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SYSTEMATICS OF CAECILIANS (AMPHIBIA: GYMNOPHIONA) OF THE FAMILY SCOLECOMORPHIDAE

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ABSTRACT.—*Nussbaum, Ronald A. 1985. Systematics of caecilians (Amphibia: Gymnophiona) of the family Scolecomorphidae. Occ. Pap. Mus. Zool. Univ. Michigan, 713: 1–49, figs. 1–10.* Caecilians of the strictly African family Scolecomorphidae are systematically reviewed, and the family is redefined. Prior to this study, the family contained a single genus and seven species. Two west African species (*bornmuelleri, lamottei*) are removed from the genus *Scolecomorphus* and placed in a new genus. Three east African species (*kirkii, uluguruensis, vittatus*) are retained in *Scolecomorphus. S. convexus* is considered to be a junior synonym of *S. kirkii* and *S. attenuatus* a junior synonym of *S. uluguruensis*. Univariate and multivariate analyses of morphometric and meristic characters by sex are given, and a key to genera and species is provided. Biogeography of African caecilians is discussed briefly.

Key words: *Amphibia, Gymnophiona, Scolecomorphidae, caecilians, Africa, systematics.*

INTRODUCTION

Taylor (1968) assigned six species of African caeciliids to the genus *Scolecomorphus* Boulenger and suggested they were distinctive enough to be placed in a separate family. Later, Taylor (1969a) proposed the new family Scolecomorphidae to accomodate these caecilians. Nussbaum (1981) described a seventh species of *Scolecomorphus* from Cameroon and suggested (Nussbaum, 1981, 1983) that (1) Taylor's diagnosis of the family Scolecomorphidae was erroneous, but that the

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family should be recognized and (2) the west African species (*bornmuelleri*, *lamottei*) of *Scolecomorphus* should be placed in a genus separate from the east African species (*attenuatus*, *convexus*, *kirkii*, *uluguruensis*, *vittatus*).

Among Taylor's (1969a) diagnostic features of the family Scolecomorphidae are: (1) no prefrontal bones, (2) a strong diastema between the prevomerine and palatine teeth, (3) palatine teeth posterior to the maxillary teeth, and (4) squamosals and parietals separated by large diastemata (zygokrotaphic skulls). Prefrontal bones had been noted earlier (Peter, 1895; de Villiers, 1938; Brand, 1956) in *Scolecomorphus kirkii* and *S. uluguruensis* and are present in all scolecomorphid skulls examined by me. The two west African species, which were not studied in detail by Taylor, do not have diastemata between the prevomerine and palatine teeth, do not have palatine teeth posterior to maxillary teeth, and have solidly-roofed (stegokrotaphic) skulls. These contradictions to Taylor's description of the family Scolecomorphidae need to be reconciled.

The purpose of this paper is to present a systematic review of the scolecomorphid Gymnophiona. The family is redefined, a new genus is constructed for the west African scolecomorphids, and two east African species, *Scolecomorphus attenuatus* and *S. convexus*, are placed in synonymy with *S. uluguruensis* and *S. kirkii*, respectively.

METHODS AND MATERIALS

All available specimens of the family Scolecomorphidae were studied, including the holotypes and paratypes of all nominate species. Standard measurements were taken from alcoholic specimens with dial calipers. The sex of each alcoholic specimen was determined by direct examination of the gonads, and the state of the reproductive organs was recorded. Both dried and cleared and alizarin stained skeletal material were available for some species. Specimens examined are listed in the respective species accounts. Acronyms used are: AMNH—American Museum of Natural History; BMNH—British Museum of Natural History; CAS—California Academy of Sciences; CM—Carnegie Museum; FMNH—Field Museum of Natural History; LACM—Los Angeles County Museum; MCZ—Museum of Comparative Zoology, Harvard; MNHNP—Muséum National d'Histoire Naturelle, Paris; MRAC—Musém Royal de l'Afrique Centrale; NMW—Naturhistorisches Museum Wien; TM—Transvaal Museum; UMMZ—University of Michigan Museum of Zoology; USNM—

United States National Museum; UZMC—Universitetets Zoologisk Museum, Copenhagen; ZMB—Zoologisches Museum Humboldt Universität; ZMH—Zoologisches Museum Universität Hamburg.

FAMILY ACCOUNT
SCOLECOMORPHIDAE TAYLOR

DIAGNOSIS.—Gymnophiona that lack stapes and foramina ovales, have no internal processes on the pseudoangular bones, have no levator quadrati muscles, and have a distinctive hyobranchial apparatus in which the flattened distal ends of the fourth branchial arch are connected by a transverse bar above the larynx.

DESCRIPTION.—There are no secondary annuli; the number of primary annuli ranges from 120 to 153 and the number of vertebrae from 131 to 165. There are no dermal scales in the annular folds, or, rarely, a few tiny vestigial scales may be present in posterior folds. Two collars are present, each usually with a dorsal, transverse groove. Annuli are usually complete anteriorly, but may be fused dorsally and/or ventrally, especially along the middle and posterior parts of the body. The mouth is subterminal. The vestigial eyes are attached to, and move with, the tentacles and may be exposed when the tentacles are extruded. Normally, the eyes are under bone as there are no orbits. The tentacular apertures are positioned ventrolaterally on the snout below the nostrils even with, or slightly anterior to, the anterior margin of the mouth. Each tentacle has an external subglobular base that is surrounded partly or entirely with a groove and a central opening through which the body of the tentacle passes when extruded or retracted. There is no tail. Instead, there is a terminal shield without annuli, which is supported by vertebrae. The terminus is bluntly rounded and flattened ventrally. The longitudinal vent lies in a shallow, oval depression only a few millimeters longer than the vent. The tongue is without narial plugs.

The paired, unfused elements of the skull (Figs. 1 and 4) are the nasals, frontals, parietals, septomaxillae, prefrontals, squamosals, quadrates, premaxillae, maxillopalatines, and prevomers. There are no orbits, and temporal fossae may be present (*Scolecomorphus*) or absent (n. gen.). The tentacular apertures of the skull are longitudinal grooves located near the anterior ends of the prefrontals. The openings do not pass through solid bone as in some Gymnophiona, rather, they are formed by the free edges of the septomaxillae, prefrontals, and maxillopalatines. The os basale is formed as in other caecilians, with the sides of the parasphenoidal portion of the os basale converging anteriorly into a rostrum that separates the posterior ends of the two prevomers. Basipterygoid processes are present. The side-walls of the braincase extend dorsolaterally from its floor and are visible in ventral view, contrary to the situation in other families in which the side-walls are vertically oriented and not visible in ventral view. The processus pterygoideus of the quadrate may be strongly or weakly developed. There is a gap between the quadrate and maxillopalatine that is bridged by the squamosal. The choanae are formed by processes of the maxillopalatines and prevomers. The dentigerous bones are the premaxillae, maxillopalatines, and prevomers. Diastemata between the prevomerine and palatine series of teeth may be present (Fig. 4) or absent (Fig. 1). The teeth are of variable size, conical, elongate, usually curved posteriorly, and monocuspid.

Each ramus of the lower jaw consists of two compound elements, the pseudodentary and the pseudoangular (Figs. 2 and 5). The latter element lacks the internal process for muscle attachment that is present in other gymnophionans. The retroarticular processes of the pseudoangulars, present in all caecilians, are curved dorsally behind the quadrates. Teeth are present on the pseudodentary; there are no splenial teeth.

The hyobranchial skeleton is cartilaginous as in all caecilians. It consists of a hyoid arch and four branchial arches (Fig. 3). The ceratohyals are joined to each other and to the first branchial arch by a short basibranchial. The second branchial arch is free from the other hyobranchial elements, being suspended by muscles. The third and fourth branchial arches form a complex structure. The bar between the distal ends of the fourth ceratobranchials is unique to this family.

CONTENT.—Two genera: *Crotaphatrema*, n. gen., with two species and *Scolecomorphus* with three species.

DISTRIBUTION.—Equatorial Africa: *Crotaphatrema*, gen. nov., occurs in southwestern Cameroon; *Scolecomorphus* occurs in Malawi, Tanzania, and possibly Kenya.

REMARKS.—The diagnosis presented above differs considerably from Taylor's (1969a) original diagnosis. Taylor emphasized the absence of prefrontal bones, which are present; the presence of diastemata between the palatine and prevomerine teeth, which occur in only one of the two genera (*Scolecomorphus*); the presence of temporal fossae, which are found only in species of *Scolecomorphus*; and the presence of spines on the phallodeum (penis). Wake (1972) could not find the spines on the phallodeum of *Scolecomorphus uluguruensis* that were described and illustrated by Noble (1931) and Taylor (1968, 1969a). But, calcified (alizarin positive) spines are clearly present on the phallodea of specimens of *S. uluguruensis* and *S. vittatus* available to me. These spines can be seen easily by gross examination of everted phallodea, and they are visible in x-ray plates of specimens with retracted phallodea. Phallodeal spines are not known to occur outside the family Scolecomorphidae, but, as they have not yet been demonstrated in all scolecomorphid species, I refrain from considering them diagnostic of the family.

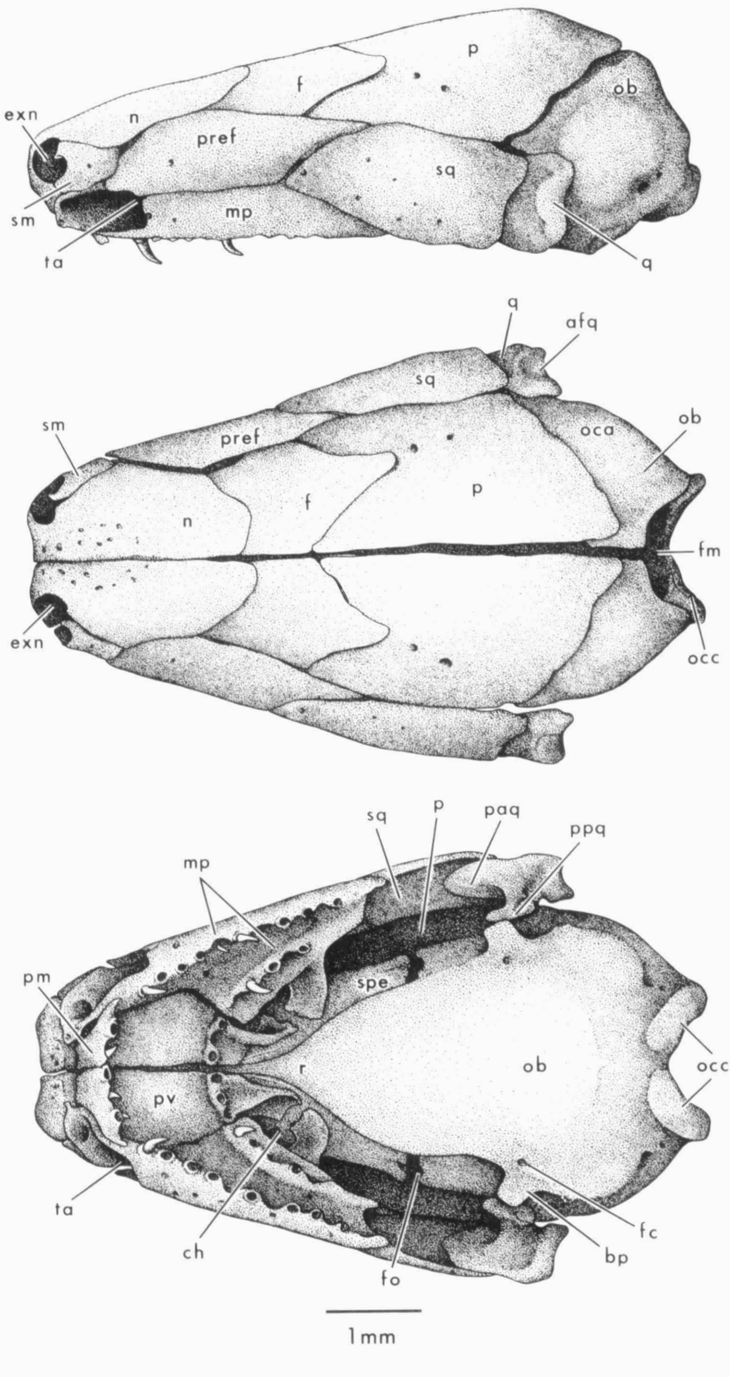
Naylor and Nussbaum (1980) and Nussbaum and Naylor (1982) described aspects of the trunk musculature of scolecomorphids. Nussbaum (1983) briefly characterized the jaw-closing muscles of the family.

CROTAPHATREMA new genus

TYPE SPECIES.—*Crotaphatrema bornmuelleri* (Werner).

DIAGNOSIS.—Scolecomorphids without temporal fossae; without diastemata between the prevomerine and palatine series of teeth; and with the maxillary series of teeth extending further posteriorly than the palatine series.

DESCRIPTION.—The skull (Fig. 1) is relatively solid, with less freedom of movement of the upper jaw arcade compared to members of the genus *Scolecomorphus*. The squamosal is braced against the parietal dorsally, closing the temporal fossa, which is open in *Scolecomorphus*. Closure of the temporal fossa is effected by a process of the parietal, which extends laterally to contact the squamosal and anteriorly to close the small space between the posterior ends of the frontal and prefrontal. This is different from the situation in stegokrotaphic skulls of other gymnophionan families (some ichthyophiids and caeciliids) in which the temporal fossa is closed by the dorsal portion of the squamosal. The processus pterygoideus of the quadrate is well developed and positioned to buttress against the basipterygoid process of the os basale when the upper cheek arcade is compressed medially. The basipterygoid process is more strongly developed than in *Scolecomorphus*. The premaxilla is small with only one-fifth to one-third as many teeth as the maxilla. The maxillary series of teeth extends posteriorly two to four teeth further than the palatine series. The prevomerine series of teeth is continuous with the palatine series. The choanal passage is defined by two prominent flanges, one on the prevomer and the other on the pars palatina of the maxillopalatine. The hyobranchial apparatus is illustrated in Fig. 3.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CONTENT.—Two species: *Crotaphatrema bornmuelleri* (Werner) and *Crotaphatrema lamottei* (Nussbaum).

ETYMOLOGY.—The generic name is derived from *krotaphos* (Gr.) meaning the temple of the head and *atrema* (Gr.) meaning without holes, in reference to the lack of temporal fossae. Gender neuter.

DISTRIBUTION.—Southwestern Cameroon; known only from the type localities of the two species.

REMARKS.—There is a possibility that species of this genus differ in reproductive mode from species of the sister genus, *Scolecomorphus*. *Scolecomorphus kirkii* and *Scolecomorphus uluguruensis* are viviparous, and *Scolecomorphus vittatus* is likely to be viviparous. Ovulated eggs of these three species are small (about 1.0 mm diameter), and large, nearly term, embryos have been observed in the oviducts of *S. kirkii* and *S. uluguruensis*.The mass of these embryos greatly exceeds the mass of the ovulated eggs, indicating transfer of nutrient between the female and embryos. The ovarian eggs of one of the five known specimens of the genus *Crotaphatrema* (the holotype of *C. lamottei*) greatly exceed the size of ovulated eggs of viviparous *Scolecomorphus*, suggesting that species of *Crotaphatrema* may be oviparous.

CROTAPHATREMA BORNMUELLERI (Werner) new combination

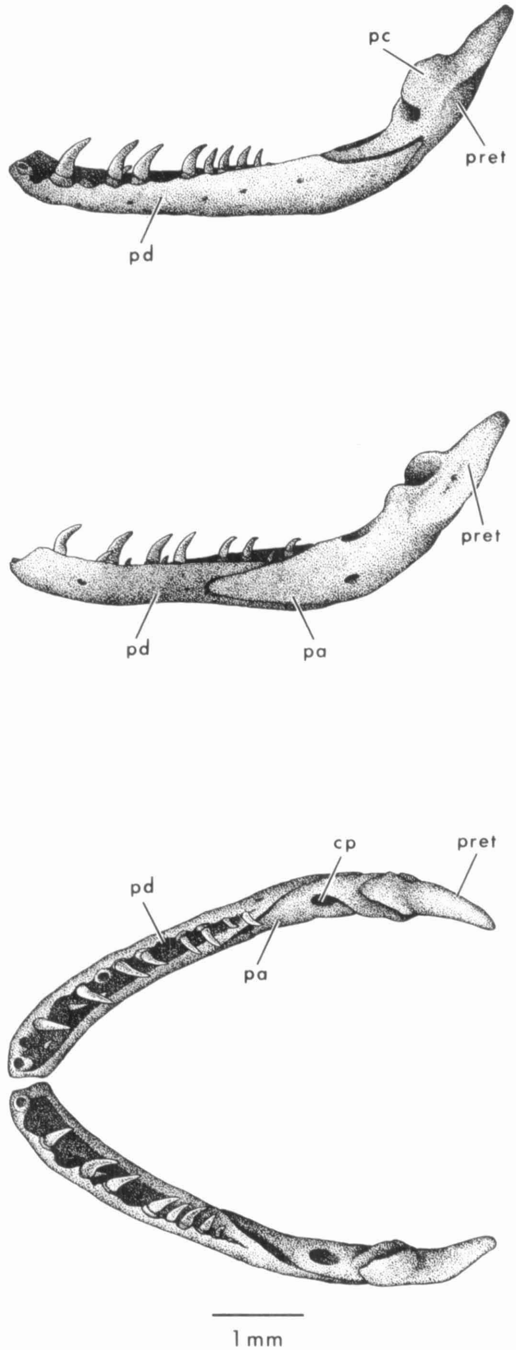
Herpele bornmuelleri Werner, 1899:144. Type-locality, "Victoria, Kamerun". Holotype, NMW 14859, mature male, collected in 1893 by Alfred Bornmüller.

Scolecomorphus bornmuelleri: Taylor 1968:636. First use of combination.

REFERRED SPECIMENS.—Known only from the holotype.

DIAGNOSIS.—A species of *Crotaphatrema* that differs from its single congener, *C. lamottei*, by having fewer vertebrae (113 versus 124–133), fewer primary annuli (107 versus 115–128), more dentary teeth (35 versus 22–28), and a differently-shaped head. The head of *C.*

FIG. 1. Skull of *Crotaphatrema lamottei*, lateral, dorsal, and ventral views. Drawn from UMMZ 174497, mature male, paratopotype, 224 mm TL. *afq*—articular facet of quadrate; *bp*—basipterygoid process; *ch*—choana; *exn*—external naris; *f*—frontal; *fc*—cartoid foramen; *fm*—foramen magnum; *fo*—foramen opticum; *mp*—maxillopalatine; *n*—nasal; *ob*—os basale; *oca*—otic capsule; *occ*—occipital condyle; *p*—parietal; *paq*—processus ascendens of quadrate; *pm*—premaxilla; *ppq*—processus pterygoideus of quadrate; *pref*—prefrontal; *pv*—prevomer; *q*—quadrate; *r*—parasphenoidal rostrum of os basale; *sm*—septomaxilla; *spe*—sphenethmoid; *sq*—squamosal; *ta*—tentacular aperture.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bornmuelleri is parallel-sided with a rounded snout, whereas the head of *C. lamottei* is subtriangular in dorsal outline.

DESCRIPTION.—The following description is from the holotype, which is slightly desiccated with the left side of the head partly dissected, but otherwise in good condition. The dorsum is brown, having the appearance of a slightly dried specimen. The venter is light cream-tan; in life the specimen was probably lavender above and cream below. The line separating the dorsal from the ventral coloration is sharp but uneven (undulating). The darker dorsal coloration extends downward to the mid-lateral line or slightly below posteriorly, but, anteriorly the dark dorsal band stops above the mid-lateral line. The dorsal band of dark color extends onto the head but does not include the upper jaws or tip of the snout. The area around the external nares has the lighter coloration of the venter. The terminus of the body above the venter is dark, but the cloacal opening is included in the lighter ventral coloration.

The collars are indistinct; each collar has a central, transverse, dorsal groove. The first 9 or 10 annuli are complete dorsally; the remainder are fused mid-dorsally. The annular grooves that define annuli 6 to 20 are slightly offset mid-dorsally, perhaps resulting from a developmental anomaly. All of the annuli are fused mid-ventrally, except the last 3 to 4. There are no scales in the annular folds.

The sides of the head are nearly parallel in dorsal outline, and the snout is rounded. The external nares are visible in dorsal view, each with a flap-like valve just inside the opening. The tentacular apertures are below, and slightly posterior to, the external nares, somewhat closer to the lips than to the nares, and about 1.0 mm anterior to the mouth. The tentacular apertures are not visible in dorsal view. The tentacles are extruded, measure 1.0 and 1.3 mm in length, and are clavate in shape. The mouth is subterminal, with the snout projecting 2.4 mm.

The nonannular terminal shield is 6.6 mm long. The more-or-less circular vent lies on the ventral surface of the terminal shield; the posterior limit of the vent is 1.0 mm from the terminus of the shield. The terminus is curved downward and somewhat laterally compressed.

Measurements (in mm) are: total length, 277; body width, 10; head

FIG. 2. Lower jaws of *Crotaphatrema lamottei*; lateral (top), medial (center), and dorsal views. Drawn from UMMZ 174497. *cp*—canalis primordialis; *pa*—pseudoangular; *pc*—processus condyloides of pseudoangular; *pd*—pseudodentary; *pret*—processus retroarticularis.

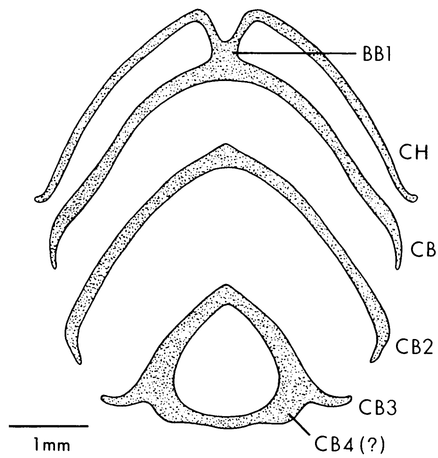


FIG. 3. Hyobranchial skeleton of *Crotaphatrema lamottei* (UMMZ 174497). *BB1*—first basibranchial; *CB1*—first ceratobranchial; *CB2*—second ceratobranchial; *CB3*—third ceratobranchial; *CB4*—possibly fourth ceratobranchial; *CH*—ceratohyal.

length (from tip of snout to first nuchal groove), 10.5; head width, 6.3; internarial distance, 2.7; and tentacular aperture-narial distance, 1.3.

Counts: primary annuli, 107; vertebrae, 113; premaxillary-maxillary teeth, 32; prevomerine teeth, 6; left palatine teeth, 6; right palatine teeth, 6; dentary teeth, 35; splenial teeth, 0.

The teeth are monocuspid, with the antero-medial teeth of each series somewhat larger and more strongly recurved than the posterior teeth. There is a small diastema between the prevomerine and palatine series of teeth on each side caused by the slight interposition of the choana. The distance between the choanae is 1.1 mm, and there are no valves apparent inside them. The tongue is smooth, without narial plugs, and was apparently free in front (the tongue has been slightly dissected).

REMARKS.—The diastemata between the prevomerine and palatine series of teeth are very small (a single tooth would fill each gap), suggesting that not all members of this species have these diastemata. The situation is completely different in *Scolecomorphus* spp., in which the palatine series are displaced posteriorly to the extent that all, or almost all, of the palatine teeth lie behind the maxillary teeth, with conspicuous gaps between the prevomerine and palatine series.

CROTAPHATREMA LAMOTTEI (Nussbaum) new combination

Scolecomorphus lamottei Nussbaum 1981:265. Type-locality, "Mont Oku, 2,300 m, Cameroon." Holotype MNHNP 1979-7441, mature female, collected November 1975 by Maxime Lamotte.

REFERRED SPECIMENS.—MNHNP 1979-7441 (holotype), 1979-7444 (paratopotype); UMMZ 174495-6 (formerly MNHNP 1979-1942-3) (paratopotypes).

DIAGNOSIS.—A species of *Crotaphatrema* that differs from its single congener *C. bornmuelleri* by having more vertebrae (124–133 versus 113), more primary annuli (128–155 versus 107), fewer dentary teeth (22–28 versus 35), and a differently-shaped head; the head of *C. lamottei* is subtriangular in dorsal outline, whereas that of *C. bornmuelleri* is parallel-sided with a rounded snout.

DESCRIPTION.—The following description is of the holotype. The dorsal coloration is tan-brown, probably lavender in life; the ventral coloration is cream. The dorsal and ventral coloration are sharply delimited anteriorly, but less sharply defined posteriorly. The upper jaws and area surrounding the tentacles are cream-colored, but the tip of the snout is tan-brown like the rest of the dorsal surface of the head.

The head is subtriangular in dorsal outline, with the snout projecting 1.9 mm anteriorly from the recessed mouth. The external nares are visible in dorsal view, but the tentacular apertures are not. Flap-like valves occur inside the external nares. The tentacular apertures are below, and slightly posterior to, the external nares and even with the anterior margin of the mouth. The tentacles are extruded about 1.0 mm and directed downward and slightly forward. The tentacles are large and clavate. There are no indications of the vestigial eyes on the extruded portions of the tentacles. The tentacular apertures are surrounded by shallow grooves, and the openings are oriented ventrolaterally.

The two collars are defined by three transverse nuchal grooves; the first nuchal groove is indistinct or missing dorsally. The second collar is divided dorsally by a transverse groove. The primary annuli are distinct dorsally but fused ventrally. There are no scales in the annular grooves. The cloacal opening is oval-shaped, longitudinally oriented, and contained within the terminal shield. The terminal shield is 3.8 mm long.

The teeth are conical, monocuspid, and curved posteriorly. The premaxillary-maxillary teeth are larger than the prevomeropalatine teeth. The anterior teeth of the premaxillary-maxillary and dentary series are enlarged relative to the posterior teeth of the same series. There are no diastemata between the prevomerine and palatine series of teeth. The maxillary series of teeth extend further posteriorly than do the palatine series. The tongue is without narial plugs, unpigmented and fused to the gum in front. The choanae are 0.9 mm apart with no obvious valves.

Measurements (in mm): total length, 318; body width, 10; head length (snout to first nuchal collar), 9.5; head width, 5.9; internarial distance, 1.1; and tentacular aperture-narial distance, 1.3.

Counts: primary annuli, 128; vertebrae, 133; premaxillary-maxillary teeth, 30; prevomeropalatine teeth, 15; dentary teeth, 22; splenial teeth, 0.

The ovaries contain enlarged, yolky ova; there are no oviductal ova nor embryos.

VARIATION.—The three paratopotypes are very similar to the holotype. Their coloration is lilac-lavender dorsally and cream ventrally. The tan-brown dorsal coloration of the holotype results from slight drying. What appear to be vestigial eyes can be seen embedded in the dorsal bases of the extruded tentacles of two of the paratopotypes (UMMZ 174495-6). Vestigial scales occur deep in the grooves of two posterior annuli of UMMZ 174496, but were not seen in other grooves. The smallest paratopotype (MNHNP 1979-7444) has smaller and more numerous dentary teeth than the others, suggesting that dentary teeth may enlarge and decrease in number with age in this species. The only male (UMMZ 174496) has fewer primary annuli (115 versus 127–128) and fewer vertebrae (124 versus 127–133) than the three females. This suggests sexual dimorphism in number of body segments in this species, parallel to that which definitely occurs in the three species of *Scolecomorphus* (see below). See Nussbaum (1981) for further description of the paratopotypes.

REMARKS.—Females mature between 196 and 262 mm total length. The only known male is mature (enlarged, multilobed, white testes) at 224 mm total length. The reproductive mode is unknown, but the presence of large (>2.0 mm), yolky, ovarian eggs in the holotype suggests the possibility that the species is oviparous.

SCOLECOMORPHUS Boulenger

Scolecomorphus Boulenger, 1883:48. Type-species *Scolecomorphus kirkii* Boulenger, 1883, by monotypy.

Bdellophis Boulenger, 1895:412. Type-species *Bdellophis vittatus* Boulenger, 1895, by monotypy.

DIAGNOSIS.—Scolecomorphids with temporal fossae, with diastemata between the prevomerine and palatine series of teeth, and with all or most of the palatine teeth posterior to the maxillary teeth.

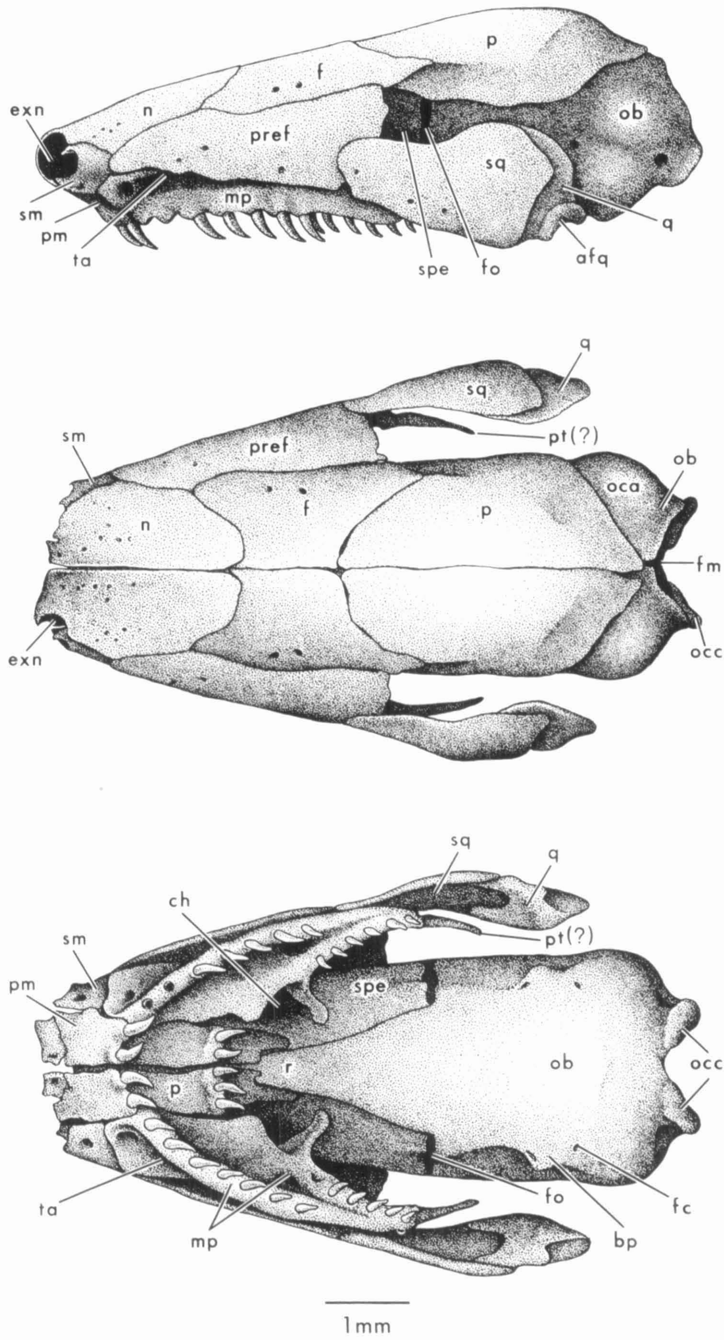
DESCRIPTION.—The distinctive temporal fossa of this genus lies between the parietal and squamosal and is limited anteriorly by the prefrontal (Fig. 4). The fossa is more-or-less open posteriorly, depending on the degree of compression of the movable squamosal-quadrate bar against the braincase. The squamosal articulates anteriorly with the prefrontal and maxillopalatine and posteriorly with the quadrate. The processus pterygoideus of the quadrate is weakly developed or absent. The basipterygoid process of the os basale is present, but poorly developed compared to that of *Crotaphatrema* spp. There is a slender posterior extension of the maxillopalatine that may be part of the latter bone or a remnant of the pterygoid. The lateral walls of the braincase are visible in ventral view as a result of the narrowness of the parasphenoidal and rostral portions of the os basale. The choanal openings are not as strongly delimited by bone as they are in species of *Crotaphatrema*. There is a choanal process on the maxillopalatine but none on the prevomer. The prevomers are long, slender bones with 1 to 3 teeth on each one and are arranged in a single transverse row. The prevomerine teeth are separated from the palatine teeth by a wide gap, which includes part of the choanal structure. The first palatine tooth usually is positioned even with the last maxillary tooth, and the palatine series are laterally displaced so that the palatine teeth appear to function as a continuation of the maxillary series.

The hyobranchial apparatus (illustrated by Brand, 1956 and Nussbaum, 1977) is very similar to that of *Crotaphatrema*.

Males of *Scolecomorphus* spp. are smaller and have fewer primary annuli and vertebrae than females (see species accounts). Two of the three included species (*kirkii* and *uluguruensis*) are viviparous, suggesting that viviparity may be characteristic of the genus. Embryos have large gills, each with three rami and numerous subbranches or fimbriae.

CONTENT.—Three species: *Scolecomorphus kirkii* Boulenger, *S. uluguruensis* Barbour and Loveridge, and *S. vittatus* (Boulenger).

DISTRIBUTION.—The genus is confined to eastern equatorial Africa. It definitely occurs in Malawi and Tanzania. The genus also has been reported in Kenya (Taylor, 1969b), and in Rhodesia and Zambia (Taylor, 1968), but these are questionable records. The Kenyan record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may be a *lapsus calami*, as Taylor's (1969b) statement is ambiguous. The Rhodesian and Zambian records are tenuous sight records. No voucher specimens exist for any of these three countries.

REMARKS.—Barbour and Loveridge (1928:179) reduced *Bdellophis* Boulenger to a synonym of *Scolecomorphus* Boulenger by showing that the single character, "eyes distinct," that distinguished *Bdellophis* from *Scolecomorphus*, was invalid.

The species of *Scolecomorphus* have been poorly defined. Boulenger's (1883) diagnosis of *S. kirkii* was essentially a diagnosis of the genus, as no other species of *Scolecomorphus* was known at that time. Again, Boulenger's (1895) diagnosis of *Bdellophis* (=*Scolecomorphus*) *vittatus* was not comparative, as "*Bdellophis*" was monotypic. Subsequent diagnoses—those of Barbour and Loveridge, 1928 and Taylor, 1968—are confusing and inadequate, largely because these authors failed to account for geographic and ontogenetic variation and because artifactual characteristics are included in the diagnoses and descriptions. There are too few specimens available for study, too few localities, and too few cases of sympatry to allow unequivocal taxonomic conclusions within the genus. However, it is relatively certain that *S. attenuatus* is a junior synonym of *S. uluguruensis* and that *S. convexus* is a junior synonym of *S. kirkii*. The remaining taxa, *S. kirkii*,*S. uluguruensis*, and *S. vittatus*, appear to be valid species.

SCOLECOMORPHUS KIRKII Boulenger

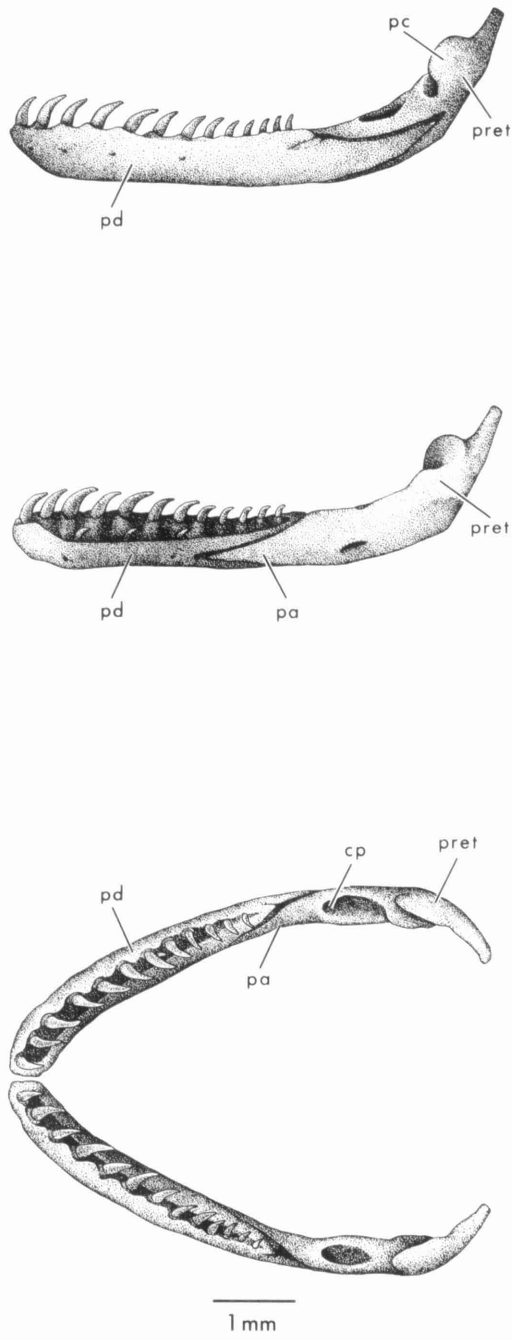
Scolecomorphus kirkii Boulenger, 1883:48. Type locality, "probably from the vicinity of Lake Tanganyika." Holotype, BMNH 1946.9.5.58, mature female, sent to the British Museum by Sir J. Kirk.

Scolecomorphus kirkii kirkii: Loveridge, 1953:332.

Scolecomorphus convexus Taylor, 1968:637. Type locality, "Uhehe, Deutsch-Ost. Africas" [Uhehe was a district of Tanganyika, now the area around Iringa in the south-central highlands of Tanzania]. Holotype, ZMH A00268 (formerly 1358), mature female, collected in 1897 by Dr. Stierling. *New Synonym.*

REFERRED SPECIMENS.—AMNH A20871 (Malawi, Shire Highlands), A53239-41 (Malawi, Zomba Plateau, 4,500 feet [1370 m] eleva-

FIG. 4. Skull of *Scolecomorphus vittatus* drawn from UMMZ 172067, mature male, 233 mm TL. *pt*—possibly a vestigial pterygoid. Other abbreviations defined in legend for Figure 1.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tion), A53242-3 (Malawi, Cholo Mountain, 3,600 feet [1100 m] elevation), A57874 (skeleton, no locality data); BMNH 92.12.31.43-4 (Malawi, Shire Highlands), 93.10.26.94-5 (Malawi, Zomba), 1946.9.5.58 (holotype, formerly No. 82.1.6.23); CM 61021 (Malawi, Zomba); FMNH 189150 (Malawi, Cholo District, dried skull and alcoholic body), 189151 (Malawi, Cholo District, Cholo Mountains, 3,600 feet [1100 m] elevation); MCZ 16305 (Tanzania, Mufindi-Njombe Road, 60 miles [98 km] south of Mufindi), 27101-2, 27104-5, 27107, 27109-15, 27117, 27119, A99844-6 (Malawi, Cholo District, Cholo Mountains), 27106 (Malawi, Cholo District, Cholo Mountains, 3,600 feet [1100 m] elevation, dried skull and alcoholic body), 27120 (Malawi, Cholo District, Cholo Mountains, 3,600 feet [1100 m] elevation, dried skull); MNHNP 1894 434 (Malawi, Zomba); MRAC 101889 (Tanzania, Uluguru Mountains, Vallée de la Mungula, 1,300 m), 101891-7 (Tanzania, Uluguru Mountains, Bunduki, 1,300–1,400 m); TM 25584-5 (Malawi, Cholo Mountains), 26719-22, 26724, 26726-7 (Tanzania, Uluguru Mountains); UMMZ 179334 (Tanzania, Mpwapwa District, Dodoma Region, Mafwemiro Forest Reserve, 6°41'S latitude, 36°31'E longitude, Chugu Peak, 2,000 m); UZMC R0258 (Malawi, Namadzi); ZMH A00268-9, formerly 1358-9 (holotype and paratopotype, respectively, of *Scolecomorphus convexus*).

DIAGNOSIS.—A species of *Scolecomorphus* in which the dark, olive-brown dorsal coloration of adults extends onto the lateral surfaces to, or slightly onto, the ventral surfaces, but does not encircle the body. The entire venter is light yellowish-olive in preservative, pinkish in life.

DESCRIPTION.—The following description is of the holotype. The dorsal coloration is dark olive-brown, covering the upper three-fourths of the body. The venter, including the chin, throat, and undersurface of the terminal shield, is yellowish-olive to flesh-colored. The borders between the dorsal and ventral coloration are somewhat diffuse.

The head is subtriangular in dorsal view with a rounded snout. The snout projects 1.4 mm beyond the mouth. External nares are visible in dorsal view, but the tentacular apertures are not. Distinct valves are visible in the external nares. The tentacular apertures are ventrolaterally oriented, located below and slightly behind the external nares, and even with the anterior margin of the mouth.

The first nuchal groove is indistinct so that the first collar is continuous (fused) with the head. The third nuchal groove is distinct dorsally but incomplete ventrally, resulting in ventral fusion of the second

FIG. 5. Lower jaws of *Scolecomorphus vittatus* (UMMZ 172067). Lateral (top), medial (center), and dorsal views. Abbreviations defined in legend for Figure 2.

collar and the first annulus. There is a short, transverse, dorsal groove on each of the two collars. The first few annuli are complete but the remainder are fused dorsally and ventrally. There is an oval impression around the longitudinal vent on the undersurface of the terminal shield. The terminal shield is 4.5 mm in length.

The teeth are elongate, conical, monocuspid, and curved posteriorly. Teeth of each series are larger anteriorly, but only slightly so in the dentary series. The dentary teeth are small relative to teeth of the other series. The palatine series of teeth begin precisely at the level where the maxillary series end.

Measurements (in mm): total length, 288; body width, 7; head length (snout to first nuchal groove), 6.5; head width, 4.5; internarial distance, 1.8; tentacular aperture-narial distance, 1.4.

Counts: primary annuli, 147; vertebrae, 157; premaxillary-maxillary teeth, 19; left palatine teeth, 6; right palatine teeth, 6; prevomerine teeth, 5; dentary teeth, 24; splenial teeth, 0.

The ovaries contain yolked follicles; there are no oviductal embryos.

VARIATION.—The 60 specimens of *Scolecomorphus kirkii* available for study may be grouped geographically into a relatively large sample of 38 from the southern highlands of Malawi, a smaller sample of 17 from the Uluguru Mountains of Tanzania, and an even smaller sample of three from the south-central highlands of Tanzania. Two specimens, including the holotype, are of uncertain provenance.

The coloration of all specimens is basically the same and similar to that of the holotype (see above) with the following exceptions. In younger (smaller) specimens, the dorsal coloration is more dorsally restricted. In adults from southern Malawi, the dorsal coloration extends somewhat further ventrally and may actually encircle the body just anterior to the vent, compared to adults from the Uluguru Mountains in which the venter is never encroached upon by dorsal coloration. Two of the specimens (the holotype and paratopotype of *Scolecomorphus convexus*) from the south-central highlands of Tanzania are too badly dried to determine details of coloration, although the two are clearly bicolored like other *S. kirkii*. The third specimen from this area (MCZ 16305) has a color pattern that falls within the range of variation of both the southern sample (Malawi) and the northern sample (Uluguru), but has a pattern (no ventral encroachment of dorsal coloration) more frequently encountered in the northern sample. TM 26726 from the Uluguru Mountains is a mutant form with a variegated dorsal pattern anteriorly on the head and neck. No sexual dichromatism is evident.

The ranges of morphometric and meristic variation for the samples from Malawi and the Uluguru Mountains are summarized in Tables 1

TABLE 1

Scolecomorphus kirkii, SOUTHERN MALAWI:
MORPHOMETRIC AND MERISTIC VARIATION

Characteristic	Mean	Range	Standard Deviation	N
Total length (mm)				
♂♂	276	215–312	24	14
♀♀	350	288–463	50	18
Body width (mm)				
♂♂	7.1	6–8	0.66	14
♀♀	8.8	7–11	1.11	18
Head length (mm)				
♂♂	8.0	6.8–9.8	0.85	14
♀♀	8.2	6.5–9.2	0.74	17
Head width (mm)				
♂♂	5.1	4.1–6.0	0.59	14
♀♀	5.5	4.5–6.8	0.63	18
Internarial distance (mm)				
♂♂	2.1	1.5–2.6	0.35	14
♀♀	2.1	1.7–2.6	0.29	17
Tentacular aperture-narial distance (mm)				
♂♂	1.4	1.0–1.8	0.22	14
♀♀	1.4	1.2–1.6	0.14	17
No. primary annuli				
♂♂	134.6	130–142	3.5	14
♀♀	145.2	140–152	3.0	18
No. vertebrae				
♂♂	146.1	141–155	4.0	14
♀♀	155.9	150–165	3.4	18
No. premaxillary-maxillary teeth				
♂♂	19.6	15–23	2.3	14
♀♀	19.0	16–22	1.7	17
No. prevomeropalatine teeth				
♂♂	18.1	13–21	2.2	14
♀♀	17.7	14–24	2.6	17
No. dentary teeth				
♂♂	26.8	18–34	4.7	14
♀♀	25.5	20–31	3.5	17
Total length/body width				
♂♂	38.7	33.8–44.6	3.2	14
♀♀	40.0	32.9–49.4	4.8	18
Total length/head length				
♂♂	34.8	30.7–40.0	2.8	14
♀♀	42.9	35.6–53.2	4.3	17
Total length/head width				
♂♂	54.3	50.2–60.9	3.1	14
♀♀	63.9	54.4–71.1	4.9	18
Head length/head width				
♂♂	1.6	1.4–1.8	0.13	14
♀♀	1.5	1.3–1.7	0.12	17

TABLE 2

Scolecomorphus kirkii, Uluguru Mountains, Tanzania: Morphometric and Meristic Variation

Characteristic	Mean	Range	Standard Deviation	N
Total length (mm)				
♂♂	199	163–234	50	2
♀♀	315	300–337	15	5
Body width (mm)				
♂♂	6.5	6–7	0.71	2
♀♀	9.2	8–10	0.84	5
Head length (mm)				
♂♂	6.1	5.2–7.0	1.27	2
♀♀	7.9	7.3–8.5	0.53	5
Head width (mm)				
♂♂	4.2	4.0–4.4	0.28	2
♀♀	4.9	4.4–5.5	0.47	5
Internarial distance (mm)				
♂♂	1.5	1.4–1.6	0.14	2
♀♀	1.9	1.7–2.0	0.13	5
Tentacular aperture-narial distance (mm)				
♂♂	1.3	1.2–1.3	0.07	2
♀♀	1.4	1.4–1.4		5
No. primary annuli				
♂♂	138.0	136–140	2.8	2
♀♀	149.0	147–151	1.6	5
No. vertebrae				
♂♂	147.0	147–147		1
♀♀	160.8	159–163	1.5	5
No. premaxillary-maxillary teeth				
♂♂	15.0	14–16	1.4	2
♀♀	15.0	14–16	0.7	5
No. prevomeropalatine teeth				
♂♂	10.5	9–12	2.1	2
♀♀	12.8	12–14	0.8	5
No. dentary teeth				
♂♂	18.0	16–20	2.8	2
♀♀	21.0	16–24	3.5	5
Total length/body width				
♂♂	30.3	27.2–33.4	4.4	2
♀♀	34.5	30.0–40.6	3.8	5
Total length/head length				
♂♂	32.4	31.3–33.4	1.5	2
♀♀	40.1	36.5–44.0	2.7	5
Total length/head width				
♂♂	47.0	40.8–53.2	8.8	2
♀♀	65.4	55.1–73.9	7.9	5
Head length/head width				
♂♂	1.4	1.3–1.6	0.21	2
♀♀	1.6	1.5–1.8	0.12	5

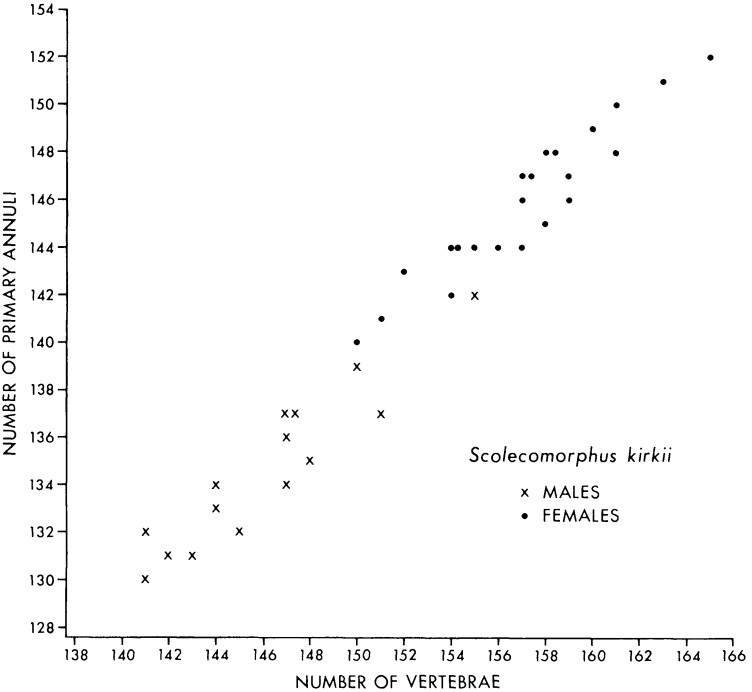

FIG. 6. Scatter diagram illustrating positive correlation between the number of primary annuli and the number of vertebrae. Females nearly always have more primary annuli and vertebrae than males.

and 2. The small size of the Uluguru sample prohibits detailed statistical comparisons, but the following conclusions and suggestions can be drawn. Females attain larger maximum size than males in both geographic areas. Females have more primary annuli and vertebrae than males in both samples (also see Fig. 6). Larger samples may show that *Scolecomorphus kirkii* from the Uluguru Mountains of Tanzania have more primary annuli and vertebrae and fewer teeth on all series than those from southern Malawi.

Morphometric and meristic data (in mm) for the three specimens from the south-central highlands of Tanzania are as follows. MCZ 16305: total length, 330; body width, 9; head length, 8.2; head width, 5.3; internarial distance, 1.8; tentacular aperture-narial distance, 1.5; primary annuli, 153; vertebrae, 161; premaxillary-maxillary teeth, 18; prevomeropalatine teeth, 10; dentary teeth, 20; splenial teeth, 0; a mature female. ZMH A00268 (holotype, *Scolecomorphus convexus*): total length, 485; body width, 14; head length, 9.2; head width, 6.0; internarial distance, 2.4; tentacular aperture-narial distance, 1.6; primary annuli, 154; vertebrae, 165; premaxillary-maxillary teeth, 20; prevomeropalatine teeth, 13; dentary teeth, 19; splenial teeth, 0; mature female. ZMH A00269 (paratopotype, *S. convexus*): total length, 234; body width, 7; head length, 7.0; head width, 4.0; internarial distance, 1.4; tentacular aperture-narial distance, 1.4; primary annuli, 121; vertebrae, 133; premaxillary-maxillary teeth, 19; prevomeropalatine teeth, 17; dentary teeth, 10 right side, left side uncountable; splenial teeth, 0; indeterminate sex and stage of maturity. The first two specimens are assignable to *S. kirkii*, but the third specimen has fewer primary annuli and vertebrae than any known *S. kirkii* and may be a specimen of *S. vittatus* or a representative of an undescribed species. Unfortunately, the coloration and other characteristics of importance are indeterminate because of poor preservation.

REMARKS.—The smallest known male, 163 mm total length, has slightly enlarged testicular lobes and appears to have been maturing when preserved. The smallest known female, 288 mm total length, is mature.

Scolecomorphus convexus Taylor (1968) is based on a desiccated specimen of *S. kirkii*. Characteristics of the holotype of *S. convexus* fall within the range of *S. kirkii*, except for the unusual architecture of the vent region, which Taylor failed to recognize is an artifact resulting from desiccation. The cloacal openings of all *Scolecomorphus* lie in an oval-shaped structure formed by the walls of the cloaca beneath the integument. In well-preserved specimens, the oval structure appears as a slight depression or elevation. But in dried specimens the integument on either side of the cloacal opening either collapses, resulting in an elevated cloacal structure as in the holotype of *S. convexus*, or folds over the cloaca. The latter condition can be seen in the paratopotype of *S. convexus*, which may be a specimen of *S. vittatus* (see above). Other poorly preserved specimens have altered cloacal architecture as well. Examples are BMNH 1946.9.5.59, the holotype of *S. vittatus*, and BMNH 92.12.31.44, a specimen of *S. kirkii*.

SCOLECOMORPHUS ULUGURUENSIS Barbour and Loveridge

Scolecomorphus uluguruensis Barbour and Loveridge, 1928:180. Type-locality, "Nyingwa, Uluguru Mountains, Tanganyika Territory." Holotype, MCZ 12193, mature male, collected 19 October 1926 by Tanzanian collectors for Arthur Loveridge.

Scolecomorphus kirkii attenuatus: Loveridge, 1953:333. First use of combination.

Scolecomorphus kirkii uluguruensis: Loveridge, 1957:307. First use of combination.

Scolecomorphus attenuatus Barbour and Loveridge 1928:181. Type-locality, "Nyingwa, Uluguru Mountains, Tanganyika Territory." Holotype, MCZ 12294 [originally MCZ 12194], mature female, collected 15 October 1926 by Tanzanian collectors for Arthur Loveridge. *New Synonym.*

Referred Specimens.—AMNH A22643, A25220-3 (paratopotypes); CAS 11519-20, 63082-3 (paratopotypes); CM 8694-5 (paratopotypes); FMNH 14975-6 (Tanzania, Uluguru Mountains, Bagilo, 5,000 feet [1520 m], paratypes); 18343 (paratopotype); LACM 35479 (Tanzania, Uluguru Mountains, Bunduki, 5,000 feet [1524 m]); MCZ 12183 (Tanzania, Uluguru Mountains, Vituri, 2,000 feet [610 m]), 12191 (Bagilo, paratype), 12193 (holotype), 12194-205, 12207-10, 12213-4, 12217-29, 12231-3, 12235-42, 12244-51, 12253-69, 12271-7, 12280, 12282-8 (paratopotypes), 12206, 12234, 12260, 12284 (paratopotypes, dried skulls and alcoholic skins and bodies), 12294-5 (holotype and paratopotype, respectively, of *Scolecomorphus attenuatus*); MNHNP 1931 60 (paratopotype); MRAC 11102 (paratopotype), 101890 (Tanzania, Uluguru Mountains, Vallée de la l'Ululu-Ndogo, affluent de la rive droite de la Mgeta á 500 m en aval de la chute de la Mgeta, 1,500 m); UMMZ 90661 (2 specimens; paratopotypes); USNM 73236-7 (paratopotypes).

Diagnosis.—A *Scolecomorphus* in which the ventral surface, except for the extremes, is darkly colored like the dorsum. The chin and throat, and the ventral surface of the terminus of the body, are cream-colored (pink in life). The head is smaller and the snout more acuminate than in other species of the genus.

Description.—The following description is of the holotype. The dorsal coloration is dark olive-brown grading into the slightly lighter olive-brown of the mid-ventral region. The chin and throat are cream-colored. The ventral terminus (posteriormost 12 mm), including the area around the cloacal opening, is also cream-colored.

The head is triangular to subtriangular in dorsal view with an acuminate snout. The snout projects 1.5 mm in front of the mouth. The external nares, but not the tentacular apertures, are visible in dorsal view. The tentacular apertures are oriented ventrolaterally and positioned below and behind the external nares, slightly anterior to the anterior margin of the mouth.

The first nuchal groove is indistinct, the second distinct, and the third distinct dorsally but not ventrally. Both collars have a short, transverse groove dorsally, the one on the second collar being much longer. The annuli are fused ventrally throughout; the first 9–10 annuli are distinct dorsally, but the rest are fused dorsally. The shape of the cloacal opening is obscured by the everted, spinous phallodeum. The terminal shield is 4.6 mm in length.

The teeth are monocuspid, conical, elongate and curved posteriorly; the teeth of each series increase in size anteriorly. The palatine series of teeth begins at the level (along the anterior-posterior axis) where the maxillary series ends.

Measurements (in mm): total length, 212; body width, 7; head length (snout to first nuchal groove), 6.4; head width, 4.0; internarial distance, 1.6; tentacular aperture-narial distance, 1.0.

Counts: primary annuli, 130; vertebrae, 141; premaxillary-maxillary teeth, 16; left palatine teeth, 3; right palatine teeth, 3; prevomerine teeth, 5; dentary teeth, 18; splenial teeth, 0.

VARIATION.—Most (107) of the 112 specimens of *Scolecomorphus uluguruensis* available for study are paratopotypes. Three specimens are from Bagilo (5,000 feet [1500 m] elevation), a site 2,500 feet [760 m] lower than the type locality (Nyingwa) in the Uluguru Mountains. One specimen is from Vituri (2,000 feet [600 m]) in the Ulugurus. Most of the available specimens are adults. Therefore, there is little opportunity to study geographic and ontogenetic variation in this species.

There is very little variation in coloration among the paratopotypes, except for the extent to which the anterior and posterior portions of the ventral surface of the body are light-colored. The mid-ventral dark coloration may extend anteriorly and/or posteriorly to nearly obscure the light area. Usually, about 6–40 mm of either end is light-colored ventrally. One of the paratopotypes (MCZ 12217), a small (164 mm TL), immature female, is light-colored mid-ventrally, with the dark coloration encroaching from the sides. It is apparent from the condition of this latter specimen, that young individuals have dark dorsums and light venters and that the dark dorsal coloration spreads with age down the sides to eventually encircle the body. Melanophores first spread down the annular grooves and then down the annular folds. Only the ventral extremes of the head and body remain light-colored to a variable extent in older (larger) individuals.

The three specimens from Bagilo are colored similarly to those from the type locality. However, it appears that the development of the dark ventral coloration proceeds at a different rate, relative to total length, at the Bagilo site. FMNH 14976 is a small (159 mm TL), immature female in which mid-ventral encroachment of melanophores is incomplete, so that a narrow (1.8 mm wide), mid-ventral, white band is present. MCZ 12191 is a larger (249 mm TL), mature, female from Bagilo in which encroachment of melanophores onto the venter is nearly complete, but there remains a narrow, irregular, white, midventral line. Specimens from the type locality (Nyingwa) are completely encircled by melanophores at midbody by the time this size is attained. The third specimen from Bagilo (FMNH 14975, 295 mm TL, mature female) is relatively large and has a body completely encircled with melanophores.

The single specimens from Bunduki and Vituri are typically colored.

The holotype and paratopotype of *Scolecomorphus attenuatus*, here considered to be specimens of *S. uluguruensis*, are colored like the latter. There is no evident sexual dichromatism in *S. uluguruensis*.

Morphometric and meristic variation for the paratopotypic sample is summarized in Table 3. As with *Scolecomorphus kirkii*, it is evident that females of *S. uluguruensis* grow to larger size and have more primary annuli and vertebrae (Fig. 7) than do males.

The three female specimens from Bagilo have low numbers of primary annuli and vertebrae (Table 4), compared to females of the paratopotypic series, and a larger sample from Bagilo would probably show that the differences are statistically significant. The two non-paratopotypic males from Bunduki and Vituri are similar morphometrically and meristically to the paratopotypes (Table 4).

REMARKS.—The smallest mature male *Scolecomorphus uluguruensis* examined was 212 mm TL, the largest immature male was 172 mm TL, and four male specimens that appeared to be maturing when preserved ranged in size from 158 to 195 mm TL. The smallest mature female measured 236 mm TL, whereas the largest immature female was 229 mm TL.

Scolecomorphus attenuatus Barbour and Loveridge is here considered to be a junior synonym of *S. uluguruensis* Barbour and Loveridge. Loveridge (1953, 1957, 1961) considered *S. attenuatus* to be a northern subspecies of *S. kirkii*, but Taylor (1968) recognized *S. attenuatus* as a valid species. The color pattern of *S. attenuatus* is identical to that of *S. uluguruensis*, and the two known specimens of *S. attenuatus* were collected at the type locality of *S. uluguruensis*. The more slender body of *S. attenuatus* noted by Barbour and Loveridge (1928) results at least in part from the very poor state of preservation of the holotype and paratype. Both specimens appear to have been preserved long after they died. The "jet-black color" (Barbour and Loveridge, 1928:181) of *S. attenuatus* is not presently evident; both specimens are purplish-brown dorsally. Barbour and Loveridge (1928:181) reported that the

TABLE 3

Scolecomorphus uluguruensis:
MORPHOMETRIC AND MERISTIC SUMMARY

Characteristic	Mean	Range	Standard Deviation	N
Total length (mm)				
♂♂	233	158–311	32	36
♀♀	272	146–330	41	53
Body width (mm)				
♂♂	7.5	6–9	0.91	36
♀♀	8.1	5–11	1.43	53
Head length (mm)				
♂♂	6.1	4.9–7.4	0.64	36
♀♀	6.1	4.5–9.2	0.76	53
Head width (mm)				
♂♂	4.4	3.6–4.4	0.40	36
♀♀	4.2	3.1–4.8	0.35	53
Internarial distance (mm)				
♂♂	1.5	1.1–1.8	0.16	36
♀♀	1.5	1.1–1.8	0.16	53
Tentacular aperture-narial distance (mm)				
♂♂	1.0	0.7–1.4	0.15	36
♀♀	1.0	0.7–1.3	0.13	53
No. primary annuli				
♂♂	129.7	124–136	2.9	36
♀♀	141.6	132–149	3.1	53
No. vertebrae				
♂♂	140.4	135–147	3.3	36
♀♀	151.4	141–160	3.4	53
No. premaxillary-maxillary teeth				
♂♂	17.6	16–20	1.2	36
♀♀	16.6	12–19	1.4	53
No. prevomeropalatine teeth				
♂♂	14.5	11–19	1.8	36
♀♀	14.5	12–20	1.7	53
No. dentary teeth				
♂♂	19.8	14–25	2.0	36
♀♀	19.5	12–25	2.5	53
Total length/body width				
♂♂	31.3	24.9–43.2	4.1	36
♀♀	33.8	23.9–42.4	4.2	53
Total length/head length				
♂♂	37.9	32.0–43.2	3.4	36
♀♀	44.4	30.4–53.9	5.1	53
Total length/head width				
♂♂	53.0	38.5–62.0	5.2	36
♀♀	64.1	41.7–78.6	7.2	53
Head length/head width				
♂♂	1.4	1.2–1.7	0.12	36
♀♀	1.4	1.2–1.9	0.13	53

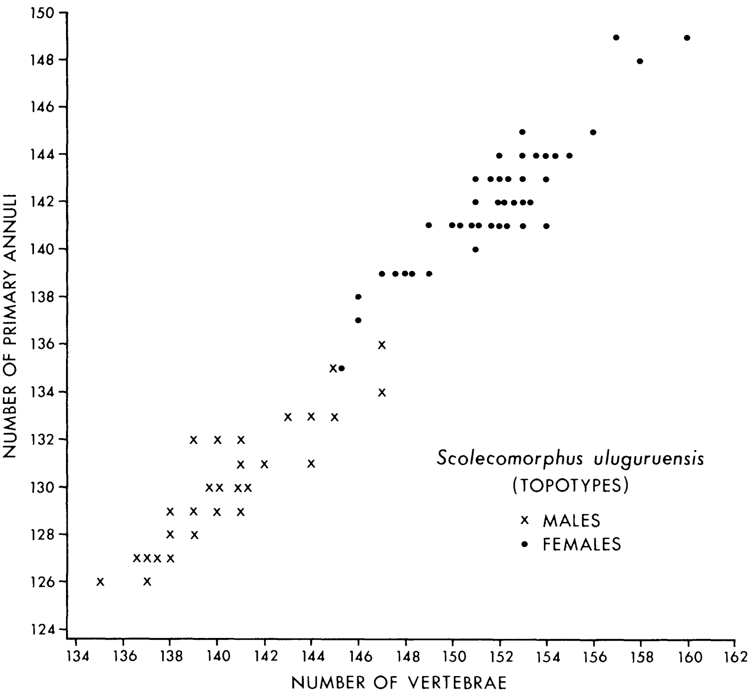

FIG. 7. Scatter diagram illustrating positive correlation between the number of primary annuli and the number of vertebrae. Females nearly always have more primary annuli and vertebrae than males.

"snout is more bluntly rounded" in *S. attenuatus* compared to *S. uluguruensis*. The snout of the holotype of *S. attenuatus* is more rounded than is usual for *S. uluguruensis*, but the shape of the snout is not outside the range of variation expected in *S. uluguruensis*. Of overriding importance is the unusual color pattern of the two specimens of *S. attenuatus*, which is precisely the same as that of *S. uluguruensis* and was not observed in any other gymnophionan species. I conclude that *S. attenuatus* is based on two slightly aberrant and poorly preserved specimens of *S. uluguruensis*.

SCOLECOMORPHUS VITTATUS (Boulenger)

Bdellophis vittatus Boulenger, 1895:412. Type-locality, "Usambara, German East Africa." Holotype, BMNH 1946.9.5.59 (formerly 1895.5.29.6), sex and stage of development indeterminant, received from Dr. F. Werner.

TABLE 4

MORPHOMETRIC AND MERISTIC VARIATION IN NON-PARATOPOTYPIC *Scolecomorphus uluguruensis*

	FMNH 14975 Bagilo	FMNH 14976 Bagilo	MCZ 12191 Bagilo	LACM 35479 Bunduki	MCZ 12183 Vituri	MCZ 12294 *S. attenuatus* holotype	MCZ 12295 *S. attenuatus* paratype
Sex	♀	♀	♀	♂	♂	♀	♂
Maturity	mature	immature	mature	mature	?	mature	mature
Total length (mm)	295	159	249	238	226	352	252
Body width (mm)	8	6	8	7	6	8	7
Head length (mm)	6.5	5.0	6.1	6.8	6.6	9.1	6.8
Head width (mm)	4.8	3.5	4.2	5.1	4.5	6.0	4.6
Internarial distance (mm)	1.4	1.3	1.3	1.7	1.4	2.1	1.5
Tentacular aperture-narial distance (mm)	1.0	0.8	0.7	1.1	1.0	2.0	0.8
No. primary annuli	131	132	127	125	132	141	124
No. vertebrae	143	141	141	136	139	150	136
No. premaxillary-maxillary teeth	15	15	16	20	16	14	18
No. vomerine teeth	3	4	4	5	3	5	5
No. palatine teeth (right side)	3	4	4	5	4	5	6
No. palatine teeth (left side)	4	4	5	5	5	6	6
No. dentary teeth	16	18	17	20	18	20	26

Scolecomorphus vittatus: Barbour and Loveridge, 1928:178. First use of combination.

REFERRED SPECIMENS.—AMNH A23509, A23512 (Tanzania ?, Nguelo), A23510-1 (Tanzania, Usambara Mountains); BMNH 95.11.15.2 (Tanzania, Usambara Mountains), 1909.6.5.6 (Kenya, Mombasa); FMNH 189148 (Tanzania, Uluguru Mountains, Nyange, dried skull and alcoholic body); LACM 35480-2 (Tanzania, Uluguru Mountains, Bunduki, 5,000 feet [1520 m]), 35688 (Tanzania, Ukaguru (sic) Mountains, Mandege, 5,300 feet [1615 m]); MCZ 10301, 12179 (Tanzania, Uluguru Mountains, Bagilo), 12181-2 (Tanzania, Uluguru Mountains, Vituri), 12187 (Tanzania, Usambara Mountains, Amani), 12188 (Tanzania, Usambara Mountains, Mt. Lutindi), 12189 (Tanzania, Usambara Mountains, Phillipshof), 25010-1 (Tanzania, Usambara Mountains, Magrotto Mountain), 28602 (Tanzania, Tanga Province, Handeni, Matembo); NMW 9172 (Tanganyika Territory, Ugano (sic)); TM 21140 (Tanzania, Usambara Mountains, Magrotto Mountain); UMMZ 65044 (2 specimens; Tanzania, Usambara Mountains, Amani), 172066-7 (Tanzania, North Pare Mountains, Kifula, Ugweno); USNM 226753 (Tanzania, North Pare Mountains, Kifula, Ugweno); UZMC R0240 (Tanzania, Usambara Mountains, Amani, Bomole Hill); ZMB 22260 (Tanzania, Usambara Mountains, Amani), 22262 (Tanzania, Usambara Mountains, Lungusa), 22769 (Tanzania, Usagara (sic)), 73353 (Tanzania?, Buloa (sic)).

DIAGNOSIS.—A relatively large-headed species of *Scolecomorphus* with a bluntly rounded snout, and with a distinctly bicolor pattern in which the lighter (yellow-cream) ventral color is more extensive than the darker (reddish-brown) dorsal color. The dark dorsal coloration may be restricted to the extent that it forms a narrow dorsal stripe continuous from the region near the external nares to the terminus of the body. The light ventral coloration on such specimens includes the margins of the upper lips, the underside of the snout, and occasionally even the area around the external nares; the light ventral coloration may extend up onto the dorsal surface of the tip of the terminal shield. At the other extreme, the dark dorsal coloration may be widened into a band that extends about half way down the lateral surfaces of the body.

DESCRIPTION.—The holotype is in poor condition. The body is flattened and the tissues considerably softened. The sex and condition of the gonads cannot be determined.

The reddish-brown dorsal stripe of the holotype extends from the external nares to the tip of the terminal shield. The margins of the upper jaw are light cream-colored like the venter. The vestigial eyes are clearly visible on the partially extruded tentacles.

The head is relatively wide with a bluntly rounded snout. The snout extends 1.5 mm anteriorly of the mouth. The unsegmented terminal shield is 4.7 mm long. The cloacal opening is in a depression bordered by raised lateral folds, the folds resulting from contortion of tissues caused by preservation.

Measurements (mm): total length, 172; body width, 6; head length, 5.5; head width, 4.0; internarial distance, 1.4; tentacular aperture-narial distance, 1.0.

Counts: primary annuli, 122; vertebrae, 132; premaxillary-maxillary teeth, 19; left palatine teeth, 4; right palatine teeth, 5; prevomerine teeth, 5; dentary teeth, 24; splenial teeth, 0.

VARIATION.—The 33 specimens of *Scolecomorphus vittatus* available for study are from scattered localities, seldom with more than two or three specimens from any single locality. The lack of large homogeneous samples precludes detailed analyses of ontogenetic and geographic variation.

It is clear, however, that the color pattern develops as described for the other species. Very small individuals have a narrow, reddish-brown dorsal stripe with the rest of the body yellowish-cream. Melanophores increase in number and spread ventrolaterally with age, but at different rates in different populations. The result is geographic variation in the width of the dorsal stripe of adults. From the limited data available, it appears that adults from the Usambara Mountains of northeastern Tanzania have the narrowest dorsal stripes and the brightest (yellow) ventrolateral color. Adults from the North Pare Mountains, to the northwest of the Usambaras, have more extensive dark dorsal bands, which extend ventrolaterally past the midlateral line. The ventrolateral, light coloration is a duller cream. Adults from the Uluguru Mountains to the south are colored more like those from the North Pare Mountains than those from the Usambaras.

Morphometric variation for the total sample of *Scolecomorphus vittatus* is summarized in Table 5. As with the other two species of *Scolecomorphus*, it is evident that females have more primary annuli and vertebrae than males, although the differences do not appear to be as great as in the other species. This may result partly from the geographic heterogeneity of the *S. vittatus* sample.

REMARKS.—The largest immature male measures 154 mm TL. This specimen (MCZ 12189) is from Mt. Lutindi in the Usambara Mountains. MCZ 12187, from Amani in the Usambaras, is already mature at 141 mm TL. These limited data indicate microgeographic variation in the size of males when maturity is attained. The smallest available female (160 mm TL) had partially destroyed urogenital organs and the state of maturity could not be determined. All other available females were mature, the smallest measuring 212 mm TL.

MORPHOLOGICAL DIFFERENTIATION OF *SCOLECOMORPHUS* SPECIES

A leading student of East African herpetology, in comparing *Scolecomorphus vittatus* to *Schistometopum gregorii* (Boettger), once wrote "It is difficult to see how [*Schistometopum gregorii*] can stand as a distinct species, though probably a good colour race. . . . All the other characters mentioned by Boettger are now recognized as being well within the range of [*Scolecomorphus*] *vittatus*." (Loveridge, 1925:765). These two species, which Loveridge would have synonymized, are now assigned to separate families. Loveridge's confusion dramatizes the difficulty in diagnosing caecilians from external morphology.

The three species of *Scolecomorphus* are diagnosed here primarily by differences in coloration, and these differences may be confusing, es-

TABLE 5

Scolecomorphus vittatus:
MORPHOMETRIC AND MERISTIC VARIATION

Characteristic	Mean	Range	Standard Deviation	N
Total length (mm)				
♂♂	213	141–312	56	15
♀♀	281	160–376	75	8
Body width (mm)				
♂♂	6.3	4–8	1.22	15
♀♀	7.9	6–12	1.96	8
Head length (mm)				
♂♂	6.9	5.0–9.4	1.23	15
♀♀	8.2	5.9–10.0	1.72	8
Head width (mm)				
♂♂	4.6	3.4–6.0	0.73	15
♀♀	5.6	3.2–7.4	1.52	8
Internarial distance (mm)				
♂♂	1.8	1.2–2.3	0.40	15
♀♀	2.0	1.0–2.6	0.55	8
Tentacular aperture-narial distance (mm)				
♂♂	1.2	0.8–1.6	0.28	15
♀♀	1.3	0.9–1.5	0.23	8
No. primary annuli				
♂♂	131.1	120–148	9.0	15
♀♀	135.8	129–145	5.9	8
No. vertebrae				
♂♂	142.5	131–158	8.4	15
♀♀	146.6	138–158	7.2	8
No. premaxillary-maxillary teeth				
♂♂	18.4	15–25	2.5	14
♀♀	19.5	14–24	3.2	8
No. prevomeropalatine teeth				
♂♂	14.9	9–21	3.4	14
♀♀	15.0	9–19	3.4	8
No. dentary teeth				
♂♂	22.6	17–29	3.9	15
♀♀	25.5	19–31	5.2	8
Total length/body width				
♂♂	34.1	25.9–46.8	6.1	15
♀♀	35.9	26.7–46.1	6.7	8
Total length/head length				
♂♂	30.9	25.0–38.3	4.0	15
♀♀	33.9	27.1–38.0	3.5	8
Total length/head width				
♂♂	46.6	33.6–61.0	7.7	15
♀♀	51.2	35.6–66.3	9.7	8
Head length/head width				
♂♂	1.5	1.3–1.7	0.13	15
♀♀	1.5	1.2–1.9	0.22	8

pecially in regard to the differentiation of *S. kirkii* and *S. vittatus*. Differences in features other than coloration are analyzed below.

Body proportions.—Ratios have been used frequently in caecilian systematics to describe differences in shape. For example, Skelton-Bourgeois (1961) attempted to define some species of *Scolecomorphus* in Tanzania by their body proportions. But, aside from the notorious statistical properties of ratios, they are of little practical use for identification of caecilians because of their wide variance (Tables 1–3, 5), much of which is explained by variance in body size (Table 6).

Covariance and regression analyses were used here to compare body proportions of the three species of *Scolecomorphus*. The variables body width, head length, head width, internarial distance and tentacular aperture-narial distance and the covariate total length were first subjected to analysis of covariance. If the requirement of the covariance model of equal slopes between strata (taxa) was satisfied, then the mean values for each variable adjusted for size (total length) were compared across taxa. Scheffé's multiple comparison test was used to determine differences at $p<0.05$. For characters in which the equal slopes criterion was not met, the slopes themselves were considered to be species-specific characters and were tested for significant differences. The data were not transformed, and males and females were analyzed separately.

Females are the larger sex in all three species of *Scolecomorphus* (Table 1–3, 5). Females average 17 (*S. uluguruensis*) to 58 (*S. kirkii*, Uluguru Mountains) percent longer than males.

TABLE 6

Correlation (Coefficients) between Body Size (Total Length) and Ratios as Descriptors of Shape

	Scolecomorphus kirkii		*Scolecomorphus uluguruensis*		*Scolecomorphus vittatus*	
	♂♂ (15)	♀♀ (23)	♂♂ (36)	♀♀ (53)	♂♂ (11)	♀♀ (8)
Total length/body width	0.524*	0.625*	0.600*	0.294*	0.793*	0.572
Total length/head length	0.279	0.779*	0.675*	0.720*	0.792*	0.748*
Total length/head width	−0.171	0.450*	0.763*	0.870*	0.845*	0.203
Head length/head width	−0.377	−0.360	0.191	0.208	0.469	−0.202
Head length/internarial distance	−0.671*	−0.234	0.244	0.321*	−0.207	−0.093
Head length/tentacular aperture-narial distance	−0.399	0.565*	−0.072	0.108	−0.064	0.449

*Significant at $P<0.05$

Sexual dimorphism in other measured characters is indicated in Table 7. Although the sexual differences are small, some are statistically significant. Female *S. kirkii* have wider bodies for a given length than males, and males and females of this species have different slopes for the regressions of head length, head width, internarial distance, and distance between the tentacular aperture and external naris on total length. In all cases, the slope is greater for males (Table 8). There are no significant sexual differences in slopes and adjusted means for *S. vittatus*. For *S. uluguruensis*, there are no sexual differences in slopes, but the adjusted means of head length, head width, internarial distance and tentacular aperture-narial distance differ between the sexes in this species. In all cases, males have the higher adjusted mean, indicating that males have relatively larger heads than females.

Comparisons of body proportions between species of *Scolecomorphus* by sex are summarized in Tables 9 (males) and 10 (females). Comparison of means adjusted to total length was valid only for body width (males and females) and head length (males only). The null hypothesis of equal slopes among taxa was falsified for the other regressions. Males of *S. uluguruensis* have significantly wider bodies and shorter heads than males of *S. kirkii* and *S. vittatus* (Table 11). The body width of females does not vary significantly among taxa.

Probability values for slope differences among taxa for those regressions that did not meet the requirements of the covariance model are given in Table 12.

Body Segmentation.—In the mid-body region of caecilians, each primary annulus (body segment) is associated with one ribbed vertebra. In the neck there are a few vertebrae that are not associated with primary annuli, and the terminus of the vertebral column of most caecilians consists of a series of increasingly smaller vertebrae that have either small or no ribs and are not associated with primary annuli. The vertebral column of forms with unsegmented terminal shields may end anterior to the terminal shield as in *Siphonops* spp. or extend into the terminal shield as in the scolecomorphids. Scolecomorphids, and all other caecilians I have examined, have more vertebrae than primary annuli because of the additional vertebrae at either end of the column, but, because of the one-to-one relationship between vertebrae and primary annuli for most of the length of the body, the numbers of each are highly positively correlated both within and between populations.

At first thought, body size would not be expected to influence the number of body segments within homogeneous samples, because individuals do not add body segments as they grow. However, if the

TABLE 7

ANALYSIS OF COVARIANCE OF MORPHOMETRIC CHARACTERS OF *Scolecomorphus* SPECIES BY SEX: MEANS ADJUSTED TO BODY SIZE (TOTAL LENGTH)

	Adjusted Mean		F-test (P) Equal Slopes	F-test (P) Equal Adjusted Means
Body width				
S. kirkii			0.660	0.033*
♂♂ (n=15)	7.6	(0.24)[1]		
♀♀ (n=23)	8.7	(0.18)		
S. vittatus			0.694	0.460
♂♂ (n=14)	6.7	(0.28)		
♀♀ (n=8)	7.1	(0.39)		
S. uluguruensis			0.213	0.592
♂♂ (n=38)	7.9	(0.17)		
♀♀ (n=56)	7.8	(0.13)		
Head length				
S. kirkii			[0.040][2]	—
♂♂	—	—		
♀♀	—	—		
S. vittatus			0.610	0.882
♂♂	7.38	(0.173)		
♀♀	7.33	(0.238)		
S. uluguruensis			0.617	<0.001*
♂♂	6.52	(0.097)		
♀♀	5.96	(0.078)		
Head width				
S. kirkii			[0.022]	—
♂♂	—	—		
♀♀	—	—		
S. vittatus			0.186	0.596
♂♂	4.84	(0.196)		
♀♀	5.02	(0.268)		
S. uluguruensis			0.389	<0.001*
♂♂	4.60	(0.049)		
♀♀	4.14	(0.040)		
Internarial distance				
S. kirkii			[0.002]	—
♂♂	—	—		
♀♀	—	—		
S. vittatus			0.595	0.531
♂♂	1.89	(0.084)		
♀♀	1.79	(0.116)		
S. uluguruensis			0.452	0.002*
♂♂	1.57	(0.027)		
♀♀	1.45	(0.022)		

(*Continued*)

TABLE 7 (*Continued*)

	Adjusted Mean		F-test (P) Equal Slopes	F-test (P) Equal Adjusted Means
Tentacular aperture-narial distance				
S. kirkii			[<0.001]	—
♂♂	—	—		
♀♀	—	—		
S. vittatus			0.345	0.081
♂♂	1.30	(0.055)		
♀♀	1.12	(0.075)		
S. uluguruensis			0.932	<0.001*
♂♂	1.09	(0.026)		
♀♀	0.96	(0.021)		

[1]Values in parentheses are standard errors of adjusted means
[2]P-values in brackets are those that indicate unequal slopes
*Indicates significantly different adjusted means

TABLE 8

STATISTICS FOR REGRESSIONS THAT HAVE UNEQUAL SLOPES BETWEEN SEXES IN *Scolecomorphus kirkii*: INDEPENDENT VARIABLE IS TOTAL LENGTH

	Regression Coefficient	r^2	F-test (P) (H^0: b=0)	Intercept
Head length				
♂♂	0.024	0.498	0.003	1.420
♀♀	0.010	0.469	<0.001	4.689
Head width				
♂♂	0.021	0.787	<0.001	−0.646
♀♀	0.011	0.621	<0.001	1.609
Internarial distance				
♂♂	0.012	0.706	0.001	−1.193
♀♀	0.004	0.365	0.002	0.807
Tentacular aperture-narial distance				
♂♂	0.007	0.669	<0.001	−0.456
♀♀	0.000	0.007	0.707	1.332

TABLE 9

ANALYSIS OF COVARIANCE OF MORPHOMETRIC AND MERISTIC CHARACTERS OF *Scolecomorphus* SPECIES: MEANS ADJUSTED TO BODY SIZE (TOTAL LENGTH), MEASUREMENTS IN MM, VARIABLES UNTRANSFORMED

MALES

	Adjusted Mean		F-test (P) Equal Slopes	Regression Coefficient	r^2	Intercept
Body width			0.904			
S. kirkii (n = 15)	6.6	(0.21)[1]		0.0138	0.303*	3.367
S. vittatus (n = 14)	6.6	(0.21)		0.0170	0.612*	2.603
S. uluguruensis (n = 38)	7.5	(0.12)		0.0151	0.265*	3.894
Head length			0.321			
S. kirkii	7.25	(0.149)		0.2370	0.498*	1.420
S. vittatus	7.32	(0.147)		0.0194	0.764*	2.729
S. uluguruensis	6.26	(0.085)		0.0154	0.569*	2.590
Head width			[0.010][2]			
S. kirkii	4.68	(0.099)		0.0209	0.787*	−0.646
S. vittatus	4.78	(0.098)		0.0099	0.606*	2.408
S. uluguruensis	4.45	(0.057)		0.0091	0.519*	2.285
Internarial distance			[<0.001]			
S. kirkii	1.92	(0.057)		0.0121	0.706*	−1.193
S. vittatus	1.88	(0.057)		0.0062	0.744*	0.430
S. uluguruensis	1.54	(0.033)		0.0025	0.242*	0.948
Tentacular aperture-narial distance			[0.046]			
S. kirkii	1.30	(0.042)		0.0069	0.669*	−0.456
S. vittatus	1.31	(0.042)		0.0036	0.525*	0.450
S. uluguruensis	1.04	(0.024)		0.0026	0.312*	0.415
No. primary annuli			[0.003]			
S. kirkii	133.0	(1.20)		0.0014	0.000	135.060
S. vittatus	131.1	(1.19)		0.0946	0.466*	109.840
S. uluguruensis	129.8	(0.69)		0.0021	0.000	129.100
No. vertebrae			[0.002]			
S. kirkii	144.7	(1.23)		0.0289	0.036	154.020
S. vittatus	142.4	(1.22)		0.0927	0.506*	121.660
S. uluguruensis	140.4	(0.71)		0.0002	0.000	140.250
No. premaxillary-maxillary teeth			0.346			
S. kirkii	18.7	(0.48)		0.0386	0.172	8.783
S. vittatus	18.8	(0.48)		0.0218	0.259	13.725
S. uluguruensis	17.7	(0.28)		0.0110	0.079	15.045
No. prevomeropalatine teeth			0.410			
S. kirkii	16.4	(0.57)		0.0530	0.265*	3.267
S. vittatus	15.8	(0.56)		0.0436	0.540*	5.600
S. uluguruensis	14.7	(0.33)		0.0277	0.211*	8.044

(*Continued*)

TABLE 9 (*Continued*)

MALES

	Adjusted Mean		F-test (P) Equal Slopes	Regression Coefficient	r^2	Intercept
No. dentary teeth			[0.001]			
S. kirkii	24.6	(0.81)		0.1548	0.661*	– 15.929
S. vittatus	24.1	(0.80)		0.0368	0.277	14.976
S. uluguruensis	20.1	(0.46)		0.0391	0.299*	10.766

[1] Standard error of adjusted mean in parentheses
[2] P-values in brackets are those that indicate unequal slopes
* Significant at P <0.05

TABLE 10

ANALYSIS OF COVARIANCE OF MORPHOMETRIC AND MERISTIC CHARACTERS OF *Scolecomorphus* SPECIES: MEANS ADJUSTED TO BODY SIZE (TOTAL LENGTH), MEASUREMENTS IN MM, VARIABLES UNTRANSFORMED

FEMALES

	Adjusted Mean		F-test (P) Equal Slopes	Regression Coefficient	r^2	Intercept
Body width			0.096			
S. kirkii (n = 23)	8.0	(0.25)[1]		0.0099	0.224*	5.569
S. vittatus (n = 8)	8.1	(0.37)		0.0199	0.584*	2.275
S. uluguruensis (n = 56)	8.5	(0.15)		0.0225	0.446*	1.963
Head length			[0.017]			
S. kirkii	7.41	(0.149)		0.0100	0.469*	4.689
S. vittatus	8.39	(0.220)		0.0217	0.900*	2.119
S. uluguruensis	6.47	(0.088)		0.0136	0.449*	2.460
Head width			[0.002]			
S. kirkii	4.82	(0.104)		0.0109	0.621*	1.609
S. vittatus	5.71	(0.153)		0.0164	0.657*	0.983
S. uluguruensis	4.47	(0.061)		0.0076	0.553*	2.203
Internarial distance			[0.031]			
S. kirkii	1.92	(0.053)		0.0037	0.365*	0.807
S. vittatus	2.07	(0.079)		0.0050	0.475	0.620
S. uluguruensis	1.54	(0.031)		0.0173	0.157*	1.009
Tentacular aperture-narial distance			[0.023]			
S. kirkii	1.31	(0.038)		0.0002	0.007	1.332
S. vittatus	1.27	(0.056)		0.0023	0.565*	0.595
S. uluguruensis	1.04	(0.022)		0.0025	0.301*	0.313

(*Continued*)

TABLE 10 (*Continued*)

FEMALES							
	Adjusted Mean		F-test (P) Equal Slopes	Regression Coefficient	r^2	Intercept
No. primary annuli			0.190			
S. kirkii	146.0	(0.95)		0.0174	0.056	152.230
S. vittatus	135.8	(1.41)		0.0054	0.005	137.280
S. uluguruensis	141.2	(0.56)		0.0212	0.052	135.310
No. vertebrae			0.203			
S. kirkii	157.0	(1.00)		0.0222	0.076	164.750
S. vittatus	146.7	(1.48)		0.0029	0.001	147.440
S. uluguruensis	151.1	(0.59)		0.0190	0.044	145.860
No. premaxillary-maxillary teeth			0.721			
S. kirkii	17.5	(0.42)		0.0148	0.098	12.997
S. vittatus	19.6	(0.63)		0.0156	0.134	15.108
S. uluguruensis	16.8	(0.25)		0.0084	0.062	14.241
No. prevomeropalatine teeth			[0.009]			
S. kirkii	15.2	(0.54)		0.0468	0.423*	0.256
S. vittatus	15.2	(0.80)		0.0214	0.228	8.959
S. uluguruensis	14.9	(0.32)		0.0086	0.039	12.102
No. dentary teeth			0.083			
S. kirkii	22.4	(0.66)		0.0261	0.095	15.313
S. vittatus	25.9	(0.97)		0.0633	0.855*	7.671
S. uluguruensis	20.1	(0.39)		0.0302	0.254*	11.157

[1] Standard error of adjusted mean in parentheses
* Significant at $P < 0.05$

larger individuals of a population are larger by virtue of having more body segments, then a positive correlation between total length and both the number of primary annuli and the number of vertebrae would occur. In limbless, burrowing forms such as caecilians, in which there are likely to be functional design limitations on the size and number of body segments per unit body length, body size variation may be determined virtually by variation in the number of body segments. These speculations are supported by the patterns of within- and between-sex covariation of size and number of body segments in the species of *Scolecomorphus*.

The regression coefficients and r^2-values for the number of primary annuli and the number of vertebrae versus total length are positive within sexes of all three species of *Scolecomorphus* (Tables 9–10). But the relationships are weak, and statistically significant only for the male population of *S. vittatus*. The samples of both sexes of this latter species are small and geographically heterogeneous which are conditions that obscure the meaning of the relatively high r^2-value for males.

TABLE 11

RESULTS OF MULTIPLE COMPARISON (SHEFFÉ) OF SIZE-ADJUSTED MEANS (TABLES 9 AND 10): RESULTS ARE GIVEN ONLY FOR THOSE COMPARISONS THAT MET THE COVARIANCE MODEL REQUIREMENT OF EQUAL SLOPES

	S. kirkii vs. *S. vittatus*		*S. kirkii* vs. *S. uluguruensis*		*S. vittatus* vs. *S. uluguruensis*	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Body width	NS	NS	**	NS	**	NS
Head length	NS	—	**	—	**	—
Number primary annuli	—	**	—	**	—	**
Number vertebrae	—	**	—	**	—	**
Number premaxillary-maxillary teeth	NS	**	NS	NS	NS	**
Number prevomeropalatine teeth	NS	—	**	—	NS	—
Number dentary teeth	—	**	—	NS	—	**

NS = not significant at 0.95 level
** = significant at 0.95 level

TABLE 12

P-SCORES (F-TEST) FROM COMPARISON OF SLOPES (TABLES 9 AND 10) OF VARIABLES REGRESSED ON TOTAL LENGTH: SCORES ARE PROVIDED ONLY FOR THOSE COMPARISONS THAT DID NOT MEET THE COVARIANCE MODEL REQUIREMENT OF EQUAL SLOPES IN A THREE-WAY COMPARISON

	S. kirkii vs. *S. vittatus*		*S. kirkii* vs. *S. uluguruensis*		*S. vittatus* vs. *S. uluguruensis*	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Head length	—	0.003	—	0.287	—	0.035
Head width	0.022	0.172	<0.001	0.071	0.739	0.011
Internarial distance	0.023	0.492	<0.001	0.068	0.002	0.011
Tentacular aperture-narial distance	0.110	0.026	0.005	0.008	0.337	0.831
Number primary annuli	0.101	—	0.924	—	0.002	—
Number vertebrae	0.036	—	0.486	—	0.002	—
Number prevomeropalatine teeth	—	0.186	—	0.001	—	0.284
Number dentary teeth	0.004	—	<0.001	—	0.892	—

The between-sex pattern of covariation of total length and number of body segments provides stronger evidence that size is determined largely by the number of body segments (rather than size of each body segment) in *Scolecomorphus*. The larger sex (females) of all three species have more primary annuli and vertebrae than the smaller sex (Figs. 6–7; Tables 1–3, 5).

The higher number of body segments in females may be related to reproductive potential. The ova and embryos of caecilians are arranged linearly, those of each side often alternating in position so that individual ova and/or embryos do not lie side-by-side. This arrangement apparently is necessary because of the extremely limited space in the coelom. An increase in coelomic capacity that would be effective in increasing the reproductive potential of females depends on increasing the length rather than the diameter of the coelom. In burrowing forms like the scolecomorphids, the diameter of the body is probably determined by locomotory limitations.

TOOTH COUNTS.—It is well-known that the number of teeth varies (usually positively) with body size in many species of amphibians. The r^2-values in Tables 9–10 indicate that the relationship between the number of premaxillary-maxillary teeth and total length is positive for both sexes of all three *Scolecomorphus* species, but that the relationships are not significant at $p<.05$. The same tables indicate that the effect of total length on the number of prevomeropalatine teeth and dentary teeth is positive in all cases, and significantly so in eight of the twelve cases.

The slopes of regressions of tooth numbers on total length are the same for the two sexes in all cases except for the dentary teeth of *Scolecomorphus kirkii* (Table 13). Sexual dimorphism and interspecific variation in tooth numbers are evident in *Scolecomorphus*, as can be seen from examination of the adjusted means and p-values of Tables 9–10, but, the differences are small, and tooth numbers could not be used to diagnose species.

MULTIVARIATE COMPARISON OF *SCOLECOMORPHUS* SPECIES

The three species of *Scolecomorphus* differ significantly in a number of morphometric and meristic traits. However, none of these traits, when used alone, will unambiguously identify individuals to species because the ranges of variation broadly overlap. It is of interest, therefore, to determine whether combinations of morphometric and meristic characters can be used to accurately identify individuals. In the present case, because individuals already have been assigned to three groups based on pattern of coloration, discriminant function analysis is the appropriate method for studying the multivariate relationships of individuals.

Quadratic discriminant functions generally have better discriminatory power than linear functions in systematic studies (Blackith and

TABLE 13

ANALYSIS OF COVARIANCE OF TOOTH COUNTS OF *Scolecomorphus* SPECIES BY SEX: MEANS ADJUSTED TO BODY SIZE (TOTAL LENGTH)

	Adjusted Mean		F-test (P) Equal Slopes	F-test (P) Equal Adjusted Means
Number premaxillary-maxillary teeth				
S. kirkii			0.348	0.012
♂♂ (n = 15)	20.1	(0.68)		
♀♀ (n = 23)	17.6	(0.52)		
S. vittatus			0.734	0.898
♂♂ (n = 14)	18.8	(0.71)		
♀♀ (n = 8)	18.7	(0.98)		
S. uluguruensis			0.747	<0.001
♂♂ (n = 38)	17.8	(0.23)		
♀♀ (n = 56)	16.4	(0.18)		
Number prevomeropalatine teeth				
S. kirkii			0.831	<0.001
♂♂	19.8	(0.78)		
♀♀	15.0	(0.59)		
S. vittatus			0.254	0.136
♂♂	15.7	(0.77)		
♀♀	13.5	(1.05)		
S. uluguruensis			0.083	0.159
♂♂	14.8	(0.31)		
♀♀	14.2	(0.25)		
Number dentary teeth				
S. kirkii			[0.003][2]	—
♂♂	28.3	(1.24)		
♀♀	23.0	(0.95)		
S. vittatus			0.243	0.658
♂♂	24.0	(0.90)		
♀♀	23.3	(1.23)		
S. uluguruensis			0.486	<0.001
♂♂	20.7	(0.36)		
♀♀	18.9	(0.29)		

[1]Values in parentheses are standard errors of adjusted means
[2]P-values in brackets are those that indicate unequal slopes
*Indicates significance at P <0.05

Reyment, 1971), and this appears to be true in the present study. Assuming that the three groups have been accurately defined based on coloration, then 88.0 percent of male *Scolecomorphus* would be accurately assigned to species using linear discriminant functions of morphometric and meristic variates (listed in Tables 14–15) and equal prior probabilities of classification, with improvement to 97.0 percent accuracy using quadratic functions. Unfortunately, the small sample size of female *S. vittatus* disallows the use of quadratic discriminant functions for that group, and linear functions were used instead. In the latter case, 95.4 percent of females were accurately assigned to species. The constants and coefficients for linear functions are listed in Tables 14–15.

Canonical discriminate functions were determined for the three species by sex, and the distributions of individuals on the two canonical variates are shown in Figures 8 and 9. Among males (Fig. 8), *Scolecomorphus uluguruensis* forms a cluster that is distinct from both *S. kirkii* and *S. vittatus*. *S. uluguruensis* is separated from the latter two species almost entirely by the first canonical variate, which accounts for 90.4 percent of the variance. The second canonical variate, which accounts for the remaining variance, partially separates *S. kirkii* and *S. vittatus*. The latter species has the widest scatter on the second canonical variate, and this may reflect the geographical heterogeneity of the *S. vittatus* sample.

For the female sample, the two canonical variates were more nearly equal in size, with only 64.8 percent of the variance accounted for by the first canonical variate. Again, however, the first component largely separates *Scolecomorphus uluguruensis* from both *S. kirkii* and *S. vittatus*, and the second component entirely separates the latter two species (Fig. 9).

The results of discriminant function analysis and canonical discrimi-

TABLE 14

LINEAR DISCRIMINANT FUNCTIONS FOR MALE *Scolecomorphus*

	S. kirkii	*S. vittatus*	*S. uluguruensis*
Constant	−923.150	−901.500	−855.050
Total length	−1.339	−1.371	−1.262
Body width	9.811	9.882	12.266
Head length	26.314	26.001	22.219
Head width	56.455	58.228	59.971
Internarial distance	−59.063	−61.100	−64.755
Tentacular aperture-narial distance	−6.285	−5.191	−15.347
No. primary annuli	−2.717	−2.856	−2.465
No. vertebrae	13.285	13.298	12.610
No. premaxillary-maxillary teeth	10.395	10.840	10.852
No. prevomeropalatine teeth	−2.596	−2.872	−2.741
No. dentary teeth	1.968	1.749	1.341
N	15	14	38

TABLE 15

LINEAR DISCRIMINANT FUNCTIONS FOR FEMALE *Scolecomorphus*

	S. kirkii	*S. vittatus*	*S. uluguruensis*
Constant	−887.620	−815.480	−809.030
Total length	−0.229	−0.319	−0.233
Body width	−1.234	−1.434	−0.450
Head length	29.100	30.526	27.063
Head width	−4.824	0.464	−3.484
Internarial distance	0.428	−1.407	−4.730
Tentacular aperture-narial distance	−53.941	−62.722	−57.909
No. primary annuli	6.310	6.329	6.357
No. vertebrae	4.368	3.804	3.979
No. premaxillary-maxillary teeth	5.373	5.989	5.270
No. prevomeropalatine teeth	1.025	0.703	1.156
No. dentary teeth	0.241	0.592	0.103
N	23	8	56

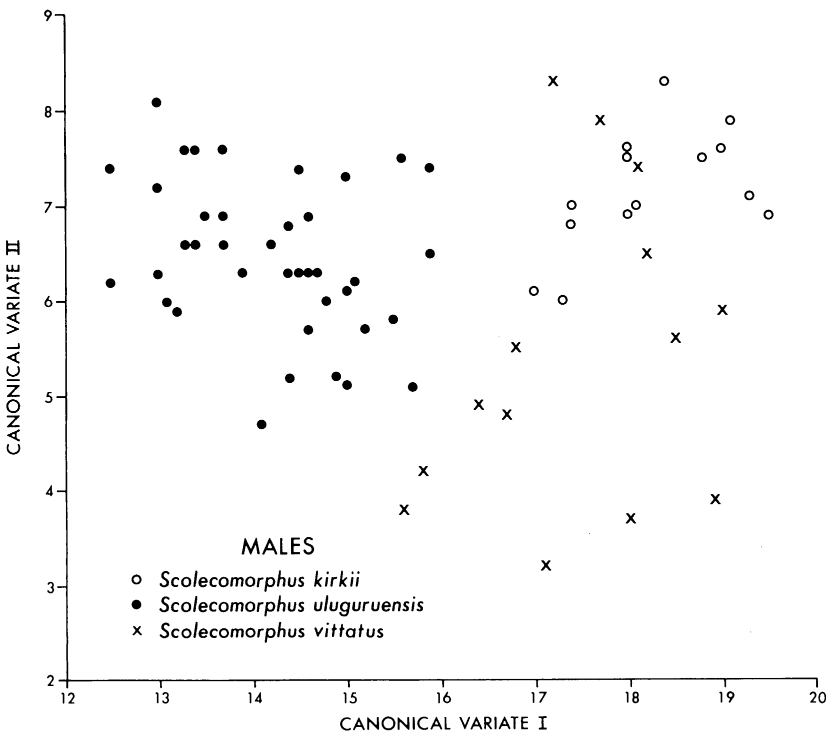

FIG. 8. Scatter of individual males on the two canonical variates. The first canonical variate accounts for 90.4 percent of the variance.

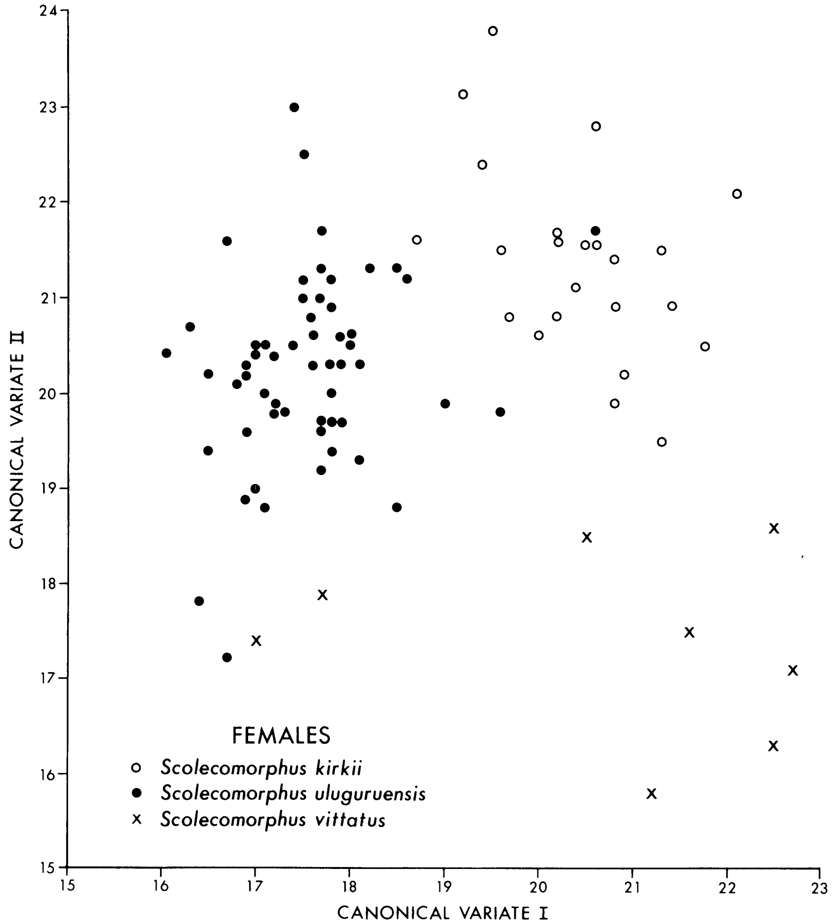

FIG. 9. Scatter of individual females on the two canonical variates. The first canonical variate accounts for 64.8 percent of the variance.

nant function analysis based on morphometric and meristic characters largely confirm the taxonomic distinctness of the three species of *Scolecomorphus* as defined by coloration alone. Reexamination of those few individuals misclassified by these methods did not convince me that they were originally misclassified on the basis of their coloration. Instead, it appears that some combination of their morphometric characteristics is extreme compared to the average for their group. For example, the single female *S. uluguruensis* that is assigned to another species (*S. kirkii*) by discriminant function analysis and clusters with *S. kirkii* in canonical analysis (Fig. 9) is the largest female by 22 mm total length and has relatively the largest head of the *S. uluguruensis* sample. The unusually large size of this specimen undoubtedly accounts for its misclassification. The color pattern is unequivocally that of *S. uluguruensis*.

KEY TO SCOLECOMORPHID CAECILIANS

1. Prevomerine and palatine teeth in continuous series, not interrupted by choanae; palatine series of teeth do not extend posterior to maxillary series of teeth (*Crotaphatrema*) 2
   Prevomerine and palatine series of teeth interrupted by choanae; palatine series of teeth extend posterior to maxillary series of teeth (*Scolecomorphus*) 3
2. Fewer than 115 primary annuli; head parallel-sided, snout rounded; more than 28 dentary teeth . . . . *Crotaphatrema bornmuelleri*
   More than 114 primary annuli; head subtriangular, snout acuminate; fewer than 29 dentary teeth . . *Crotaphatrema lamottei*
3. Dark dorsal coloration encroaches onto mid-ventral region completely encircling the midbody in large juveniles and adults; area under chin and throat and ventral region of terminus of body are light-colored . . *Scolecomorphus uluguruensis*
   Dark dorsal coloration does not encroach onto ventral surface except possibly in immediate vicinity of cloacal opening 4
4. Dark dorsal coloration extends onto lateral surfaces past mid-lateral line to or slightly onto ventral surface; dorsal coloration may nearly or completely encircle body in vicinity of cloacal opening . . . . . . *Scolecomorphus kirkii*
   Light ventral coloration (yellow to cream) more extensive than dark dorsal coloration; dark dorsal coloration may be restricted to a narrow dorsal stripe or band, or may extend half way down lateral surfaces of body . . . . *Scolecomorphus vittatus*

DISCUSSION

The fauna and flora of the isolated, forested highlands ($\geq$ 1,500 m elevation) of equatorial East Africa have long been claimed to bear closer affinities to their counterparts in West Africa than to the flora and fauna of the surrounding lowland savannahs and plains (Gregory, 1896). Loveridge (1933), for example, calculated that 31 percent of amphibian and 100 percent of reptilian genera that occur in the Uluguru and Usambara Mountains of Tanzania also occur in West Africa. Unfortunately, it is difficult to assess the purported herpetological relationship between the two regions because comparisons have been based on species lists assembled from diverse sources that do not include detailed cladistic analyses.

Caecilians are potentially excellent subjects for the study of east-west

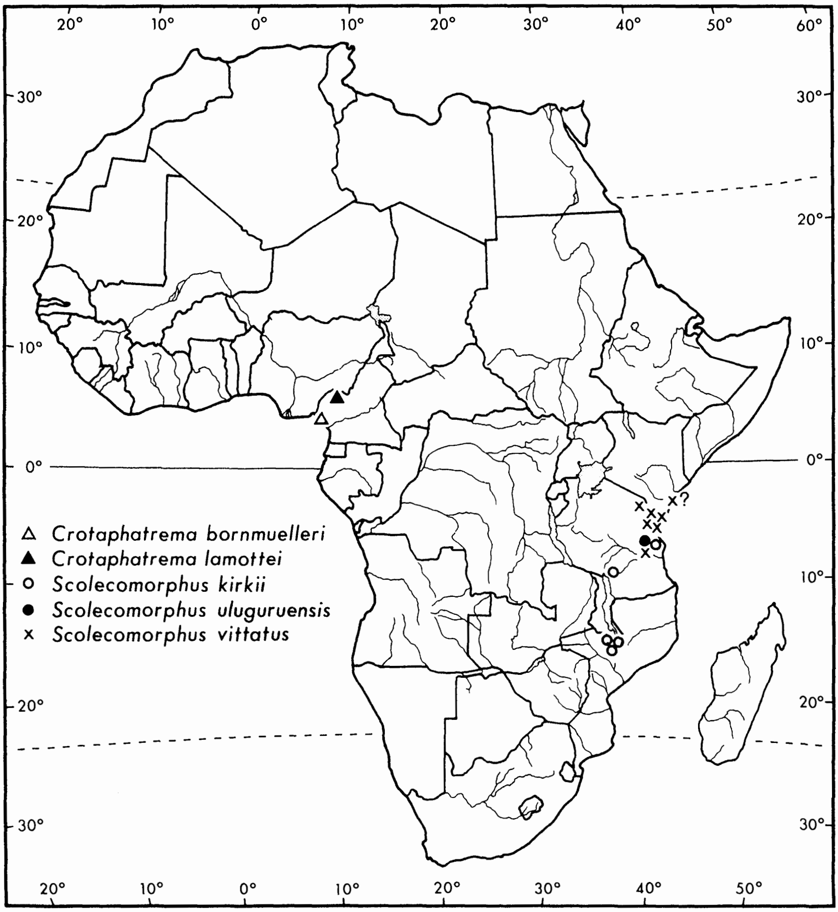

FIG. 10. Distribution of scolecomorphid caecilians. The question mark indicates a Kenyan locality for *Scolecomorphus vittatus* at the seaport of Mombasa that needs verification.

disjunctions in equatorial Africa because they have limited means of dispersal and have restrictive habitat requirements. Furthermore, the distribution of African caecilians as a group apparently is disjunct, with a western group centered around the Gulf of Guinea and an eastern group ranging from west-central Ethiopia to southern Malawi. However, the absence of caecilians from central equatorial Africa (Burundi, Rwanda, eastern Zaire, Uganda) may be artifactual, as caecilians are notoriously difficult to collect and the region is poorly known herpetologically.

There are two families and eight genera of caecilians in Africa. The family Scolecomorphidae is disjunct with one West African and one East African genus (Fig. 10). Of the six genera of African caeciliids, two (*Herpele*, *Idiocranium*) are West African, two (*Afrocaecilia*, *Boulengerula*) are East African, and two (*Geotrypetes*, *Schistometopum*) occur in both West and East Africa. Studies in progress indicate that *Herpele* and *Idiocranium* are distinctive western forms with no close relationship to other African caecilians and that *Afrocaecilia* and *Boulengerula* form a closely related pair of East African genera. With the division of *Scolecomorphus* into eastern and western genera, *Geotrypetes* and *Schistometopum* remain the only caecilian genera represented on both sides of the African continent. Detailed anatomical studies of these latter two genera are needed to determine whether the disjunctions are real at the generic level.

SUMMARY

Caecilians of the strictly African family Scolecomorphidae were systematically reviewed. Prior to this study, the family consisted of a single genus, *Scolecomorphus*, with two West African (*bornmuelleri lamottei*) and five East African (*attenuatus*, *convexus*, *kirkii*, *uluguruensis*, *vittatus*) species. It was shown that the West and East African forms differ markedly in skull morphology, to the extent that the family had to be redefined and a new genus, *Crotaphatrema*, named for the two West African species. *Scolecomorphus attenuatus* was placed in junior synonymy with *S. uluguruensis*, and *S. convexus* in junior synonymy with *S. kirkii*.

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