

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.

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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

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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 *Scolecomorphus 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; (\bar{x} = 84.0) primary annuli and 20–31 (\bar{x} = 26.0) secondary annuli (Table 1). Variation in primary counts is probably due to Parker's inclusion of the two collar folds in his counts; variation in secondaries is probably due to my inclusion of the short postvent annuli. The vent has 6–8 lobes and is subterminal.

Parker reported that the specimens were "blue-grey above, lighter beneath." They have faded in preservative to greyish-brown to yellow-brown dorsally, and cream-colored ventrally. The skin of the lower jaw margin and of that around the eye, tentacle, and nostril is also cream-colored.

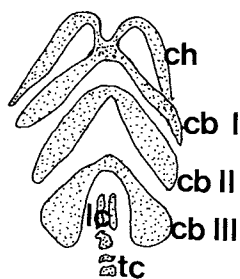
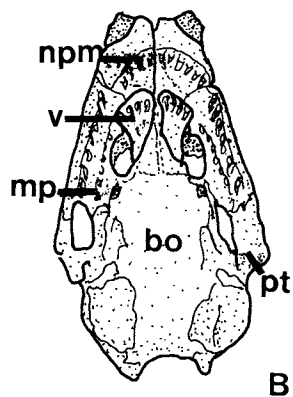
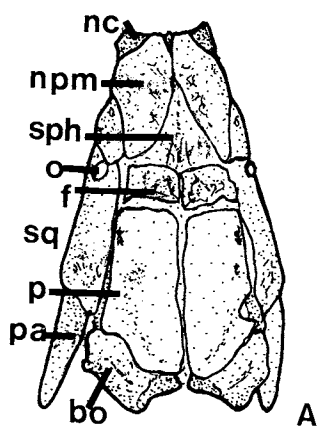
Osteology

The skull has several unique features which were mentioned by Parker ('36): the great reduction of the frontals, the concomitant nasopremaxillary contact with the squa-

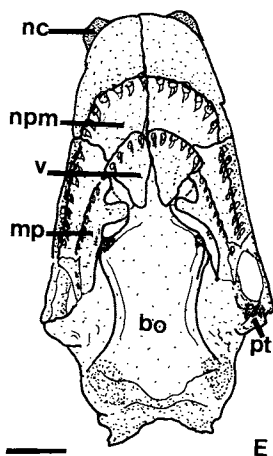
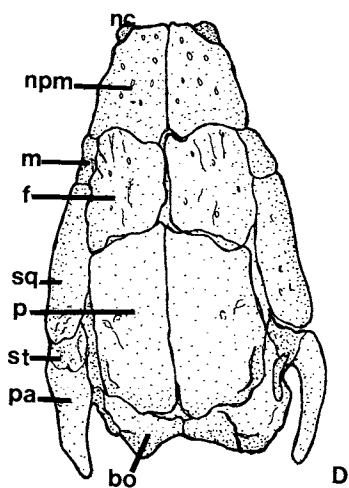
mosal, and the large nasofrontal fontanelle that exposes much of the dorsal surface of the sphenethmoid. The absence of pre- and postfrontals and ectopterygoids was also noted. Taylor ('69) reiterated these characters. They are indicated in Figure 1A–C, and compared to those of a more 'typical' skull (*Afrocaecilia taitana*; Fig. 1D–F).

These and other osteological features can be evaluated in more detail based on cleared and stained (Fig. 1) and sectioned material. In the skull of a specimen 113 mm in total length (MCZ 21811; skull 5.2 mm long), the nasopremaxillary bones are separated medially, approaching contact only for the second 10% of their lengths. Anteromedially they diverge to expose the mesethmoid process, which is more fully ossified than in most other species (Fig. 2) (see Wake and Hanken, '82). The connecting bar of the nasal component to the premaxillary is very thin; the nasal process widens only in the middle of its length. The cartilaginous nasal cupulae are unusually large, and project bilaterally so as to square the outline of the snout. The posteromedial 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

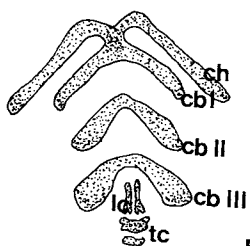
Fig. 1. Skulls of *Idiocranium russeli* (A–C) and *Afrocaecilia taitana* (D–F). Note reduction of dermal elements of *I. russeli*. A. *taitana* is a small but not miniaturized species. A. Dorsal views. B,E. Ventral views. C,F. Hyoid apparatus. Camera lucida drawings of skulls to same scale. Cartilage is heavily stippled. Abbreviations: bo, basioccipital; cb, ceratobranchial; ch, ceratohyal; f, frontal; lc, laryngeal cartilages; m, maxilla; mp, maxillo palatine; nc, nasal cupula; npm, nasopremaxillary; o, orbit; p, parietal; po, pseudangular; pq, pterygoquadrate; sq, squamosal; sph, sphenethmoid; st, stapes; tc, tracheal cartilage; v, vomer. Bar = 0.1 mm.



C



E



F

TABLE 1. Measurements (mm) and counts for *Idiocranium russeli*

Sex	Specimen No.	Total length	Primary annuli	Secondary annuli	Head length	Head width at nostrils	Head width at jaw articulation	Eye to tentacle	Eye to nostril	Tentacle to nostril	Body width	Vertebrae
♀	MCZ 21811	113	83	26	5.3	1.4	3.4	1.4	2.1	0.7	3.5	91
BMNH												
♀	1946.9.5.77	111	82	26	5.2	1.2	3.2	1.4	1.9	0.7	3.3	90
♀	1946.9.5.84	105	87	30	5.3	1.4	3.3	1.4	2.0	0.5	4.2	93
♀	1946.9.5.73	104	84	29	5.2	1.6	3.1	1.3	1.7	0.6	5.0	94
♂	1946.9.5.76	104	85	22	5.2	1.3	3.2	1.4	1.9	0.6	4.3	91
♂	1946.9.5.83	104	83	25	5.2	1.2	3.5	1.7	2.2	0.6	4.2	91
♀	1946.9.5.72	103	83	27	5.2	1.8	3.2	1.4	1.8	0.5	3.5	90
♀	1946.9.5.78	102	82	28	5.0	1.0	3.0	1.1	1.5	0.4	3.4	90
♀	1946.9.5.71	102	87	27	5.3	1.1	3.5	1.4	1.8	0.6	4.1	92
♀	MCZ 20946	99	82	25	4.9	0.9	3.0	1.4	1.9	0.6	4.0	89
♀	MCZ 21812	96	85	29	4.5	1.0	2.9	1.1	1.6	0.5	3.4	90
BMNH												
♀	1946.9.5.74	96	84	26	—	—	—	—	—	—	—	90
♀	1946.9.5.80	95	86	27	5.0	1.0	2.9	1.3	1.9	0.5	3.8	92
♀	1946.9.5.79	95	85	24	5.1	1.2	3.0	1.3	1.7	0.5	3.7	90
♀	1946.9.5.75	94	82	24	5.1	1.4	3.4	1.4	1.7	0.5	4.0	91
♀	1946.9.5.86	85	85	31	4.9	1.1	3.0	1.3	1.7	0.5	3.9	88
♂	1946.9.5.81	77	83	26	4.6	1.0	2.5	1.3	1.5	0.4	2.5	91
Imm	1946.9.5.85	67	85	29	3.8	0.9	2.6	1.0	1.5	0.4	2.9	90
Imm	1946.9.5.82	50	86	24	3.9	0.45	1.9	0.8	1.2	0.3	1.7	86
CAMBRIDGE*												
♀	1	104	83	24	4.8	1.0	3.0	1.4	1.7	0.5	4.4	—
♂	2	105	81	28	5.4	1.1	2.3	1.3	1.3	0.5	4.0	—
Imm	3	61	81	26	3.3	0.8	2.1	0.8	1.2	0.3	2.2	—
Imm	4	73	86	25	3.3	0.8	2.4	0.9	1.4	0.4	2.6	—
♀	5	88	84	29	4.3	0.9	2.2	1.0	1.5	0.4	3.6	—
Imm	6	65	86	29	3.5	0.6	2.0	0.5	1.2	0.3	2.2	—
♀	7	95	82	25	4.7	1.1	2.9	1.6	1.6	0.4	3.5	—
♀	8	110	84	23	6.6	1.4	2.4	1.5	2.4	0.5	3.5	—
♂	9	104	83	30	5.0	1.2	3.3	2.2	1.8	0.6	3.9	—
♂	10	107	84	27	4.5	1.1	2.8	1.3	1.8	0.5	3.5	—
♀	11	110	81	29	4.2	0.9	2.7	1.2	1.6	0.4	4.0	—
♀	12	103	82	25	4.3	1.0	3.4	1.2	1.6	0.5	3.7	—
♀	13	96	82	27	3.8	1.0	2.9	1.1	1.5	0.4	3.4	—
♂	14	98	85	30	4.5	1.0	3.2	1.1	1.5	0.5	3.2	—
♂	15	113	85	31	4.9	1.0	3.3	1.4	1.8	0.5	4.1	—
♀	16	109	85	32	4.0	1.0	3.1	1.2	1.6	0.5	4.3	—
♀	17	98	83	24	4.7	0.9	2.9	1.3	1.7	0.5	4.0	—
♂	18	86	29	72	3.1	0.8	2.2	0.9	1.3	0.4	3.0	—

(continued)

TABLE 1 (contd.). Measurements (mm) and counts for *Idiocranium russeli*

Sex	Specimen No.	Total length	Primary annuli	Secondary annuli	Head length	Head width at nostrils	Head width at jaw articulation	Eye to tentacle	Eye to nostril	Tentacle to nostril	Body width	Vertebrae
Imm	19	67	81	26	3.2	0.8	2.3	1.0	1.5	0.4	2.8	—
♂	20	74	84	27	3.8	0.8	2.5	1.0	1.4	0.4	2.1	—
♀	21	112	83	30	5.1	1.1	3.3	1.7	1.6	0.5	4.0	—
Imm	22	62	83	25	3.9	0.9	2.3	1.0	1.3	0.4	2.9	—
♂	23	77	86	31	3.7	0.9	2.4	1.1	1.4	0.4	3.1	—
♀	24	99	87	27	4.0	0.8	3.2	1.1	1.7	0.4	4.0	—
♀	25	111	88	29	5.0	1.0	3.2	1.3	1.7	0.4	4.0	—
Imm	26	73	86	25	3.5	0.9	2.2	0.9	1.3	0.5	2.9	—
♀	27	89	82	25	3.8	0.9	2.8	1.0	1.5	0.5	3.1	—
♂	28	113	85	31	5.2	1.1	3.1	1.4	1.8	0.6	4.0	—
x			84.0	26.0								90.5

*Cambridge specimen numbers are the author's, not catalogued numbers.

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 columellar component is short and has a cartilage-capped articular surface that abuts the quadrate. The stapedia foot plate is very large, filling a concomitantly large oval window. The stapes is not perforated by the stapedia 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

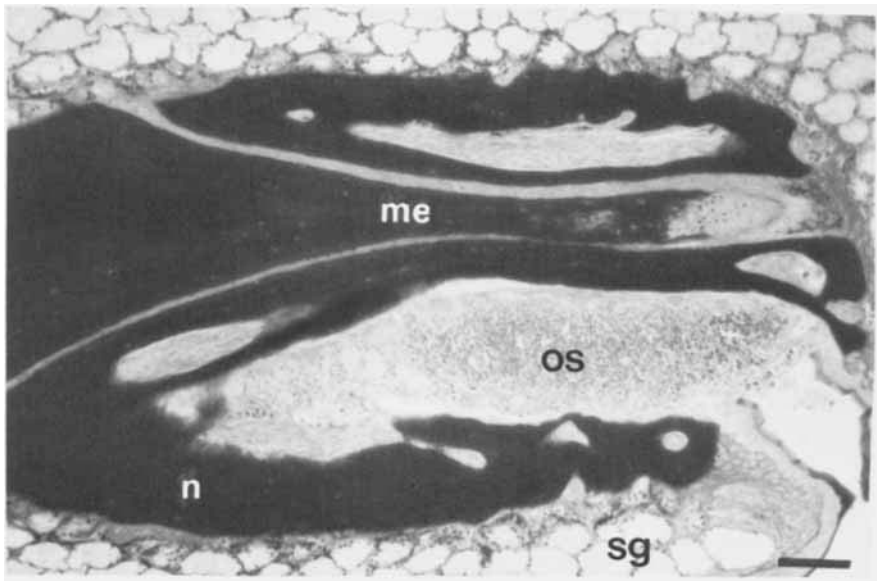


Fig. 2. Photomicrograph of frontal section through top of skull of *I. russeli*. Note gap between nasopremaxillae, exposed extent of mesethmoid–sphenethmoid complex, and scant cartilage at anterior end of mesethmoid. Abbreviations: me, mesethmoid; n, nasal; os, olfactory sac; sg, skin glands. Bar = 0.1 mm.

TABLE 2. Tooth data for *Idiocranium russeli**

Specimen No.	Dentary teeth	Splénial teeth	Tooth counts†		Stage‡ (%)						
			Premaxillary–maxillary teeth	Vomeropalatine teeth	a	b	c	d	e	f	g
BMNH											
1946.9.5.72	24	1	30	21	5.4	6.9	13.1	5.4	5.4	58.5	5.4
1946.9.5.74	17	4	28	23	1.6	10.2	9.4	7.9	4.7	56.7	9.4
MCZ 21811	20	4	26	23	1.0	3.8	5.7	6.7	0	69.5	14.3

*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.)

statistical analysis, but it suggests that variation in tooth number in adults is not highly correlated with size (or probably age).

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 bicapital 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-

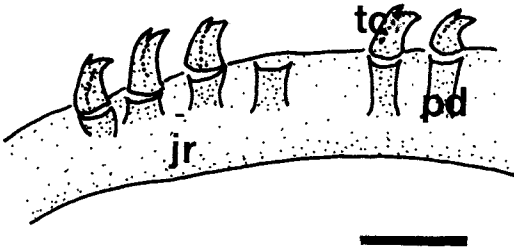


Fig. 3. Camera lucida drawing of lingual view of teeth of *I. russeli*. Tooth crowns are bicuspid, the labial cusp small. Abbreviations: jr, jaw ramus; pd, pedicel; tc, tooth crown. Bar = 0.5 mm.

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 vertebra. Further, the neural arch of the last vertebra is incomplete dorsally.

Myology

The general pattern of head and body musculature is that of non-rhinatremitid 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 interhyoideus posterior muscle is large and fan-shaped, originating on fascia overlying body wall musculature and inserting posteroventrally on the retroarticular process (Fig. 5A). The interhyoideus 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 Kühlenbeck ('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

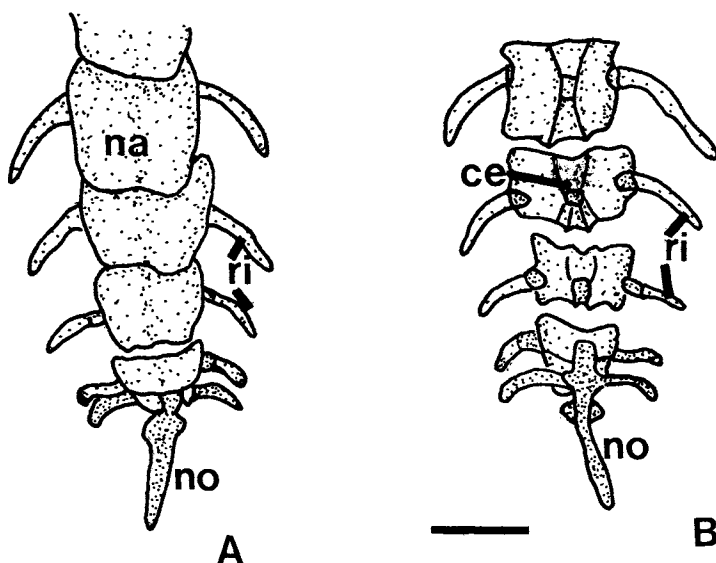


Fig. 4. Camera lucid drawings of posteriormost vertebrae of a specimen of *I. russeli* 113 mm in total length. Note increased retention of cartilage (heavily stippled) in centrum, articulations with ribs, and rib ends in progressively more posterior vertebrae, so that the terminal

vertebra is represented only by cartilaginous flanges, and the terminal cartilaginous notochord is retained throughout life. A. Dorsal view. B. Ventral view. Abbreviations: ce, centrum; na, neural arch; no, notochord; ri, rib. Bar = 1.0 mm.

olfactory bulb. The tentacles are extrusible structures, protracted 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 crys-

talline, 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 nonichthyophiid 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

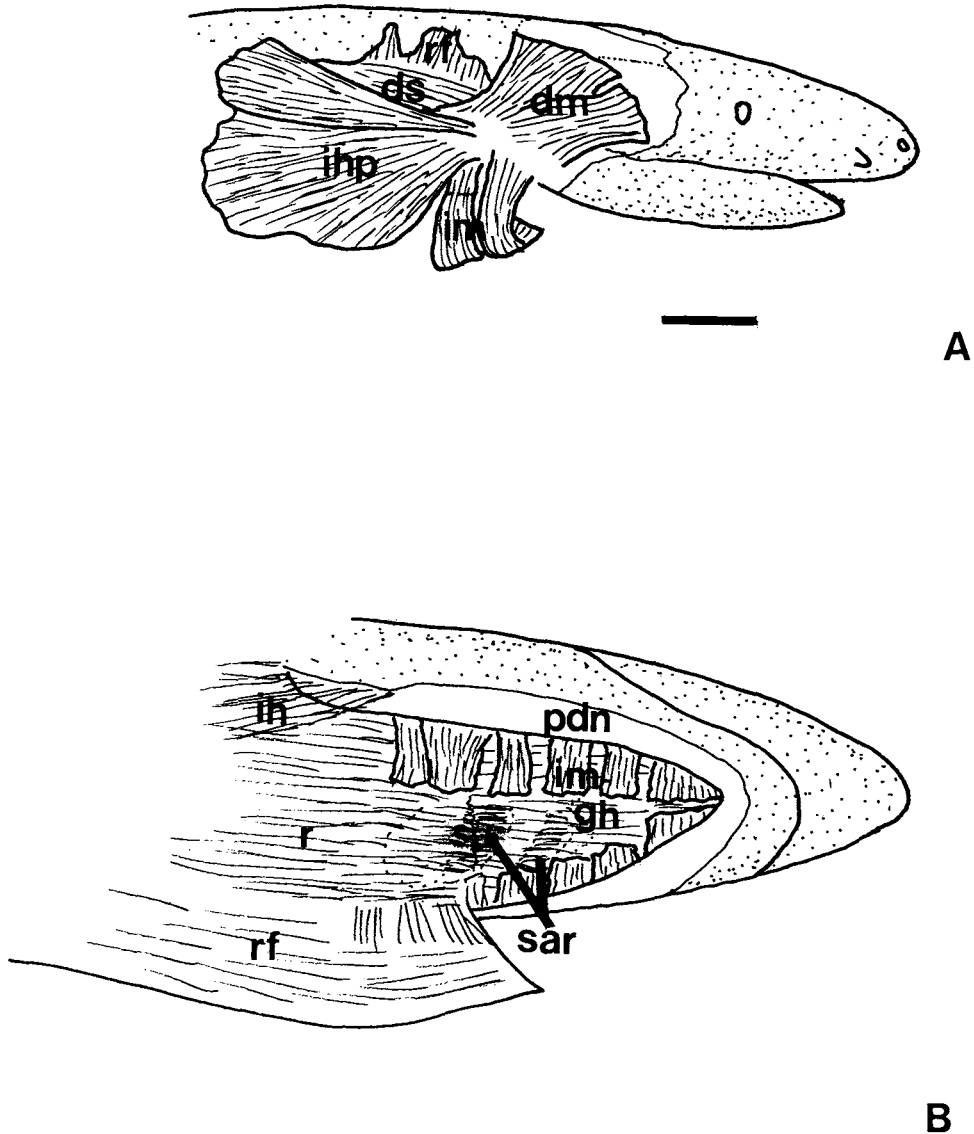


Fig. 5. Camera lucida drawings of head musculature of *I. russeli*. Depressor mandibulae is in two bundles; intermandibularis is of numerous bundles; interhyoideus posterior, an adductor of the jaw, has dorsal and ventral components. A. Right lateral view. B. Ventral view. Hyobranchial apparatus is indicated by dotted

lines, and associated musculature by heavy lines. Abbreviations: dm, depressor mandibulae; ds, dorsal spinal musculature; gh, geniohyoid; ih, interhyoideus; ihp, interhyoideus posterior; im, intermandibularis; pdn, pseudodentary; r, rectus cervicis; rf, reflected flap; sar, subarcualis rectus. Bar = 1.0 mm.

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

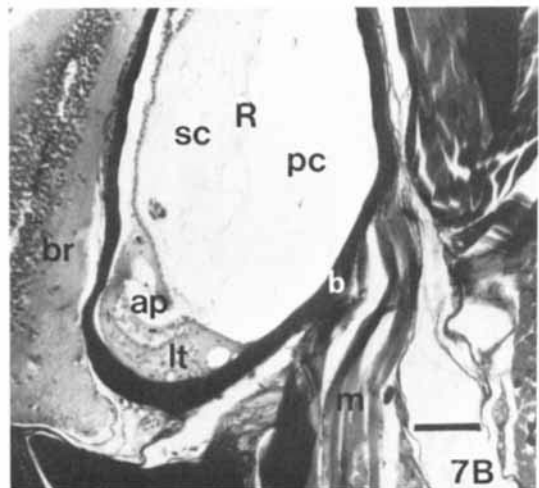
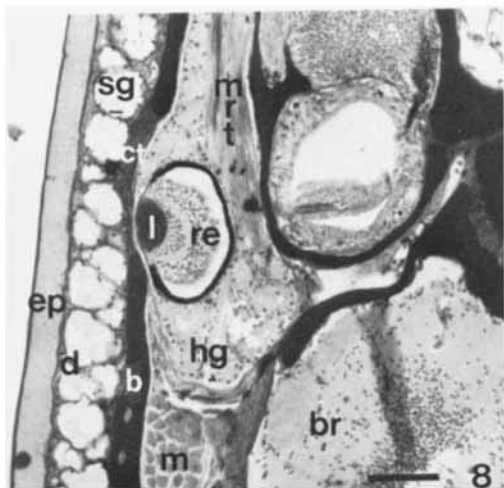
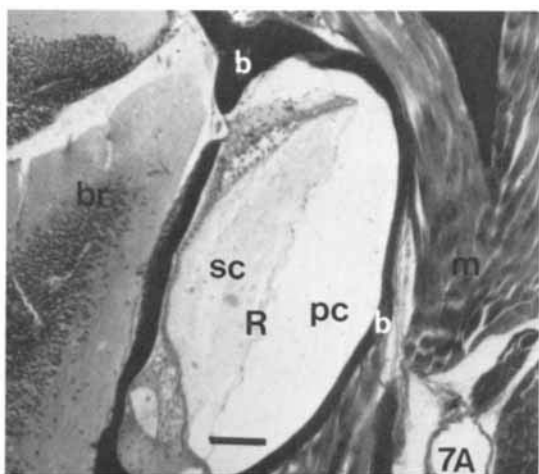
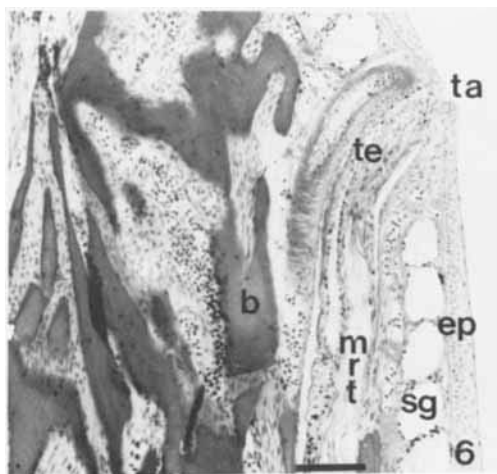


Fig. 6. Frontal section through right tentacle of *I. russeli*, illustrating lumen and retractor musculature. Abbreviations: b, bone; ep, epidermis; mrt, musculus retractor tentaculæ; sg, skin gland; ta, tentacle aperture; te, tentacular epithelium. Bar = 0.1 mm.

Fig. 7. Sections (7A, 7B) of inner ear of *I. russeli*. A. Dorsal anterior component. B. Medial posterior component including amphibian papilla. Abbreviations: ap, amphibian papilla; b, bone; br, brain; lt, limbic tissue;

m, muscle; pc, perilymphatic cistern; R, Reissner's membrane; sc, saccular cavity. Bars = 0.1 mm.

Fig. 8. Frontal section through left eye of *I. russeli*. The eye is very small and heavily covered by skin, but has a well developed lens and retina. The eye lies in the Harderian gland, and atop the tentacular retractor muscle. Abbreviations: b, bone; br, brain; d, dermis; ep, epidermis; hg, Harderian gland; l, lens; m, muscle; mrt, musculus retractor cloacae; re, retina; sg, skin gland. Bar = 0.1 mm.

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 gastrosplenic 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. There 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

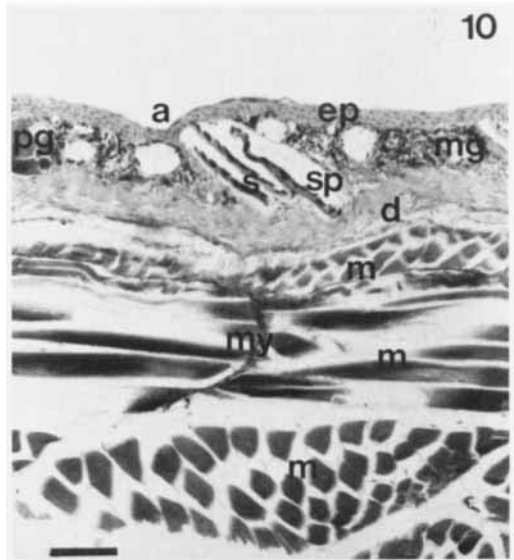
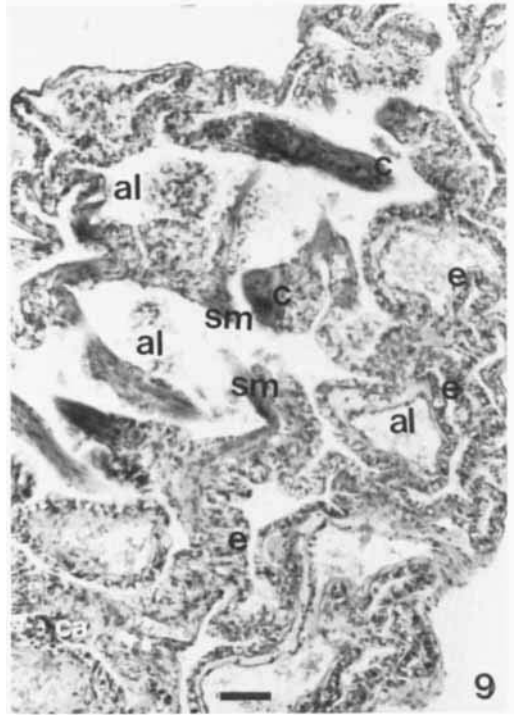


Fig. 9. Frontal section through mid-lung of *I. russeli*. Note the ends of the cartilaginous semicircular support structures, the associated smooth muscle fibers, and the complexly elaborated respiratory epithelial surface. Abbreviations: al, alveolus; c, cartilage; ca, capillary; e, epithelium; sm, smooth muscle. Bar = 0.1 mm.

Fig. 10. Frontal section through posterior body wall of *I. russeli*. Note skin glands, scale structure (mineralized denticles atop connective tissue base plate), and association of scale pocket and annulus with segmental muscle septum. Abbreviations: a, annulus; ep, epidermis; m, muscle; mg, mucous gland; my, myotomal septum; pg, poison gland; s, scale; sp, scale pocket. Bar = 0.1 mm.

('72). 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 0.8×0.45 mm in diameter. Taylor ('72) reported that the largest scale from one specimen that he observed was 1.4×1.6 mm, with several approximately 1.0×1.5 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 circumventing a free-living larval stage; Wake, '77b, '82). Sanderson reported that many females were found coiled around clutches of eggs with embryos in diverse stages of development. These specimens are not deposited in any museum, according to my multiple inquiries. The females and clutches were found as the mat of swamp grasses was rolled back, revealing the females with their young atop pedicels of earth, surrounded by "moats" of water. Sanderson reported that the females spat at him as they were uncovered — a functional near-impossibility, to my notion.

Sexual maturity, as indicated by gonad maturation, occurs at > 70 mm total length. The gonads of a 67-mm specimen are undifferentiated; a 77-mm male has paired testes, each of a single lobe. Females 85 mm and longer have mature ovaries containing ova of several size classes, and Parker ('36) reported a 90-mm female with a laid clutch of eggs. These sizes at maturity are smaller than suggested by Parker. Nothing is known

of growth in the species, nor even size at 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. russeli* 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 locules contain maturing spermatids, 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

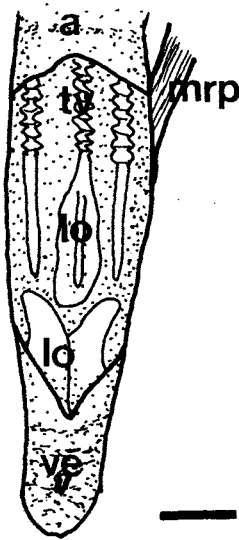


Fig. 11. Camera lucida drawing of unverted cloacal male intromittent organ. The phalloseum is the posterior part of the cloaca which is extruded through the vent and inserted into the vent of the female to effect sperm transport. The pattern of lobes and ridges is species-specific. Cloaca is opened ventrally and pinned open, exposing entire surface. Abbreviations: a, annulus; lo, lobes; mrp, retractor muscle of the phalloseum; tv, transverse connective tissue ridges; ve, vent. Bar = 1.0 mm.

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

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

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 caeciliid, 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-pseudarticular 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 quadrate 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 "dictate" 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 progenesis (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 β , 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 progenesis 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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