Studies on Amphisbaenians (Reptilia)
8. Two Genera of Small Species from East Africa
(Geocalamus and Loveridgea)

CARL GANS¹ AND DAVID M. KRAKLAU²

ABSTRACT

This study, the last of this series, reports on most known specimens, including all types, of the amphisbaenian genera Geocalamus and Loveridgea, characterizing two species of each. Redefinition of species allows assignment of a specimen from Ushora to G. acutus rather than G. modestus, and introduces new records extending the range of the former into Tanzania. We confirm Loveridge's observation that L. ionidesii is viviparous. A key to the species is included, as are some comments on specimens of the sympatric forms of Ancylocranium and Chirindia.

INTRODUCTION

The African continent contains 58 described species pertaining to 12 genera of amphisbaenians (Gans, 1967, 1987). Most of the genera extend over quite large ranges: thus the generalized (= rounded-headed, Gans, 1968) Chirindia occupies a belt from Tanzania south to Natal (Broadley and Gans, 1978a), Zygaspis from southern Malawi south to South Africa, and thence north through west central Africa to Zaire (Saiff, 1970; Broadley and Gans, 1975, 1978b; Stevens, 1974); and Cynisca from Gabon to Sénégal (Gans, 1987). The spade-snouted genera Monopeltis and Dalophia also have vast ranges (Broadley et al., 1976; Gans, 1976; Gans and Latifi, 1971; Gans and Lehman, 1973). In contrast, the keel-snouted genera appear geographically more restricted. Although the highly derived Ancylocranium ranges from southern Tanzania to Somalia, each of its species has a very localized range (Gans and Kochva, 1966) and the monotypic genus Baikia (known from only eight specimens, Dunger, 1965) occurs only in central Nigeria.

The present study, the last of this series, reports on two small genera, the keel-snouted Geocalamus Günther (1880) and the round-headed Loveridgea Vanzolini (1951b), both from East Africa (Kenya and Tanzania). Each

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includes two species. These forms are here reviewed, on the basis of all available specimens. For the species *Loveridgea ionidesii*, we report on extremely large and previously incompletely analyzed series of 459 specimens deriving from the spectacular collecting efforts of the late C. J. P. Ionides. We also report on an additional amphisbaenian record for Tanzania.

**MATERIALS**

The approximately 512 specimens discussed derive from the following collections (identified by abbreviations throughout the text) and we are grateful to the curators (names given in parentheses) for assistance with loans or hospitality during visits. A complete table of meristic data has been deposited in the herpetology department of the American Museum of Natural History. Loveridge (1956b) noted that part of the material collected by C. J. P. Ionides was deposited at the Tanzania Game Department Collection in Dar es Salaam. This is the only material reported for the group that could not be located. A statistical test of the three major subsets of this material (BM, MCZ, NMK) showed some differences that are reported in the account of *Loveridgea ionidesii*. These and the discovery of the embryos justify the reexamination of all of this material.

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<tr>
<th>AMNH</th>
<th>American Museum of Natural History, New York City, New York (C. W. Myers and R. G. Zweifel)</th>
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<tr>
<td>BMNH</td>
<td>British Museum (Natural History), London, England (A. G. C. Grandison, N. Arnold, and A. Stimson)</td>
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<td>CG</td>
<td>Carl Gans Collection, Ann Arbor, Michigan</td>
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<td>Carnegie Museum, Pittsburgh, Pennsylvania (C. J. McCoy, Jr.)</td>
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<td>Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (J. Gosse)</td>
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<td>KMH</td>
<td>Kim M. Howell Collection, Dar es Salaam</td>
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<td>Museum of Comparative Zoology, Cambridge, Massachusetts (E. E. Williams)</td>
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<td>National Museum of Kenya, Nairobi, Kenya (Alex MacKay)</td>
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<td>Senckenbergische naturforschende Gesellschaft, Frankfurt-am-Main, Germany (K. Klemmer)</td>
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<td>VC</td>
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<td>ZMB</td>
<td>Zoologisches Museum der Universität, Berlin, D.D.R. (G. Peters)</td>
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Methods of measurement and description are those described in Gans and Alexander (1962) and Gans (1966, 1987).

**STATUS**

The genus *Geocalamus* has been recognized and left without significant discussion since the 1941 review of African amphisbaenians by Loveridge.

In 1947, Laurent reviewed the generic status of African amphisbaenians. Loveridge (1941) had placed all African round-nosed amphisbaenians, except the species *feae* and *degrysi*, into the genus *Amphisbaena*. However, Laurent retained only *dolichomenta*, *phylofiniens*, *quadrifrons*, and *violacea* in the otherwise South American *Amphisbaena*. He placed the East African species into *Chirindia* and the West African species into *Cynisca*. In 1950, Battersby described *Amphisbaena ionidesii*. Vanzolini (1951a, 1951b) extended the generic separation of African and American “*Amphisbaena*” by assigning *phylofiniens* and *ionidesii* to his new *Loveridgea*, and *dolichomenta* and *quadrifrons* to a genus now known as *Zygaspis*. Broadley and Gans (1978b) later noted that *violacea* belonged with the genus *Zygaspis*, restricting the genus *Amphisbaena* to South America.

Both *Geocalamus* and *Loveridgea* are easily recognizable externally, the former by the short, curved snout coupled with the postcephalic groove, and the latter by the four pairs of regular and enlarged cephalic shields. Coupled with the internal characteristics adduced by Vanzolini (1951a, 1951b; see also Gans, 1978), these suggest that the genera are valid.
KEY TO THE SPECIES OF 
GEOCALAMUS AND LOVERIDGEA 

1. Snout laterally compressed to form vertical keel; sulcus between head and first body annulus. Pectoral scales differentiated, interannular sutures forming posteriorly open chevron in this region. 196–243 body annuli. ............ (Geocalamus) 2

Snout not compressed laterally; head region fusiform. Pectoral scales not differentiated, interannular sutures crossing ventral surface at right angles to long axis. 237–257 body annuli. ............ (Loveridgea) 3

2. 196–226 body annuli; 19–24 caudal annuli; suture between nasal and first supralabial complete; two infralabials, rarely three; four postgenials in first row; ventral caudal surface past autotomy site never completely pigmented. ............ G. acutus 238–243 body annuli; 26–27 caudal annuli; suture between nasal and first supralabial incomplete; three infralabials; two postgenials in first row, occasionally four; ventral caudal surface, past autotomy site, completely pigmented. ............ G. modestus

3. Eye obvious externally; in discrete ocular. Frontals fused medially. 20–26 caudal annuli; autotomy at the 8th to 11th caudal annulus. Four precloacal pores. Medium sized (79–184 mm body length). ... L. ionidesii

Eye not obvious externally; no discrete ocular. Discrete frontals in partial or complete contact at a medial suture. 19–20 caudal annuli; autotomy at the fifth or sixth caudal annulus. Six precloacal pores. Generally larger sized (165–195 mm body length). ............ L. phylofiniens

GENUS GEOCALAMUS GÜNTER

Geocalamus Günther, 1880: 234. Type species: Geocalamus modestus, by monotypy. See discussion in Loveridge (1941: 401) and Vanzolini (1951b: 114).

DIAGNOSIS: Generally small to medium-size amphibiaenians with vertically oval head (snout-vent length of adults 190–250 mm); rostral shield reaching posteriorly to contact prefrontal shields, keeping discrete nasals from medial contact and being broadly visible in dorsal view; rostral and some adjacent shields sometimes keratinized; oculars and large postoculars distinct; neither a discrete precocular nor a supraocular; pair of enormous prefrontal shields in broad contact along the midline and reaching large frontoparietals posteriorly, enclosing an azygous (frontal) shield between them; sometimes with tiny occipitals; angulus oris lying at back of posterior suture of third supralabial; various segments of the temporal region, the postocular, and the frontoparietals lying dorsal to this supralabial; a small triangular postsupralabial; it and segments dorsal to it comprising dorsal part of first body annulus.

Lower jaw covered with small mental, postmental, and two or three infralabials; posterior half of latter representing a postinfralabial; first row of small segments following postmental; this shield only as wide as median pair of these postgenial segments, as lateral ones show but narrow contact; second row of small postgenial segments lying in postinfralabial zone and forming ventral portion of first body annulus; next one or two body annuli narrow and filled with small segments forming postcephalic groove.

Length of next six to seven annuli differing dorsally and ventrally from subequal lateral position; nuchal region showing anteriorly open V, although ventral neck region composed of posteriorly open V with midlines filled with imbricate segments; posterior body annuli regular, crossing the trunk at right angles; lateral sulci present, but dorsal and ventral sulci indicated only by alignment of sutures; four (sometimes two) precloacal pores; caudal autotomy sites always present, but occasionally difficult to discern; distal tip of tail usually regularly segmented, leading into terminal cone.

The generic diagnosis (Vanzolini, 1951b) includes the following characteristics: “Snout compressed, bent. Basipterygoid processes, parts posteriores choanarum and supratemporalis absent. Nasal bones very small. Den- tition: 3 premaxillary; 3 maxillary; and 6 mandibular teeth.”

Geocalamus acutus Sternfeld


Fig. 1. Map to note localities mentioned in text. Msuega was not located.

**DIAGNOSIS:** Species of *Geocalamus* with three supralabials and two infralabials; suture complete between nasal and first supralabial; only a single temporal segment between postocular and supralabial in first body annulus; four to eight small postgenial segments in second row between infralabials; body annuli 196 to 226, caudal annuli 19 to 24; autotomy site (when externally obvious) at fifth to ninth caudal annulus.

**FIGURES:** Figures 2 and 3 show views of the head, figure 4A segment proportions as well as pattern at midbody, figure 5A lateral view of tail and caudal region, figure 6A ventral surface of cloacal region, figures 18 and 19 body proportions, and figure 20 distribution of characters.

**DESCRIPTION:** *Geocalamus acutus* is a small to medium-size amphisbaenian. Specimens are a uniform plumbeous brown dorsally, lighter ventrally. Anteriorly, the darker pigmentation usually starts dorsally on the pa-
Fig. 2. *Geocalamus acutus*, dorsal, lateral, and ventral view of head of CG 4069. The line equals 1 mm to scale. Shields identified by numbers are: 1, rostral; 2, first supralabial; 3, second supralabial; 4, third supralabial; 6, nasal; 7, prefrontal; 8, ocular; 9, azygous frontal; 10, parietal; 11, mental; 12, first infralabial; 13, second infralabial; 16, postmental; 18, first row of postgenials; 19, second row of postgenials; 21, postocular temporal; 22, temporal.

Rietals, which are rarely unpigmented. The dorsoposterior corner of the postoculars is sometimes darkened. Anterior and lateral cephalic shields and segments are usually unpigmented (although the thickened keratinization of the keel lends it a darker hue). The narrowed nuchal annuli lack lightly pigmented segmental centers, or have reduced ones, so the nuchal region may appear lightly banded. Laterally the trunk color fades and the central pigmented portion of each segment shrinks, occasionally producing a checkerboard pattern two to six segments ventral to the lateral sulcus. The dorsal color becomes progressively darker toward the tail. The dorsal and lateral surfaces of the caudal end are a dark chocolate brown. Some segments of the ventral surface of the tail may be pigmented within the first postcloacal annuli (particularly the autotomy annulus); however, the ventral surface of the tail is commonly white and rarely are more than half of the segments pigmented. (A juvenile, MCZ 41115, is an exception with most of its subcaudal surface pigmented. In SMF 11831, the segments of the ventral surface of the tail, anterior to the autotomized and healed portion, appeared dusky over their entire surface. However, the ventral surface is lighter than the dorsolateral surfaces and the central dark zones drop out laterally in the typical checkerboard pattern.) The dorsal trunk segments are “a delicate flesh-pink in life” (Loveridge, 1936).

The snout is prognathous. A thickened keratinized sheath covers the rostral. In large
adults it may extend more thinly over the prefrontals and the median azygous (frontal) shield. The head is vertically oval in cross section; the neck is narrowed, then the body increases gradually to a greater and horizontally oval cross section by midtrunk. The shields of the anterior head show few major fusions. A large protruding rostral shield, which is broadly visible in dorsal view, posteriorly abuts the prefrontal shields, separating the small nasals medially. A pair of large prefrontal shields meet along the midline; and posteriorly diverge to enclose the anterior half of a medial diamond-shaped azygous shield. Posteriorly, each prefrontal broadly contacts the large frontoparietals lateral to the azygous. The pair of occipitals narrow medially and taper laterally.

The first supralabial is small and completely separated from the nasal. The second supralabial reaches the top of the nasal. The third supralabial is longer than high. The oculars and large postoculars are separate. The variably sized (compare figs. 2 and 3) triangular temporal lies between the third supralabial and the postocular. The prefrontal/ frontoparietal suture bisects the eye. The rectangular ocular lies diagonally above the second and the third supralabial suture. There are three supralabials and two infralabials; the angulus oris lies near the posterior edge of these shields. One specimen (MCZ 41114) shows a unilateral tiny supralabial, beneath the nasal, anterior to this series. (See Taxonomic Notes.) The postsupralabial is tiny; dorsally and ventrally it does not appear to correspond to discrete segments. (The postsupralabial and its fused dorsal and ventral continuations do not obviously represent remnants of a first body annulus. Also, MCZ 70165, preserved with the mouth open, suggests that the angulus oris lies at the tip of the triangular postsupralabial.)

The rostral is broadly visible in ventral view. The deep lower jaw is partially inset into the ventral surface of the snout. In ventral view, the mental appears as wide as the rostral portion of the labial edge; it tapers posteriorly to contact the narrower shield-shaped postmental. The first infralabials are large and the second almost twice as large (CG 4392 and BMNH 1966.909 have three infralabials, as they show a small discrete shield between the first and third); only the first contacts the postmental. The posterior portion of the enormous second infralabials extends into the postinfralabial zone. A first row of four small segments follows the mental; the median pair of these postgenial segments lies immediately posterior to the postmental; the lateral segments rarely make contact. A second row of four to eight, most

commonly six, elongate postgenial segments follows (rarely is a segment of the first row continuous with one of the second); the posterior aspect of these may form the ventral portion of a first body annulus. The next one or two body annuli (here counted as the first) are narrow and filled with small segments forming the postcephalic groove laterally and ventrally behind the head.

The width, measured along the side, of the next five body annuli increases, the sixth being the widest. The dorsal interannular sutures form a shallow, anteriorly open V (with the medial region filled with imbricate segments) as the lateral extent of the head shields terminates anterior to the middorsal position (back of the occipitals). The back of the sixth annulus forms a more obtuse posteriorly open V and by the tenth or so annulus the posterior body annuli are regular, crossing the trunk at right angles. In ventral view, the second through seventh annuli break medially into irregular segments, they are generally shorter ventrally than laterally, and the two or more thereafter longer. This generates a posteriorly open postpectoral V.

Specimens have 196 to 226 body annuli, from the first segments posterior to the angulus oris up to and including the pore-bearing precloacal row. There are no obvious intercalations or fusions, except for a spiral displacement just anterior to the cloaca. At midbody an annulus contains 16 to 20 dorsal segments, each generally twice as long as wide, and 18 to 22 ventral ones, the medial about 80 percent as wide as long. The cloacal region corresponds to three to five lateral annuli. The tail bears 19 to 24 caudal annuli, the last

being partly incorporated into an oval caudal tip. The variably expressed autotomy site (21 specimens have complete tails, 4 have broken and at least partially healed tails, and 2 have broken and unhealed tails) falls between the 5th and 9th caudal annulus.

There are four (2 in the Dodoma specimen) relatively small round precloacal pores or pore scars, each inset into a lateral corner of the posterior edge of one of the median segments of the last body annulus. The elongate precloacal shield consists of two wide median plus two to three narrower flanking segments (total 6–8), and the precloacal edge bears a few tiny triangular segments. The narrow postcloacal edge is formed of 11 to 18 segments.

The trunk is generally horizontally oval; however, it becomes slightly higher than wide just anterior to the cloacal region and the tail is slightly compressed vertically. The lateral sulci start at the level of the 45th body annulus and extend down to some 10 annuli anterior to the level of the cloaca, are filled with small triangular segments and, at mid-body, are approximately one-half as wide as one of the flanking segments. The middorsal and midventral sulci are indicated only by alignment of intersegmental sutures.

**RANGE:** Southeastern Kenya to northeastern Tanzania.

**SPECIMENS AND OTHER RECORDS:** **Kenya:**
- Galana, Kilifi: MCZ 70164, 70165; NMK L/1921. Samburu, near Voi: BMNH 1963.506 (Loveridge, 1923a, 1923c), BMNH 97.11.17.15. Voi, flats of the Msinga Plantation (estate) and near the northwest foot of Mt. Mbololo: BMNH 1966.909; CG (unnumbered, ex MCZ); MCZ 41114–41116, 41121, 41122 (Loveridge, 1936, 1956a); MRAC 15147, USNM 217447 (ex MCZ 41123); VA (ex MCZ 41117; 41119); ZMB 22297 (lectotype of *Geocalamus acutus* Sternfeld, 1912; Loveridge, 1941; Nieden, 1913). Voi, East Tsavo Park airstrip (construction): CG 4061, 4062, 4372, 4373, 4380–4384, 4391, 4392. Voi, East Tsavo park road: CG 4921, 4370–4373, 4377–4379. **Tanzania:** No further data: ZMB 21941 (lectoparatype of *Geocalamus acutus* Sternfeld, 1912).
- Moshi, SMF 11831 (formerly 5433a) [holotype *Geocalamus noltei*, Boettger, 1913; Loveridge, 1957 (checklist); Mertens, 1922]. Usora (Uschora, 15 km west of Ussure, or Usure, D. G. Broadley in litt.), Iramba dist.: MCZ 18293 (Loveridge, 1923c, 1941, 1944a). Dodo: KMH 6058.

**BIOLOGICAL MISCELLANEA:** Specimens were found in sandy soil on the flats at Msinga Estate not far from the Voi River, in upland...
savannah, not associated with gallery forest (Loveridge, 1937, 1941) and were collected at Voi one day after drenching rains (Loveridge, 1937, 1956a). The stomach of a large amphibiaenid contained a young worm or caecilian, another some skin of what may have been a caterpillar. In all there was much soil and grit (Loveridge, 1936, 1941, 1956a). No signs of gestation were noted in specimens taken at Voi between 7 and 13 April (Loveridge, 1941).

During construction of an airstrip at Voi (7–8 August 1969), CG collected 12 specimens dug up by bulldozers in sandy soil. Widening of a road crossing the Aruba creek above Aruba Dam approximately 3 km north-east of the Voi gate of Tsavo National Park, Kenya, provided an opportunity to check the distribution of specimens along a 2 km transect after intermittent light rains during the night. A bulldozer was widening a trail by about 3 m and cutting the top 20 cm of soil. Rain had penetrated less than 15 cm. No Geocalamus were found in the blackish soil of the narrow flood plain; however, most were taken in the immediately adjacent reddish sandy soil (2–4 m above stream level), with concentration of specimens reduced further away from (and approximately 4–8 m above) the river. Animals were in definitely formed tunnels. Frequency of cut specimens (50%) suggested that many showed head-up vertical orientation, perhaps associated with recent rainfall (CG, personal obs.).

A damaged specimen (MCZ 18293) was recovered from the stomach of a banded mongoose (Mungos mungo colonus; Loveridge, 1923a, 1923c, 1944a).

TAXONOMIC REMARKS: The skull has been illustrated and discussed (Zangerl, 1944; Vanzolini, 1951a, 1951b; also mentioned in Bellairs, 1950).

Specimens had 134 to 135 vertebrae (3 on neck, 106 on trunk, 4 cloacal, 21–22 caudal), and an atlas with a tiny hypocentrum. Vertebrae and ribs have been described (Zangerl, 1945). The dermal vertebral ratio is 2:1 on the trunk, and 1:1 on the tail (Alexander and Gans, 1966). CG 4262 has poorly everted hemipenes.

The types match the description well. The very large and stout holotype of Geocalamus noltei does have an autotomized and healed tail. This confirms Loveridge's (1941) comment that the name is a synonym of G. acutus. The “absence” of an eye represents an adult condition and the other characteristics adduced in the posthumous Boettger (1913) paper represent individual variation.

The illustration in Loveridge (1941) is faulty in showing a tiny extra supralabial. Only one specimen (MCZ 41114) showed such a segment azygously; in the illustrated specimen, the line indicates the limit of the heavy rostral keratinization, rather than a discrete segment.

The damaged specimen from Ushora once was ascribed to Geocalamus modestus (cf. Loveridge, 1941); however, this specimen appears to be a G. acutus. The cephalic keratinization of this seemingly juvenile specimen is restricted to the rostral. The suture between nasal and first supralabial is complete, unlike G. modestus. Its number of body annuli is 196, 46 less than the lowest value of the rest of G. modestus and even 13 less than the significantly lower values for G. acutus. Its autotomy site is lower than that of any other G. modestus, but all of the values of this small aggregate sample fall within the range of G. acutus. Finally, it has two rather than three infralabials, which is the pattern in G. acutus.

The assignment of this specimen to Geocalamus acutus is confirmed by the new record of G. acutus from Dodoma, which also has very low counts of body annuli plus being unique in having only two precloacal pores. The low count of body annuli and minor differences from the populations in southeastern Kenya suggest that there may be a distinct population of G. acutus (description of which is deferred in hopes that a more nearly adequate sample may come to hand). However, the geographically intermediate sample does not show intermediacy in characteristics and thus maintains the concept that the two forms of Geocalamus represent distinct species. In any case, there is merit to a search for additional specimens of this species in north-central and northeastern Tanzania.

Some of the head scale characteristics of Geocalamus modestus appear in individual specimens of G. acutus. Examples are BMNH 1966.909 and CG 4392 which have three infralabials and USNM 217447 which shows
Fig. 7. *Geocalamus modestus*. Dorsal, lateral and ventral view of head of BMNH 1946.9.1.12. The line equals 1 mm to scale.
the more extensive pattern of cephalic keratinization.

_Geocalamus modestus_ Günther


**DIAGNOSIS:** Species of _Geocalamus_ with three supralabials and 21/2 infralabials; suture between the nasal and first supralabial incomplete near its anterior end; multiple temporal segments between postocular and third supralabial; four to seven small postgenial annuli in second row between infralabials; body annuli 238 to 243, caudal annuli 26 to 27; autotomy site at sixth to eighth caudal annulus.

**FIGURES:** Figures 7 and 8 show views of head, segments are named in figure 2, figure 4B shows segment proportions as well as pattern at midbody, figure 5B lateral view of tail and caudal region, figure 6B ventral surface of cloacal region, figures 18 and 19 body proportions, and figure 20 distribution of characters.

**DESCRIPTION:** _Geocalamus modestus_ is a small to medium-size amphisbaenian. Specimens are a uniform plumbeous brown dorsally, lighter ventrally. Anteriorly, the darker pigmentation always starts on the paretials. The dorsoposterior corner of the postoculars is sometimes darkened. Anterior and lateral cephalic shields and segments are unpigmented (although the thickened keratinization of the keel lends it a darker hue). The lightly pigmented segmental centers are reduced on the narrowed nuchal annuli, so that the nuchal region seems lightly banded. Laterally the trunk color fades and the central pigmented portion of each segment shrinks; also the color drops out in a checkerboard pattern, two to three segments ventral to the lateral sulcus. The dorsal color becomes more intense along the back, being darkest toward the tail. The dorsal and lateral surfaces of the caudal end are a dark chocolate brown. Some segments of the ventral surface of the tail start to be pigmented within the first postcloacal annuli; all ventral segments are pigmented near and posterior to the autotomy annulus.

The dorsal trunk segments are "plumbeous," ventral segments "somewhat transparent" in life (Loveridge, 1923c).

The snout is prognathous. A thickened keratinized sheath covers the rostral, prefrontals, and the median azygous (frontal) shield. The head is vertically oval in cross section; the neck is narrowed, then the body increases gradually to a greater and horizontally oval cross section by midtrunk. The shields of the anterior head show few major fusions. A large protruding rostral shield, which is broadly visible in dorsal view, posteriorly abuts the prefrontal shields, separating the small nasal shields medially. A pair of enormous prefrontal shields meet widely along the midline; posteriorly they diverge to enclose the anterior half of a medial diamond-shaped azygous (frontal) shield. Posteriorly, each prefrontal broadly contacts the large frontoparietals lateral to the azygous (frontal). The pair of occipitals narrow medially and taper laterally.

The first supralabial is small and incom-
pletely separated from the nasal so that the anterior end of the common suture is absent. The second supralabial is as tall as the top of the nasal. The oculars and large postoculars are separate. The prefrontal/frontoparietal suture bisects the eye. The rectangular ocular lies diagonally above the second and the very large third supralabial suture. There are three supralabials and 2½ infralabials. The tiny postsupralabial is followed dorsally by a series of irregular segments that reaches the ventral edge of the postocular. (The postsupralabials and their dorsal continuation may represent remnants of a first body annulus; however, as these segments are even small in specimens of *G. acutus*, the counts of body annuli are given as starting after this zone.)

The rostral is broadly visible in ventral view. The deep lower jaw is partially inset into the ventral surface of the snout. The contact of the mental with the labial edge appears as wide as that of the rostral; posteriorly, the mental tapers to contact the narrower postmental. The first infralabials are small and the second twice as large; medially, both about the variably diamond-shaped postmental. The posterior portion of the large third infralabial extends into the postinfraceralial zone. A first row of small segments follows the mental, the median pair of these postgenial segments lies immediately posterior to the postmental; the lateral segments make only point or narrow contact. A second row of small postgenial segments follows; these form the ventral portion of the first body annulus. The next one or two body annuli are narrow and filled with small segments forming the postcephalic groove extending around the sides and bottom of the back of the head.

The width, measured along the side, of the next five body annuli increases, the sixth being the widest. The dorsal interannular sutures form an anteriorly open V (with the midline filled with imbricate segments) as the lateral extent of the head shields terminates anterior to the middorsal position (back of the occipitals). The back of the sixth annulus forms a more obtuse posteriorly open V and by the tenth or so annulus the posterior body annuli are regular, crossing the trunk at right angles. In ventral view, the second through sixth annuli break medially into small irregular segments, the next two are shorter ventrally than laterally, and the two or more thereafter much longer until the regular annuli are reached. This generates a posteriorly open postpectoral V.

Specimens have 238 to 243 body annuli, from the first segments posterior to the annulus oris up to and including the pore-bearing precloacal row. There are no obvious intercalations or fusions, except for a spiral displacement just anterior to the cloaca. At midbody an annulus contains 16 to 18 dorsal segments, each generally twice as long as wide and 18 to 20 ventral ones, the medial about 80 percent as wide as long. The cloacal region corresponds to three lateral annuli. The tail bears 26 or 27 caudal annuli, the last being partly incorporated into an oval caudal tip and the autotomy site (at which 2 tails from 4 specimens are broken) falls between the sixth and eighth caudal annulus.

There are four (once two) round precloacal pores, each inset into the center of the posterior edge of one of the median segments of the last body annulus. The elongate precloacal shield consists of two wide median plus two to three narrower flanking segments, and the precloacal edge bears a few tiny triangular segments. The narrow postcloacal edge is formed of 14 to 17 segments.

The trunk is generally horizontally oval; however, it becomes slightly higher than wide just anterior to the cloacal region and the tail is slightly compressed vertically. The lateral sulci start at the level of the 45th body annulus and extend to some 10 annuli before the level of the cloaca, contain small triangular segments, and at midbody are approximately one-half as wide as one of the flanking segments. The middorsal and midventral sulci are indicated only by alignment of intersegmental sutures.

**Range:** Central Tanzania.

**Specimens and Other Records:** Tanzania: Ikikuyu and Mpwapwa, Usgo dist.: BMNH 1946.9.1.10–1946.9.1.12 [syntypes *Geocolamus modestus* Günther, 1880; Bouleger, 1885 (illustrations); Loveridge, 1923c, 1941, 1944a (detailed discussion of history), 1957 (checklist); Nieden, 1913 (mention); Strauch, 1881; Werner, 1910 (key)]. Ikikuyu, some 80 mi south of Mpwapwa: MCZ 18294 (Loveridge, 1923a, 1941).

**Biological Miscellanea:** This species oc-
cupies upland savannah (Loveridge, 1937). The Ikikuyu specimen was taken in sandy soil (Loveridge, 1923a). Mpwapwa is also a locality for *Chirindia mpwapwaensis* taken while searching for *Geocalamus modestus* (Loveridge, 1932, 1944a).

**TAXONOMIC REMARKS:** The counts of the three syntypes agree with the original description. The mouth of one of them (BMNH 79.11.13.9:RR1946.9.1.11) had previously been cut open, extending the angulus oris.

Most of the specimens were taken in the vicinity of Ikikuyu and Mpwapwa and this small series shows only minor geographic variability.

**GENUS LOVERIDGEA VANZOLINI**


**DIAGNOSIS:** Generally small and slender-size amphisbaenians (snout-vent length of adults between 150 and 200 mm) with trunk rounded and long, conical noncompressed head covered with four pairs of enlarged shields, namely nasals, prefrontals, frontals, and parietals (the third, frontal, pair may be medially fused); rostral shield invisible in dorsal view; oculars discrete or fused to anterodorsal tip of second supralabial; neither preoculars nor postoculars, but three supralabials and three infralabials; no occipitals; one large postsupralabial which may be divided to form a temporal; both forming dorsal part of the first body annulus.

Lower jaw covered with a small mental, a postmental, and three infralabials, followed by a large postinfralabial or a small one with an enormous malar; first row of two to three small segments between infralabials contacts postmental; followed by irregular second row of small postgenial segments; pectoral scales not differentiated, interannular sutures crossing ventral surface at close to right angles to long axis.

Lateral sulci present, but dorsal and ventral sulci only indicated by alignment of sutures; four to six oval precloacal pores in both sexes; caudal autotomy site always present; tip of tail usually leading into unsegmented caudal cone.

The generic diagnosis (Vanzolini, 1951a, 1951b) includes the following characteristics of the skull: "Snout compressed, strongly bent. The premaxilla forms an anterior vertical keel. Basipterygoid processes and supratemporals absent. Partes posteriores choanarum present sometimes reduced. Quadrate rod-like. Dентition: 7 premaxillar; 4 maxillary; and 6 [actually 7 per Tornier, 1899] mandibular teeth."


**DIAGNOSIS:** Species of *Loveridgea* with eye apparent externally through a discrete ocular; frontals fused medially to form a V-shaped azygous shield; slightly less than three supralabials and three infralabials; first postsupralabial fused with postocular, second enormous and in medial contact with parietal, and third narrow; first postinfralabial narrow, in medial contact with enormous malar; two rows of postgenials, two to three segments in the first row, four irregularly (3–5) in the second; eight (7–10) postmalars; no occipitals; body annuli 232–257; caudal annuli 20–26; four round precloacal pores; autotomy site at the 8th to 11th caudal annulus (10–20% autotomized and healed); 12–16 dorsal and 14–18 ventral segments to a midbody annulus; medium size (79–184 mm body length).

**FIGURES:** Figures 9 and 10 show views of head, figure 4C segment proportions as well as pattern at midbody, figure 5C lateral view of tail and caudal region, figure 6C ventral surface of cloacal region, figures 18 and 19 body proportions, and figure 20 distribution of characters.

**DESCRIPTION:** *Loveridgea ionidesii* is a small to medium-size species. The syntypes are faded to a uniform pale brown. More recently collected specimens show an even brown dorsal color with the center of each segment very slightly more densely colored. Anteriorly, the pigmentation is rather dense on the parietals, less so on the temporals and sometimes the back of the frontals. The more anterior segments occasionally show a blotchy pattern.
The anterior and posterior ends of the trunk are more densely pigmented than the middle of the trunk; particularly the distal cap of autotomized and healed caudal tips is very dark. Laterally on the trunk, the color fades. Pigmented segments drop out in a checkerboard pattern, about one row of segments dorsal to the lateral sulcus, although some specimens have much of the venter pigmented. The segments on the underside of the tail generally are pigmented, although more lightly than those on the dorsal surface; segments of the lateroventral (not medioventral) edges of the tail tend to be colorless, producing a checkerboard pattern. (The ventral caudal surface is occasionally unpigmented.) Some postcloacals may be densely pigmented, others not. The autotomy annulus and the adjacent annuli are densely pigmented.

The rounded snout is prognathous and the head shields are not differentially keratinized. The rostral shield is invisible in dorsal view. Four pairs of enlarged shields, namely the nasals, prefrontals, (fused) frontals, and parietals cover the dorsal surface of the head. The nasals are always in broad contact along the dorsal midline and, along with the rostral, form the tip of the snout. Dorso-posteriorly, each nasal abuts one of the paired prefrontals. The shorter frontals are medially fused to produce a single V-shaped shield. The sub-triangular parietals form the posteriormost enlarged pair; their narrow and extended posterior tips lie at the level of the first body annulus. Posteriorly, they abut the medial pair of rectangular segments of the second body annulus (occipitals?); the next lateral segments of this annulus are significantly enlarged.

The first supralabial is elongate and dorsally makes point contact with the nasal and prefrontal; the second supralabial is taller, contacts the prefrontal, frontal (in point contact), and triangular ocular, through which the eye is visible. The third supralabial is higher than long and dorsally abuts the parietal. The posterior tip of the third supralabial may extend slightly beyond the angulus oris which corresponds to the posterior suture of the third infralabial. However, the suture between the postsupralabial and post-infralabial shields is deeper than that between other cephalic shields. The oculars are distinct, but there are no postoculars. The enormous postsupralabial dorsally abuts the parietal shields; all of these form the dorsal portion of the first body annulus.

The rostral is broadly visible in ventral view. The deep lower jaw is partially inset into the ventral surface of the snout. In ventral view, the mental starts as wide as the rostral portion of the labial edge, but slims down posteriorly to contact the anterior edge of the narrower shield-shaped postmental. The mental is flanked by smaller first infralabials. The postmental is flanked by first infralabials and much larger second ones. It has only point contact with the enormous malars. The third infralabial is narrowly rectangular and the single postinfralabial is smaller. The small postgenial segments of the first row number 2 (to 3), there are generally 3 (3-5) in the second and occasionally a third row with 4 to 5. Rarely are one or both lateral segments of the first row continuous with the second. However, the medial segment of the first row may extend to lie between the first and second rows. The “postmalar” row comprises generally 8, rarely 7 to 10 segments; they and the postinfralabials form the ventral portion of the first body annulus.

The ventral portions of the second to fifth body annuli are narrowed. Fewer than 1 percent of the specimens show ventral interruptions forming intercalated dorsal half-annuli in the anterior quarter of the trunk. The dorsal portion of the second through sixth body annuli is very slightly longer than the lateral and ventral ones. Pectoral scales are not otherwise differentiated; the more posterior interannular sutures cross the ventral surface at close to right angles to the long axis.

Specimens have 232 to 257 body annuli, from the first segments posterior to the angulus oris up to and including the pore-bearing precloacal row. One or very rarely two intercalations or fusions, sometimes involving a spiral displacement, occur just anterior to the cloacal of most specimens. At midbody an annulus contains 12 to 16 dorsal segments, generally slightly longer than wide, and 14 to 18 ventral ones, the medial about twice as wide as long. The cloacal region corresponds to three to four lateral annuli. The tail bears 20 to 26 caudal annuli, the last being partly
Loveridgea ionidesii. Dorsal, lateral, and ventral view of head of CG 1831. The line equals 1 mm to scale. Shields identified by numbers are: 1, rostral; 2, first supralabial; 3, second supralabial; 4, third supralabial; 5, first postsupralabial (if horizontally divided, upper part is temporal; 6, nasal; 7, prefrontal; 8, ocular; 9, fused frontal; 10, parietal (medial enlarged segments posterior to these would be called occipitals); 11, mental; 12, first infralabial; 13, second infralabial; 14, third infralabial; 15, first postinfralabial; 16, postmental; 17, malar; 18, first row of postgenials; 19, second row of postgenials; 20, postmalar segments.
incorporated into a narrow and vertically oval caudal tip. The variably expressed autotomy site (at which half the observed tails were broken and at least partially healed) falls between the 8th and 11th caudal annulus.

There are four generally substantial round to suboval precloacal pores (rarely pore scars, lacking cores), each inset into the posterior edge of one of the median segments of the last body annulus. (As far as could be checked the pores of sexually mature males always had a 50% larger diameter than those of females, and all pore scars occurred on females.) The elongate precloacal shield consists of two wide median plus two to six narrower flanking segments (total 4–8). The narrow postcloacal edge is formed of 10 to 16 segments.

The head is pointed and vertically oval in the preocular region, becoming of rounded cross section thereafter. The nuchal region barely narrows. Past it the trunk increases in diameter and has a generally round, slightly oval horizontal, cross section. The trunk is generally horizontally oval; however, it becomes slightly higher than wide just anterior to the cloacal region and the tail is slightly compressed vertically. The lateral sulci start at the level of the 45th body annulus and extend down to the level of the cloaca and, at midbody, are filled with some imbricate segments in a gap as wide as the flanking segments which are in turn approximately one-half as wide as the adjacent segments. The middorsal and midventral sulci are indicated only by alignment of intersegmental sutures.

**RANGE:** Southern District, Tanzania.


**BIOLOGICAL MISCELLANEA:** A plot of the times that specimens had been collected (fig. 13) indicates that Ionides obtained most specimens during the months from December through May, summer in southern Tanzania. A specimen, MCZ 52542 (180 + 22 mm), from Liwale, contained two embryos measuring 76 and 77 mm (Loveridge, 1955); however, these embryos were no longer with the specimen. MCZ 162443, although in poor condition, also contained an early embryo, but no trace of eggshell. More advanced embryos were seen in VM (ex MCZ 50015). All had been collected during the month of October. This confirms that the species seems to be viviparous (and explains why so few embryo-containing specimens are in collections).

Ionides noted that specimens betrayed their presence by pushing up little heaps of still damp black soil in areas from which the river had recently receded (Loveridge, 1951). Specimens were taken from the stomachs of *Amblyodipsas polypleys hildebrandti*, *A. ionidesii*, *Chlororhinophis carpenteri livaleensis*, and *Atractaspis bibroni*. Some of the amphisbaenians contained nematodes (Loveridge, 1955).

**TAXONOMIC REMARKS:** Dermal vertebral
Fig. 10. *Loveridgea ionidesii*. Dorsal, lateral, and ventral view of head of MCZ 162457.

ratio is 2:1 on trunk, and 1:1 on tail (Alexander and Gans, 1966).

The type series, which has been subdivided into multiple collections, and the numerous topotypes were available for analysis. As only some of the material had been examined for the original description, we are able to refine the diagnosis. It is interesting to note how the substantial series of specimens deposited in the BMNH, MCZ, and NMK differ. The BMNH series contains 162 specimens from Liwale, the MCZ contains 188, and the NMK contains 30. The sample means plus standard errors of body annuli are BMNH 249.7 ± 0.27, MCZ 248.2 ± 0.32, and the NKM 247.7 ± 1.14. Maxima are BMNH 257, MCZ 261, and NKM 256 and minima BMNH 238, MCZ 237, and NKM 240.

The ranges given document the distinctness of the species. However, 4 out of the 459 specimens examined (MCZ 162455, 162461, 162480, 162488, all from Tunduru) showed partial separation of the frontal, by a medial groove of variable width. Also one specimen (MCZ 162464 also from Tunduru) showed a bilateral separation of the enormous temporal into small rectangular postsupralabials with very large temporals dorsal to them. Both of these conditions resemble those shown by *Loveridgea phylofiniens*.

The material from Kilwa appears to represent a distinct geographical variant as the series has a markedly reduced number of body and also lower caudal annuli (fig. 20). The first and the second postgenial rows each have only two segments. One specimen out of the set of five did not match the pattern, suggesting variability or mixed locality.

*Loveridgea phylofiniens* (Tornier)


**DIAGNOSIS:** Species of *Loveridgea* lacking a discrete ocular and eye not externally apparent (in adults); discrete frontals in contact at medial suture; fusion on midline sometimes irregular or partial; three supralabials and three infralabials; third supralabial fused with postocular; first postsupralabial followed dorsally by large temporal which is in contact with parietals; two rows of postgenials, two to five segments in the first row, four irregularly (2–5) in the second; third
infralabial enormous, first postinfralabial smaller; no malar shield; no occipitals, although middorsal segments of second body annulus slightly modified; body annuli 240–258; caudal annuli 19–20; six oval precloacal pores; autotomy site at fifth or sixth caudal annulus (50% autotomized and healed); 14–16 dorsal and 16–17 ventral segments per midbody annulus; medium size (165–195 mm body length).

FIGURES: Figures 14 and 15 show views of head, segments are labeled in figure 9. Figure 15 shows lateral photograph of head with mouth open to show site of angulus oris; figure 4D segment proportions as well as pattern at midbody; figure 5D lateral view of tail and caudal region; figures 6D ventral surface of cloacal region; figure 17 caudal tip recently broken and partially healed; figures 18 and 19 body proportions; and figure 20 distribution of characters.

DESCRIPTION: Loveridgea phylofiniens is a small to medium-size species of Loveridgea. The syntypes are faded to a uniform pale brown. More recently collected specimens show an even brown dorsal color with the
center of each segment slightly more densely colored. The more anterior and posterior ends of the trunk are more densely pigmented than the middle of the trunk; particularly the distal cap of autotomized and healed caudal tips is very dark. Laterally on the trunk, the color fades. Pigmented segments drop out in a checkerboard pattern, about one row of seg-

Fig. 13. *Loveridgea ionidesii*. Seasonal distribution of times at which collections were made. Embryos were found in a specimen collected during October.
ments dorsal to the lateral sulcus. The segments on the underside of the tail are pigmented, although at a density less than that of the dorsal surface. Some caudal segments along the lateroventral (not medioventral) edges tend to show drop out of pigment in a checkerboard pattern.

The rounded snout is prognathous and the head shields are not differentially keratinized. The rostral shield is invisible in dorsal view.

Fig. 14. *Loveridgea phylofiniens*. Dorsal, lateral, and ventral view of head of ZMB 15669a. The line equals 1 mm to scale.
Fig. 15. *Loveridgea phylofiniens*. Dorsal, right lateral, and ventral view of head of ZMB 15669a.

Four pairs of enlarged shields, namely the nasals, prefrontals, frontals, and parietals cover the dorsal surface of the head. The nasals are always in broad contact along the dorsal midline and, along with the rostral, form the tip of the snout. Dorsoposteriorly, each nasal abuts one of the paired prefrontals. The shorter frontals abut on the midline; however, the medial suture may be asym-

Fig. 16. *Loveridgea phylofiniens*. ZMB 15669b from Udzidji, Tanzania. Photograph showing specimen with mouth open to show angulus oris.

Fig. 17. *Loveridgea phylofiniens*. ZMB 15669b (top) and MCZ 47902 (bottom), both from Udzidji, Tanzania, showing (bottom) of a recently broken and healing tail, compared to one (top) in which integumentary cap has closed completely. Note that broken surface contains gaps from which the fusiform muscle fascicles have pulled out. The broken surface of the caudal vertebra is exposed and the integument of the autotomy annulus has folded inward, signaling closure.
metrical and sometimes partial (4 of 6 specimens have half the zone fused). The wedge-shaped parietals represent the posteriormost enlarged pair; their posterior tips lie on the level of the first body annulus. Posteriorly, they abut the medially modified but only slightly enlarged middorsal (occipital?) segments of the second body annulus.

The first supralabial is elongate and dorsally contacts the nasal and prefrontal; the second is taller, contacts the prefrontal and frontal, and appears to have fused with the ocular, although the eye is not apparent externally (in the adults available). The third supralabial is longer than high and contacts the frontal and parietal. Neither oculars nor postoculars are distinct. The posterior edge of the third supralabial marks the angulus oris. The postsupralabial is squarish and contributes to the dorsal portion of the first body annulus. A very large temporal lies dorsal to the postsupralabial and abuts the parietal shields.

The rostral is broadly visible in ventral view. The deep lower jaw is partially inset into the ventral surface of the snout. In ventral view, the mental starts as wide as the rostral portion of the labial edge, but slims down posteriorly to contact the anterior edge of the narrower shield-shaped postmental. The mental is flanked by smaller first infralabials, the second and third being much larger. The postmental has only point contact with the enormous third infralabial. The single postinfra labial is smaller. The small postgenial segments of the first row number 2 to 5, as do those of the second row. In 50 percent of the specimens one or both lateral segments of the first row are continuous with the second. There is no discrete malar shield. A “postmalar” row lying between the postinfra labials forms the ventral portion of the first body annulus.

The ventral portions of the second and third body annuli are narrow and their small segments are irregular. The second or third body annulus is ventrally narrowed and in some specimens is ventrally interrupted to form an intercalated dorsal half-annulus. The dorsal portion of the second through sixth body annuli is longer than the lateral and ventral parts. Pectoral scales not otherwise differentiated,
more posterior interannular sutures across the ventral surface at close to right angles to the long axis.

Specimens have 240 to 258 body annuli, from the first segments posterior to the angulus oris up to and including the pore-bearing precloacal row. One or two intercalations or fusions, sometimes involving a spiral displacement just anterior to the cloaca, occur in the second half of most specimens. At midbody an annulus contains 14 to 16 dorsal segments, generally slightly longer than wide, and 16 to 17 ventral ones, the medial about twice as wide as long. The cloacal region corresponds to three to four lateral annuli. The tail bears 19 to 20 caudal annuli, the last being partly incorporated into a narrow and oval caudal tip. The variably expressed autotomy site (at which 3 out of 6 specimens had broken and at least partly healed tails) falls between the fifth and sixth caudal annuli.

There are six substantial round to suboval precloacal pores, each set into the posterior edge of one of the median segments of the last body annulus. The elongate precloacal shield consists of two wide median plus three to four narrower flanking segments (total 8–10). The narrow postcloacal edge is formed of 12 (to 15) segments.

The head is vertically oval in the preocular region, becoming of rounded cross section thereafter. The nuchal region barely narrows and the trunk has a generally round, slightly oval horizontal, cross section. The trunk is generally horizontally oval; however, it becomes slightly higher than wide just anterior to the cloacal region and the tail is slightly
Fig. 20. *Geocalamus* and *Loveridgea*. Histograms of character distribution.

compressed vertically. The lateral sulci start at the level of the 45th body annulus and extend down to the level of the cloaca, and at midbody are filled with some imbricate segments in a gap as wide as the flanking segments which are in turn approximately one-half as wide as the adjacent segments. The middorsal and midventral sulci are indicated only by alignment of intersegmental sutures.

**RANGE:** Known only from the vicinity of the type locality.

**SPECIMENS AND OTHER RECORDS:** Tanzania: Udjidji (Ujiji), Ruanda: MCZ 47901–
47904 (includes skull) (Loveridge, 1942, 1944b); ZMB 15669a, b [syntypes Amphisbaena phylofiniens Tornier, 1899, 1900; Loveridge, 1923b, 1924, 1941, 1942, 1957 (checklist); Monard, 1931 (mention); Nieden, 1913 (mention); Werner, 1910 (key)].

Fig. 20—Continued.
BIological Mickey: The medial premaxillary and dentary teeth are elongated (Werner, 1910).

Specimens have been reported for upland savannah (Loveridge, 1937), the low-lying rice fields of Ruanda, a few miles east of Ujiji, and the sandy country near Lake Tanganyika at least 20 miles south of Ujiji (Loveridge, 1941). Notes refer to moist sand or laterite soil (Loveridge, 1944b).

Taxonomic Remarks: The counts of the two syntypes agree with the original description. The specimen listed first in the original account and the only one with a complete type locality is here designated as lectotype.

Comments on Other Amphibians from Tanzania

The series of Loveridgea ionidesii from the plateau locality of Tunduru, Tanzania, included a single and quite interesting (misidentified) specimen (MCZ 162505) of Chirindia that seems to be intermediate between C. orientalis (previously known only from the coastal locality of Mikindani) and C. swynnertoni (known only from central Mozambique and eastern Zimbabwe; cf. Gans and Rhodes, 1967; Broadley and Gans, 1978a). The specimen overlaps the character range of both forms in number of caudal annuli (23), pore number (6), number of midbody segments (12 + 12), and in general rounding of the head. It agrees with C. orientalis, rather than C. swynnertoni in that the parietals are somewhat larger and posteriorly convex rather than concave. However, in number of body annuli (240) it agrees with C. swynnertoni (236–265) rather than C. orientalis (256–271), as it does with relative tail length (BL + TL = 133 + 16 mm), and in lack of contact between the points of the triangular mental and postgenial. It is interesting to note the extent to which the inland records agree. Except for the very substantial gap in the geographic range, the specimen would suggest the specimens are conspecific in which case C. swynnertoni would have priority. As noted earlier (Broadley and Gans, 1978a), the northern portion of Mozambique remains a potentially critical region for understanding the distribution of the African herpetofauna.

Through the courtesy of Dr. D. G. Broadley, it is possible to correct a set of errors in the key to the subspecies of Ancylocranium (Gans and Kochva, 1966). All of these refer to the variously subdivided segments of the temporal region. As noted correctly in the descriptions and illustrations, there are three discrete patterns. A. somalicum has the region subdivided into small rectangular segments; hence part of couplet 1 is transposed as now written, it should contrast “temporals variably fused” . . . 2. with “small rectangular segments on the side of the head immediately posterior to the rostral”. . . . 5. In couplet one, the character “mental and postmental fused/discrete” should be transposed. In couplet 2, one should add that A. barkeri has these “temporals fused into narrow vertical strips” and in contrast that A. ionidesii has “a large triangular segment on the side of the head immediately following upon the rostral.”

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