. The pterygoid separates into anterior and posterior parts, connected by a ligament,

and the anterior part shifts laterally, broadening the interpterygoid vacuity. The quadrate develops a new platelike anterior extension, the quadratojugal process. A longitudinal dorsal ridge develops on the vomer, dividing the nasal cavity into medial and lateral chambers. Tooth number in the outer (maxillopalatine) tooth row increases greatly.

Having observed this ontogenetic pattern, two questions arise: (1) What features of this pattern are plesiomorphic for caecilians? (2) Can the inferred plesiomorphic metamorphic pattern shed any light on the problem of lissamphibian monophyly?

The Plesiomorphic Metamorphic Pattern.—A biphasic life history involving metamorphosis from a free-living larval stage occurs in all caecilians of the families Rhinatrematidae (Taylor, 1968; Wake, 1989), Ichthyophiidae (Sarasin and Sarasin, 1887–1890; Taylor, 1968; Breckenridge et al., 1987), and Uraeotyphlidae (Parker and Dunn, 1964; Wilkinson, 1992) for which the life histories are known (reviewed by Wake 1977, 1992). These are generally agreed to be the three most basal caecilian families (Nussbaum, 1977, 1979; Duellman and Trueb, 1986; Hedges et al., 1993). Several genera of the derived family Caeciliidae (probably paraphyletic; see Hedges et al., 1993) also have free-living larvae and metamorphosis (Wake 1977, 1992): the South American caeciliid *Siphonops* (Spengel, 1876; Edgeworth, 1925), the African caeciliid *Sylvacaecilia* (Largen et al., 1972; Wake, 1987), and the Seychellean caeciliid *Grandisonia* (Brauer, 1899; Parker, 1941, 1958; Taylor, 1968). Other caeciliids for which the life history are known are either direct-developing or viviparous (Wake 1977, 1992). Given this distribution, metamorphosis is clearly plesiomorphic for caecilians.

A review of the extensive literature on the skull of *Ichthyophis* (larvae: Müller, 1835; Thyng, 1906; Norris and Hughes, 1918; Edgeworth, 1925; de Jager, 1939; Ramaswami, 1947; adults: Wiedersheim, 1879; Engelhardt, 1924; Taylor, 1969; both: Sarasin and Sarasin, 1887–1890; Peter, 1898; Visser, 1963; Badenhorst, 1978) shows that species of this genus undergo a palatal metamorphosis similar to that outlined above for *Epicrionops*, though this has not been widely recognised. Significant differences include: (1) a deep tentacular groove or canal in the maxillopalatine develops as the tentacular apparatus migrates forward; (2) the "postfrontal" forms (this region is occupied by the extension of the maxillopalatine in *Epicrionops*); (3) the pterygoid does not divide into anterior and posterior parts; (4) a long cartilaginous extension of the pterygoid process present in larvae degenerates to connective tissue (Peter, 1898; de Jager, 1939; Visser, 1963); 5) the parasphenoid fuses with

the (already fused) pleurosphenoid, otic capsules, and occiput to form the basal (Peter, 1898; Ramaswami, 1947; Visser, 1963). Of these five differences, the first involves a derived state of adult *Ichthyophis*, for which the condition in *Epicrionops* is considered primitive (Nussbaum, 1977, 1979; Trueb, 1993). The second and third involve uniquely derived states of Rhinatrematidae or of *Epicrionops* (Nussbaum, 1977; Trueb, 1993), and thus the state in *Ichthyophis* must be considered primitive. For the last two, the lack of information on larvae of a suitable outgroup (e.g., *Eocaecilia*; Jenkins and Walsh, 1993) makes the polarity of the states uncertain.

Information on metamorphic changes in other caecilian taxa is sparse. The classic study of caecilian skull development by Marcus et al. (1935) described early embryonic and juvenile stages of a species of *Grandisonia*, but their intermediate stage was apparently of the closely related (Nussbaum and Ducey, 1988; Hass et al., 1993; Hedges et al., 1993), direct-developing *Hypogeophis rostratus*. The skull of this *Hypogeophis* embryo shows many similarities to the skull of larval *Epicrionops* and *Ichthyophis*; in particular, the maxillary part of the maxillopalatine extends back only to the middle of the choana, and the temporal region is open, due to the splint-like squamosal (see their fig. 2a and 2b, redrawn by de Beer, 1937, as figs. 6 and 7, pl. 73, but note that labelling of the palatal bones is badly confused). Similar conditions probably occur in *Grandisonia*; Parker (1941) noted the caudad extension of the maxilla at metamorphosis. The "late larval" skull of *Sylvacaecilia* illustrated by Wake (1987, fig. 1) is actually a young postmetamorphic specimen (Specimen H. 145/14 of Largen et al., 1972; M. H. Wake, pers. comm.), and thus not relevant, but it is clear that in both *Sylvacaecilia* and *Uraeotyphlus* there is a caudad extension of the premaxillary-maxillary tooth row at metamorphosis (Largen et al., 1972; Wilkinson, 1992).

In summary, most features of palatal metamorphosis seen in *Epicrionops* are also present in *Ichthyophis*, and thus can be considered plesiomorphic for caecilians. Furthermore, at least part of this shared metamorphic pattern, namely the caudad extension of the maxilla around the subtemporal fenestra, occurs in *Grandisonia*, can be inferred to occur in *Sylvacaecilia* and *Uraeotyphlus*, and appears to be recapitulated in the direct-developing *Hypogeophis*.

Palatal development in *Dermophis mexicanus*, the one viviparous caecilian that has been studied (Wake and Hanken, 1982), does not recapitulate the plesiomorphic larval palatal structure or metamorphic pattern. More generally, the "dentitional metamorphosis" around the time of birth in all viviparous caecilians (Parker,

1956; Parker and Dunn, 1964; Wake, 1976, 1980) has no apparent relationship to the metamorphic changes seen in caecilians with free-living larvae.

Lissamphibian Monophyly.—As noted above, recent molecular evidence (Hedges and Maxson, 1993) supports the emerging consensus that the Lissamphibia, containing caecilians, frogs, and salamanders, is monophyletic. However, even if the Lissamphibia is monophyletic with respect to other living tetrapods (i.e., amniotes), it may not be monophyletic with respect to fossil taxa (Milner, 1988, 1993; Bolt, 1991).

Many of the morphological synapomorphies used to define the Lissamphibia involve the open temporal region and the loss of a number of skull roofing bones (Bolt, 1991; Trueb and Cloutier, 1991; Trueb, 1993). For these to be valid synapomorphies, the solidly roofed skull of many caecilians must be secondarily derived (Nussbaum, 1977, 1979, 1983; Trueb, 1993). However, *Eocaecilia micropodia*, the recently discovered fossil caecilian from the Early Jurassic of Arizona, has a solidly roofed skull (Jenkins and Walsh, 1993). *Eocaecilia* also has many skull roofing bones not present as independent elements in Recent adults. Thus lissamphibian synapomorphies involving an open skull roof may need to be reevaluated.

The fact that all Recent amphibians—including caecilians, as the current study makes clear—have a morphologically distinct larval palate, and an abrupt metamorphosis to the adult palatal form (Rose and Reiss, 1993), suggests that features of palatal metamorphosis might serve as synapomorphies uniting the Lissamphibia. To do so, such features must be (1) shared among the three groups, and (2) lacking in outgroups.

Unfortunately, it is difficult to define features of palatal metamorphosis shared among the three groups, because the palate of anuran larvae is almost completely cartilaginous, whereas that of caecilian larvae is almost completely ossified. Even leaving anurans aside, there are some striking differences between the palatal metamorphosis of caecilians and that of salamanders. These include the occurrence in salamanders of: (1) a shift of the inner tooth row from the rostral to the caudal margin of the vomer, due to outgrowth of a large anterior extension of the palatal process (Clemen and Greven, 1974; Clemen, 1979); (2) extensive remodelling of the palatopterygoid, involving separation of the palatine from the pterygoid and subsequent resorption or fusion to the vomer (Larsen, 1963; Jurgens, 1971; Clemen and Greven, 1977; Clemen, 1979); and (3) a caudal shift in the jaw joint, similar to, if less extreme than, that seen in anurans (Wassersug and Hoff, 1982).

Nevertheless, such differences are irrelevant from a cladistic standpoint. What matters is that two metamorphic changes are shared by caecilians and salamanders: (1) a laterad shift of the anterior end of the pterygoid, with consequent widening of the interpterygoid vacuity, and (2) a caudad extension of the maxilla (Wintrebert, 1922; Stadtmüller, 1924; Wilder, 1925; Lebedkina, 1960, 1964; Larsen, 1963; Clemen and Greven, 1974, 1977; Greven and Clemen, 1985; Reilly, 1986; adults are reviewed by Trueb, 1993). Further, one can argue that both changes occur in an accentuated form in frogs: (1) the space corresponding to the interpterygoid vacuity widens, when the anterior quadratocranial commissure is replaced by the posterior maxillary process (reviewed by Reiss, 1993; Rose and Reiss, 1993); (2) the maxilla extends caudad from its initial ossification center. Thus these two palatal changes at metamorphosis can be interpreted as shared characters of the Lissamphibia. This interpretation is supported by evidence that the pattern of palatal metamorphosis in salamanders and frogs, at least, is ancient. Anuran tadpoles of modern aspect are known from the Lower Cretaceous (Estes et al., 1978) and many fossil salamanders, dating back at least to the Upper Cretaceous (Batrachosauroididae; Estes, 1981), and possibly to the Middle Jurassic (Evans et al., 1988) or Upper Triassic (Ivakhnenko, 1978), have the typical larval morphology of the palate.

To show that these metamorphic changes are lacking in outgroups is not difficult, because a distinct larval palatal morphology has not been recognized for any non-lissamphibian "amphibian," though larval palatal structure is known for many advanced temnospondyls (Boy, 1972, 1974, 1987, 1988, 1990; Milner, 1982; Olson, 1985; Werneburg, 1986, 1991; Dilkes, 1991; Schoch, 1992), the microsauro *Microbrachis pelikani* (possibly a neotene; Carroll and Gaskill, 1978), and a few discosauriscid anthracosaurs (Špinar, 1952; Ivakhnenko, 1981; Werneburg, 1985).

Importantly, larvae are known for many of the fossil taxa thought to be closely related to lissamphibians. For example, a recent cladistic study of temnospondyls and lissamphibians supported the hypothesis that the dissorophoid temnospondyl family Branchiosauridae is the stem group of the Lissamphibia (Trueb and Cloutier, 1991). Most branchiosaurids appear to be neotenic forms that never metamorphose. Post-metamorphic specimens were recently reported for one branchiosaur species, but no metamorphic changes occur in the palate (Werneburg, 1991).

The greatest reported difference between larval and juvenile palates among fossil amphib-

ians is found in another dissorophoid temnospondyl, *Amphibamus grandiceps* (Milner, 1982; but see Boy, 1987, for comments on attribution of larval specimens), which has also been considered close to lissamphibian ancestry (Watson, 1940; Bolt, 1979, 1991; Milner, 1982, 1988, 1993; Trueb and Cloutier, 1991). In *Amphibamus* a caudal shift in the jaw articulation occurs between large larvae and small juveniles, similar to that seen during metamorphosis in salamanders and frogs (Wassersug and Hoff, 1982). However, such a shift is a common feature of juvenile growth in temnospondyls, and *Amphibamus* shows few other metamorphic changes in the palate: by late larval stages all bones are formed, the maxillary arcade is complete, and the interpterygoid vacuity is large, unlike caecilians, salamanders, or frogs, but like all other known temnospondyl larvae. In contrast to lissamphibians, in many temnospondyl species the interpterygoid vacuity is reduced in relative size with larval and juvenile growth (e.g., Olson, 1985; Boy, 1988, 1990; Dilkes, 1991).

In summary, neither of the metamorphic changes shared by caecilians and salamanders is known from any fossil amphibian group, including those thought close to lissamphibian ancestry, yet it can be argued that both are shared by anurans. Thus it appears that a pronounced palatal metamorphosis—incorporating a widening of the interpterygoid vacuity and a caudad extension of the maxilla—is a valid synapomorphy of the Lissamphibia.

Acknowledgments.—I thank Dr. Marvalee H. Wake for her kindness in allowing me to examine specimens of *Epicrionops* and *Ichthyophis*, and her generous help throughout the study. Dr. C. J. Cole of the American Museum of Natural History loaned the embryonic specimen. For comments on the manuscript I thank G. Graffin, F. A. Jenkins, Jr., A. R. McCune, K. Z. Reiss, C. S. Rose, A. P. Russell, M. H. Wake, and C. F. Wellstead. The research was supported by a U. S. National Science Foundation (NSF) Dissertation Improvement Grant.

LITERATURE CITED

- BADENHORST, A. 1978. The development and the phylogeny of the organ of Jacobson and the tentacular apparatus of *Ichthyophis glutinosus* (Linné). Ann. Univ. Stellenbosch, Ser. A II (Sool.) 1:1–25.
- BEMIS, W. E., K. SCHWENK, AND M. H. WAKE. 1982. Morphology and function of the feeding apparatus in *Dermophis mexicanus* (Amphibia: Gymnophiona). Zool. J. Linn. Soc. 77:75–96.
- BOLT, J. R. 1979. *Amphibamus grandiceps* as a juvenile dissorophid: evidence and implications. In M. H. Nitecki (ed.), *Mazon Creek Fossils*, pp. 529–562. Academic Press, New York.
- . 1991. Lissamphibian origins. In H.-P. Schultze and L. Trueb (eds.), *Origins of the Higher Groups of Tetrapods*, pp. 194–222. Cornell University Press, Ithaca, New York.
- BOY, J. A. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Perm, SW-Deutschland). Abh. hess. Landesamtes Bodenforsch. 65:1–137.
- . 1974. Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli; Karbon–Trias). Paläontol. Z. 48:236–268.
- . 1987. Studien über die Branchiosauridae (Amphibia: Temnospondyli; Ober-Karbon–Unter-Perm). 2. Systematische Übersicht. Neues Jahrb. Geol. Paläontol. Abh. 174:75–104.
- . 1988. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäisch-ten Rotliegend (? höchstes Karbon–Perm). 1. *Sclerocephalus*. Paläontol. Z. 62:107–132.
- . 1990. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäisch-ten Rotliegend (?höchstes Karbon–Perm). 3. *Onchiodon*. Paläontol. Z. 64:287–312.
- BRAUER, A. 1899. Beiträge zur Kenntniss der Entwicklung und Anatomie der Gymnophionen. II. Die Entwicklung der äusseren Form. Zool. Jahrb., Abt. Anat. Ontog. Tiere 12:477–508.
- BRECKENRIDGE, W. R., S. NATHANIEL, AND L. PEREIRA. 1987. Some aspects of the biology and development of *Ichthyophis glutinosus* (Amphibia: Gymnophiona). J. Zool. (London) 211:437–449.
- CANNATELLA, D. C., AND D. M. HILLIS. 1993. Amphibian relationships: phylogenetic analysis of morphology and molecules. Herpetol. Monogr. 7:1–7.
- CARROLL, R. L., AND P. GASKILL. 1978. The Order Microsauria. Mem. Am. Philos. Soc. 126:1–211.
- CLEMEN, G. 1979. Experimentelle Veränderungen am knöchernen Gaumenbogen der Axolotl–Larve und ihre Auswirkungen während der Metamorphose. Zool. Anz. 203:23–34.
- , AND H. GREVEN. 1974. Morphologische Untersuchungen an der Mundhöhle von Urodelen. I. Die Gaumenzähne von *Salamandra salamandra* (L.) (Salamandridae: Amphibia). Forma Functio 7:249–280.
- , AND ———. 1977. Morphologische Untersuchungen an der Mundhöhle von Urodelen. III. Die Munddachbezeichnung von *Ambystoma mexicanum* Cope (Ambystomatidae: Amphibia). Zool. Jahrb., Abt. Anat. Ontog. Tiere 98:95–136.
- DE BEER, G. R. 1937. The Development of the Vertebrate Skull. Oxford University Press, London.
- DE JAGER, E. F. J. 1939. The gymnophione quadrate and its processes, with special reference to the processus ascendens in a juvenile *Ichthyophis glutinosus*. Anat. Anz. 88:223–232.
- DE QUEIROZ, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. Syst. Zool. 34:280–299.
- DILKES, D. W. 1991. Reinterpretation of a larval dissorophoid amphibian from the Lower Permian of Texas. Can. J. Earth Sci. 28:1488–1492.
- DUELLMAN, W. E., AND L. TRUEB. 1986. Biology of Amphibians. McGraw Hill, New York.
- EDGEWORTH, F. H. 1925. On the autostylism of Dipnoi and Amphibia. J. Anat. 59:225–264.

- ENGELHARDT, F. 1924. Tentakelapparat und Auge von *Ichthyophis*. Jena. Z. Naturwiss. 60:241-304.
- ESTES, R. 1981. Gymnophiona/Caudata. In P. Wellnhofer (ed.), *Handbuch der Paläoherpetologie*, Teil 2, pp. i-xvi, 1-115. G. Fischer, Stuttgart.
- ESTES, R., Z. V. ŠPINAR, AND E. NEVO. 1978. Early Cretaceous pipid tadpoles from Israel (Amphibia: Anura). *Herpetologica* 34:374-398.
- EVANS, S. E., A. R. MILNER, AND F. MUSSETT. 1988. The earliest known salamanders (Amphibia, Caudata): a record from the Middle Jurassic of England. *Geobios* (Lyon) 21:539-552.
- GADOW, H. 1901. Amphibia and reptiles. In S. F. Harmer and A. E. Shipley (eds.), *The Cambridge Natural History*, vol. 8, pp. i-xi, 1-668. [1958 reprint]. Wheldon and Wesley, Ltd., Condicote, England.
- GREVEN, H., AND G. CLEMEN. 1985. Metamorphosebedingte Veränderungen der Zähne und zahntragenden Knochen im Munddach von *Salamandra salamandra* (L.) (Amphibia, Urodela). *Verh. dtsch. zool. Ges.* 78:162.
- HASS, C. A., R. A. NUSSBAUM, AND L. R. MAXSON. 1993. Immunological insights into the evolutionary history of caecilians (Amphibia: Gymnophiona): relationships of the Seychellean caecilians and a preliminary report on family-level relationships. *Herpetol. Monogr.* 7:56-63.
- HEDGES, S. B., AND L. R. MAXSON. 1993. A molecular perspective on lissamphibian phylogeny. *Herpetol. Monogr.* 7:27-42.
- , 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). *Herpetol. Monogr.* 7:64-76.
- HETHERINGTON, T. E., AND M. H. WAKE. 1979. The lateral line system in larval *Ichthyophis* (Amphibia: Gymnophiona). *Zoomorphology* (Berlin) 93:209-225.
- HUMASON, G. L. 1979. *Animal Tissue Techniques*. 4th Ed. W. H. Freeman, San Francisco.
- IVAKHNENKO, M. F. 1978. Urodelans from the Triassic and Jurassic of Soviet Central Asia. *Paleontol. J.* 1978:362-368.
- . 1981. Discosauriscidae from the Permian of Tadzhikistan. *Paleontol. J.* 1981:90-102.
- JENKINS, F. A., JR., AND D. M. WALSH. 1993. An Early Jurassic caecilian with limbs. *Nature* (London) 365:246-250.
- JURGENSEN, J. D. 1971. The morphology of the nasal region of Amphibia and its bearing on the phylogeny of the group. *Ann. Univ. Stellenbosch, Ser. A* 46(2):1-146.
- LARGEN, M. J., P. A. MORRIS, AND D. W. YALDEN. 1972. Observations on the caecilian *Geotrypetes grandisonae* Taylor (Amphibia Gymnophiona) from Ethiopia. *Monit. Zool. Ital. Suppl.* 4:185-205.
- LARSEN, J. H. 1963. The cranial osteology of neotenic and transformed salamanders and its bearing on interfamilial relationships. Ph.D. Diss., University of Washington, Seattle.
- LEBEDKINA, N. S. 1960. Development of the bones of the palatal arch in the caudate Amphibia. *Dokl. Akad. Nauk SSSR Biol. Sci. Sect. (Engl. Transl.)* 131:218-220.
- . 1964. The development of the dermal bones of the basement of the skull in Urodela (Hynobiidae). *Tr. Zool. Inst. Akad. Nauk SSSR* 33:75-172.
- MARCUS, H., E. STIMMELMAYR, AND G. PORSCH. 1935. Beitrag zur Kenntnis der Gymnophionen XXV. Die Ossifikation des *Hypogeophisschädels*. *Morphol. Jahrb.* 76:375-420.
- MILNER, A. R. 1982. Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois. *Palaeontol.* 25:635-664.
- . 1988. The relationships and origin of living amphibians. In M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods*, Vol. 1, pp. 59-102. Clarendon Press, Oxford.
- . 1993. The Paleozoic relatives of lissamphibians. *Herpetol. Monogr.* 7:8-27.
- MÜLLER, J. 1835. Über die Kiemenlöcher der jungen *Coecilia hypocyanea*. *Arch. Anat. Physiol. wiss. Med.* 1835:391-398.
- NOBLE, G. K. 1927. The value of life history data in the study of the evolution of the Amphibia. *Ann. New York Acad. Sci.* 30:31-128.
- NORRIS, H. W., AND S. P. HUGHES. 1918. The cranial and anterior spinal nerves of the caecilian amphibians. *J. Morphol.* 31:488-560.
- NUSSBAUM, R. A. 1977. Rhinatrematidae: a new family of caecilians (Amphibia: Gymnophiona). *Occas. Pap. Mus. Zool. Univ. Michigan* 682:1-30.
- . 1979. The taxonomic status of the caecilian genus *Uraeotyphlus* Peters. *Occas. Pap. Mus. Zool. Univ. Michigan* 687:1-20.
- . 1983. The evolution of a unique dual jaw-closing mechanism in caecilians (Amphibia: Gymnophiona) and its bearing on caecilian ancestry. *J. Zool. (London)* 199:545-554.
- , AND P. K. DUCEY. 1988. Cytological evidence for monophyly of the caecilians (Amphibia: Gymnophiona) of the Seychelles archipelago. *Herpetologica* 44:290-296.
- OLSON, E. C. 1985. A larval specimen of a trematopod (Amphibia: Temnospondyli). *J. Paleontol.* 59:1173-1180.
- PARKER, H. W. 1941. The caecilians of the Seychelles. *Ann. Mag. Nat. Hist., Ser. 11* 7:1-17.
- . 1956. Viviparous caecilians and amphibian phylogeny. *Nature* (London) 178:250-252.
- . 1958. Caecilians of the Seychelles Islands with description of a new subspecies. *Copeia* 1958:71-76.
- , AND E. R. DUNN. 1964. Dentitional metamorphosis in the Amphibia. *Copeia* 1964:75-86.
- PARSONS, T. S., AND E. E. WILLIAMS. 1962. The teeth of Amphibia and their relation to amphibian phylogeny. *J. Morphol.* 110:375-390.
- , AND ———. 1963. The relationships of the modern Amphibia: a re-examination. *Q. Rev. Biol.* 38:26-53.
- PETER, K. 1898. Die Entwicklung und funktionelle Gestaltung des Schädels von *Ichthyophis glutinosus*. *Morphol. Jahrb.* 25:555-628.
- PUSEY, H. K. 1939. Methods of reconstruction from microscopic sections. *J. R. Microsc. Soc.* 59:232-244.
- RAMASWAMI, L. S. 1941. Some aspects of the cranial morphology of *Uraeotyphlus narayani* Seshachar (Apoda). *Rec. Ind. Mus. (Calcutta)* 43:143-207.
- . 1947. Apodous Amphibia of the Eastern

- Ghats, South India. *Curr. Sci. (Bangalore)* 16:8-10.
- REILLY, S. M. 1986. Ontogeny of cranial ossification in the eastern newt, *Notophthalmus viridescens* (Caudata: Salamandridae), and its relationship to metamorphosis and neoteny. *J. Morphol.* 188:315-326.
- REISS, J. O. 1993. Development and evolution of the amphibian palate. Unpubl. Ph.D. Thesis, Harvard Univ., Cambridge.
- ROSE, C. S., AND J. O. REISS. 1993. Metamorphosis and the vertebrate skull: ontogenetic patterns and developmental mechanisms. In J. Hanken and B. K. Hall (eds.), *The Vertebrate Skull*, Vol. 1, pp. 289-346. University of Chicago Press, Chicago.
- SARASIN, P., AND F. SARASIN. 1887-1890. Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon in den Jahren 1884-1886. II. Zur Entwicklungsgeschichte und Anatomie der ceylonesischen Blindwühle, *Ichthyophis glutinosus*. C. W. Kreidels Verlag, Wiesbaden.
- SCHMIDT, A., AND M. H. WAKE. 1990. Olfactory and vomeronasal systems of caecilians (Amphibia: Gymnophiona). *J. Morphol.* 205:255-268.
- SCHOCH, R. R. 1992. Comparative ontogeny of early Permian branchiosaurid amphibians from south-western Germany. Developmental stages. *Palaeontogr. Abt. A Palaeozool.-Stratigr.* 222:43-83.
- SPENGEL, J. W. 1876. Das Urogenitalsystem der Amphibien. I. Theil. Der anatomische Bau des Urogenitalsystems. *Arb. zool.-zootom. Inst. Würzburg* 3:1-114.
- ŠPINAR, Z. V. 1952. Revision of some Moravian Discosauriscidae. *Ústřední ústav geol. Rozpr.* 15:1-146.
- STADTMÜLLER, F. 1924. Studien am Urodelenschädel. I. Zur Entwicklungsgeschichte des Kopfskeletts der *Salamandra maculosa*. *Z. Anat. Entwicklungsgesch.* 75:149-225.
- SZARSKI, H. 1962. The origin of the Amphibia. *Q. Rev. Biol.* 37:189-241.
- TAYLOR, E. H. 1968. The Caecilians of the World: A Taxonomic Review. Univ. Kansas Press, Lawrence.
- . 1969. Skulls of the Gymnophiona and their significance in the taxonomy of the group. *Univ. Kansas Sci. Bull.* 48:585-687.
- THYNG, F. W. 1906. Squamosal bone in tetrapodous Vertebrata. *Proc. Boston Soc. Nat. Hist.* 32:387-425.
- TRUEB, L. 1993. Patterns of cranial diversity among the Lissamphibia. In J. Hanken and B. K. Hall (eds.), *The Skull*, vol. 2, pp. 255-343. University of Chicago Press, Chicago.
- , AND R. CLOUTIER. 1991. A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). In H.-P. Schultze and L. Trueb (eds.), *Origins of the Higher Groups of Tetrapods*, pp. 223-313. Cornell University Press, Ithaca, New York.
- VISSER, M. H. C. 1963. The cranial morphology of *Ichthyophis glutinosus* (Linné) and *Ichthyophis monochrous* (Bleeker). *Ann. Univ. Stellenbosch, Ser. A* 38:67-102.
- WAKE, M. H. 1976. The development and replacement of teeth in viviparous caecilians. *J. Morphol.* 148:33-64.
- . 1977. The reproductive biology of caecilians: an evolutionary perspective. In D. H. Taylor and S. I. Guttman (eds.), *The Reproductive Biology of Amphibians*, pp. 73-101. Plenum Press, New York.
- . 1980. Fetal tooth development and adult replacement in *Dermophis mexicanus* (Amphibia: Gymnophiona): fields versus clones. *J. Morphol.* 166:203-216.
- . 1987. A new genus of African caecilian (Amphibia: Gymnophiona). *J. Herpetol.* 21:6-15.
- . 1989. Metamorphosis of the hyobranchial apparatus in *Epicrionops* (Amphibia: Gymnophiona: Rhinatrematidae): replacement of bone by cartilage. *Ann. Sci. Nat. Zool. Biol. Anim.*, 13° Ser. 10:171-182.
- . 1992. Reproduction in caecilians. In W. C. Hamlett (ed.), *Reproductive Biology of South American Vertebrates*, pp. 112-120. Springer-Verlag, New York.
- , AND J. HANKEN. 1982. Development of the skull of *Dermophis mexicanus* (Amphibia: Gymnophiona), with comments on skull kinesis and amphibian relationships. *J. Morphol.* 173:203-223.
- WASSERSUG, R. J., AND K. HOFF. 1982. Developmental changes in the orientation of the anuran jaw suspension: a preliminary exploration into the evolution of anuran metamorphosis. *Evol. Biol.* 15: 223-246.
- WATSON, D. M. S. 1940. The origin of frogs. *Trans. R. Soc. Edinb.* 60:195-231.
- WERNEBURG, R. 1985. Zur Taxonomie der jungpaläozoischen Familie Discosauriscidae ROMER 1947 (Batrachosauria, Amphibia). *Freiberg. Forschungsh. C* 400:117-139.
- . 1986. Branchiosaurier aus dem Rotliegenden (Unterperm) der ČSSR. *Z. geol. Wiss. Berl.* 14: 673-686.
- . 1991. Die Branchiosaurier aus dem Unterrotliegend des Dohleener Beckens bei Dresden. *Veroeff. Naturhist. Mus. Schloss Bertholdsburg Schleusingen* 6:75-99.
- WIEDERSHEIM, R. 1879. Die Anatomie der Gymnophionen. G. Fischer., Jena.
- WILDER, I. W. 1925. The Morphology of Amphibian Metamorphosis. Smith College, Northampton, Massachusetts.
- WILKINSON, M. 1992. On the life history of the caecilian genus *Uraeotyphlus* (Amphibia: Gymnophiona). *Herpetol. J.* 2:121-124.
- WINTREBERT, P. 1922. La voute palatine des Salamandridae. *Bull. Biol. Fr. Belg.* 56:277-426.

Accepted: 16 October 1995.

APPENDIX 1

Specimens were examined from the following collections: American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Louisiana State University Museum of Zoology (LSUMZ); and private collection of M. H. Wake, University of California, Berkeley (MHW). *Epicrionops bicolor* Boulenger—Larvae: 66 mm TL (LSUMZ 27293), 89 mm TL (LSUMZ 27261, sectioned), 89 mm TL (LSUMZ 27291), 125 mm TL (LSUMZ 27289); 161 mm TL (LSUMZ 27254, sectioned), 165 mm TL (LSUMZ 27267), 206 mm TL (LSUMZ 27245). Adults: 231 mm TL (LSUMZ 27266), 247 mm TL (LSUMZ 27265). *Epicrionops petersi* Taylor—Embryo: 58 mm TL (AMNH

1454, sectioned). Larva: 101 mm TL (LSUMZ 27306). Late metamorphic: 193 mm TL (LSUMZ 27317). Adult: 221 mm TL (LSUMZ 27312, sectioned), 335 mm TL (LSUMZ 27319). *Ichthyophis kohtaoensis* Taylor—Larvae: 66 mm TL (two: sectioned as MHW series 447 and 448). *Ichthyophis* sp.—Larva: 112 mm TL larva (FMNH 76340, North Borneo, sectioned).

Abbreviations Used in Figures.—aow = anterior orbital wall; bas = basal; ca = cupola anterior; ch = choana; ci = cartilago infranarina; co = cartilago obliqua; csb = "Choanenschleimbeutel"; dlp = dorsolateral process of palatine; ect = ectopterygoid; f = frontal; fc = carotid foramen; fj = jugular foramen; fon = orbitonasal foramen; Hg = Harderian gland; j = jugal; jo = Jacobson's organ (lumen); ld = lacrimal duct(s); lon

= lamina orbitonasalis; mpl = maxillopalatine; mwj = medial wall of chamber for Jacobson's organ; mx = maxilla; n = nasal; nc = nasal cavity; p = parietal; pl = palatine; pm = premaxilla; pn = paries nasi; poch = postchoanal process of palatine; ppch = prechoanal process of solum nasi; ppt = pterygoid process of quadrate; pqj = quadratojugal process of quadrate; ps = parasphenoid; psa = pseudoangular; pt = pterygoid; q = quadrate; qj = quadratojugal; se = sphenethmoid; sm = septomaxilla; sn = septum nasi; son = solum nasi; sq = squamosal; st = stapes; tf = tentacle fold; tm = taenia marginalis; tn = tectum nasi; tr = trabecula; v = vomer; I_d = dorsal olfactory nerve; V_1 = deep ophthalmic branch of trigeminal; V_2 = maxillary branch of trigeminal.

Journal of Herpetology, Vol. 30, No. 1, pp. 39–46, 1996
Copyright 1996 Society for the Study of Amphibians and Reptiles

Extreme Chromosomal Polytypy in a Population of *Sceloporus grammicus* (Sauria: Phrynosomatidae) at Santuario Mapethé, Hidalgo, México

IRENE GOYENECHEA, FERNANDO MENDOZA-QUIJANO,
OSCAR FLORES-VILLELA, AND KENT M. REED¹

Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, A.P. 70-399,
México D.F., 04510, Mexico and

¹Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin 53201, USA

ABSTRACT.—The karyotypic status of the mesquite lizard, *Sceloporus grammicus*, was investigated at two localities at Santuario Mapethé, Hidalgo, México. A total of 23 different karyotypes was recorded from the 36 individuals examined. Individual lizards were heterozygous at up to four chromosomes. Karyotypic differences were attributed to Robertsonian fission/fusions and pericentric inversions involving the macrochromosomes. The polymorphisms generally conformed to Hardy-Weinberg equilibrium suggesting a lack of underdominance for most rearrangements. The extreme chromosomal polytypy observed at Santuario Mapethé is hypothesized to result from parapatric hybridization between two chromosome races.

RESUMEN.—Se estudió el estatus cariotípico de la lagartija *Sceloporus grammicus* de dos localidades en Santuario Mapethé, Hidalgo, México. Se registraron un total de 23 cariotipos diferentes de 36 individuos examinados. Las lagartijas fueron heterocigotas hasta en 4 pares cromosómicos. Las diferencias cariotípicas se atribuyeron a fisiones/fusiones Robertsonianas y a inversiones pericéntricas ue involucran a los seis pares macrocromosómicos. Los polimorfismos se conformaron generalmente de acuerdo al equilibrio Hardy-Weinberg, lo que sugiere una ausencia de subdominancia para la mayoría de los rearreglos. La extrema politipia cromosómica observada parece ser el resultado de hibridación parapátrica entre dos razas cromosómicas.

Few species of vertebrates exhibit the extreme chromosomal polytypy observed in the mesquite lizard *Sceloporus grammicus* complex. Previous cytogenetic studies revealed eight distinct chromosome races in a relatively small area of the central Mexican plateau (Hall, 1983; Porter and Sites, 1986; Arévalo et al., 1991;

Sites, 1993). The races (cytotypes) are defined primarily by Robertsonian (centric fission) rearrangements and include LS (Low Standard, $2n = 32\phi$), HS (High Standard, $2n = 32$), F6 ($2n = 34$), F5 ($2n = 34$), F5+6 ($2n = 36$), FM1 ($2n = 40-44$), FM2 ($2n = 44-46$), and FM3 ($2n = 38-42$). In addition to the fixed differences which

LINKED CITATIONS

- Page 1 of 2 -



You have printed the following article:

Palatal Metamorphosis in Basal Caecilians (Amphibia: Gymnophiona) as Evidence for Lissamphibian Monophyly

John Reiss

Journal of Herpetology, Vol. 30, No. 1. (Mar., 1996), pp. 27-39.

Stable URL:

<http://links.jstor.org/sici?sici=0022-1511%28199603%2930%3A1%3C27%3APMIBC%28%3E2.0.CO%3B2-3>

This article references the following linked citations. If you are trying to access articles from an off-campus location, you may be required to first logon via your library web site to access JSTOR. Please visit your library's website or contact a librarian to learn about options for remote access to JSTOR.

Literature Cited

The Ontogenetic Method for Determining Character Polarity and its Relevance to Phylogenetic Systematics

Kevin De Queiroz

Systematic Zoology, Vol. 34, No. 3. (Sep., 1985), pp. 280-299.

Stable URL:

<http://links.jstor.org/sici?sici=0039-7989%28198509%2934%3A3%3C280%3ATOMFDC%3E2.0.CO%3B2-6>

A Larval Specimen of a Trematopsid (Amphibia: Temnospondyli)

Everett C. Olson

Journal of Paleontology, Vol. 59, No. 5. (Sep., 1985), pp. 1173-1180.

Stable URL:

<http://links.jstor.org/sici?sici=0022-3360%28198509%2959%3A5%3C1173%3AALSOAT%3E2.0.CO%3B2-D>

Caecilians of the Seychelles Islands with Description of a New Subspecies

H. W. Parker

Copeia, Vol. 1958, No. 2. (Jun. 18, 1958), pp. 71-76.

Stable URL:

<http://links.jstor.org/sici?sici=0045-8511%2819580618%293%3A1958%3A2%3C71%3ACOTSIW%3E2.0.CO%3B2-G>

LINKED CITATIONS

- Page 2 of 2 -



Dentitional Metamorphosis in the Amphibia

H. W. Parker; E. R. Dunn

Copeia, Vol. 1964, No. 1. (Mar. 26, 1964), pp. 75-86.

Stable URL:

<http://links.jstor.org/sici?sici=0045-8511%2819640326%293%3A1964%3A1%3C75%3ADMITA%3E2.0.CO%3B2-V>

The Relationships of the Modern Amphibia: A Re-Examination

Thomas S. Parsons; Ernest E. Williams

The Quarterly Review of Biology, Vol. 38, No. 1. (Mar., 1963), pp. 26-53.

Stable URL:

<http://links.jstor.org/sici?sici=0033-5770%28196303%2938%3A1%3C26%3ATROTMA%3E2.0.CO%3B2-1>

The Origin of the Amphibia

Henryk Szarski

The Quarterly Review of Biology, Vol. 37, No. 3. (Sep., 1962), pp. 189-241.

Stable URL:

<http://links.jstor.org/sici?sici=0033-5770%28196209%2937%3A3%3C189%3ATOOTA%3E2.0.CO%3B2-X>

A New Genus of African Caecilian (Amphibia: Gymnophiona)

Marvalee H. Wake

Journal of Herpetology, Vol. 21, No. 1. (Mar., 1987), pp. 6-15.

Stable URL:

<http://links.jstor.org/sici?sici=0022-1511%28198703%2921%3A1%3C6%3AANGOAC%3E2.0.CO%3B2-C>