The Morphology of *Idiocranium russeli* (Amphibia: Gymnophiona), With Comments on Miniaturization Through Heterochrony

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**ABSTRACT**  *Idiocranium russeli* is among the smallest species of caecilians. The morphology of the skull (e.g., small, widely spaced dermal elements, retention of cartilaginous remnants) and of the posterior vertebrae (incomplete development, retention of a postvertebral notochord) indicate that heterochrony, or change in timing of development, has resulted in the miniaturization of the species. The pattern is apparently a progenetic one, characterized by early offset of development (see Alberch et al., '79). Other unique features of osteology (e.g., extensive sphenethmoid development) correlate with the burrowing habit of the species and may have arisen to compensate for progenetic effects. Several features of the myology, neurology, and visceral morphology are correlated with miniaturization as well. Reproductive maturity occurs at approximately 75 mm total length; gonads are proportionately small, but other aspects of reproductive morphology are typical of direct-developing caecilians.

*Idiocranium russeli* is one of the smallest caecilian species. Collected only once near the Cameroon–Nigerian border in 1934–1935 by the British Museum (Natural History) expedition led by Ivan T. Sanderson, the species is characterized by a number of unique characters. Several (reviewed below) were listed by Parker ('36) in the type description. Aspects of the ecology and behavior were recounted by Sanderson ('37). Forty-eight paratypes were reported by Parker ('36) to be in the British Museum (Natural History) and the Museum of Zoology, Cambridge University, U.K. Available for study were the holotype (BMNH 1936.3.4.29) and 16 paratypes from the BMNH, 28 specimens from Cambridge, and three specimens from the Museum of Comparative Zoology, Harvard University. Investigation of *Idiocranium* provides information relevant to several problems in evolutionary morphology. Little was known of its morphology; thus its relationships to other gymnophione taxa are not well assessed. Miniaturization as a developmental and evolutionary phenomenon is receiving renewed attention (Hanken, '84); heterochrony, or alteration of developmental “program,” has been proposed as a mechanism for such phenomena (Gould, '77; Alberch et al., '79). Analysis of heterochrony in a lineage presumably already constrained developmentally and phylogenetically by body elongation and limb loss may yield insight into pattern of evolution. This study analyzes characters of *Idiocranium* common to the gymnophione lineage, and the nature of variation of these characters in a miniaturized taxon. It considers how small size may be achieved, and how the morphological characteristics of the taxon are correlated with its biology, especially its fossorial habits and its direct-development mode of reproduction. A comparison with other West African caeciliids also may be instructive in the absence of opportunities to recollect the species, if it still exists.

**MATERIALS AND METHODS**

Forty-eight specimens (27 females, 13 males, and eight juveniles) of *Idiocranium russeli* were examined, ranging from 50 mm total length (TL) immatures to among the largest known adults (114 mm TL). Fifteen specimens were X-rayed, one cleared and...
stained with alizarin, one cleared and stained with alizarin and sudan black, two cleared and stained with alizarin and Alcian blue, and two prepared as serial frontal sections (head and tail) stained with hematoxylin–eosin, picro-ponceau, or Mallory’s trichrome. In addition, gonads, kidney, urogenital ducts, lung, and skin were prepared for histological examination, and scales were stained and mounted. The head and body wall musculature were dissected before clearing and staining. Other West African taxa (Geotrypetes seraphini, G. grandisonae, Herpele squalostoma, Schistometopum thomense, and Scalcomorphus kirkii) were variously X-rayed, cleared and stained, dissected, and sectioned for comparison of morphological characters. Table 1 presents counts and measurements of various characters. The morphology and some features of the natural history of the species are reported here, for the paratype series constitutes the entire sample of this unique genus and species.

RESULTS

External morphology

The type description (Parker, ‘36) summarizes many of the salient features of external morphology. The eye is visible as a small, dark dot beneath the skin of the head; the snout is long and pointed, the mandible underslung. The tentacle is globular, nearer the nostril than the eye. Parker reported 83–90 (mode 86) primary annuli and 21–29 (mode 24) secondary annuli, presumably for the full sample of 49 specimens. For my sample of 47, I find 81–88; (x = 84.0) primary annuli and 20–31 (x = 26.0) secondary annuli (Table 1). Variation in primary counts is probably due to Parker’s inclusion of the two collar folds to square the outline of the snout. The posterior divergence of the nasopremaxillaries exposes much of an exceptionally well-ossified sphenethmoid complex. Dorsally the sphenethmoid is domed and smooth, and its medial suture is complete. There are no sutures between any of the dermal elements, and they are usually separated by gaps of 0.25–0.5 mm. The small frontals lie adjacent to the nasopremaxillary posterior projections, the squamosals, and the front ends of the parietals. The maxillaries are excluded from contact with the frontals by the long nasopremaxillae, a condition unique among caecilians. The eye socket is formed of the posterior margin of the maxillary and the anterior margin of the squamosal, but socket size and eye position may vary. In one cleared and stained specimen, the left socket is poorly formed, nearly occluded by the squamosal. In that specimen and one other, one eye lies...
### TABLE 1. Measurements (mm) and counts for Idiocranium russeli

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<tr>
<th>Sex</th>
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<th>Head width at nostrils</th>
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(continued)
HETEROCHRONY AND MINIATURIZATION IN CAECILIANS

under the squamosal, the other in the socket. The squamosal overlaps the quadrate posteriorly and the dentigerous part of the maxillary anteriorly. The posterolateral margin of the parietal overlaps the otic capsule. The left and right otic elements are separated dorsomedially.

Ventrally, the fused maxillopalatine bears two rows of teeth, the nasopremaxillary a single row (the medial continuation of the labial tooth row) and the vomer a single row (the continuation of the lingual tooth row). The palatine forms the lateral and posterior margins of the choanae. The vomers are small and form the medial borders of the choanae. They are widely separated medially and expose the length of the sphenethmoid.

The os basale, into which otic capsules and occipital elements are incorporated, has lateral flanges anterior to the otic capsules which bear cartilaginous surfaces that articulate with the quadrate. Anterolaterally, there are dorsal (orbital cartilage remnant) and ventral (trabecular remnant) bars of cartilage between the os basale and the sphenethmoid. The pterygoquadrate is very large and bears the angled articulation surface for the lower jaw. The stapes is large and block-like. The columnellar component is short and has a cartilage-capped articular surface that abuts the quadrate. The stapedial foot plate is very large, filling a concomitantly large oval window. The stapes is not perforated by the stapedial artery.

The lower jaw consists of two elements: the dentigerous pseudodentary and the pseudarticular. The latter bears a long retroarticular process which is 1.0 mm of the 3.8 mm length of the jaw. A small (0.15 mm) remnant of Meckel’s cartilage lies between the juncture of the two elements of the jaw, even in large adults.

**Teeth**

The teeth of *I. russeli* are bicuspid and recurved (Fig. 3), similar to those of other African caeciliids (Wake and Wurst, ’79). The teeth located medially on the rami of the dentaries are considerably larger than those more posteriorly. Tooth replacement patterns were analyzed for the three cleared and stained specimens. A virtually full complement of stage F teeth (mature, ankylosed, functional; see Wake, ’76, ’80b) is maintained in each tooth row (see Table 2). Replacement crowns in stages a–d (rarely e) were present for most loci. The sample is too small for

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**Table 1 (contd.). Measurements (mm) and counts for *Ichthyolamia russeli***

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*Cambridge specimen numbers are the author’s; not catalogued numbers.*
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*Data are taken from cleared and stained specimens.

-Tooth counts are of stage f teeth.

-Stages a–e are developing tooth crowns; stage f is that of ankylosed, functional crowns; stage g is the unoccupied space of a shed tooth. (See Wake, '76, and text for discussion.)

Vertebrae and ribs

There are slightly fewer vertebrae in the column than in other caecilians, except for members of the genus *Grandisonia* which also has some diminutive species. Individuals in a sample of 19 *I. russeli* have 86–94 (\(\bar{x} = 90.5\)) vertebrae. The atlas has a small centrum and has the large atlantal cotyles mentioned by Wake ('70) for caecilians. The articular facets have a deep cartilaginous pad. The structure of the remaining vertebrae resembles that reported by Wake ('80c) for other caecilians. The vertebrae are block-like, rather than elongate. All vertebrae but the atlas have posteriorly directed dia- and parapophyses for articulation with the bicipital ribs. The second through eighth or ninth vertebrae have a slight keel on the neural arch where dorsal head muscles insert. All of the vertebrae have the pronounced ventral keel characteristic of caecilians and many other fossorial forms. A small block of notochord remains in the center of the centrum of each vertebra, as noted by Lawson ('66) and Wake ('70).

The most noteworthy aspect of the vertebral column is the reduced development of the posterior components. Even in the large-
est (113 mm TL) specimen cleared and stained, the notochord is retained throughout life. It extends as a rod posterior to the terminal vertebra (Fig. 4A–B). It is connected to the unmineralized notochordal component of the centrum of the penultimate and last vertebrae. Paired small lateral blocks of cartilage lie beside the posterior notochord, and intervertebral joints may have been forming before and after these blocks, for the notochordal cartilage is less dense and resembles ontogenetic segmentation formation. A block of notochordal cartilage, reduced in size in each vertebra anteriorly in the sequence, occurs independently in the third and fourth posteriormost vertebrae. This component is not embryonic cartilage (Alcian blue positive) in the more anterior vertebrae. The dia- and parapophyses are also cartilaginous on the terminal vertebrae. Ribs are partially mineralized on the second and third posteriormost vertebrae, and entirely cartilaginous on the last vertebrae. Further, the neural arch of the last vertebra is incomplete dorsally.

**Myology**

The general pattern of head and body musculature is that of non-rhinatrematid caecilians. The head musculature is characterized by a large, fan-shaped depressor mandibulae that appears to have anterior and dorsal components (Fig. 5A). These originate from the parietals and squamosals, and insert anterodorsally on the retroarticular process of the lower jaw. The three adductor muscles are small, and the interhyoides posterior muscle is large and fan-shaped, originating on fascia overlying body wall musculature and inserting posteromedially on the retroarticular process (Fig. 5A). The interhyoides posterior major has dorsal and ventral components. It is likely involved in jaw ad-duction, as suggested by Nussbaum (’77, ’83) and demonstrated by Bemis et al. (’83) in *Dermophis mexicanus*. The muscle is shorter than in many species (Wake, personal observation), originating over the first four body segments. The intermandibularis is distinctly segmental (Fig. 5B). Four extrinsic eye muscles are present, one of only 2–3 fibers. Because of their positions, I infer that these are rectus superior, r. inferior, and obliquus inferior; the attenuate muscle is probably the r. externus.

The trunk musculature is relatively invariant in caecilians (Naylor and Nussbaum, ’80, Nussbaum and Naylor ’82). The musculature of *Idiocranium* is much like that of *Geotrypetes seraphini* as summarized by Nussbaum and Naylor (’82), though I am not convinced of the extent of myosepta in the obliquus externus superficialis muscle.

**Brain and spinal cord**

The topology of the brain is that of most caecilians, with large olfactory bulbs, dorsal and ventral olfactory tracts, enlarged cerebral hemispheres that expose a median pineal–thalamic complex, small medullary lobes, and a recurved diencephalon. Some comparisons of *Idiocranium* with data on other species from the literature, especially Kuhlenbeck (’22), are warranted. Concomitant with the elongation of the anterior end of the skull, the olfactory lobes are relatively larger and somewhat more tapered anteriorly. The Jacobson’s organ is small and embedded in the Harderian gland. The cranial nerve complement is typical of caecilians. Large dorsal and ventral olfactory nerves are present; the trigeminal and facial are also large, as are their ganglia. The optic nerves are very small, and the trochlear nerve is absent. The abducens innervates the retractor tentaculi muscle. The tongue is innervated by the glossopharyngeal and hypoglossal nerves. The vagus nerve originates from some six roots.

The hindbrain tapers into the spinal cord. A complex "spinal accessory" nerve includes components of spinal nerves 1 and 2. Paired spinal nerves serve each body segment. Anteriorly, they exit through foramina in the vertebrae, but after the first six, exit intervertebrally.

**The tentacle**

The paired tentacles are chemosensory structures whose lumina open to the Jacobson’s organ, then to the epithelium of the
olfactory bulb. The tentacles are extrusible structures, protacted and retracted by extrinsic muscles which are homologous to the retractor and levator bulbi of other amphibians. They are derived from the rectus externus and levator mandibulae, respectively (see Wake, '85 for review).

The tentacle of *Idiocranium* lies in a channel in the maxilla, emerging just behind and below the nostril. The tentacle is "globular" (Parker, '36; Taylor, '68) as opposed to elongate. The channel epithelium of the tentacle is continuous with the epidermis, and the epithelium of the outer wall of the tentacle is also epidermal (Fig. 6). A connective tissue cover is perforated by the lumen, which is lined by a scant columnar epithelium. The retractor tentaculi muscle is very long, probably concomitant to the extreme anterior emergence of the tentacle. The tentacular channel is lubricated by secretions of the Harderian gland.

**Eye**

The structure of the eye is discussed in detail in Wake '85 and compared with other species. It is summarized here. The socket is formed of the maxillary-squamosal margins. The orbit lies under a thick layer of glandular skin. The lens is well developed and crystalline, adherent to the cornea and retina, and the cornea is attached to the overlying dermis (Fig. 8). The retina has the eight-layered structure typical of nearly all vertebrates. An attenuate optic nerve is present, as are four tiny extrinsic muscles. The large Harderian gland fills the back part of the socket.

**The ear**

The optic capsule is proportionately large and dilated in *Idiocranium*, and the large stapes is free in the oval window. The inner ear is similar to that reported by Wever ('75) and Wever and Gans ('76), and White and Baird ('82) for nonichthyophioid caecilians. *Idiocranium* has a small papilla neglecta and a large amphibian (auditory) papilla. The amphibian papilla lies in a recess, and is partially covered by an arm of limbic tissue, so that the aperture is reduced (Fig. 7B). The saccular macula is elongate, as are the sacculus itself and the perilymphatic cistern. The latter structures are separated by a well-defined Reissner's membrane (Fig. 7A,B).

**Lung**

Only the right lung is well developed, the left represented by a very small outpocketing. In a 104-mm-TL specimen the lung is 13
mm long, or 12.5% total length — proportionally shorter than in other taxa of caecilians (Wake, personal observation). However, the lung has the complex organization typical of caecilians. The lung is compartmented and highly vascularized, with a large, elongate pulmonary artery and pulmonary vein, and many capillaries underlie the epithelium. The lung is supported along most of its length by independent, branched, semicircles of cartilage (Fig. 9) as in several other species (Marcus, '23; Wake, '74; Pattle et al., '77). Furthermore, Marcus and Wake both noted that smooth muscle connected the free ends of the cartilages. Marcus tentatively indicated and Wake elaborated upon a passive
recoil mechanism of inspiration, as cartilages rebound following smooth muscle contraction during expiration, which is also facilitated by body wall contraction.

**The heart and the general circulation**

The heart begins at 26.4% TL in the body. In the 104-mm TL specimen, it is 6.25 mm long, elongate, and has thin-walled paired atria and a muscular elongate tapering ventricle. The interior of the ventricle is thrown into many potential channels by the elongate muscular cords. The vessels entering and leaving the heart are much more elongate than the general diagrams in Lawson ('70) indicate. The common carotids are paired at the level of their emergence from the heart and branch only as they enter the head. A
single right systemic arch is present, whence issues the dorsal aorta. The pulmonary trunk contributes the right pulmonary artery, and a single large pulmonary vein enters the atrium from the lung. The general pattern of vascularization is as Lawson ('70) described for *Hypogeophis*.

**Other visceral organs**

The liver in the specimens dissected is ±20 mm long, or 20% of the total length. It has 20–28 fan-like lobes, and its surface has a scattering of melanophores. A small, saccular gall bladder is attached to the penultimate lobes. The spleen is small (4 mm long), reddish, and spindle-shaped, attached to the body wall and the stomach by the mesogaster and the gastroplenic ligament. The pancreas is large, pale, and diffusely massed on the mesentery of the intestine. The stomach is recognizable as an elongate, highly muscular region of the gut tube; the intestine is somewhat coiled, an unusual state for caecilians. The "rectum," immediately preceding the cloaca, is a dilated rather thin-walled region of the intestine. The cloaca receives the intestine and the urogenital ducts of both sexes (see below).

**Integument**

The skin is composed of a thin, slightly keratinized epidermis and a thick dermis that contains mucous and "poison" glands, melanophores, capillaries, and dermal scales (Fig. 10). Numerous capillaries lie just under the epidermal basement membrane. The dermis contains thick layers of fibrous and some elastic connective tissue. The melanophores lie just under the epidermis, and over the scale pockets, and beside the poison and mucous glands.

The skin glands are a monolayer in the dermis, and are of two major types (Fig. 10). Mucous glands are small (0.5–0.8 mm diameter) and lie just under the epidermis. They are several per body segment, with ducts to the surface of the epidermis. They are typically vacuolated and have basal nuclei around their periphery. The "poison" glands are much larger, typically 0.13 mm in diameter. There are usually 2–3 per body segment in a sagittal section; hence they are numerous around the body. The glands are filled with a granular acidophilic secretory product. The glands have large ducts to the skin surface.

The scales occur in the posterior body segments, as described for the species by Taylor.
The scales lie in pockets bounded by connective tissue in the dermis. Typically there are two pockets per segment in a sagittal section of dorsal skin. Each pocket contains three scales per section. Each scale is composed of an unmineralized base plate that appears to be a bilayer of connective tissue, and a series of dorsal mineralized denticles of diverse shapes (Fig. 10). Each scale has a thin cellular (generative?) layer on its ventral side. The scales are small relative to those of other species; a sample of 15 from several annuli averages 0.8 \( \times \) 0.45 mm in diameter. Taylor ('72) reported that the largest scale from one specimen that he observed was 1.4 \( \times \) 1.6 mm, with several approximately 1.0 \( \times \) 1.5 mm. Scales are dorsoventrally flattened and ovoid in shape (Fig. 10). The denticles are flatter and further apart than in most species (Wake, personal observation), and arranged in typical concentric circles. I do not observe the "fore to aft" increase in size reported by Taylor; scales show much variation in size within pockets and among annuli.

**Urogenital morphology and reproductive biology**

The reproductive biology of the species is known only from the report of Sanderson ('37). The taxon is one of several direct developers (eggs laid on land, development through metamorphosis before hatching; thus inferences about age at first reproduction cannot be made. The sample includes 26 females, 13 males, and eight immatures.

The testes of *I. russelli* are reduced, 1–5 lobes on each side (one specimen has a large lobe only on the right side). Lobes reduce slightly in length posteriorly. The length of the testis is 5–10 mm, or 5–10% of the total length of the animal, in contrast to the 10–20% typical of adult males of most species. The testes show active spermatogenesis, with many loculi in different stages of development in each lobe (see Fig. 34, Wake, '68). A large proportion of loculi contain maturing spermatozoids, and several have evacuating ducts that enter the longitudinal duct in the center of the testis. Three to six transverse ducts extend to the anterior part of the kidney, and sperm are eventually transported by the archinephric ducts (see below). Well-developed interstitial tissue is present, and the spermatogenic cycle is in a late stage 4 (Wake, '68).

The paired Müllerian glands (derived from the Müllerian ducts; see Wake, '70a, '80c) are some 8 mm long and adjoin the cloaca. They are composed of series of simple tubular glands whose lumina are continuous with the central lumen of the duct. The columnar secretory cells have large, granular basal nuclei. The cells are densely packed so that nuclei appear to be in 2-3 layers. The lumen of the duct is lined with ciliated epithelial cells. Secretory activity is correlated with active spermatogenesis and perhaps sperm transport among terrestrial animals (see discussion in Wake, '80c).

The cloaca is described by Wake ('72) and compared to that of other species. That of *Idiocranium* has the typical sites of entrance of archinephric ducts, Müllerian glands and oviducts, with no partitioning relative to the intestinal aperture. Cloacae are simple; both sexes have a dimorphic but apparently species-specific organization of dorsal, ventral, and transverse muscles and connective tissue structure. The vent is transverse, with 10–12 lobes. As in all other species of caecilians, the terminal part of the cloaca is eversible, constituting an intromittent organ for sperm transport and internal fertilization when inserted into the vent of the female. A stout retractor muscle extends from the ventral body wall to the phallodeum. *Idiocranium* lacks blind sacs, a feature of cloacal
specimen is composed of deep columnar cells, and is hypertrophied and somewhat convoluted. The cells appear swollen, probably due to fluid accumulation. Numerous capillaries lie in the thin fibromuscular layer bounding the epithelium, suggesting hypervascularization. This condition, coupled with the presence of a single lysed ovum in the anterior region of the duct, suggests that 1) ovulation has just begun, or 2) laying of the clutch has just occurred.

The morphology of the paired, elongate kidneys is generally typical of that of all terrestrial species (Wake, '68). Glomeruli usually occur in pairs—a condition not often observed in other species, and perhaps a vestige of their segmental origin in this diminutive species.

The archinephric or Wolffian duct is the sole unit of urine transport in both sexes (Wake, '70a). No accessory urinary ducts are present. In females, the ducts transport urine only. Collecting ducts from multiple nephrons join the archinephric duct. In males, the ducts also transport sperm. The sperm exit the transverse ducts into unmodified nephrons, whose collecting ducts bear the sperm to the archinephric ducts.

The fat bodies are well developed, 4–10 lobes on each side, held by the mesentery of the gonad. The length of the fat body unit is 15–30 mm, correlated with body size. There are no observable differences between the sexes.

Males have the urinary bladder attached by mesentery to the m. retractor cloacae. In Idiocranium the anterior lobe is four times as long as the posterior and extends fully beyond the mesentery. In females the bladder lobes are nearly equal, the anterior only slightly longer than the posterior. See Wake ('70b) for comparative data.

DISCUSSION

Miniaturization and functional morphology in Idiocranium

The proportions of a number of organs and some of the unique aspects of their structure in Idiocranium are associated with the unusually small size of the species. Lungs, liver, and gonads are relatively smaller than in other caecilians. The number of testis lobes is more highly variable than observed in other taxa.

Several features of the skull are associated with miniaturization and its mode of acquisition (see below). Truncation of development

morphology presumed primitive (see Wake, '72) and has sets of muscles that form pronounced ridges and terminate in the phalldem (Fig. 11).

The ovaries are paired, elongate (8–17 mm), hollow sacs containing ova in three stages of development. A class of 4–10 large (1.0–1.4 mm × 0.6–0.9 mm) yolky ova is present in each ovary, each ovum surrounded by a flattened, follicular monolayer. The largest class of ova may be at maximum size, for the state of the oviduct (see below) and the presence of a cytolyzed ovum in it suggest that ovulation has just begun (see Wake, '68, for comparative data on ovarian structure). A class of greater numbers (6–15) of vitellogenic ova (0.5–0.7 mm diameter) and clusters of 15–25 previtellogenic oocytes (0.2–0.3 mm diameter) are interspersed among the well-yolked ova. Corpora lutea were observed in the one ovary sectioned.

The oviducts are elongate (40–50 mm), reaching from the end of the liver to their entrance into the cloaca. Development of the oviducts is discussed by Wake ('70a). The luminal epithelium of ducts of the sectioned

Fig. 11. Camera lucida drawing of uneverted cloacal male intromittent organ. The phallodeum is the posterior part of the cloaca which is extruded through the vent and inserted into the vent of the female to effect sperm transport. The pattern of lobes and ridges is species-specific. Cloaca is opened ventrally and pinned open, exposing entire surface. Abbreviations: a, annulus; lo, lobes; mrp, retractor muscle of the phalloderm; tv, transverse connective tissue ridges; ve, vent. Bar = 1.0 mm.
is suggested by the reduction of the frontals, the large dorsal fontanelle, the large cartilaginous nasal cupulae, the small vomers, and the absence of sutures or overlap among many dermal elements. The dorsal and ventral fontanelles are particularly construed as evidence for truncation; for comparison with an ontogenetic series of *Dermophis mexicanus*, a Central American caecilian, indicates that the stage of development of the elements forming the fontanelles in *Idiocranium* is that of a midterm fetus of *Dermophis*, were dermal bone development to cease in *Dermophis* at that stage.

A number of components of the skull remain cartilaginous throughout life in *Idiocranium*. Several of these are typical of all caecilians: the hyoid apparatus is rarely mineralized (Wake, personal observation). The rims of the nasal capsules and the anterior component of the mesethmoid process remain cartilaginous in virtually all taxa of caecilians, even in large, old specimens. Yet throughout life, *Idiocranium* retains small blocks of orbital and trabecular cartilage at the juncture of the sphenethmoid complex and the os basale and a small block of Meckel’s cartilage at the pseudodentary–pseudarticulation junction. This is a characteristic of a number of small species (*Grandisonia alternans* and *G. brevis*, J. Straub, personal communication; *Afrocaecilia taitana*, Wake, personal observation) but is an ontogenetic feature of *Dermophis mexicanus*. Diverse functions (viz., kinesis, shock absorption during burrowing) have been suggested (Straub, personal communication), but never tested. In *Dermophis*, the cartilages are completely replaced by bone in older adults, the Meckel’s cartilage first, the trabecular second, and the orbital last. Furthermore, in *Idiocranium* the nasal cupulae are larger and of a more defined shape throughout life than in other species. Yet, the mesethmoid process is less cartilaginous, and more ossified in older specimens than in other caecilians.

Some features of the skull of *Idiocranium* probably are consequences of miniaturization correlated with demands of function and habitat, rather than simple consequences of cessation of development. I suggest that the extensive mineralization of the sphenethmoid complex, including its domed shape and rounded completeness dorsally and ventrally, and the extensive ossification of the mesethmoid are correlated with the burrowing mode of the species and compensate for the reduction of the dermal elements. The particular shape of the nasal cupulae may also facilitate burrowing.

Yet other features may be correlated with the demands of feeding mechanics. Morphology and osteology suggest a typical "strong bite" mechanism (see Bemis et al., ’83). The long retroarticular process and the large number of teeth in this small taxon may facilitate such a mode of feeding. Nothing is known of prey preferences in *Idiocranium*; I have not been able to identify prey from 50-year-old gut contents. Skulls of *Idiocranium* have large articulation facets of the lateral flanges of the os basale and the quadrate. These are present in the skulls of other small species, such as *Afrocaecilia taitana*. However, they are present in larvae and juveniles of *Geotrypetes grandisonae* and juveniles of *G. seraphini* and *D. mexicanus*, but not in large adults of these taxa. The juncture of these elements is firmly bound by fibrous connective tissue in large adults. It is tempting to suggest increased skull kinesis in small species to allow strong bites on large prey, especially given the loose quadrates and squamosal associations, which occurs as a developmental phase in other taxa (see Wake and Hanken, ’82). This awaits corroboration.

The morphology of special sensory units is apparently correlated with miniaturization. The eyes are reduced, correlated with fossoriality, not miniaturization. However, both the olfactory and the otic components are disproportionately large in *Idiocranium*. The olfactory lobes of the brain are elongate; the otic capsules are inflated, the inner ear well developed, and the oval window and footplate of the stapes proportionally large for caecilians. Hanken (’84) has suggested that in urodeles the sensory capsules have a minimum functional size, which, if met, dictates skull conformation in miniature forms. In other words, other elements of the skull may be reduced further than those of the sensory units, which get no smaller than their functional minimum. These units therefore “dicate” skull proportions as a consequence of relative growth. This principle may apply in *Idiocranium* to olfactory and otic components.

Vertebral development also suggests truncation of development. Retention of a post-tail notochord and lack of ossification of terminal vertebrae and ribs suggest that development stopped before these elements were completed. Development in caecilians is highly cephalized, the last body segments
forming well after gastrulation is complete (Wake, unpublished observation). An individual embryo, fetus, or juvenile is in effect an ontogenetic series as a consequence of this anteroposterior sequence of development. Yet, only Idiocranium retains the notochord and terminal chondrification in adulthood. A diversity of developmental variations of terminal ends of tails obtains, including the postnotochordal tail of lungfish and salamanders (Percy, '62), and of some teleosts (Meunier and Kirschbaum, '78, '79), but these are unlike the skeletal variance in Idiocranium. I do not see that any functional advantage can be attributed to such vertebrae and suggest that their lack of development is correlated with a genetic or epigenetic truncation of development.

The evolutionary mechanism through which miniaturization in this taxon is achieved appears to be the heterochronic phenomenon of progensis (Gould, '77; Alberch et al., '79) which typically results in paedomorphosis and size decrease. The epigenetic alteration of the developmental program relative to other species of caecilians that produces the osteological, myological, and other features of small size in Idiocranium may be a consequence of early initiation of \( \beta \), the offset of development signal. This hypothesis is corroborated by the presence of a number of features of structure in large Idiocranium as noted above that are features of fetal, larval, or juvenile stages of other, related, species. Another heterochronic mode, neoteny, with prolonged growth, characteristically produces paedomorphosis not necessarily associated with size change. When size is affected through neoteny, however, it is in the direction of gigantism, not miniaturization, and hypertrophy of elements, not reduction.

All of the evidence points to progensis as the phenomenon responsible for much of the structure, and possibly much of the biology, of Idiocranium. Corroboration awaits analyses and comparison of the "ontogenetic trajectory" of the species, and recollection in order to contribute crucial data on population biology, ecology, and behavior.

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