

Development of the Skull of *Dermophis mexicanus* (Amphibia: Gymnophiona), With Comments on Skull Kinesis and Amphibian Relationships

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ABSTRACT The development of the skull of *Dermophis mexicanus* (Caeciliidae) is described and compared to that of other caecilians. The chondrocranium is well developed in embryos of 25 mm total length (TL); ossification begins in the quadrate and the articular element of the lower jaw at about 30 mm TL. The occipital arch then ossifies, followed by the dorsal and lateral dermal bones, then the ventral endochondral and dermal elements. The stapes ossifies at 55 mm TL. The amount of skull roofing increases during ontogeny, although the anterior rims of the nasal capsules, the anterior part of the mesethmoid, and the hyoid apparatus remain cartilaginous throughout life. *Dermophis mexicanus* lacks many primary embryonic ossification centers reported by Marcus et al. ('35) for *Hypogeophis*; presence of these ossification centers has been presumed to be indicative of a primitive skull morphology derived with little modification from archaic amphibians ("stegocephalians"). The fetal skull is highly kinetic, and some kinesis is retained in adults. We suggest that fetal skull kinesis and early ossification of jaw suspension elements are functionally related to the intraoviducal feeding mode of this viviparous species. Based on this evidence, together with the observed ossification pattern and bone homologies, we conclude that stegokrotaphy (complete skull roofing) in caecilians is a derived condition, correlated with fossoriality, and does not indicate a direct relationship of caecilians to any known early amphibian taxon.

Caecilians have perhaps the most highly derived skeletal morphology of all Recent amphibians. They possess a suite of characters, including complete loss of limbs and limb girdles, that represents a set of adaptations for the burrowing locomotion typical of the group. In contrast to the skull of most urodeles and anurans, the skull of adult caecilians is robust and heavily ossified, with considerable overlap of bones, connective tissue binding, and fusion of many elements. Because of the superficial resemblance of the caecilian skull to that of archaic armored amphibians ("stegocephalians"), skull morphology of caecilians has been used both in assessing the relationships among the Recent Amphibia, and in general discussions of the evolution of the tetrapod skull (for example, DeBeer, '37; Edgeworth, '25, '35; Parsons and Williams, '63; Kesteven, '44; Goodrich, '30; Marcus, '09; Marcus et al., '33; Schmalhausen, '68; Carroll and Currie, '75; Romer, '50, '66). However, these authors have debated whether

the characteristic features of the caecilian skull 1) represent the primitive amphibian condition little changed from the Paleozoic era, or 2) are secondarily derived adaptations for terrestrial burrowing that evolved from the "reduced" morphology typical of other recent amphibians.

Descriptions of skull development in caecilians rely heavily on the correct assessment of homology and inferred function of individual elements. Yet, knowledge of caecilian osteology is based on examination of either dried adult skulls or wax reconstructions from serial sections of stained heads, usually including only single specimens of a few species. Useful descriptions of osteology and development of *Ichthyophis glutinosus* (Sarasin and Sarasin, 1887, 1887-1890; Peter, 1898) and *Hypogeophis*, primarily *rostratus* (Brauer, 1897, 1899;

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Marcus, '09, '10, '22; Marcus et al., '33, '35; Lawson, '63; Gewolf, '23), have been presented. A few general discussions of particular morphological problems have referred to aspects of development (Wiedersheim, 1879; Peters, 1879, 1880, 1881; Parker, '41; Marcus et al., '35; Ramaswami, '41, '42, '43, '48; Peter, 1895, 1898; Eifertinger, '33; DeBeer, '26; de Jager, '38, '39a,b,c, '47; DeVilliers, '36, '38; Els, '63; Visser, '63; Winslow, 1898). Some ontogenetic material has therefore been available, but only for *H. rostratus* is the early developmental series nearly complete, and it lacks more advanced specimens necessary for direct assessment of the ossification sequence. Further, Marcus's sample of *Hypogeophis* included both *rostratus* and *alternans*, the latter now referred to a different genus (*Grandisonia*: Taylor, '68, '69).

Availability of a complete ontogenetic series of *Dermophis mexicanus* has allowed us to analyze chondrocranium development and the ossification sequence of endochondral and dermal elements in this derived species (Taylor, '68, '69; Wake, '80b; Nussbaum, '79). Comparison of these data with descriptions of skull development of *I. glutinosus*, *H. rostratus*, and *G. alternans* permits assessment of homologies and variation in developmental pattern within the order Gymnophiona and therefore facilitates analysis of relationships among extinct and extant amphibians. Also, we are able to discuss the extent and role of skull kinesis in this species, in the context of fetal adaptation and phylogenetic significance.

MATERIALS AND METHODS

Specimens of *Dermophis mexicanus*, a terrestrial, burrowing, viviparous caeciliid, were collected at several times of the year from a locality near San Rafael, Pie de la Cuesta, in northwestern Guatemala. Several females in

each sample were pregnant, thereby providing a virtually complete embryonic and fetal ontogenetic series that complemented an equally complete juvenile-adult series. Fetuses hatch from the egg membrane approximately 2 months after fertilization, at which time they are approximately 25 mm total length (TL). Yolk is resorbed at hatching when the young begin feeding actively upon maternal oviducal secretions. Gills are resorbed approximately 3 months after fertilization. Fully metamorphosed young are born at 110–150 mm TL after a total gestation period of 1 year (see Wake, '80a,b for details).

Specimens used in the description of cranial development (30 of 25–77 mm TL, 10 of 100–150 mm TL, and 2 exceeding 300 mm TL) were cleared and differentially stained for bone and cartilage by a procedure slightly modified from the techniques of Dingerkus and Uhler ('77) and Wassersug ('76). An ontogenetic series of sectioned skulls was also available for comparison. All specimens will be deposited in the Museum of Vertebrate Zoology, University of California, Berkeley.

Estimates of relative size of the head sensory organs follow the method of Hanken ('80). Relative lengths of the eye, nasal capsule, and otic capsule equal the proportion of total skull length occupied by each of these structures, expressed as a percentage.

RESULTS

Chondrocranial development

TL 29 mm. (Figs. 1a and 5A). The chondrocranium is 4.5 mm long. Parachordal and trabecular cartilages are well established, as are the occipital condyles. The notochord, not yet sheathed in cartilage, extends into the basihyophyseal fenestra below the brain. The orbital cartilages are elongate and supported by the

Abbreviations

a, atlas	fr, fetal tooth rows	or, orbital cartilage	ptq, pterygoquadrate
af, alveolar foramen	h, hyoid skeleton	ot, otic capsule	q, quadrate
an, angular	jf, jugular foramen	p, parietal	rp, retroarticular process
ar, articular	m, maxilla	pa, pseudoangular	s, splenial
bs, basisphenoid	mc, Meckel's cartilage	pal, palatine	se, sphenethmoid
c, coronoid	me, mesethmoid	pan, pila antotica	sen, septum nasi
ca, copula anterior	mn, mentomeckelian	pc, parachordal cartilage	sn, solum nasi
cf, carotid foramen	mp, maxillopalatine	pcd, posterior condyle	sq, squamosal
ch, choana	mpc, mediopalatal cavity	pd, pseudodentary	st, stapes
d, dentary	nc, notochord	pf, prefrontal	su, supraethmoid
e, eye	nca, nasal capsule	pi, processus internus	tc, trabecular cartilage
en, external naris	npm, nasopremaxilla	pm, premaxilla	tf, tentacular foramen
ex, exoccipital	or, orbit	por, preoptic root	tfs, temporal fossa
f, frontal	ob, os basale	pp, prenasal process	tm, taenia marginalis
frm, foramen	oc, occipital condyle	pq, palatoquadrate	v, vomer

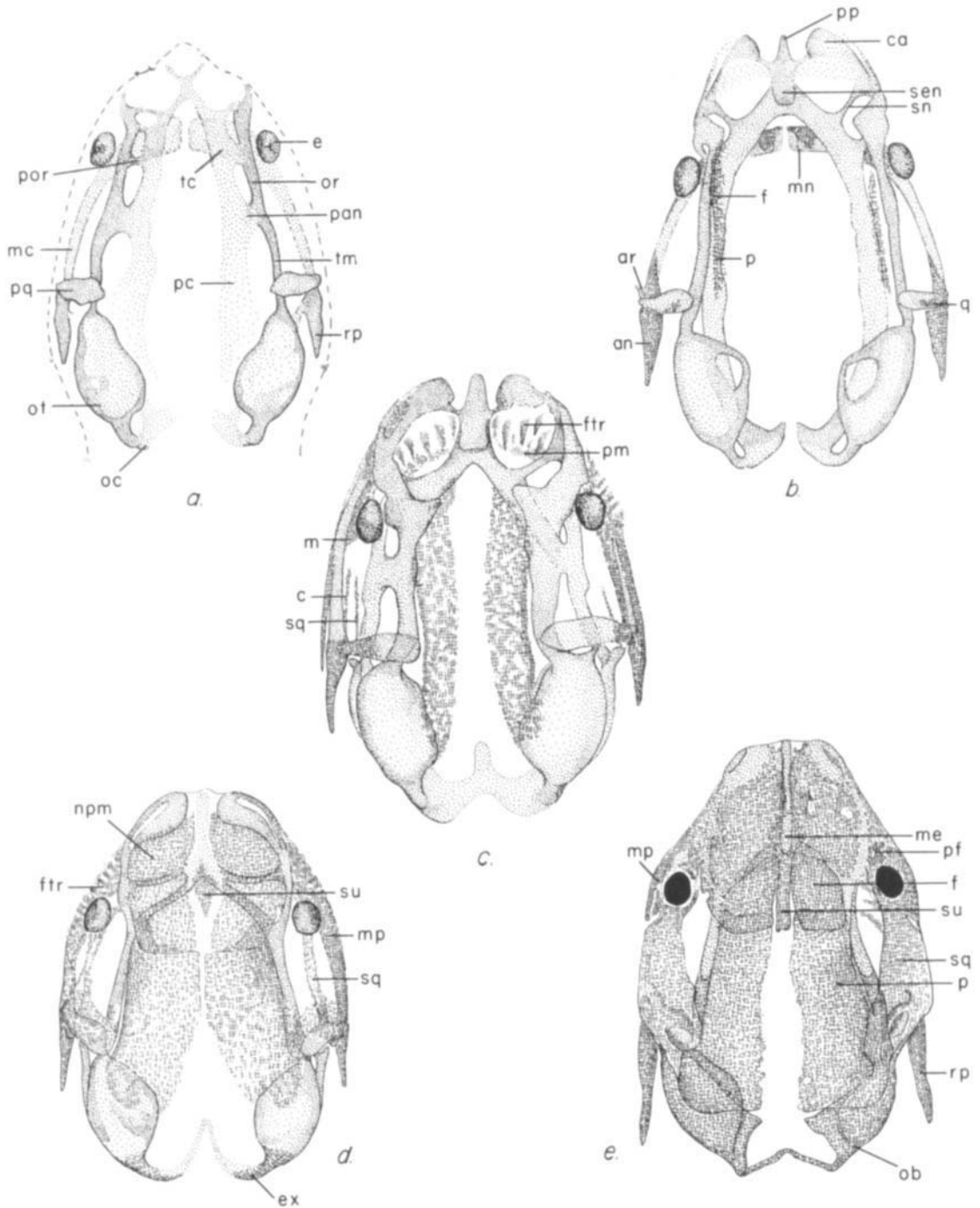


Fig. 1. Growth and ossification of the chondrocranium in *D. mexicanus* (dorsal view). Total specimen length and skull length (in parentheses) in millimeters: a, 29.0 (4.5); b, 33.0 (4.7); c, 44.5 (5.3); d, 51.8 (5.7); e, 68.6 (6.7). Cartilage stippled; bone and teeth cross-hatched. Elements are labeled as they first appear. See list of abbreviations.

stout pilae antoticae; posteriorly the orbital cartilages connect to the taenia marginales, then to the otic capsules. The roof of each otic capsule is incomplete; ventrally the jugular foramina are large. The nasal capsules are poorly formed. The septum nasi is complete only anteriorly; the sola nasi extend laterally almost to the cartilago obliqua. The copula anterior and prenasal processes are not yet formed. The palatoquadrate is a stout vertical element, loosely bound to the otic capsule by connective tissue; it lacks both pterygoid and ascending processes. Meckel's cartilage is well developed, with a pronounced articular facet and retroarticular process. Ossification of the articular facet and the quadrate has begun in one 29-mm specimen (Fig. 5A) but not another (Fig. 1a).

TL 35 mm. (Fig. 5B). This specimen differs only slightly from the 29-mm individual. The otic capsule and nasal septum are more complete and the pilae are oriented more vertically. Trabecular, parachordal, and orbital cartilages are well developed. The exoccipital arches are established, Meckel's cartilage has a well-developed retroarticular process, and a vertical palatoquadrate is well formed.

TL 40.5 mm. Otic capsules are more complete. The anterior extension of the notochord is encased in cartilage. The occipital condyles are stout and medial bosses are formed at the junction of the trabecular and parachordal cartilages. The components of the septum nasi are fused extensively and have a vertical prenasal process. Copulae anteriori are formed, especially medially and laterally. Opposing articular surfaces of the palatoquadrate and Meckel's cartilage are ossifying. Investing (dermal) bones have begun to sheath Meckel's cartilage anteromedially.

TL 33 mm. Developmentally, this specimen is more advanced than the 40.5-mm fetus, with more complete otic and nasal capsules and the solum nasi connected to the copulae anteriori. However, the nasal capsules still lack dorsal and ventral walls. The ventral chondrocranial components are broader and thicker than in previous stages. Ossification of the suspensorium is proceeding, including the appearance of additional dermal elements (see below and Fig. 1b).

TL 44.5 mm (Figs. 1c and 5D). The occipital condyles, palatoquadrates, and mandibles are ossifying. The otic capsules have nearly complete dorsal and ventral walls; in each, the columella is elongate but does not fill the large

foramen ovale. The nasal capsules have more extensive lateral walls and a more pronounced prenasal process.

TL 51.8 mm. (Figs. 1d and 5E). The exoccipitals are fully ossified (Figs. 1e and 5E). Ossification of palatoquadrate and Meckel's cartilage is nearly complete, and the orbital and trabecular cartilages are eroding. However, the nasal and otic capsules continue to chondrify.

TL 56.4 mm. This specimen shows less chondrocranial erosion than the 51.8-mm specimen, but the otic capsules are ossified posteriorly by extension of the exoccipital ossification. The nasal capsules have more extensive lateral walls. The prenasal process is pronounced and abuts the newly forming sphenoid plate. The stapes has begun to ossify.

TL 60.1 mm. Much of the chondrocranium is eroded. The otic capsules and stapes show greater ossification. The quadrates are nearly fully ossified, but not yet fused to either dermal bone or endochondral elements. Meckel's cartilage is eroding medially. Yet, even at this stage the nasal capsules continue to chondrify, with extensive copulae anteriori and stout lateral walls.

TL 64 mm. This specimen, though larger in body size than the preceding specimen, is less advanced developmentally. The chondrocranium is eroding posteriorly, and the otic capsules are ossified completely except for the ventral aspect. However, the anterior part of the chondrocranium, including trabecular elements, orbital cartilages and pilae, and nasal capsules, is well developed and intact. Meckel's cartilage is thin but continuous.

TL 68.6 mm and larger (Figs. 1e, 5F, and 6). The 68-mm specimen retains cartilaginous fragments in the occipital and anterior otic regions (Figs. 1e and 5F). Specifically, the orbital cartilages, dorsal remnants of the pilae, the prenasal process, and the copulae anteriori are distinct. At 70.8 mm TL (Figs. 6A-C), only the copulae, the prenasal process, vestiges of the orbital cartilages and pilae anterior to the eye, the mentomeckelian processes, and slips of Meckel's cartilage remain unossified. A 77.3-mm TL specimen has even less cartilage in these same regions. A 105-mm fetus (Figs. 6D,E,F) retains cartilage only at the anterior rim of the nasal capsule (remainder of the copula), the prenasal process (mesethmoid), the small mentomeckelian process, and the medial vestige of Meckel's cartilage. The entire hyoid apparatus is cartilaginous in specimens of all sizes.

Ossification sequence

TL 29 mm. Ossification is first apparent in the lower jaw of a 29-mm fetus (Fig. 5A). Blades of alizarin-stained bone are apparent at the mentomeckelian process, the articular, and the angular components, including the retroarticular process.

TL 33–36 mm. A 35.1-mm specimen shows no mineralization whatsoever. A 35.6-mm fetus shows ossification in several sites (Fig. 5C). The bony elements of the lower jaw are more extensive, and the splenials are present as thin blades. The quadrates are ossified ventrally; the squamosals appear as thin, membranous sheets with their posterior portions ossified. Frontals and parietals are ossified dorsolaterally and extend medially as sheets. Each of the premaxillae, maxillae, and palatines is represented by an isolated, thin sliver of bone. Several rows of mineralized teeth are present but not fused to the premaxillae and the maxillae; a few teeth are present in the unossified vomerine region. The paired exoccipitals are ossifying, continuing into the otic capsules. The basisphenoids are indicated by ventrolateral slivers of bone. One 33-mm specimen (Fig. 1b) has begun ossification only in the quadrates, in the articular process and mentomeckelian process of the lower jaw, and in thin dorsolateral blades of the frontal and parietal bones. However, a 33-mm specimen from the same clutch is more advanced than its 36-mm sibling, with nasals forming as thin, bony sheets on the dorsolateral sides of the nasal capsules, more extensive ossification of the quadrates and otic capsules, and ossification of the medial shelves of the palatines. The premaxillae and maxillae have more extensive basal blades; sheets of bone that extend dorsally from the blades foreshadow each bone's adult morphology. Ossification of the frontals and parietals is proceeding medially; in each, the leading edges of bone are thin and reticulate. The quadrates and the lower jaw are well ossified relative to other elements. The angular and articular are fused, forming the pseudoangular bone. The dentary and mentomeckelian are fused but the other components of the adult pseudodentary, the splenial and coronoid (and the rarely observed complementale), are still distinct. The otic capsule is ossifying as bone spreads from anterior (taenia marginalis) and posterior (exoccipital) sources.

TL 44.5 mm. This specimen has greater ossification of the dermal bones below the brain case (Figs. 1c and 5D). The parasphenoid sheet

is ossifying. Ossification of the basisphenoids (from the trabeculae) is extending medially, and ossified centers of the orbitosphenoids (from the preoptic roots), vomers, and pterygoids are present. The dorsal and lateral dermal elements are extending their sheets of bone medially and dorsally, respectively. Several rows of fetal teeth are present on upper and lower jaws.

TL 51.8 mm. The orbitosphenoids are ossified but are not yet joined to the cartilaginous prenasal process (Figs. 1d and 5E). Ventrally, basisphenoid ossification is spreading medially and posteriorly, joining the orbitosphenoid component. The frontals approach contact medially and overlap the parietals posteriorly. The parietals are nearly completely ossified anteriorly but not posteriorly. The palatines are fusing to the maxillae.

TL 54.5 mm. This specimen shows increased ossification of the elements mentioned above and has a single, well-developed septomaxilla at the juncture of left maxilla, nasal, premaxilla, and frontal. The stapes have begun to ossify posteriorly. Considerable ossification of the basi- and orbitosphenoid elements, especially laterally, has occurred.

TL 56.4 mm. Subsequent ossification involves the enlargement, remodelling, and in some cases fusion of those elements already present. In this specimen, the dermal bones are thin, but nearly complete, sheets that foreshadow their adult configuration. Parietals are still incomplete posteriorly. The parasphenoid sheet stops posteriorly at the anterior point of the notochordal remnant, leaving paired gaps bordered by exoccipitals, the notochordal remnant, the otic capsules, and the parasphenoid sheet.

TL 60.1 mm. Ossification of the quadrates and the pseudoangular is nearly complete and the palatoquadrate cartilage is virtually obliterated. Meckel's cartilage is much reduced in the pseudoangular region, but still is evident medially, though it diminishes posteriorly in the pseudodentary. The anterior part of the parasphenoid is constricted as the vomers enlarge.

TL 68.6 mm. The squamosals and maxillae nearly meet the frontals and parietals dorsolaterally. The nasals and premaxillae are fusing, and the latter meet at several points on their boundaries (Figs. 1e and 5F). Prefrontals are present, and a median supraethmoid has formed. Ventrally, the parasphenoid sheet is nearly completely united with the exoccipitals

and otic capsules, forming the os basale. The vomers and the anterior part of the sphenethmoid have nearly attained the shapes characteristic of adults. The fenestrae for the jaw adductor musculature are completely formed, and bordered by the margins of the pterygoids, palatines, maxillae, squamosals, and quadrates. The pterygoids are fusing to the quadrates. The parachordal cartilages are nearly obliterated, but trabecular and orbital cartilages are evident. Several rows of fetal teeth are present in a peripheral arc on the maxillae and premaxillae, and in an extensive second arc on the palatines and vomers. Lower jaw elements are more extensively ossified and the retroarticular processes are longer. Several rows of teeth are present on the pseudo-dentary; all teeth now have well-mineralized pedicels. The stapes are completely ossified.

TL 70.8 mm. In this specimen, the chondrocranium is obliterated, except for the anterior part of the mesethmoid (prenasal process), the anterior rim of the nasal capsule, and the medial remnant of Meckel's cartilage (Fig. 6A,B,C). Remaining endochondral elements are fully ossified. Frontals and parietals are nearly complete medially. The prefrontal is fusing with the maxilla to form the anterior part of the orbit. The gaps between squamosals and the frontals and parietals are smaller because of anterior extension of the squamosal shelves. The occipitootic portion of the basal unit is incomplete dorsally, and fusion with the parasphenoid is nearly complete, forming the os basale. Morphogenesis of the vomeropalatine-sphenethmoid region has continued; the vomers have enlarged and assumed their adult shape. The orbitosphenoids, basisphenoids, supraethmoid, and mesethmoid are fusing to form the sphenethmoid compound element. The retroarticular processes of the pseudoangulars are relatively more elongate.

TL 105 mm. The only cartilage remaining is that of the anterior rim of each nasal capsule and the mesethmoid part of the sphenethmoid (Figs. 6D,E,F). These components and the hyoid apparatus remain cartilaginous throughout life. Further ossification increases the mass of the elements thickening the bones in situ. Skull shape alters, becoming longer and flatter relative to that of earlier fetuses. Allometric growth of the anterior elements of the skull and the jaw effects overall elongation and flattening (Wake, unpublished data). The elongate retroarticular processes now reach the posterior end of the skull. The quadrates are still vertical elements, though they are

broadening and the pterygoid squamae are thickening. Frontals and parietals overlap the sphenethmoid medially. The parietals overlap the otic capsules posterolaterally. The occipitootic region of os basale is still open dorsally and small gaps lie between the squamosals and the dorsal elements.

TL 120, 140, 150 mm. The ossified elements continue to thicken, and such fusions as nasal-premaxilla, maxilla-palatine, pterygoid-quadrate, and those of the sphenethmoid and os basale are strengthened. Anteroposterior overlap of dorsal investing bones is more extensive, but there is no median suture. The rear margins of the squamosals are free (the anterior is part of the orbit), and the occipitootic region of os basale remains incomplete dorsally in both unborn and free-living specimens.

TL 325-375 mm. Large adult specimens (probably more than 3 years old: see Wake, '80b) retain the cartilaginous nasal capsule rims and anterior sphenethmoid. The occipitootic part of os basale is barely complete dorsally, and the dorsal edges of the squamosals are bound weakly to the parietals by connective tissue. The dorsal investing bones are in close approximation but do not overlap medially, though there is overlap at other margins (Fig. 2).

DISCUSSION

Chondrocranium

Chondrocranial development was described for *Ichthyophis* by Peter (1898), Winslow (1898), and Edgeworth ('25), for *Grandisonia alternans* and *Hypogeophis rostratus* by Marcus ('09, '10, '22) and Marcus et al. ('35), and for *Gegeneophis carnosus* by Ramaswami ('48). DeBeer ('37), in reviewing the descriptions of *Ichthyophis*, *Hypogeophis*, and *Grandisonia*, was impressed by the similar chondrocranial structure in these forms. We, too, find the structural commonalities remarkable, for they still obtain as we compare both the description of *Gegeneophis* and our *Dermophis* material to the descriptions cited by DeBeer. Thus, DeBeer's summary of development of *Ichthyophis* remains cogent for all species examined. As he did, we will simply comment on the way species differ, either from *Ichthyophis* or from each other.

The structure of the nasal capsules in adults of several additional species has been paid considerable attention by Ramaswami ('41, *Uraeotyphlus*; '43, *Gegeneophis*), Els ('63, *Schistometopum*), Brand ('56, *Scolecocomorphus*), de Jager

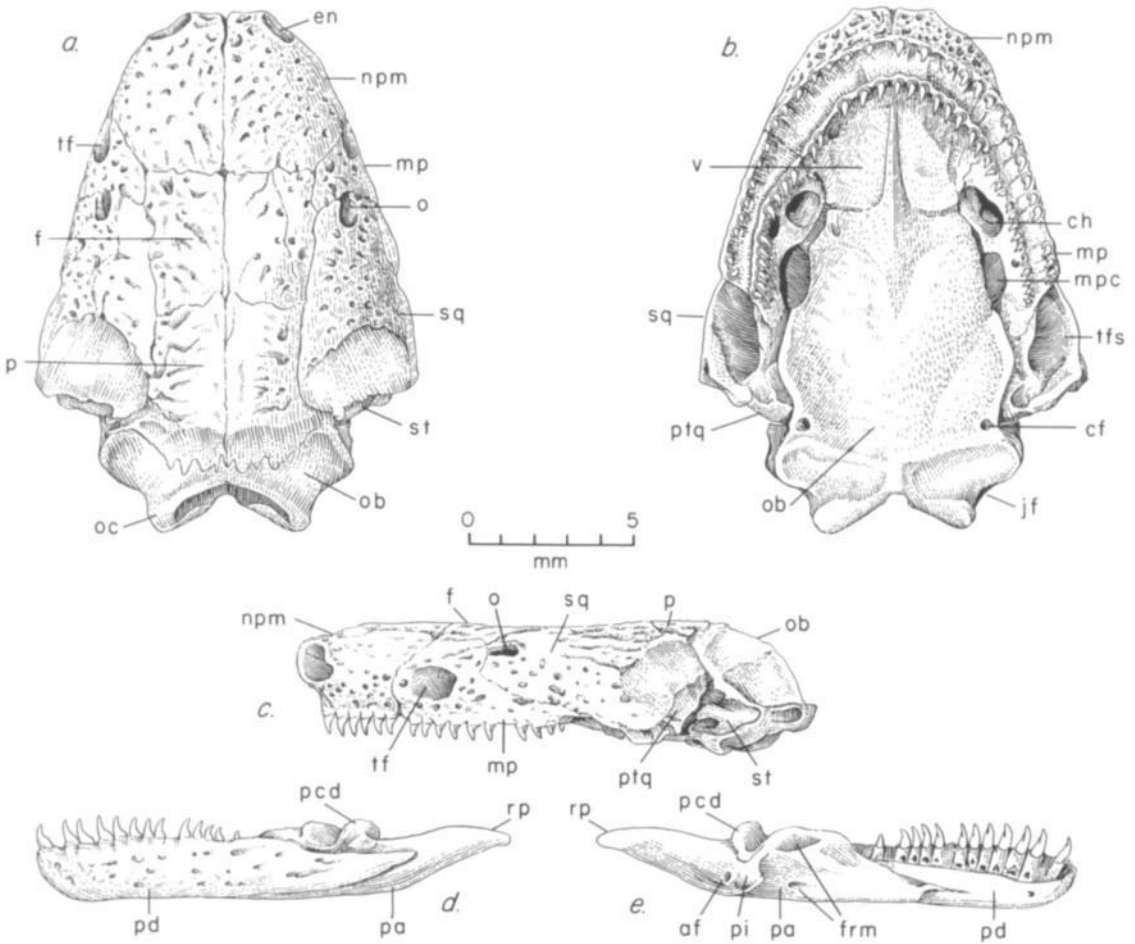


Fig. 2. Skull (a-c) and left lower jaw of 373 mm adult *D. mexicana*. Skull length 14.7 mm. Lower jaw is drawn from labial (d) and lingual (e) aspects. See list of abbreviations.

('39b, *Coecilia* [= *Oscacilia*]), and Visser ('63, two species of *Ichthyophis*). *Hypogeophis* and *Grandisonia* are the only forms known to have roofed nasal capsules, though there is an ontogenetic increase in the completeness of capsule walls. In *Dermophis*, nasal capsules remain fenestrated anteriorly, dorsally, and ventrally, but have extensive lateral walls. The solum nasi remains separate from the oblique cartilage in *Gegeneophis* (Ramaswami, '48; Fig. 2) though it is connected in other species.

The structure and development of the central region of the chondrocranium is much the same in all species. In *Dermophis*, we observe an increase in the mass of the trabecular and orbital cartilages during early ontogeny, as well as a more vertical orientation of the preor-

bitar roots and pilae antoticae, making the chondrocranium less flattened (Figs. 1 and 5). The otic capsules of *Dermophis* are proportionally large, and dorsally and laterally rounded, as are those of *Gegeneophis* but not other species for which there is information. The anterior tip of the notochord projects into the posterior part of the basihypophyseal fenestra and persists until ~70 mm TL in *Dermophis*; it was illustrated in the 25-mm *Grandisonia* by Marcus et al. ('35), and Ramaswami ('48) noted its presence in a 20-mm *Gegeneophis*.

Perhaps the most exceptional feature of the chondrocranium of *Dermophis* is the absence of both ascending and pterygoid processes of the palatoquadrate. Both processes are present and elongate in *Ichthyophis*, *Hypogeophis*,

and *Grandisonia*. Ramaswami ('48) noted the presence of an ascending process and the absence of a basal process in *Gegeneophis* but did not mention the pterygoid process. We see the appearance of the pterygoid process and the inception of a weak basal process only when the quadrate is considerably ossified (~50 mm TL); we never see an ascending process. Also, the columella-stapes never has a cartilaginous connection to the quadrate in *Dermophis*. Much emphasis has been placed by previous workers on such connections that form and then break down to form joints. We do not see these fusions in our material, bulk-stained or sectioned, though de Jager ('39a) commented on bilateral variation in these connections in heads of her *Dermophis*. These phenomena will be discussed below with the suspensorium and its significance.

Sensory capsule proportions

Cranial nervous and sensory components, particularly the brain and sensory organs, may influence both the differentiation and morphogenesis of the surrounding skull (Moss and Young, '60). Consideration of ontogenetic and interspecific differences in sensory capsule dimensions relative to head size may be valuable in analyses of the development and evolution of skull morphology and in systematic analyses (Hanken, '80). Interspecific comparisons among caecilians do not exist. However, we took appropriate measurements on our series of *D. mexicanus* in order to document ontogenetic changes in relative sensory capsule dimensions, and evaluate the relationships of this pattern of capsule growth to skull development. This information provides a basis for comparison both with other species of caecilians and with urodeles and anurans.

Relative eye size is greatest—11% of head length—in the smallest embryo and diminishes with continued growth. The proportion of eye length to head length is less than 9% (\bar{x} = 8.72%; SD = 1.18; N = 19) in embryos and fetuses smaller than 80 mm TL, less than 6% (\bar{x} = 5.56%; SD = 0.9; N = 5) in embryos between 100 and 160 mm TL (up until birth), and 5% in each of two large adults (325 mm TL). The decreasing rate of eye growth, combined with positive allometric growth of anterior elements of the skull, results in the eye lying progressively further back in the skull as the skull lengthens. In embryos less than 80 mm TL, the anterior margin of the eye lies at a level approximately 25% posterior on the length of the

skull from its anterior tip; in larger embryos it lies ~33% posterior, whereas it is nearly 40% posterior in adults. Longitudinal overlap between the eye and nasal capsule, which is often extreme in other amphibians (Hanken, '80), is not seen, for the sensory capsules are "pulled apart" as the skull lengthens.

There is little change in the relative size of the nasal capsule with skull growth. The mean head length occupied by the nasal capsule in all specimens is 24.3% (SD = 1.84, N = 26). The four smallest specimens have nasal capsule length 22.8% of head length (SD = 0.32), compared with 24.1% in the adults.

Relative length of the otic capsule decreases from 27% of skull length at 29 mm TL to 23.6% at 155 mm TL, but increases to approximately 32% in adults. However, it is difficult to make accurate measurements of otic capsule dimensions from cleared and stained specimens (especially in adults in which the otic capsule is nearly completely masked by investing bones). Therefore, we do not consider these data sufficient to document a shift in the pattern of allometric growth of the otic capsule (from negative to positive) between juveniles and adults as they suggest.

Olfaction is presumed to be the dominant sensory mode in caecilians, which utilize both specialized chemosensory tentacles and olfaction via the nares, which communicate directly with the nasal capsules. The sensory mode is reflected by the relative size of the nasal capsules, which occupy nearly 25% of overall head length in specimens of all sizes. Conversely, the eye of caecilians is covered by skin in some genera (e.g., *Dermophis*) and skin and bone in others. Retinas are well developed in all species but many other eye structures are reduced (Wake, '80c). Thus, while the caecilian eye appears to retain its function as a photoreceptor, it apparently is involved little, if at all, in prey capture in these animals, which forage nocturnally. Limited vision is correlated with relatively reduced eye size in *Dermophis*, especially adults.

Ossification sequence

In contrast to the development of the chondrocranium, which is relatively similar in all caecilians examined thus far, cranial ossification varies interspecifically. The ossification sequence of *Dermophis mexicanus* differs from that of *Ichthyophis glutinosus* (Sarasin and Sarasin, 1887-1890; Peter, 1898), *Hypogeo-*

phis rostratus and *Grandisonia alternans* (Marcus et al., '35), and *Gegeneophis carnosus* (Ramaswami '48). Further, *D. mexicanus* lacks several primary ossification sites. These sites are presumed to be homologous to distinct, separate bones present in adult skulls of certain primitive fishes and archaic amphibians, and to be present (albeit fused) in adult caecilians (Marcus et al., '35). Below, we first will summarize briefly the ossification sequence of *D. mexicanus* presented earlier and then review pertinent information concerning cranial ossification in other caecilians. This information is included in Table 1. Last, we will discuss the implications of our findings for ideas of skull function and evolution in caecilians.

In *D. mexicanus*, the palatoquadrate and the articular component of Meckel's cartilage ossify first, well before the inception of other bone anlagen. Next to ossify are blade-like anlagen of the nasals, premaxillae, frontals, parietals, squamosals, maxillae, palatines, exoccipitals, and more of the lower jaw (by ~40 mm TL). These are followed by the vomers, pterygoids, elements of the sphenethmoid complex, the basal elements, and the stapes, which ossifies by 55 mm. These elements enlarge by ossification in situ. Fusion of the maxilla-palatine begins at 50 mm TL and the prefrontal joins at 68 mm. Fusion of nasal and premaxilla (and septomaxilla when present), and quadrate and pterygoid occurs by 65 mm TL. The otic capsules ossify at 55 mm TL.

Precocious ossification of jaw suspension elements in *Dermophis* is similar to the condition Peter (1898) reported for *Ichthyophis*, in which the quadrate and medial and articular elements of Meckel's cartilage are ossified in Stage 1B embryos. Ramaswami ('48) reported that in a 45-mm *Ichthyophis* ossification begins with the maxilla, palatine, pleurosphenoid, and parasphenoid, whereas the occipital region remains cartilaginous. He did not mention any ossification of the quadrate or Meckel's cartilage. Peter (1898) and DeBeer ('37, after Peter) noted that the occipital region (the basal elements in Peter's 1C embryo) is next to ossify in that genus. Peter reported ossification of nasal, frontal, vomer, pterygoid, parabasal, ethmoid, "trabecular," and sphenoid centers in a 100-mm larva, with ossified turbinals by 160 mm. DeBeer concluded that the stapes, quadrate (in contrast to *D. mexicanus*), and sphenethmoid mineralize "late."

The ossification sequence in *Hypogeophis* is different (Marcus et al., '35). However, the observations of Marcus et al. are difficult to inter-

pret because the three specimens they analyzed actually represent two taxa in different but related genera—two *Grandisonia alternans* (25 mm TL and 68 mm TL) and one *Hypogeophis rostratus* (44 mm TL). Marcus's claim ('08) that the development of the two is identical pertains to early, prechondrocranial development. Further, *H. rostratus* of the sizes of the *G. alternans* reported by Marcus et al. are distinctly different in ossification pattern (Wake, unpublished data). Given the variation in ossification sequence among species we have examined and those reported in the literature, we see little reason to assume identity of the ossification in *H. rostratus* and *G. alternans*, so the conclusions of Marcus et al. ('35) about the number of anlagen and their sequence of ossification must be viewed with caution. Further, our whole-specimen staining procedure allows for precise resolution of skeletal configuration so that some of the problems of serial reconstruction (e.g., whether or not bone splints are joined) are minimized. We suspect that some of the reports of multiple elements (cf. Marcus et al., '35) and side-to-side variation (cf. de Jager, '39a) have resulted from either staining artifacts or the difficulty of interpreting complicated structures from reconstructions.

In the stage 40 (25 mm TL) embryo of *G. alternans*, only the vomers and palatines are ossified, near but separate from the teeth. The intermediate-sized (44 mm TL) stage 47 embryo of *H. rostratus* has many more sites of ossification—the lower jaw itself has nine elements (Eifertinger, '33); nasals, frontals, prefrontals, parietals, squamosals, premaxillae, maxillae, sphenethmoid, and parasphenoid have also appeared. The auditory capsules fuse to the exoccipitals, basioccipitals, and supraoccipitals, as these elements ossify. The quadrate is fused to the quadratojugal and is continuous with the stapes. In the larger (68 mm) embryo of *G. alternans*, ossified anlagen for orbitosphenoids (preoptic roots of the orbital cartilages), pleurosphenoids (in the orbital cartilages and metoptic roots), periorbitals, septomaxillae, lachrymals, interparietal, and presphenoid (mesethmoid) have appeared. The stapes is also ossified and separate from the quadrate.

Ramaswami ('48) partially described the ossification sequence of *Gegeneophis carnosus* in his account of chondrocranial development in the species. In a 51-mm embryo, the nasal, premaxilla, and septomaxilla are ossified and fused into a single element, as are the maxilla and palatine. The quadrate and the columellar

TABLE 1. Summary of inception of ossification of cranial bones, and their fusions

TL (mm)	Bones																						
	Mn	D	Sp	C	Sa	An	Ar	Pr	Co	Q	Qj	N	L	Pm	M	Sm	Pf	Sq	St	F	P	Ip	Pal
25					*?			*	*		*					R						*	G
30	D	D				D	D			D													
35	I	I	DI			I	I			I?		D		D	D			D		D	D		D
40				D								D											
45	H	H	H	H	H	H	H	H	H	H	H	H	H	H	IH		H	H		IH	H		I
50										Ge	Ge	Ge	Ge	Ge	Ge	Ge			Ge				Ge
55																D			D				
60																							
65																							
70													G			G							G
75																							
80																							
90																							
95																							
100														I									I
100+																							I

Key:

Bones:

Mn Mentomeckelian
D Dentary
Sp Splenial
C Coronoid
Sa Surangular
An Angular
Ar Articular
Pr Prearticular

Co Complementale
Q Quadrate
Qj Quadratojugal
N Nasal
L Lacrimal
Pm Premaxilla
M Maxilla
Sm Septomaxilla

Pf Prefrontal
Sq Squamosal
St Stapes
F Frontal
P Parietal
Ip Interparietal
Pal Palatine

Pt Pterygoid
V Vomer
Ex Exoccipital
Bo Basisoccipital
So Supraoccipital
Pro Prootic
Ot Otic capsule

Ps Parasphenoid
BS Basisphenoid
Su Supraethmoid
Os Orbitosphenoid
Pl Pleurosphenoid
Me Mesethmoid

process of the stapes are united; ossification is nearly complete in the retroarticular process of the pseudoangular, and beginning in the stapes (Ramaswami, '48: Fig. 4a). In an 81-mm larva (Ramaswami, '48: Fig. 4b) the eye is covered by a flange of the maxillopalatine, the parasphenoid and quadrate are fused, the pleurosphenoid free, the septa of the otic capsules ossified, and the quadrate united with both the pseudoangular and the columella. (Ramaswami commented that both of these "unions" will break down and form joints).

There are major problems in evaluating these ossification sequences and comparing them with that of *D. mexicanus*. First, all of the studies cited above are based on observations of only a few developmental stages. (The Sarasins, Brauer, and Marcus et al. had excellent material for observation of early development but little of later stages crucial to analysis of ossification.) Second, the only study primarily concerned with ossification (Marcus et al., '35) is based on one specimen from each of only three stages, and these three specimens represent two species now referred to different genera. Third, in no study was any attempt made to look in an ordered way at each element as we have attempted to do. Each author ad-

dressed either specific regions of the skull or specific problems such as fusion or kinesis, so some elements were paid little attention. Lastly, terminology is inconsistent, although DeBeer ('37) attempted to resolve the confusion; thus it is difficult to establish homologies among elements observed in different species by different workers.

Some comparisons and generalizations are possible. The lower jaw ossifies earlier in *Dermophis*, *Ichthyophis*, and *Gegeneophis* than in *Hypogeophis* and *Grandisonia*. The quadrate ossifies early in *Dermophis* and *Ichthyophis* in contrast to most other forms examined. Early ossification of the suspensorium in *Dermophis* may be correlated functionally with the inception of intraoviducal feeding and attendant utilization of jaws and specialized fetal teeth (shed at birth), in these viviparous forms. Ossification occurs at approximately 30 mm TL, the size at which yolk is exhausted completely and the switch to maternal nutrition via epithelial secretion takes place (Wake, '77a,b; '80a,b; see below).

Dermal bones of the skull proper appear next. In *Ichthyophis* and *Dermophis*, dorsal and lateral elements appear first (nasals, premaxillae, maxillae, frontals), but in *Hypogeo-*

																			Fusions in adults					
Pt	V	Ex	Bo	So	Pro	Ot	Ps	Bs	Su	Os	Pl	Me	PA	PD	MP	NPmSm	OB	PtQ	MPf	Se	QQj	PaQ		
	G		*	*	*						*											*	*	
	D													D	D									
H	D	H	H	H		D	D	D	H	D	I			D	D								H	
									D						DGe	Ge		D						
			I?	I?	I?	I?																		
												G	G	G?	G	G?	D			D		D	D	
							G?				Ge													
	I	I																						
								I	I	I	I													

Fusions:

PA Pseudoangular
 PD Pseudodentary
 MP Maxillopalatine

NPmSM Nasal-premaxilla-septo-maxilla
 Ob Os basale
 PtQ Pterygoquadrate

MPf Maxilla-prefrontal
 Se Sphenethmoid

QQj Quadrate-quadratojugal
 PaQ Palatoquadrate

Genera: D *Dermophis*; G *Grandisonia*; Ge *Gegeneophis*; H *Hypogeophis*; I *Ichthyophis*

* = not found in *Dermophis*; ? = question re precision of time of inception; R = rarely seen in taxon.

Note: *Dermophis* allocation based on our data; *Hypogeophis* and *Grandisonia* from Marcus et al. ('35); *Ichthyophis* from Peter (1898) and Ramaswami ('48); *Gegeneophis* from Ramaswami ('48). The pattern of development of each of the latter is difficult to compare with that of *Dermophis* because of lack of fully representative ontogenetic sequences and because the states of certain elements are not reported in the literature.

phis and *Grandisonia* ventral elements (vomeres and palatines) ossify first. In *D. mexicana*, the dorsal and lateral elements have a similar pattern of ossification. A ventrolateral rod (nasal, premaxilla, maxilla, squamosal) or lateral strut (frontal, parietal) ossifies initially; subsequent ossification proceeds as a broad sheet that extends dorsally and medially from these anlagen. [Peter (1898) also refers to "lamellae."] Ossification is seen next in the occipital region of the skull in all forms, though there is much variation in shape and number of anlagen. For example, *Dermophis* lacks the numerous isolated patches of bone on the floor of the braincase that characterize *Hypogeophis* and *Grandisonia* (Marcus et al., '35). Instead, the floor of the braincase is formed from paired, parasphenoid sheets; ossification proceeds in a lateral to medial direction. In *Dermophis* the vomeres and pterygoids ossify late; this pattern contrasts to that of *Hypogeophis* and *Grandisonia*, but is similar to that of *Ichthyophis*. Late ossification of sphenethmoid elements and the stapes characterizes all caecilians examined thus far.

The greatest discrepancy between our observations of *Dermophis* and those reported for other caecilians concerns the number of dis-

tinct, embryonic ossification centers that contribute to the adult skull. Marcus et al. ('35) claimed that embryonic *Hypogeophis* have at least 36 distinct cranial elements, many of which subsequently fuse in varying combinations to produce the 14 + separate bones of the adult skull (not including components of the lower jaw or the second member of paired bones). DeBeer ('37) was quite interested in these observations because of his concern for establishing the identity of morphological units. He looked carefully for examples of "fusions primordiales," in which skeletal elements separate in an ancestor arise from a single center in the descendent (and which DeBeer suggests require some "speculative" assumptions of fusion), "fusions secondaires," or bones separate early in ontogeny but which later fuse (and for which there is embryological evidence). DeBeer also sought instances in which bones present earlier in phylogeny are absent in a descendent; in place of these elements, other bones may expand to fill morphological and functional space. The data of Marcus et al. ('35) were of particular interest in this regard because they represented clear evidence of "fusions secondaires." For ease of reference, we will refer, as previous authors have, to

Marcus's data for "*Hypogeophis*." DeBeer ('37) summarized the composition of the compound bones of the adult skull of *Hypogeophis* (after Marcus et al., '35) as follows:

"basale," composed of the fused bones of the auditory capsule, exoccipitals, basioccipital, supraoccipital, parasphenoid (including the paired ossifications behind it), and pleurosphe-

noids;

"temporal," composed of fused frontal and prefrontal;

"nasopremaxilla," composed of fused nasal, premaxilla, and septomaxilla;

"maxillopalatine," composed of fused maxilla, palatine, and lachrymal, sometimes including the pterygoid as well;

"sphenethmoid," composed of fused orbitosphenoids and presphenoid (there appears to be uncertainty whether representatives of the lateral ethmoids may not be included as well);

"squamosal," composed of fused squamosal and periorbital bones;

"quadrate," composed of fused quadrate and quadratojugal;

"pseudodentary," composed of fused dentary, splenial, coronoid, supraangular, mentomeckelian;

"pseudoangular," composed of fused angular, prearticular, articular, and complementale.

Skull development in *Dermophis* does provide example of "fusions secondaire"; however, this pattern of fusion is not nearly as extensive as has been claimed for *Hypogeophis*. *Dermophis* also lacks several of the ossification centers observed by Marcus et al. ('35); we see no evidence of quadratojugal, postparietal, lacrimal, periorbital, ectopterygoid, or interparietal elements at any stage. Septomaxillae are present in only two specimens, one of which lacks the bone on one side. The stapes is always free of the quadrate and lacks a separate center of ossification for the foot plate. Multiple ossification centers fuse to form the single, median os basale and sphenethmoid elements. The sphenethmoid is composed of paired orbitosphenoids and basisphenoids and single supraethmoid ossifications, and the cartilaginous mesethmoid. The os basale includes the exoccipitals, the auditory capsules (ossified from the exoccipital and taenia marginalis contributions) and parasphenoids. Separate supra- and basioccipitals are absent and these regions os-

sify from the exoccipitals. Therefore, separate pro-otic, opisthotic, and pleurosphe- noid centers do not occur in *Dermophis*. As noted above, the "quadrate" is a pterygoquadrate, for the pterygoid process appears late and fuses to the quadrate. We recognize frontal, rather than temporal, bones, because they arise as single elements from the center of origin for the frontal and do not fuse with a prefrontal element. The maxilla, prefrontal, and palatine elements fuse to form a discrete unit. The homologies of the lower jaw components are unclear. The endochondral elements (mento- meckelian and articular, the latter with its pronounced retroarticular process) and the dentary, splenial, coronoid, and angular are present, but we observe neither a prearticular nor a supra-angular. A thin splint of bone present in some, but not all, 40- to 50-mm specimens may represent the complementare of Eifertinger ('33). Thus, there seem to be only six or seven centers of origin for the lower jaw, instead of nine.

Skulls of juvenile (190 mm TL) and adult (369 mm TL) specimens were macerated in order to determine the nature of the articulation between adjacent skeletal elements in adults (i.e., bony fusion or connective tissue), and whether any additional fusions occur after birth. The same bones were obtained in both preparations; these included paired frontals, parietals, squamosals, maxillopalatines, nasopremaxillae, vomers, pterygoquadrates, stapes, pseudodentaries, and pseudoangulars, and single sphenethmoid and basal bones (Figs. 3 and 4). Therefore, fusions are complete early, probably by birth, and though bones grow and change shape somewhat (Wake, unpublished data) additional fusions do not take place. This general observation is confirmed by observation of cleared and stained material. The cleared and stained *Dermophis* skulls indicate that the investing bones are bound less rigidly than had been inferred from dried specimens in which cartilage, and especially ligaments and other binding connective tissues, are shrunken. The skull is compact, but not the fused and tightly sutured unit as has been claimed.

Our description of skull development in *Dermophis mexicanus* differs in many respects from that currently accepted as "standard" for caecilians, a "standard" that has played a central role in many discussions of amphibian biology, generally (e.g., the relationships among the modern Amphibia—see below). We appreciate the likelihood of variation in skull devel-

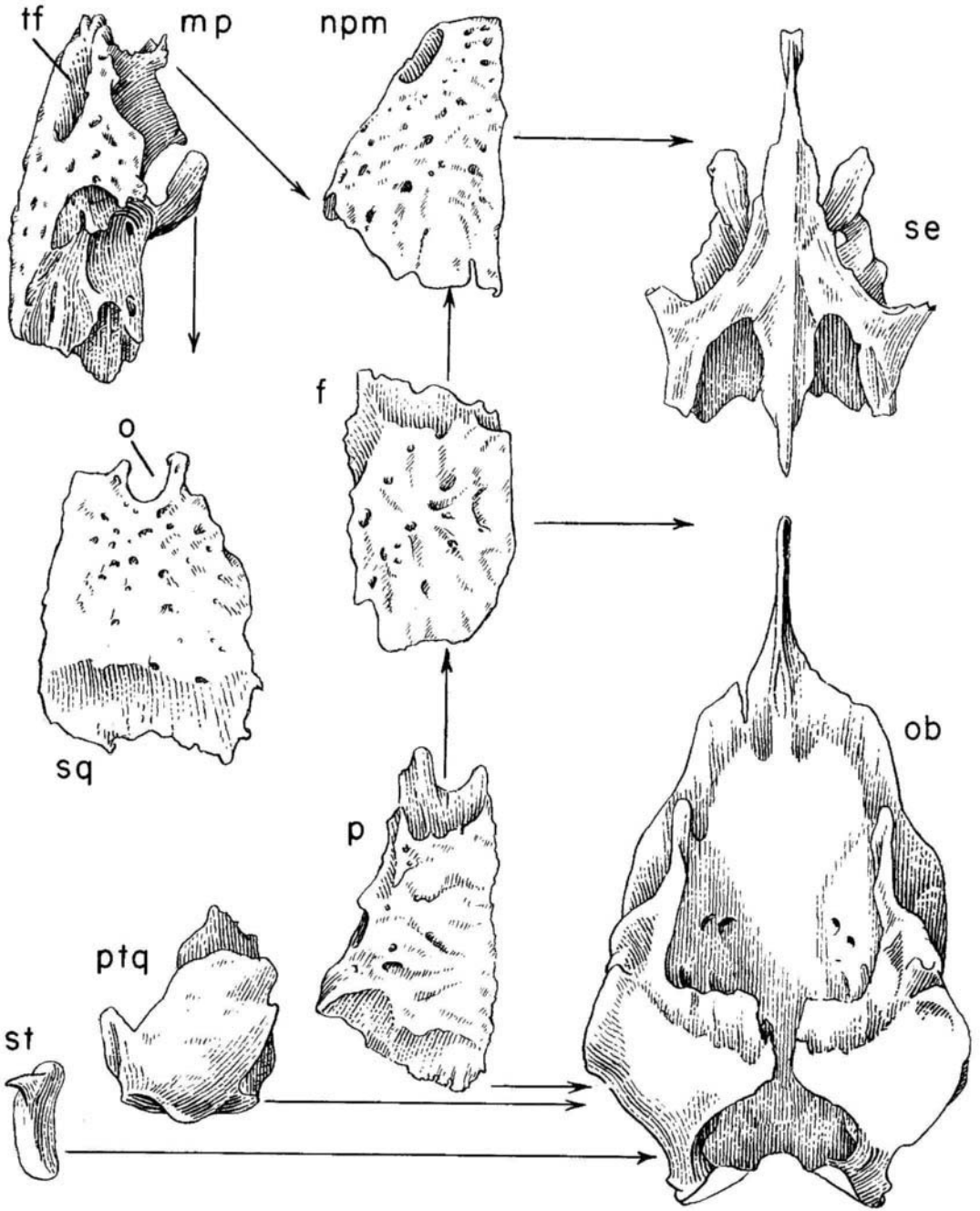


Fig. 3. Disarticulated skull (dorsal view) of 369-mm adult *D. mexicanus* illustrating size, shape, orientation, and relative position of separate elements (i.e., results of ossification and, in many cases, fusions that do not dissociate). Skull length 16.3 mm. See list of abbreviations.

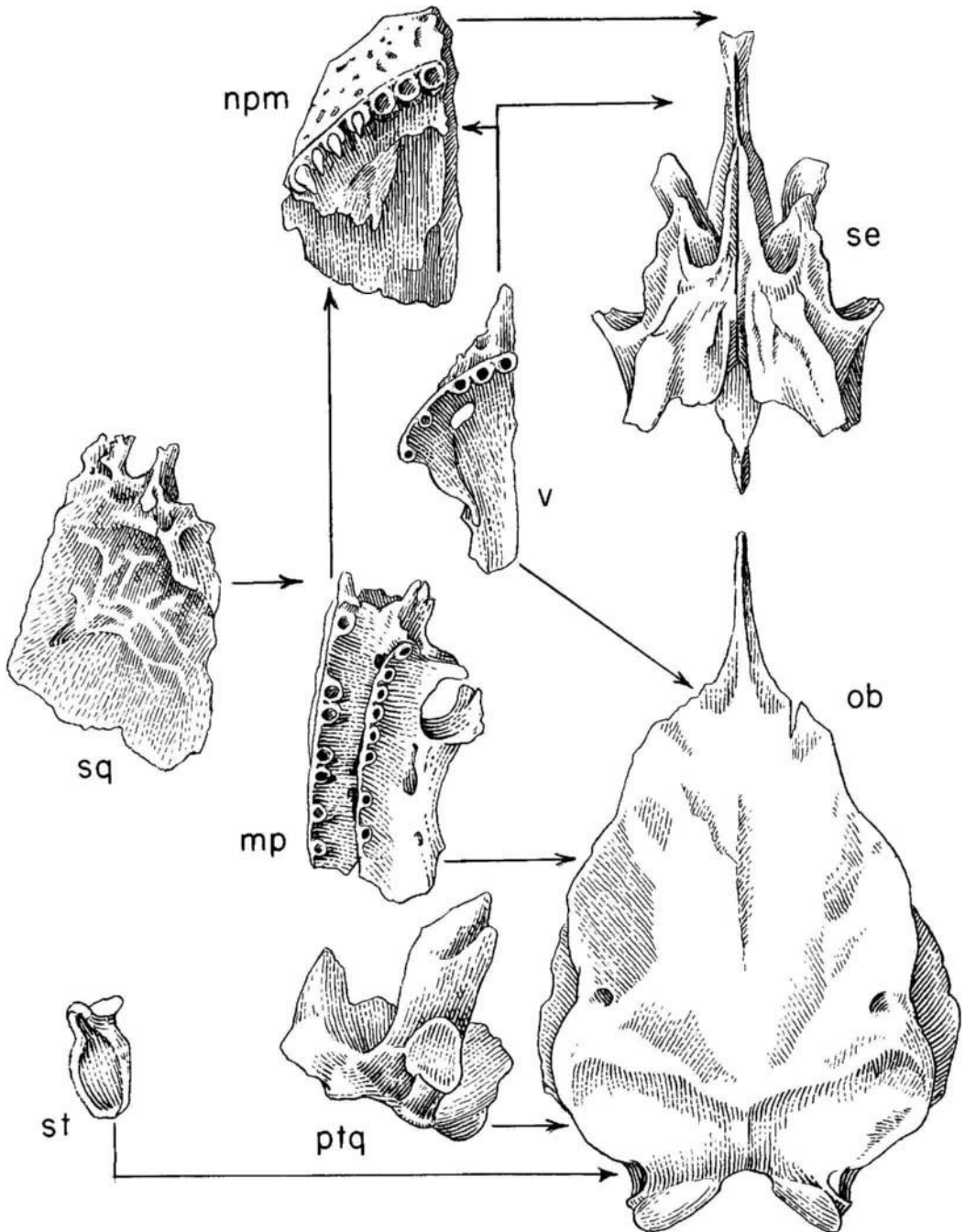


Fig. 4. Disarticulated skull (ventral view) of 369-mm adult *D. mexicanus* illustrating size, shape, orientation, and relative position of separate (i.e., unfused) elements. See list of abbreviations.

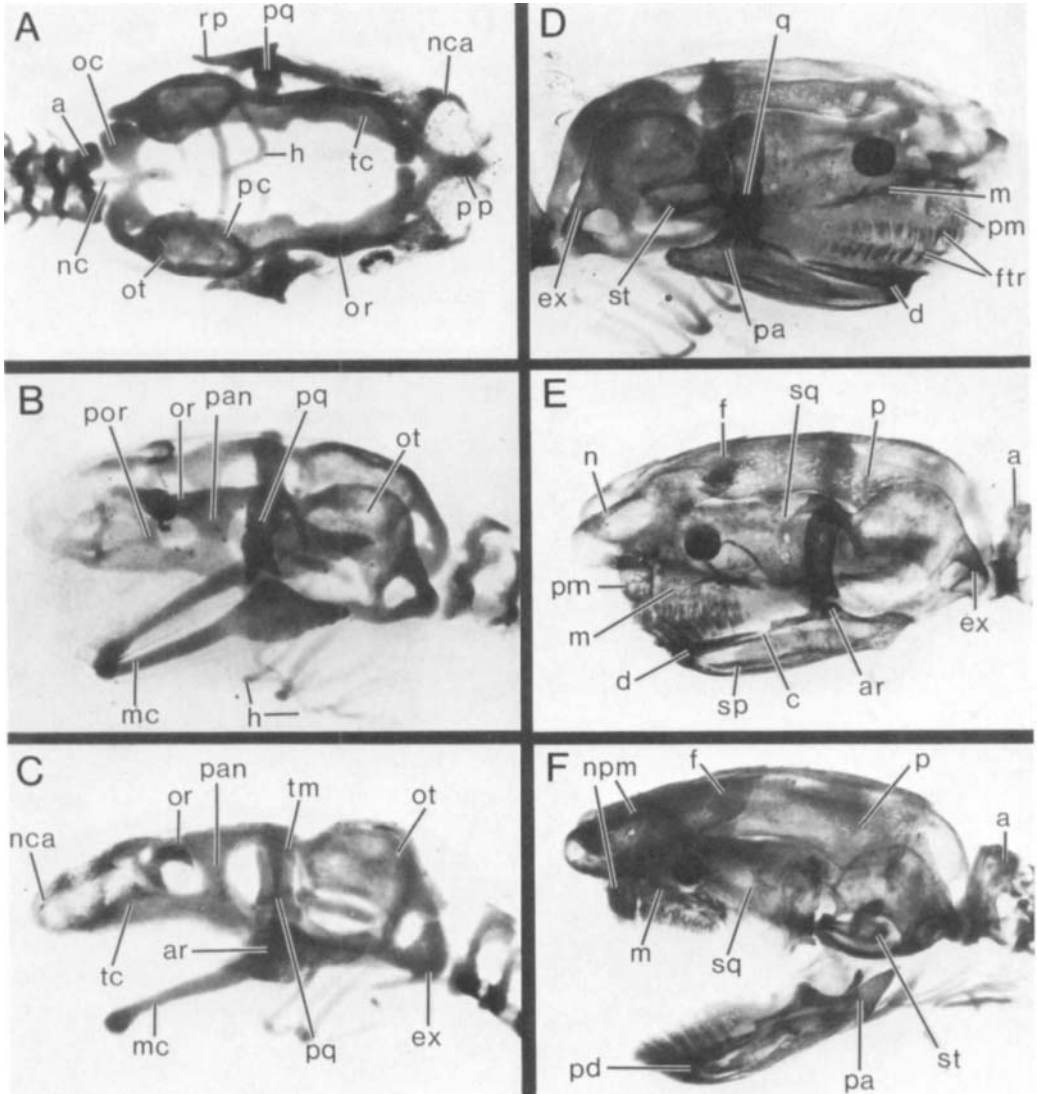


Fig. 5. Embryonic and early fetal skulls of *D. mexicanus*, cleared and differentially stained for bone and cartilage. Total specimen length and skull length (in parentheses) in millimeters: A (dorsal view), 29.0 (4.4); B, 35.0 (5.1); C, 35.6 (4.8); D, 44.5 (5.3); E, 51.8 (5.7); F (lower jaw disarticulated),

68.6 (6.7). Cartilage predominates in A-C, although some ossification (difficult to see in black-and-white photographs) is present in C; teeth, dermal roofing bones, and ossified lower jaw elements are visible in D-F. See list of abbreviations.

opmental patterns among caecilians and, further, that the pattern observed in *Dermophis* is not necessarily typical for all members of the group. Therefore, we do not wish to draw conclusions about relatedness or primitive vs. derived states within the order. These analyses await additional comparative material.

Jaw suspension and consideration of skull kinesis

For the last 100 years, morphologists who have examined caecilian skulls, and especially their development, have evaluated the components of the jaw suspension with regard to the

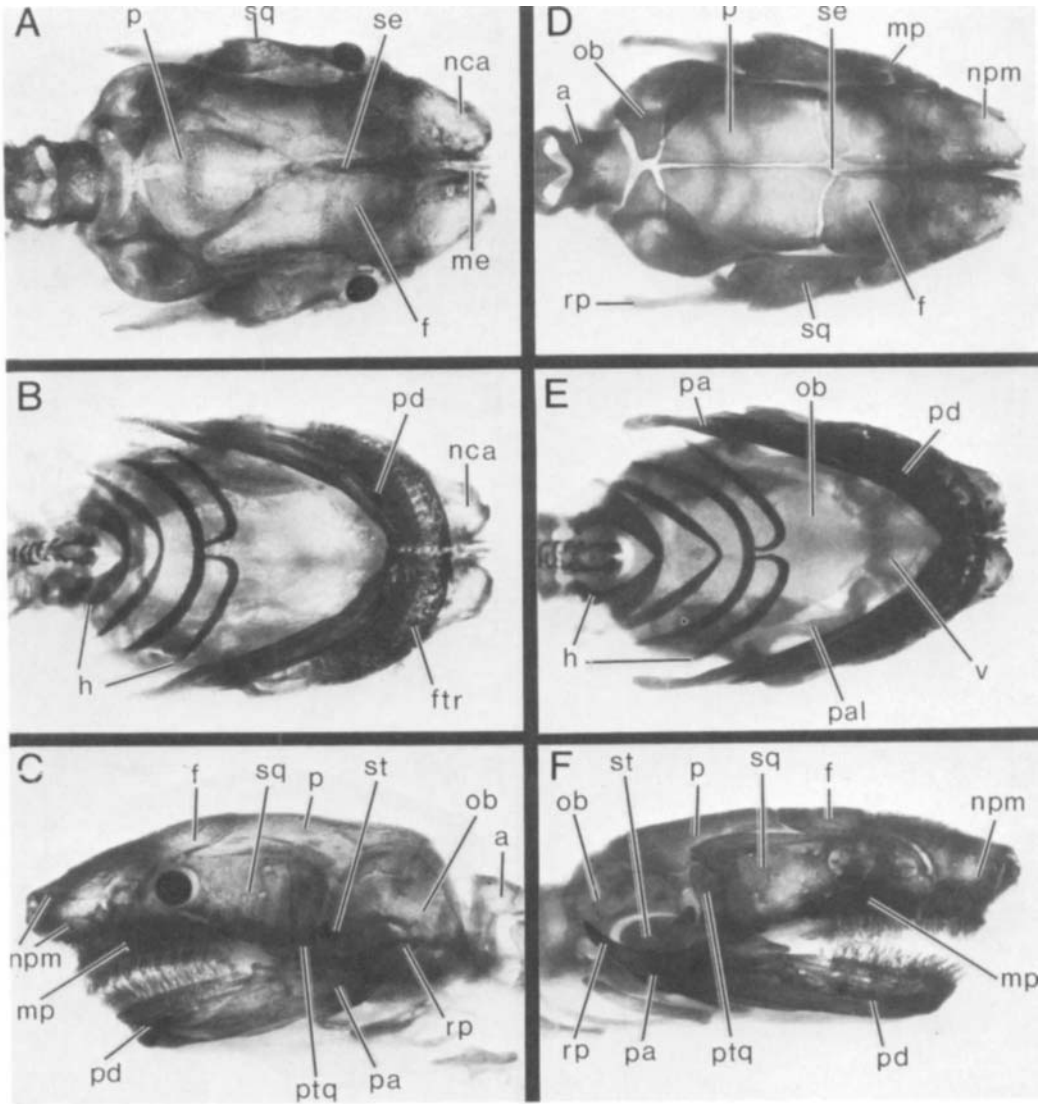


Fig. 6. Two late fetal skulls (dorsal, ventral, and lateral views) of *D. mexicanus*, prepared as in Figure 5. Total speci-

men length and skull length (in parentheses) in millimeters: A-C, 70.8 (6.4); D-F, 105.0 (7.6). See list of abbreviations.

presence and functional significance of kinesis. Further, examination of the quadrate and squamosal and their articulations, and consideration of the development and articulations of the stapes, have led to controversy about the nature of kinesis in the caecilian skull. Kinesis has been claimed for some genera but presumed absent in others. However, evidence is often only circumstantial and incomplete and the interpretations often contradictory. We will consider the problems of suspensorial type

and skull kinesis together, because the relationships of certain bones (squamosal, quadrate, stapes, and basal) are crucial to analysis of both questions.

Marcus et al. ('33), concluded that the skulls of *Hypogeophis* and *Grandisonia* are kinetic (*sensu* Versluys, '10, '12), and that movement between the two parts of the skull—the basal segment (os basale) and the quadrate segment (all other bones)—occurs at four points: 1) between the rostrum of the os basale and the

vomers, 2) between the os basale and the parietals, 3) between quadrate and stapes, and 4) between quadrate and the basitrabecular process of the os basale. In contrast, Ramaswami ('41) pointed out that none of the species he examined had movement at all four points (all did between quadrate and stapes, but often not at the other three junctures), concluding that "the Apodan skull is slowly becoming akinetic." Ramaswami and other workers have considered connective tissue binding of various bones, the absence of certain bones and/or processes, and certain fusions as evidence of the evolutionary loss of kinesis. For example, DeBeer ('37) considered the skull of *Hypogeothis* monimostylytic (quadrate bound to the skull) and slightly kinetic because "the quadrate is fixed to the squamosal" and only slight movement might be possible at other joints. [Ramaswami ('41) found no indication of such an association of quadrate and squamosal, and considered DeBeer to be in error.] DeVilliers ('38) and Brand ('56) considered the skull of *Scolecormorphus* monimostylytic because of 1) the absence of the stapes (and, therefore, of the quadratostapedial articulation), 2) the absence of the m. levator quadrati, and 3) connective tissue binding of the quadrate and squamosal. Els ('63) concluded that *Schistometopum* is monimostylytic because of 1) the synchondrosis of the stapes to the rim of the fenestra ovalis, and 2) the connective tissue binding of the quadrate and squamosal. Neither de Jager ('39c) nor Visser ('63) dealt with kinesis in *Ichthyophis*, though Edgeworth ('25) considered the skull secondarily streptostylytic (quadrate moveable); Ramaswami ('41) considered the syndesmosis of the basal and quadrate evidence of the absence of kinesis. DeVilliers ('36, '38) considered *Boulengerula* to have possible movement at the appropriate articulations, so, presumably, he thought the skull streptostylytic and kinetic. De Jager ('39b) found the skull of *Oscacilia* (then *Coecilia*) *ochrocephala* to be monimostylytic and akinetic because of 1) a cartilaginous connection between the stapes and fenestra ovalis, 2) a similar connection of the stapes and quadrate, 3) connective tissue binding of squamosal and quadrate, and 4) limitation of the basal-quadrate articulation. Ramaswami ('41) considered *Uraeothyphlus* monimostylytic and akinetic because of the syndesmosis of basal and quadrate. Finally, de Jager ('39a) believed *Dermophis mexicanus* to be monimostylytic and akinetic. She found (on one side of one specimen) the degeneration of the quadrostapedial joint and a cartilaginous

fusion of those elements, firm binding of quadrate and squamosal by dense connective tissue, and cartilaginous fusion of the stapes to the fenestra ovalis. She concluded that the basal-quadrate articulation and the m. levator quadrati must be functionless because for there to be any quadrate movement the quadrate must be able to move relative to the stapes. She also suggested, therefore, that the stapes cannot function in sound transmission.

The definition of kinesis has varied among workers. Ramaswami ('41) noted that if adjacent bones are not fused one cannot say a priori that movement is impossible; in these situations some movement may even be expected. He, therefore, accepts streptostyly, only to imply on the following page that movement is lost. Luther ('14), who considered streptostyly a primitive character in caecilians, noted in his analysis of caecilian jaw musculature that the question of kinesis was one of the degree of movement, not its presence or absence. On the other hand, Marcus et al. ('33) questioned whether the streptostyly that they described is functional because of the close binding of adjacent bones. The presence of dense connective tissue instead of bony fusion, they claimed, did not permit kinesis but, instead, served to cushion adjacent elements during burrowing.

Our data can be used to evaluate the degree of kinesis only in *Dermophis* and here our observations contradict those of de Jager ('39a). The fetal skull is highly streptostylytic and kinetic. We noted above that quadrate and articular ossify early in *Dermophis* and at the same size at which the developing embryo's yolk supply is exhausted. Beginning at this time, and continuing for the remaining several months of gestation, the fetuses actively ingest maternal oviducal secretions (Wake, '77a,b, '80a,b). We suggest that early ossification is associated with the inception of jaw movement during intraoviducal feeding. The quadrate is highly moveable, especially before the appearance of adjacent bones that will restrict its movement, and it appears that the lower jaw, with its armature of specialized fetal teeth, can be swung far forward, facilitating oviducal epithelium stimulation and ingestion of secretions. Subsequent development of the endochondral and dermal bones associated with the quadrate restrict its movement but it is never bound rigidly to other skull components. Further, we do not see any cartilaginous association of the quadrate with the stapes at any time during development, contrary to the claim by de Jager ('39a).

Adult skulls also allow movement at crucial joints, though much less than that of the fetus. We examined sectioned heads of three specimens ($325 \text{ mm} \pm 25 \text{ TL}$) and found, in each, intact synovial joints between the stapes and quadrate present on both sides of the head, and connective tissue, not cartilage, binding the stapedia foot plate in the large fenestra ovalis. Further, we found intact quadratobasal joints and dense connective tissue and muscle between the quadrate and squamosal. There are no indications that previous workers attempted to demonstrate movement (or its absence) among these bones. We therefore manipulated the skull of a freshly killed specimen, on the assumption that if movement were possible, it is at least possible in life; if there were no movement under these conditions it would be unlikely to occur in living specimens. Movement of the posterior end of the squamosal described an arc of $3\text{--}4^\circ$, and there was flexibility at its junction with the maxilla at the orbit. Significantly, this squamosal movement did not appear to involve the quadrate. When the squamosal was removed from the freshly killed specimen, the m. levator quadrati was revealed, and the pars quadrati, when grasped with a forceps on its anterior rim, moved in a 7° arc at its joints with stapes and os basale. We were not able to effect relative movement at the basal-vomer and basal-parietal joints. Therefore, it appears that the quadrate of adult *Dermophis mexicanus* is movable; the skull is streptostylic and slightly kinetic. We conjecture that de Jager may have had a juvenile specimen (she does not mention its size), and therefore observed more cartilage, as is typical of early ontogenetic stages but not of adults.

It is clear that the skull of *Dermophis mexicanus* is highly kinetic during the period of active feeding that characterizes the latter part of fetal development. This kinesis, produced by the precocious ossification of jaw suspension elements and the retarded development of adjacent elements that later will restrict movement of quadrate, is of functional significance and represents a fetal adaptation in this viviparous species. Similar precocious ossification of jaw suspension elements is known only for *Ichthyophis* (see above), which are oviparous and have free-swimming larvae. It is possible that these larvae hatch and begin active feeding relatively early in their skeletal development but, unfortunately, the timing of ossification events relative to the onset of feeding remains unknown. The relatively late develop-

ment of the quadrate and other alterations in the ossification sequence typical of the direct-developing *Hypogeophis* and *Grandisonia* may correlate with the fact that they do not feed before birth, in contrast to both oviparous species with free-living larvae and viviparous species.

The extent of kinesis in adult skulls, and its functional significance, are more difficult to establish. We suggest that, at least in adult *D. mexicanus*, the slight kinesis of the skull may be of functional significance during feeding, although in a manner different from that present in the fetus. One possibility may be its conferring an increase in the mechanical advantage of the adductor musculature similar, although not identical, to that described by Smith ('80) for reptiles. An investigation of feeding mechanics is currently under way in the senior author's laboratory.

Caecilian skulls and amphibian relationships

The composition of the caecilian skull, specifically the number, identity, and morphology of the bones present in adults and embryos, has provided valuable evidence in analyses of the relationships of caecilians to extinct and extant amphibians and in attempts to establish homologies among skull bones in all vertebrates. Some of the most critical data, cited by nearly all workers, are those of Marcus et al. ('35), who described the presence, in embryos, of several bones that subsequently fuse and are not visible as discrete elements in adults (see above). Marcus and his co-workers believed that the additional centers of ossification in caecilian embryos are homologous to individual, separate bones in the skulls of many archaic amphibians of pre-Jurassic age ("Stegocephalians"), which are otherwise lacking in all modern amphibians. Thus, they concluded that the well-developed skull roof typical of all caecilians, which is quite different from the reduced skull roof in frogs (Anura) and salamanders (Urodela), represents the primitive amphibian condition, called stegokrotaphy, in which skull roofing is complete, especially in the temporal region. Further, Marcus et al. ('33) considered stegokrotaphy in caecilians to be directly descended with little modification (except fusions) from the skulls of stegocephalians, in other words, a retained primitive feature, or plesiomorphy.

Several authors have accepted the general conclusions of Marcus and his co-workers, including DeVilliers ('36, '38), Schmalhausen ('68), and, most recently, Carroll and Currie

('75). While these authors accept the idea of a caecilian descent from early amphibians separate from other recent amphibians as proposed by Marcus et al. ('35), they all favor the Paleozoic microsaur (Microsauria) as the most likely ancestral group.

The belief of Marcus et al. ('35) that the well-developed skull of caecilians is a retained primitive feature has been challenged by many authors, however, all of whom interpret the stegokrotaphy of the caecilian skull as being secondarily derived from a reduced skull typical of other Recent amphibians. They do not deny the observations of Marcus et al. ('33) and Marcus et al. ('35) but are careful to point out the differences that still distinguish the skull of caecilians from any purported ancestor. Goodrich ('30) and DeBeer ('37) cite the lack of postfrontal and supratemporal bones in caecilians, both of which characterize primitive amphibian skulls. They believe that the solidly roofed skull of caecilians was derived secondarily from a reduced skull in response to the functional demands associated with fossoriality, as does Nussbaum ('77). Romer ('66) also favored secondary acquisition (i.e., convergence with the skull morphology of early amphibians) for the same reasons; he was impressed also with the unique, derived anatomical features shared by the Recent amphibians as identified by Parsons and Williams ('63).

Our analysis of skull development in *Dermophis* has several implications for this controversy. First, as presented above, we did not observe several of the embryonic ossification centers whose supposed presence has been used to ally caecilians and early amphibians, particularly the microsaur. Some centers (e.g., postparietal, periorbitals) are absent from all other recent amphibians. Second, there is good reason to believe that the original description of these elements in *Hypogeophis* (Marcus et al., '35) is inadequate. At best, their presence in caecilians must be considered only tentative pending confirmation in additional studies; certainly at this time their presence cannot be used to buttress a hypothesis of close caecilian relationship with any known early amphibian.

Dermophis usually has been considered stegokrotaphic, though Taylor ('69) showed some variation among his putative species (see Savage and Wake, '72). In *D. mexicanus*, development of the skull roof proceeds gradually. The gap between squamosal and parietal shrinks as the squamosal enlarges with age. A

slight space is present at birth and persists in adults as observed in cleared and stained material. Preliminary observations of kinesis, especially the demonstrated potential for relative movement at the squamosal-quadrate articulation, suggest that the skull of *D. mexicanus* is usually incompletely stegokrotaphic; complete stegokrotaphy is achieved late in ontogeny, if at all. Nothing in the pattern of development of the skull roof in *Dermophis* can be used to reject the hypothesis of secondary derivation of the well-developed cranium of caecilians from a reduced condition in an ancestral form. On the other hand there is less evidence of resemblance between the caecilian skull roof and that of primitive amphibians than has previously been assumed.

We heartily concur with the idea of a long and separate evolutionary history for caecilians, independent of frogs and salamanders, as has been expressed by Carroll and Currie ('75). However, the resemblances between the cranial morphology of caecilians and that of their purported ancestors, the microsaur, are only superficial, and many significant differences remain. Further, there are real differences in the postcranial elements, which were not within the purview of Carroll and Currie's study.

Based on our observations of skull development in *Dermophis mexicanus*, we believe that there is now little evidence for the hypothesis of primary derivation of the caecilian skull from any known early amphibian group. While our observations do not provide any direct proof of the hypothesis of secondary derivation of the well-developed skull from a reduced ancestral condition, we favor this idea in view of the likelihood of convergent evolution of a solidly roofed skull in response to the demands of the fossorial environment.

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