

Systematics and adaptive radiation of Equatorial African lizards assigned to the genera *Adolfus*, *Bedriagaia*, *Gastropholis*, *Holaspis* and *Lacerta* (Reptilia: Lacertidae)

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The Equatorial African group of lacertids comprises nine species which share a number of derived features and appear to constitute a holophyletic assemblage. Revision of the group using morphological characters analyzed by parsimony and compatibility methods results in the following taxonomic changes: *Lacerta jacksoni* = *Adolfus jacksoni*, *Lacerta echinata* = *Gastropholis echinata*, *Bedriagaia tropidopholis* = *Gastropholis tropidopholis*, *Bedriagaia moreavi* = *Gastropholis prasina*, the latter species being validated and removed from the synonymy of *Gastropholis vittata*. *Adolfus jacksoni* has most features in common with the hypothetical ancestor of the group, while *Holaspis guentheri* and the species of *Gastropholis* are the most derived forms. Geographical variation in *Adolfus alleni* is described and what is known of the ecology of the Equatorial group summarized. Most are forest dwellers with the majority of the more primitive forms living on tree boles and among litter and timber on the forest floor (*Adolfus jacksoni*, *A. africanus*, *A. vauereselli*). Another, *Holaspis guentheri*, is confined to tree boles but glides between them, while the species of *Gastropholis* appear to be climbers in flimsy vegetation and *Adolfus alleni* is ground-dwelling above the tree line. Many of the morphological features characterizing these lizards appear to be functionally related to their particular habitats.

Introduction

Nine well-defined, relatively primitive species of lacertid occur in equatorial Africa from Liberia in the west to the coasts of Kenya, Tanzania and Mozambique in the east. Most of these are associated with forest habitats. Boulenger (1920, 1921) allocated these forms to five different genera: *Lacerta* Linnaeus, 1758; *Algyroides* Bibron & Bory, 1833; *Bedriagaia* Boulenger, 1916a; *Gastropholis* Fischer, 1886; and *Holaspis* Gray, 1863, the two species placed in *Lacerta* being assigned to different subgenera, *Podarcis* Wagler, 1830 and *Centromastix* Boulenger, 1916b. Laurent (1956) raised *Centromastix* to full generic status, although this course has not been subsequently followed. Arnold (1973) pointed out that the three forms allocated to *Algyroides* are very different from the other members of the genus, which occur in Europe and include the type species, and consequently transferred them to another genus, *Adolfus* Sternfeld, 1912. He also suggested that the two species assigned to *Lacerta* did not really belong to that grouping. Current names for the species concerned are *Adolfus africanus* (Boulenger, 1906), *A. alleni* (Barbour, 1914), *A. vauereselli* (Tornier, 1902),

Bedriagaia tropidopholis Boulenger, 1916a, *Gasropholis prasina* Werner, 1904, *G. vittata* Fischer, 1886, *Holaspis guentheri* Gray, 1863, *Lacerta* (*Centromastix*) *echinata* Cope, 1862 and *L. jacksoni* Boulenger, 1899.

Abbreviations used. AMNH, American Museum of Natural History, New York; BMNH, British museum (Natural History), London; LACM, Los Angeles County Museum; MCZ, Museum of Comparative Zoology, Harvard; MNHP, Muséum Nationale d'Histoire Naturelle, Paris; MRAC, Musée Royale de l'Afrique Centrale, Tervuren; MZUT, Museo Zoologia Sistemática, Turin; NHRS, Naturhistoriska Riksmuseet, Stockholm; USNM, United States National Museum of Natural History, Washington, D.C; ZMB, Zoologisches Museum der Humboldt-Universität, Berlin.

Evidence for holophyly of the African Equatorial group

The placing of these few species in so many genera reflects a considerable degree of superficial difference between them, but it seems probable that the group is a holophyletic unit. While there is no known completely unique synapomorphy that unites them, these forms share a number of derived features, some generally uncommon in the Lacertidae, which are unknown in this combination elsewhere. Other indications of close relationship are the relatively restricted and subcontinuous range of the group and the fact that, although quite varied in morphology, they can be arranged in a branching series in which adjacent members are relatively similar.

The derived features that all or most of the nine species share are as follows.

1. Pineal fontanelle in parietal bone consistently absent. Members of three other genera, each of which appear holophyletic, may lack the pineal fontanelle, but none do so consistently. They are *Philochortus*, *Poromera* and *Nucras* (Degen, 1911). The fontanelle is nearly always absent in *Philochortus* but I detected a minute opening in two out of 27 *P. hardeggeri* examined. It is absent in only six out of 17 *Poromera fordi* checked, the size being variable in the remainder. In *Nucras*, with the apparent exception of *N. lalandii*, and perhaps also *N. scalaris* which has not been examined, the fontanelle is present in some members of each species (see Broadley, 1972)

2. Postorbital and postfrontal bones fused in all except *Holaspis guentheri*, where this condition appears to have been secondarily lost.

3. Medial area of clavicle not or only weakly expanded, with only a small fontanelle or none at all (Fig. 3). Elsewhere weak expansion is usual only in *Nucras lalandii*.

4. Nearly always a single postnasal scale on each side.

5. Parietal scale extending to the edge of the parietal table of the skull (i.e. to the outer margin of the postorbital bone).

6. Tympanic shield usually small, except in *Adolfus alleni* where the whole temporal scaling is very coarse.

7. Temporal scales often keeled, except in *Adolfus alleni*, *Holaspis guentheri* and *Gastropholis vittata*.

Relationships to other lacertids

The relationship of the Equatorial African group to other lacertids is discussed elsewhere (Arnold, in Press). Although relatively primitive, its members share derived features with other Ethiopian and advanced Saharan and Eurasian lacertids that are not usually found in the more primitive Palaearctic genera of the family (*Lacerta*, *Algyroides*, *Podarcis*, *Psammodromus*, *Gallotia*, *Takydromus* and *Platyplacopus*). These

include advanced ulnar nerve conditions, a hemipenial armature and, in most cases, an unlobed female genital sinus. The Equatorial African group is near the base of the assemblage containing the Ethiopian and advanced Saharan and Eurasian species.

The status of *Gastropholis prasina* and *Bedriagaia moreaui*

Gastropholis prasina Werner, 1904 was synonymized with *G. vittata* Fischer, 1886 by Boulenger (1921). Examination of the types and other material of these two forms shows they are in fact perfectly distinct (Table 1). The type of *Bedriagaia moreaui* Loveridge, 1936a is clearly conspecific with *G. prasina*.

Table 1. Differences between *Gastropholis vittata* and *G. prasina*.

	<i>G. vittata</i>	<i>G. prasina</i>
Individuals examined	12	2
Known maximum size (snout to vent, mm)	83	110
Head proportions		more narrow and elongate
Colouring	in spirit, brown above with broad, white, dark-edged, dorsolateral stripes; underside white	in spirit, bluish-green with a pale, greenish underside. Live animals pea green above and yellowish below (Loveridge, 1936a). A specimen collected by J. Ashe has yellowish flanks, a yellow edge to the eyelids, the thighs are yellow anteriorly and the posterior surfaces of the hind legs are grey
Supratemporal scales (number on each side)	8–12	7–8
Gular scales	21–27	27, 28
Shape of dorsal scales	distinctly but often weakly keeled; usually flattish in vertebral area, more convex elsewhere	strongly keeled and tectate
Number of dorsal scales in transverse row at mid-body	19–26	28, 32
Number of ventral scales in longest transverse row	12, occasionally 10	13, 14
Femoral pores (number on each side)	9–13	13–14
Unverted hemipenis	relatively robust	apparently slender

Table 2. Geographic variation in *Adolfus alleni*.

	Mount Kenya	Mount Elgon	Aberdare Mountains
Individuals examined	18	41	13
Maximum size (snout to vent, mm)	70	57	61
Individuals with contact between rostral and frontonasal scales	(some populations smaller)		
Number of temporal scales	6%	2.5%	69%
mean	7.0	8.06	4.61
range	5-10	6-12	3-6
Keels on dorsal scales	weak, occasionally moderate	intermediate	strong (except in Kinangop material)
Femoral pores in males (on each side)			
mean	12.75	11.77	10.14
range	12-14	10-13	8-12
Femoral pores in females (on each side)			
mean	11.44	11.50	9.50
range	10-13	10-13	9-10
Vertebral stripe	often strong	often narrow	often narrow
Vertebral stripe includes occipital scale	usually	often not	often not

Geographic variation in *Adolfus alleni*

Adolfus alleni occurs only above 2700 m in its restricted range in southwest Kenya and adjoining Uganda. So far as is known it is confined to four separate massifs: Mount Kenya, the Aberdare Mountains, Mount Elgon and the Cherangani Hills. Occurrence in the last locality is based on a specimen (BMNH 1969.2584) from Sondang, 10 500 feet (3150 m), which is very similar to ones from Mount Elgon. The populations known from more than a single individual show distinct differences (Table 2). However, samples from the alpine zones of Mount Kenya and Mount Elgon are relatively similar, even though they are separated by 300 km. In contrast, those from the highland zone of the Aberdare Mountains which is only about 50 km from that of Mount Kenya, are very different. The similarity between the first two samples may well be primitive resemblance since the features in which the Aberdare population differs from them appear to be derived, including frequent contact between rostral and frontonasal scales, very low number of temporal scales, keeling on dorsal scales often strong, and low femoral pore counts. This isolate could be given separate subspecies status, but it is more prudent to delay this until more material is available, especially as present samples suggest that, in the Aberdares and on Mount Kenya at least, there may be geographical variation within the main isolates. For instance, material from the north of the Aberdare Mountains has strongly keeled dorsal scales, while in specimens from the southern section of the range, Mount Kinangop (MHNP 23.78-81), keeling is much less developed.

Inter-relationships of the African Equatorial lacertids

Characters used

Characters were selected mainly from the skeleton and from external features, but a minority come from other parts of the body, including the tongue, nerves of the forearm, and male and female reproductive systems. The features used are listed below and their distribution summarized in Table 3. Each character or character complex is numbered. The latter, which have more than two states, are divided into binary characters, which are designated by figures after a decimal point. Each state of a binary character is indicated by 0 or 1, the former being attached to the apparent primitive condition of the character. A total of 63 characters are used. In 47, the apparent derived state occurs in more than one species and is consequently of direct use in assessing relationships. The remainder, in which the apparent derived state occurs in a single species, are included because they give some indication of how distinct some of the species are and may contribute to the determination of polarities in the first group by the production of polar incompatibilities. Characters where polar incompatibility suggests that the polarity should be reversed are indicated by asterisks. The terminology applied to the hemipenis is explained elsewhere (Arnold, 1986).

Skeleton

- 1 *Premaxilla*. Normal (0); modified to form an anterior boss (1).
- 2* *Postfrontal and postorbital bones*. Separate (0); fused (1).
- 3 *Shape of squamosal bone* (Fig. 1). Slender (0); deep, especially posteriorly (1).
- 4 *Squamosal-parietal contact* (Fig. 1). Absent (0); present (1).
- 5 *Quadrate bone* (Fig. 1). Dorso-anterior border rounded (0); dorso-anterior border angled (1).

Table 3. Distribution of character states in the African Equatorial group of lacertids.

Character Nos.	1	2*	3	4	5	6	7	8	9:1	9:2	10:1	10:2	11	12:1	12:2	13	14	15	16
<i>A. jacksoni</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. allenii</i>	0	1	0	0	0	V	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>A. africanus</i>	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>A. vauereselli</i>	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0
<i>G. echinata</i>	0	1	0	0	1	1	V	0	0	1	0	1	0	0	0	1	0	0	1
<i>G. tropidopholis</i>	0	1	1	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1
<i>G. prasina</i>	0	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	1	0	1
<i>G. vittata</i>	0	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	1	V	1
<i>H. guentheri</i>	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0

Character Nos.	17	18	19	20	21	22:1	22:2	23:1	23:2	24:1	24:2	25	26:1	26:2	27	28:1	28:2	28:3	29:1	
<i>A. jacksoni</i>	0	0	0	V	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. allenii</i>	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>A. africanus</i>	0	0	0	1	V	V	0	1	1	1	1	1	0	1	0	1	0	0	1	1
<i>A. vauereselli</i>	0	0	0	V	1	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0
<i>G. echinata</i>	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	V
<i>G. tropidopholis</i>	0	1	0	1	1	V	0	0	1	0	0	1	0	0	0	0	1	0	1	1
<i>G. prasina</i>	0	1	0	1	1	1	1	0	0	1	0	0	1	0	0	0	1	1	1	1
<i>G. vittata</i>	0	1	0	1	1	1	V	0	0	1	0	0	1	0	0	0	1	1	1	1
<i>H. guentheri</i>	1	0	0	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0

Character Nos.	29:2	30	31:1	31:2	32	33	34	35	36	37	38	39	40	41	42	43	44:1	44:2	45	
<i>A. jacksoni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. allenii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>A. africanus</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	V	0	0
<i>A. vauereselli</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>G. echinata</i>	0	0	0	0	0	0	1	0	1	0	1	1	V	0	1	1	1	0	1	1
<i>G. tropidopholis</i>	1	V	1	0	1	0	1	0	1	0	0	1	V	0	1	1	1	1	1	1
<i>G. prasina</i>	1	1	1	1	1	0	1	0	1	0	0	1	0	0	1	1	1	1	1	1
<i>G. vittata</i>	1	1	1	1	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	1
<i>H. guentheri</i>	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	0	0

Character Nos.	46	47	48	49	50	51*
<i>A. jacksoni</i>	1	0	0	0	1	1
<i>A. allenii</i>	1	0	0	0	1	1
<i>A. africanus</i>	1	0	0	0	1	1
<i>A. vauereselli</i>	0	0	0	1	1	0
<i>G. echinata</i>	0	1	1	0	0	1
<i>G. tropidopholis</i>	0	1	1	0	0	1
<i>G. prasina</i>	0	0	1	0	-	-
<i>G. vittata</i>	0	0	1	0	0	1
<i>H. guentheri</i>	1	0	0	0	-	1

0, apparently primitive state, on evidence of outgroup comparison. 1, apparently derived state, on evidence of outgroup comparison. V, variable, both 0 and 1 states present. *, characters where polar incompatibility suggests that polarity based on outgroup comparison should be reversed.

- 6 *Temporal osteoderms*. Absent (0); often some present anteriorly and dorsally (1).
- 7 *Maxilla* (Fig. 2). Not extending posterior to coronoid notch (0); extending posterior to coronoid notch (1).
- 8 *Number of scleral ossicles*. 14 scleral ossicles in each eye (0); 12 scleral ossicles in each eye (1).
- 9.1, 9.2. *Average number of presacral vertebrae in males* (Table 4). 26 or 27 (0, 0); 25 or less (1, 0); 29 or more (0, 1).
- 10.1, 10.2. *Number of long free dorsal ribs immediately posterior to thoracic ribs*. 7–9 (0, 0); 6–7 (1, 0); 10–12 (0, 1).
- 11 *Size of long free dorsal ribs immediately posterior to thoracic ribs*. Moderately elongated (0); very elongated, about twice the length of other free dorsal ribs (1).
- 12.1, 12.2 *Posterior border of medial loop of clavicle*. Present and slender (0, 0) Fig. 3c; absent (1, 0) Fig. 3d; present and thickened (0, 1) Fig. 3e.
- 13 *Transverse processes of anterior autotomic caudal vertebrae*. Directed roughly laterally (0); directed obliquely forwards (1).

External features

- 14 *Contact between postnasal and supranasal scales below level of nostril*. Absent (0); present (1).
- 15 *Number of loreal scales on each side*. Two (0); one (1).
- 16 *Row of supraocular granules*. Complete or nearly so (0); very reduced or absent (1).
- 17 *Lower eyelid*. Opaque and covered with relatively small scales (0); with a transparent 'window' made up of one or more enlarged scales (0).
- 18 *Parietal scales*. Normal (0); posterior lateral corners eroded so scales are narrowed behind (1).
- 19 *Temporal scaling*. Relatively fine (0); very coarse, 13 or fewer scales on each side, excluding the supratemporals and tympanic (1).
- 20 *Keeling on temporal scales*. Absent (0); present (1).
- 21 *Gular fold*. Present (0); absent (1).
- 22.1, 22.2 *Keeling on collar scales*. Absent (0, 0); present at sides (1, 0); present on all collar scales (1, 1).
- 23.1, 23.2 *Granules beneath collar*. Many (0, 0); reduced to about two rows (1, 0); often very scattered or absent, at least close to mid-line (1, 1).
- 24.1, 24.2 *Size of mid-dorsal scales*. Small (0, 0); somewhat enlarged (1, 0); very large (1, 1).
- 25 *Differentiation of dorsal scales*. More or less uniform in size (0); flank scales distinctly smaller than mid-dorsals.
- 26.1, 26.2 *Micro-ornamentation of dorsal scales*. Smooth (0, 0); striate, especially on tail (1, 0); pustulate, with minute tubercles (0, 1).
- 27 *Flank scales*. In close contact (0); can be widely separated by stretching skin laterally (1).
- 28.1, 28.2, 28.3 *Number of longitudinal rows of ventral body scales*. Six or eight complete rows (0, 0, 0); four complete rows and an outer row on each side which is strongly reduced anteriorly (1, 0, 0); ten rows (0, 1, 0); twelve or more rows (0, 1, 1).
- 29.1, 29.2 *Keeling on ventral body scales*. Absent (0, 0); present only on outer longitudinal row (1, 0); present on all ventral body scales (1, 1).
- 30 *Main preanal scale*. Entire (0); divided longitudinally (1).

- 31.1, 31.2 *Keeling on preanal scales*. None (0, 0); only on peripheral preanal scales (1, 0); on all preanal scales (1, 1).
- 32 *Keeling on scales beneath limbs*. Absent (0); present (1).
- 33 *Row of femoral pores*. Long, extending almost to knee (0); shortened, well separated from knee (1).
- 34 *Scales bearing femoral pores* (Fig. 4). Not or only slightly projecting, pores close together in males (0); projecting, pores well separated in males (1).
- 35 *Hind toes*. Without fringes (0); with lateral fringes of flattened, pointed, interconnected scales (1).
- 36 *Tail in mature animals*. Not more than 2.2 times snout-vent distance (0); extremely long and slender, at least 2.3 times snout-vent distance (1).
- 37 *Tail shape*. Cylindrical without lateral fringes (0); dorsoventrally flattened with lateral fringes of flattened, pointed, interconnected scales (1).
- 38 *Pad of spinous scales on dorsum of tail base* (Fig. 11). Absent (0); present (1).
- 39 *Ground colour of dorsum in alcohol*. Brownish or blackish (0); greenish (1).
- 40 *A distinct dark reticulation on dorsum*. Absent (0); present, reducing ground colour to spots, bars, or both (1).
- 41 *Pale dorsolateral stripes*. Absent (0); present (1).

Tongue, nerves, muscles, reproductive system

- 42 *Tongue surface*. Mainly squamate (0); mainly plicate posteriorly (1).
- 43 *Tongue colour in alcohol*. Dark (0); pale (1).
- 44.1, 44.2 *Ulnar nerve pattern*. A continuous independent ulnar nerve present but connected to the brachial trunk by a bridge in the lower arm (0, 0) Fig. 5b; bridge thickened, and independent ulnar nerve in upper arm attenuated (1, 0) Fig. 5c; 'varanide' arrangement with no continuous independent ulnar nerve and all fibres to lower limb passing through the brachial trunk (1, 1) Fig. 5d.
- 45 *Size of hemipenis*. Large (0); small (1).
- 46 *Intramuscular portion of hemipenial armature*. Very deeply cleft anteriorly (0); not very deeply cleft (1).
- 47 *Medial side of hemipenial armature reduced*. No (0); yes (0).
- 48 *Size of hemipenial clavulae*. Large (0); small (1).
- 49 *Shape of hemipenial clavulae*. Simple (0); complexly lobed (1).
- 50 *Exit of oviducts into genital sinus*. Ventral or terminal (0); dorsal (1).
- 51* *Female genital sinus*. Bilobed (0); unlobed (1).

Determination of polarities (Table 5)

Polarity has been determined largely by outgroup comparison using the primitive west Palaearctic lacertid assemblage (*Lacerta*, *Algyroides*, *Podarcis*, *Psammotromus* and *Gallotia*) as the outgroup. In some cases, only one condition of a character exists here, but quite frequently both do. When this occurs, the derived state is taken to be that which is infrequent and sporadically distributed. The non-coincidence of these minority states also suggests most of them are derived (Arnold, 1981, p. 12). In a few cases, ontogenetic considerations support polarity.

If the distribution of the states of all characters is compared, it would be expected that, in nearly all cases, the primitive states of each pair would sometimes occur together. Characters where the primitive state often fails to occur with the primitive state of others (polar incompatibility) may well have their true polarities reversed. A programme for compatibility analysis, described by Gauld & Underwood (1986), has

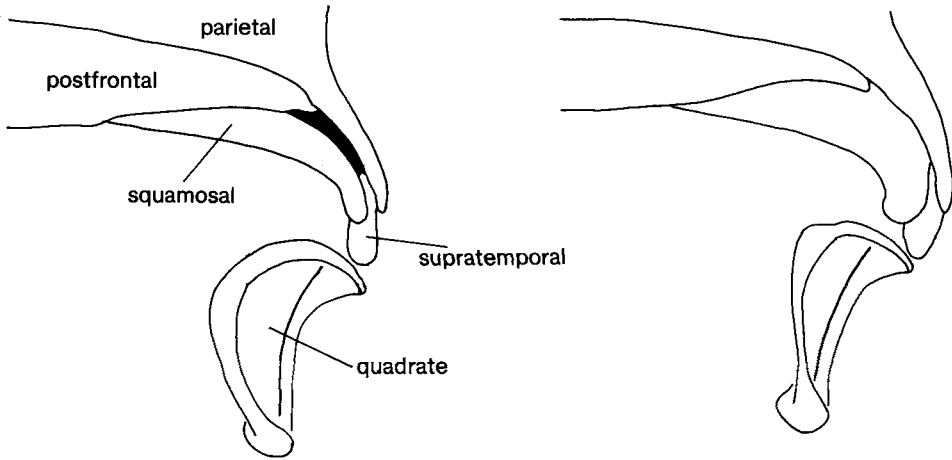


FIG. 1. Lateral view of posterior skulls showing differences in squamosal and quadrate bones (anterior to left). *Left, Adolfus jacksoni*: squamosal slender and separated from supratemporal process of parietal; quadrate with a rounded dorso-anterior border. *Right, Gastropholis vittata*: squamosal deep, especially posteriorly and in contact with supratemporal process of parietal; quadrate with angled dorso-anterior border.

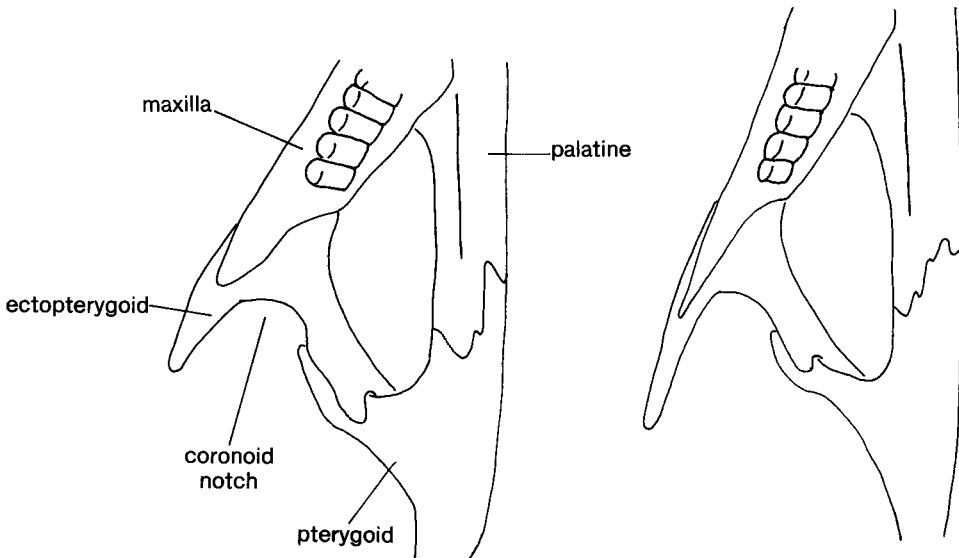


FIG. 2. Ventral view of right suborbital regions of skulls. *Left, Adolfus jacksoni*: maxilla does not extend posteriorly beyond level of coronoid notch. *Right, Gastropholis echinata*: maxilla extends posteriorly beyond level of coronoid notch.

a facility to count polar incompatibilities. When this is applied to the data set, two characters (2 and 51) have particularly high scores for polar incompatibility. If the polarities of these are reversed, the level of polar incompatibility falls abruptly. Polarity reversal in character 2, fusion of the postorbital and postfrontal bones, is initially surprising as the supposed primitive condition, in which the bones are separate, is widespread in the immediate outgroup and in more distant ones as well, and is also

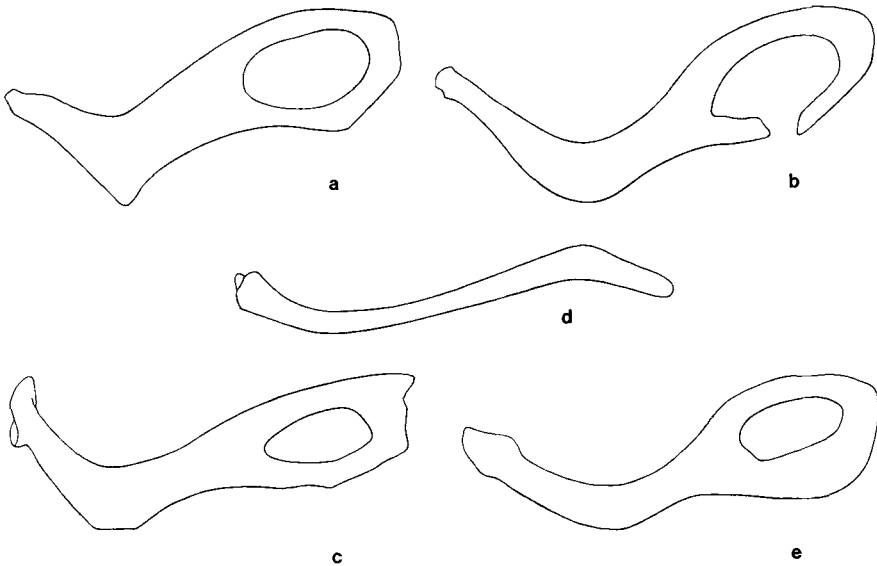


FIG. 3 Right clavicles from beneath. *a*, *Lacerta s. str.*: medial loop strongly expanded and intact, the most widespread condition in the Lacertidae. *b*, *Lacerta s. str.*: medial loop strongly expanded with loop interrupted posteriorly, a common alternative in primitive West Palaearctic lacertids. *c*, *Gastropholis echinata*: medial loop intact but only weakly expanded. *d*, *Holaspis guentheri*: posterior section of medial loop completely absent. *e*, *Adolfus vauereselli*: medial loop intact and not strongly expanded but with thickened posterior border.

supported by ontogenetic considerations. However, in the one Equatorial African form in which the bones are separate, *Holaspis guentheri*, the skull is generally weakly ossified, so a phylogenetic return to an unused condition seems feasible.

Parsimony analysis

Treatment of variable scores in parsimony analysis.

In certain characters, the score for some taxa may be variable (V), that is both the 0 and 1 states have been observed in each taxon concerned. Often such scores are treated as primitive (0), on the grounds that the 1 score is a result of independent origin within the taxon, so that it is therefore homoplastic relative to any other 1 scores and can consequently be ignored. Such a course is often appropriate with supraspecific taxa but may not be when dealing with species. This is because polymorphic present of 0 and 1 states in the same species is probably not uncommon, when dealing with the small-scale characters usual at this taxonomic level which may well be under relatively simple genetic control, so it cannot be assumed that the ancestor of such forms had a consistent 0 score. It is reasonable to consider the possibility that forms with 1 and V scores have arisen from a polymorphic ancestral species (V). In fact such a quite realistic assumption appears to be more parsimonious than assuming immediate ancestors had only the 0 condition, as fewer events are postulated. It requires fewer independent origins of new states and less total change in frequency of states (see Fig. 6).

Another reason concerns sampling problems. In most data sets, characters are checked on relatively few individuals of each species, especially if the taxon is rare or the character costly, in terms of effort, to investigate. Yet to detect a 20% polymorphi-

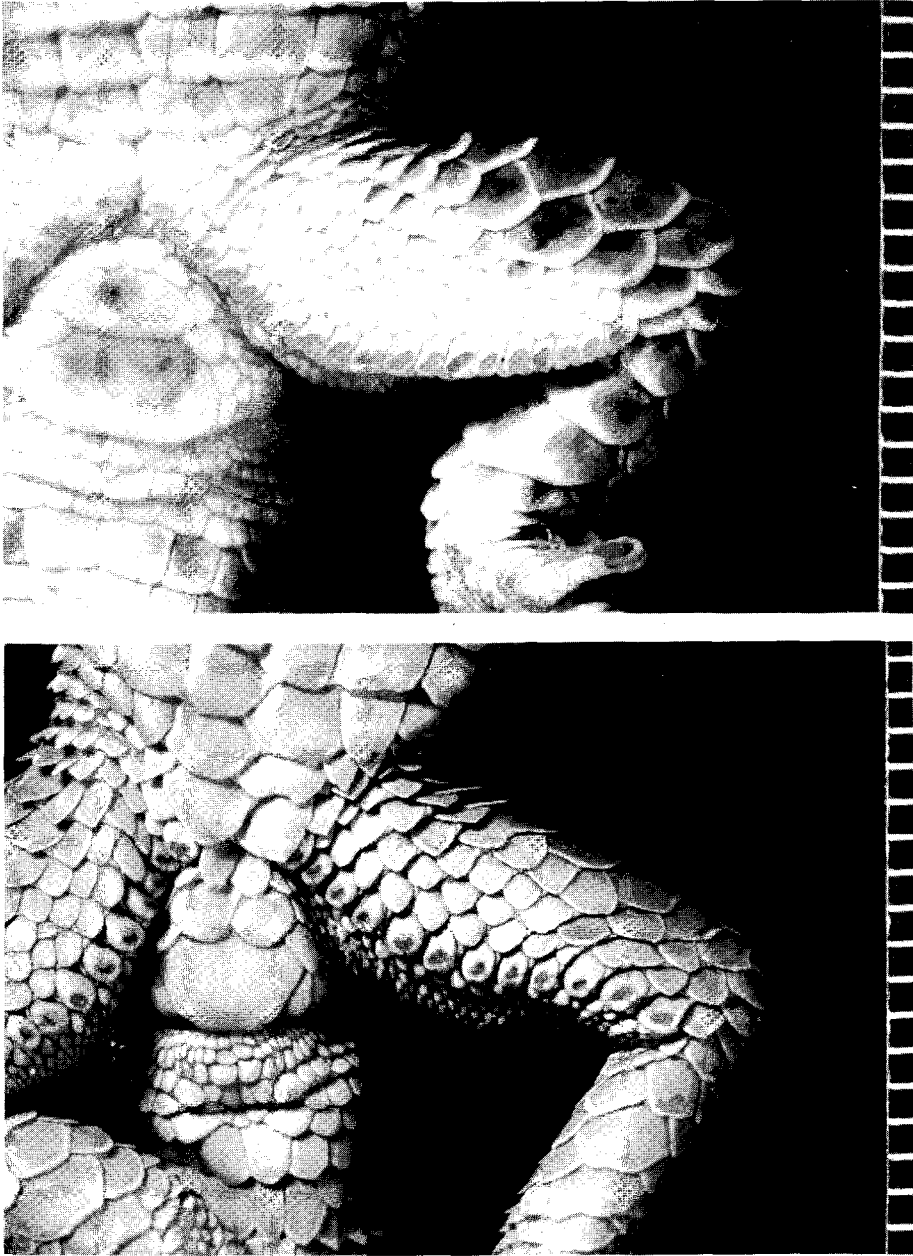


FIG. 4. Undersides of thighs of male *Adolfus jacksoni* (above) and *Gastropholis echinata* (below), showing difference in femoral pores. The pores are close together in *A. jacksoni* but well separated and projecting in *G. echinata*.

ism up to 14 individuals may have to be examined and even this may not be enough if there is geographical variation in incidence (Arnold, 1981). Consequently many 0 and 1 scores may really be undetected 0, 1 (V) scores. It therefore seems inappropriate to dispense with 0, 1 scores that happen to have been detected. Of course, 0 scores may also be undetected 0, 1 scores, but here there is no actual evidence of the presence of

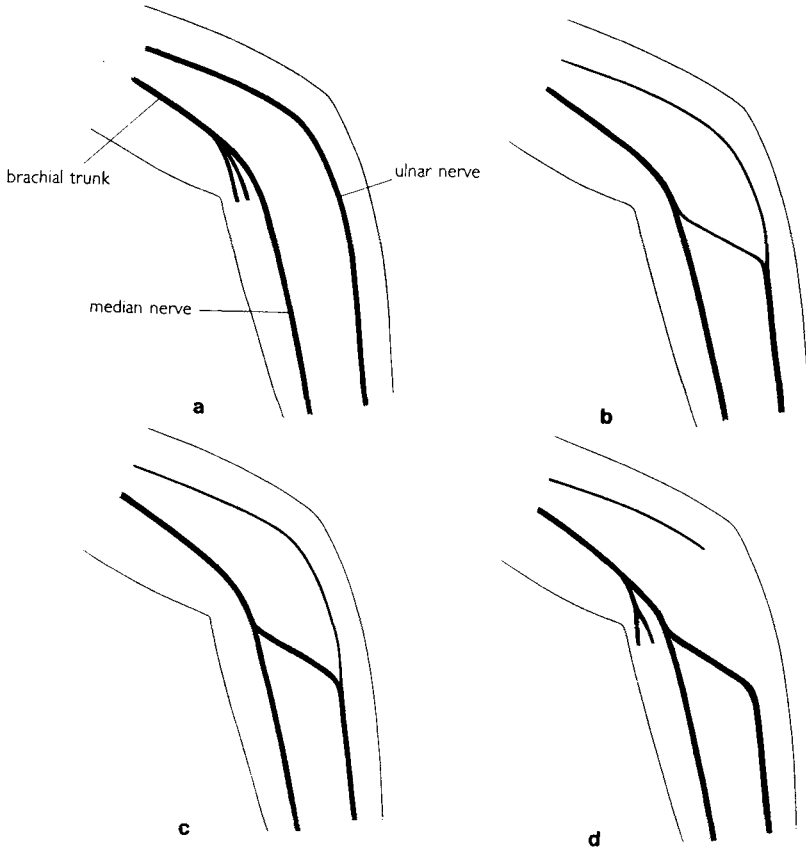


FIG. 5. Ulnar nerve patterns in lacertid lizards. *a*, 'Lacertide' pattern found in primitive Eurasian species; *b*, intermediate pattern of *A. jacksoni* and *A. alleni*; *c*, intermediate pattern of *G. echinata* and some *A. africanus*; *d*, 'varanide' pattern found in other members of the Equatorial African group, other lacertids in the Ethiopian region, and advanced Saharan and Eurasian genera.

Julien & Renous-Lécuru (1972) discuss two patterns of innervation in the lower forelimb of lizards. In the more primitive ('lacertide') condition, the ulnar nerve is completely independent of the brachial trunk, and the nerves originating from it, and follows a superficial course in the lower limb (Fig. 5a). In the more advanced ('varanide') condition, there is a common trunk in the upper arm which includes all the fibres of the ulnar nerve that serve the lower limb; these separate only below the elbow (Fig. 5d). The authors correctly report both conditions in the Lacertidae. Among the members of the Equatorial African group, the 'lacertide' condition is not found, but some species are intermediate between this and the 'varanide' condition. Thus, in *Adolfus jacksoni* and *A. alleni*, some fibres of the ulnar nerve follow the 'lacertide' course while others follow the 'varanide' one, so that an independent ulnar nerve runs from the upper to the lower forelimb but receives additional fibres in the lower limb which form a slender bridge from the brachial trunk (Fig. 5b). *Gastropholis echinata* and some *Adolfus africanus* are similar but more fibres follow the 'varanide' route, so that the bridge is thicker, and the upper part of the ulnar nerve more attenuated (Fig. 5c). In other members of the Equatorial African group, the 'varanide' condition is found and the ulnar nerve fibres in the upper arm do not reach those that pass along the brachial trunk (Fig. 5d).

the apomorphy whereas there is in a 0, 1 score. Again, if a 0 score really hides a 0, 1 condition, it is statistically likely that the 1 state is at a lower frequency than in a species represented by a 1 or 0, 1 score. In view of these arguments, V scores will be treated as derived (1) in the present analysis,

Table 4. Variation in numbers of presacral vertebrae and of pairs of inscriptional ribs.

	Presacral vertebrae															Pairs of inscriptional ribs		
	Males							Females										
	24	25	26	27	28	29	30	24	25	26	27	28	29	30	0	1	2	3
<i>Adolfus</i>																		
<i>A. jacksoni</i>			1	14								8	1		14	10	1	
<i>A. alleni</i>			1	13	4	2						11			22	6		
<i>A. africanus</i>	2	7							5						13	1		
<i>A. vauereselli</i>		2							1	1					1	2		
<i>Gastropholis</i>																		
<i>G. echinata</i>						4	3					2	2		8	6	1	
<i>G. tropidopholis</i>						1	2						2		4			
<i>G. prasina</i>						1							1		1			
<i>G. vittata</i>					1	3						1	1		4	1		

Table 5. Evidence for character polarities.

Apparent primitive state universal in outgroup:
1, 2*, 3, 4, 5, 6, 8, 11, 12, 13, 18, 19, 20, 22, 27, 29, 30, 31, 32, 34, 35, 37, 38, 45, 46, 47, 48, 49.

Apparent primitive state in majority of outgroup and broadly distributed:
7, 9, 10, 14, 15, 16, 17, 21, 23, 24, 25, 26, 28, 33, 36, 39, 40, 41, 43, 44, 50, 51*.

Apparent primitive state known to appear first in ontogeny:
2*, 6, 36.

Polarity uncertain: 42.

*—polar incompatibility suggests polarity within Equatorial group should be reversed.

Ancestral conditions	Present conditions	Number of independent origins of new states	Total changes in frequency
0	0,1	1 (0 → 1)	1 (0 → 1)
0	0	2 (0 → 1, 0 → 1)	1.5 (0 → 1, 0 → 0,1)

FIG. 6. Treatment of variable scores in parsimony analysis. The assumption, that taxa with 0 and 0,1 (V) scores for particular characters may have inherited them from ancestral species, is more parsimonious than assuming that ancestral species had only the 0 condition. It requires fewer independent origins of new states and less total change in the frequency of states.

Results

All 47 characters in Table 3, in which two or more taxa share the apparent derived state, were included. The tree was rooted by the inclusion of a hypothetical common ancestor with 0 scores for all characters. This data set was processed using Swofford's (1985) 2.4 version of his PAUP (Phylogenetic Analysis Using Parsimony) programme. For relatively small numbers of taxa, as in the present case, this is able to consider all possible trees using the 'branch and bound' method of Hendy & Penny (1982). Higher taxonomic unit character-state optimization was by the MINF method. A single tree of 68 steps with a consistency of 0.691 was produced, which is shown in Fig. 7.

Compatibility analysis

Compatibility analysis was carried out using the programme of Gauld and Underwood (1986). This conducts Le Quesne (Le Quesne, 1969) tests on all characters in which both states occur more than once, and the frequency of failure of each character (that is incompatibility with other characters) is compared with that expected on a

Le Quesne testing because the primitive state occurs in one taxon only. Other characters, considered in the reverse order of their removal during 'boil down' may also contribute to analysis. In some cases they can be substituted for members of the compatible set, or some small degree of homoplasy may be tolerated.

Le Quesne testing gives an overall randomness ratio of 0.44 and the 'boil down' process produces a compatible set of 29 characters. Fourteen of these support a group made up of *L. echinata*, *B. tropidopholis*, *G. prasina* and *G. vittata*, which will all be allocated to the genus *Gastropholis*, and referred to as such in the rest of this paper. Without this well substantiated assemblage, four characters suggest that *G. prasina* and *G. vittata* are sister species and six more indicate that this species pair is most closely related to *G. tropidopholis*. Four characters associate *A. africanus* and *A. vauereselli* and one more relates this species pair to *H. guentheri*. Character 16 associates *A. alleni* with *Gastropholis*, but a compatible set of the same size can be produced by substituting 23.1 for this, which would associate *A. alleni* with *A. africanus*, *A. vauereselli* and *Holaspis guentheri*. Character 23.1 was the last to be eliminated in 'boil down', and at this stage it had precisely the same randomness ratio (0.4) as 16, so which one was eliminated was arbitrary. Consequently it is not possible to choose between the two sets on compatibility evidence. In fact the compatible set containing 23.1 corresponds exactly to the features shared by two or more species undergoing unique transformation in parsimony analysis, so this set is preferred.

Some characters score badly in the initial 'boil down' because they are homoplastic. However, in a group like the present one, where a well substantiated subgroup can be discerned, a character may occur in both the subgroup and the remaining taxa and thus be homoplastic, but nevertheless give good information in each. Consequently, *Gastropholis* in the sense understood here, was considered as a separate entity and then the remaining taxa plus the most primitive member of the foregoing assemblage, *G. echinata*, were analyzed separately. This latter procedure did not connect *G. echinata* to the remaining forms, so the data were re-run excluding this too. In the case of *Gastropholis*, the number of characters supporting each section of the tree increased significantly. A boil down of the remaining Equatorial forms produces a small compatible set in which five characters support the affinity of *A. africanus* and *A. vauereselli*, four the association of these with *H. guentheri* and two the relationship of these to *A. alleni*. The extra characters identified in these separate compatibility analyses of the two subgroups correspond to those shared by more than one species that undergo two separate transformations in parsimony analysis. Compatibility analysis does not place *Adolfus jacksoni*.

Summary of inter-relationships

Both parsimony and compatibility analysis produce similar results. The reality of *Gastropholis* is strongly supported, as are the relationships of the four species within it, and also the relationship of *A. africanus* to *A. vauereselli*. Weaker support is given to the relationship of the latter two species to *Holaspis guentheri* and of these three to *A. alleni*. Parsimony analysis associates *A. jacksoni* with this group, but only on the basis of two characters which are subsequently reversed in one member of the assemblage. Nearly all the features of *Adolfus jacksoni* are close to those expected in the ancestor of the Equatorial African group, whereas the most derived forms in the assemblage are the members of *Gastropholis* and *Holaspis guentheri*.

Nomenclature

As already noted '*Lacerta*' *echinata*, *Bedriagaia tropidopholis*, *Gastropholis prasina* and *G. vittata* form a strongly corroborated group which, in spite of some superficial differences which were responsible for them being allocated to three genera, have a high level of resemblance to each other. This being so it is sensible to refer them all to the same genus, *Gastropholis*. *Adolfus africanus* and *A. vauereselli* are very similar and also assignable to a single genus but their apparent sister taxon, *Holaspis guentheri* has many unique features within the Lacertidae and is best retained as a monotypic genus. The relationships of *A. alleni* appear to be with the three foregoing forms and as it is quite similar to the two other *Adolfus* species, it is retained in this group. The same course is followed with *Lacerta jacksoni*, even though the evidence for allying it with *Adolfus* and *Holaspis* is relatively weak; this is because it resembles other *Adolfus* more closely than it does other members of the Equatorial group. Such a treatment is not entirely satisfactory as *Adolfus* is now clearly paraphyletic and not defined by any exclusive synapomorphies. But alternative courses are inconvenient or have other shortcomings. All the Equatorial species could be placed in the oldest available genus, *Holaspis*, but this would mask a high level of diversity, as would putting just *Holaspis guentheri* and *Adolfus* in a single genus. On the other hand, avoiding paraphyly by creating separate genera for *A. alleni* and *L. jacksoni* would divide them from generally similar forms and fail to give any indication of their affinities.

Checklist of the African Equatorial lacertids

Adolfus

Adolfus Sternfeld, 1912: 220. Type species: *A. fridericianus* (= *A. africanus*).

Adolfus africanus (Fig. 8a)

Algyroides africanus Boulenger, 1906: 570. Type locality: Entebbe, Uganda. Type: BMNH 1906.5.30.13/1946.9.3.13.

Adolfus fridericianus Sternfeld, 1912: 220. Type locality: upper Aruwimi River, Zaire. Type: ZMB 24121 (missing, January, 1987, fide G. Peters).

Range: Uganda, eastern Zaire as far south as 9.12S 26.40E (De Witte, 1953); also Cameroon west to 4.58N 9.15E.

Adolfus alleni

Algyroides alleni Barbour, 1914: 97. Type locality: northeast slope of Mount Kenya. Type: MCZ 9280.

Range: Mount Elgon, Uganda; Cherangani Hills, Mount Kenya and Aberdare Mountains, Kenya. Found above 2700 m.

Adolfus jacksoni

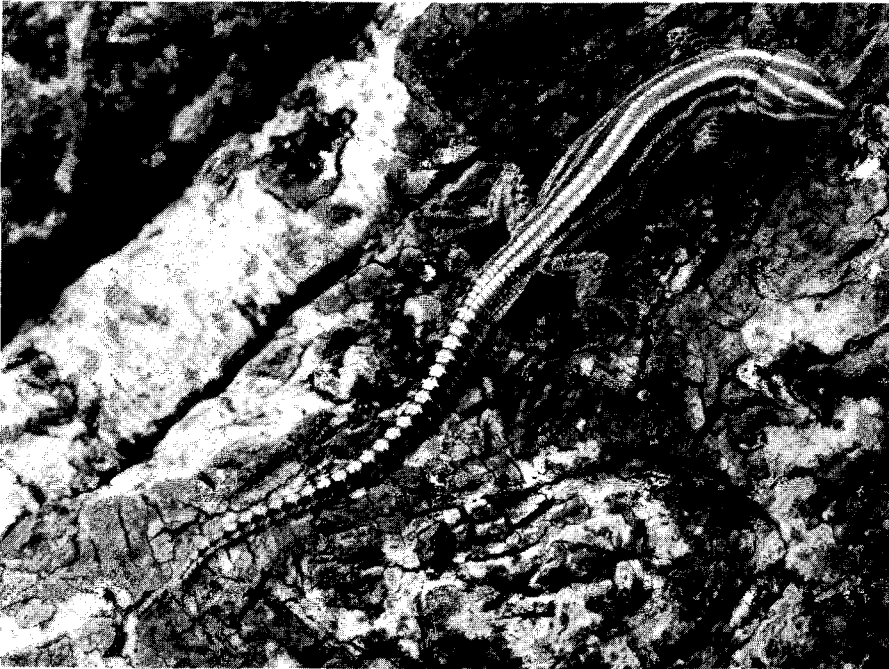
Lacerta jacksoni Boulenger, 1899: 96. Type locality: Ravine Station, Mau Mountains, Kenya. Type: BMNH 98.12.27.8/1946.9.2.99.

Lacerta jacksoni kibonotensis Lönnberg, 1907:5. Type locality: 'Kibonoto' (i.e. Kibongoto), Kilimanjaro, Tanzania. Types: NHRS YSÖ 1905385.5717, NHRS YSÖ 1906145.5718, NHRS YSÖ 1906208.5719, NHRS YSÖ 1906248.5720.

Range: Uganda, Kenya, and Tanzania west through Rwanda and Burundi(?) to eastern Zaire.



(a)



(b)

FIG. 8. Live Equatorial African lacertids photographed in the Ituri Forest, Zaire by Herbert Lang during the American Museum Congo Expedition, 1909–1915, and originally published in Schmidt (1919).

a. *Adolfus africanus*: AMNH 10534, male, length 163 mm.

b. *Holaspis guentheri guentheri*: AMNH 10709, male, length 118 mm.

Adolfus vauereselli (Tornier)

Lacerta vauereselli Tornier, 1902:701. Type locality: Kagera, west of Lake Victoria, Tanzania. Type: ZMB 17700.

Algiroides boulengeri Peracca, 1917: 351. Type locality: Fort Portal, Toro, western Uganda. Type: MZUT R2439 (3136).

Range: Western Uganda and western Tanzania, Rwanda, Burundi(?), northeastern Zaire.

Gastropholis

Gastropholis Fischer, 1886:1. Type species: *G. vittata*.

Bedriagaia Boulenger 1916a: 112. Type species: *B. tropidopholis*.

Lacerta (*Centromastix*) Boulenger, 1916b: 3. Type species: *L. echinata*.

Centromastix Laurent, 1956: 237. Type species: *L. echinata*.

Gastropholis echinata (Figs 9a, 10, 11)

Lacerta (*Zootoca*) *echinata* Cope, 1862: 189. Type locality: not stated, but probably Liberia (Loveridge, 1941). Type: USNM 5995.

Lacerta hirticauda Vaillant, 1884: 168. Type locality: Kinjaho, Assini, Ghana. Type: MNHP 6454.

Lacerta echinata Boulenger, 1885: 10.

Lacerta langi Schmidt, 1919: 492. Type locality: Medje, northeast Zaire. Type: AMNH 10525.

Centromastix echinatus Laurent, 1956: 237.

Range: Liberia, Ivory Coast, Ghana, Cameroon, Equatorial Guinea, Gabon, north and northeast Zaire.

Remarks: Loveridge (1941) revived *Lacerta langi* Schmidt, 1919 as a subspecies of *G. echinata*, but examination of a wide range of material does not support this action and *L. langi* is consequently returned to synonymy.

Gastropholis prasina (Fig. 10)

Gastropholis prasina Werner, 1904: 462. Type locality: probably Tanga, northeast Tanzania. Type: ZMB 18087.

Bedriagaia moreaui Loveridge, 1936a: 67. Type locality: Amani, Usumbara Mountains, northeast Tanzania. Type: MCZ 39799.

Range: Extreme northeastern Tanzania and adjacent southeast Kenya. Loveridge (1957) recorded another individual of this very rare lizard from Tanga; it was preserved by R. E. Moreau but its whereabouts is unknown (Moreau, personal communication, 7.3.1969). K. G. Preston-Mafham photographed a juvenile of this species in the Sokoke forest, on the coast between Malindi and Mombasa, Kenya in March 1979 and J. Ashe obtained a specimen in this region at Watumu in 1985.

Gastropholis tropidopholis (Figs 9b, 10)

Bedriagaia tropidopholis Boulenger, 1916a:112. Type locality: Madje, Ituri District, Zaire. Type: Tervuren Museum.

Range: Zaire: Madje: between Abumombasis and Modjambolija (MCZ 24797); Sankuru (Laurent, 1958); Equateur District (BMNH 1919.8.26.3); Kivu District (LACM 49518).



(a)



(b)

FIG. 9. Live Equatorial African lacertids photographed in the Ituri Forest, Zaire by Herbert Lang during the American Museum Congo Expedition, 1909–1915, and originally published in Schmidt (1919).

a. *Gastropholis echinata*, uniform phase (type of *Lacerta langi* Schmidt, 1919): AMNH 10525, female, length 275 mm.

b. *Gastropholis tropidopholis*: AMNH 10528, male, length 398 mm.



FIG. 10. Species of *Gastropholis*. Left to right: *G. prasina* (holotype of *Bedriagaia moreaui*, MCZ 39799, Amani, Usambara Mountains, Tanzania); *G. echinata*, banded phase (BMNH 1903.5.30.2, Bitye, Ja River District, Cameroun); *G. tropidopholis* (BMNH 1919.8.26.3, Equateur District, Zaire); *G. vittata* with regenerated tail (ZMB 22414, Tendaguru, Tanzania).

Gastropholis vittata (Fig. 10)

Gastropholis vittata Fischer, 1886: 1. Type locality: 'Zanzibar' (probably coast of opposite mainland). Types: BMNH 86.5.15.44–45/1946.8.4.91–92.

Gastropholis lutzei Tornier, 1900: 591. Type locality: Tanga, Tanzania. Type: ZMB 15801.

Range: Coastal Tanzania and Mozambique, from Tanga to Lumbo: Tanga; 50 miles from Bagamoyo on Handeni road (MCZ 54474–5); Morogoro (Kenya Museum); Barikwa, Liwale District (MCZ 54473); Tendaguru (ZMB 22414); Lumbo (MCZ 18307).

Holaspis

Holaspis, Gray, 1863: 152. Type species: *H. guentheri*.

Holaspis guentheri guentheri (Fig. 8b; coloured photographs – Schiøtz, 1960)

Holaspis guentheri (A. Smith), Gray, 1863: 153. Type locality: unknown. Type: BMNH 1946.8.7.3.1.

Range: Sierra Leone, Ghana, Nigeria, Cameroon, Gabon, French Guinea, Zaire, Uganda, Angola.

Holaspis guentheri laevis

Holaspis guentheri laevis Werner, 1895: 191. Type locality: Usambara Mountains, Tanzania. Type: BMNH 95.4.8.4/1946.8.7.25.

Range: Tanzania, Mozambique, Malawi.

Remarks: Loveridge's revival of Werner's subspecies appears justified and material examined here shows the colour differences mentioned in the key below.

Key to the African Equatorial lacertids

Lacertids in which the parietal foramen is consistently absent, the parietal scale extends to the edge of the parietal table and the postnasal scale is single.

- 1a Head and body very depressed, frontoparietal and occipital scales all fused, tail depressed with lateral fringes of scales. *Holaspis guentheri*, 2
- 1b Head and body not or moderately depressed, frontoparietal scales not fused to occipital, tail undepressed without fringes 3
- 2a A dark vertebral stripe on body and three dark stripes on each side
Holaspis guentheri guentheri
- 2b A dark vertebral stripe and two dark stripes on each side
Holaspis guentheri laevis
- 3a All ventral scales longitudinally keeled; 10 or more in longest transverse row 4
- 3b Keeling on ventral scales, if present, limited to outer longitudinal scale rows; not more than eight ventral scales in longest transverse row 6
- 4a Nostril in contact with first upper labial scale, temporal scaling coarse, 10 ventral scales in longest transverse row, main preanal scale(s) unkeeled *Gastropholis tropidopholis*
- 4b Nostril narrowly separated from first upper labial scale, temporal scaling fine, in most cases more than 10 ventral scales in longest transverse row, preanal scales all keeled 5
- 5a Upper parts uniform green, belly greenish; dorsal scales strongly keeled and tectate, 28–32 in transverse row at mid-body; more than 12 ventral scales in longest transverse row across belly *Gastropholis prasina*
- 5b Upper parts brown with two broad, pale dorsolateral stripes, belly white; dorsal scales distinctly but often weakly keeled, usually flattish in vertebral region, 19–26 in transverse row at mid-body; 12, occasionally 10 ventral scales in longest transverse row across belly *Gastropholis vittata*
- 6a Base of tail with a dorsal pad of long, upwardly curved scales
Gastropholis echinata
- 6b Scaling on tail unmodified 7
- 7a Six longitudinal rows of ventral scales, the outermost ones incomplete, not extending forwards to the axillae; vertebral scales very distinctly larger than those on flanks 8
- 7b Six or more longitudinal rows of ventral scales, if six then outermost rows complete; vertebral scales not or scarcely larger than those on flanks 9
- 8a Nostril in contact with first upper labial scale; dorsal scales not minutely tuberculate, 30–49 in a transverse row at mid-body; outer ventral scales unkeeled *Adolfus vauereselli*
- 8b Nostril separated from first upper labial scale; dorsal scales minutely tuberculate, 18–24 in a transverse row at mid-body; outer ventrals keeled *Adolfus africanus*
- 9a Temporal scales numerous; 37–48 dorsal scales in a transverse row at mid-body; many granules present beneath collar *Adolfus jacksoni*
- 9b Temporal scales few (3–12); 18–24 dorsal scales in a transverse row at mid-body; no granules beneath centre of collar *Adolfus alleni*

Ecology

Some idea of the habits of *Adolfus jacksoni*, *A. africanus* and *A. vauereselli* can be gained from a variety of sources including the accounts of Angel (1925, 1928), Barbour & Loveridge (1930), Boulenger (1899a, 1909, 1916b), Curry-Lindahl (1956), De Witte (1941, 1953), Laurent (1954, 1956), Lönnberg (1907), Loveridge (1936b, 1942, in litt.), Schmidt (1919), Sternfeld (1912) and data with BMNH specimens. All three are essentially montane species that are associated with woodland. They climb on standing and fallen timber, taking refuge in holes and crevices in this and beneath trunks, boughs and stones on the ground. Hunting takes place on the ground to a considerable extent.

A. jacksoni occurs from 450 m at Mombo (Loveridge, 1936b) to 2700 m and perhaps 3000 m on Kilimanjaro (Angel, 1925). It is frequently found in montane forest but often extends into clearings and more open areas (Sternfeld, 1912; Angel, 1925; Barbour & Loveridge, 1930) and in some regions is more abundant in such situations (Curry Lindahl, 1956; data with BMNH specimens). Where deforestation has occurred, it may be found on road banks (Loveridge, 1942) and buildings (Angel, 1925; BMNH specimens from Cherangani Hills, Kenya). It eats a variety of arthropods (Barbour and Loveridge, 1930; Loveridge, 1936b, 1942).

In the east of its range, *A. africanus* is found from 580 m (BMNH specimen from Kindu, Zaire) to 1750 m (De Witte, 1953), and in Cameroon at 1200 m (BMNH 1984.646–652, from Rumpi Hills). It occurs in clearings but not in really open country and does not adapt to deforestation as well as *A. jacksoni* (Loveridge, in litt.). It often hunts in litter etc.

A. vauereselli appears to be more strictly montane than the foregoing species, being found from 1000 m to 2400 m (De Witte, 1933; Laurent, 1954; Sternfeld, 1912). It too occurs in clearings and hunts among litter.

A. alleni is a very high altitude species occurring from about 2700 m to 4500 m, almost entirely above the tree line although it has been reported from bamboo forests on Mount Kinangop in the Aberdare Mountains at the lower end of its altitudinal range (Angel, 1925). More usually, it is found in the Alpine, Heather and *Hagenia-Hypericum* zones in moorland situations, where it lives on the ground, often taking refuge in dense tussocks of coarse or spiny vegetation (Loveridge, 1936b; Coe, 1967; data with BMNH specimens).

Like most of the species of *Adolfus*, *Holaspis* is associated with timber but appears to occur nearly always on the trunks and branches of standing trees, often at some height, and does not usually come to the ground (P. Agland, personal communication. D. G. Broadley, personal communication; Barbour & Loveridge 1928; De Witte, 1953; Dungen, 1967; H. Lang in Schmidt, 1919; Laurent, 1964; Loveridge, 1951, 1953; A. P. Mead, personal communication; Perret and Mertens, 1957; Schiøtz & Volsøe, 1959). It is an active hunter, often investigating crevices (P. Agland) in which it also frequently hides (H. Lang in Schmidt, 1919; Laurent, 1964; Loveridge, 1951) and is extremely agile, moving with ease on vertical and overhanging surfaces (H. Lang in Schmidt, 1919). *Holaspis* is unique among lacertids in being able to glide between trees. This was first formally reported by Schiøtz & Volsøe (1959), who observed one lizard travelling a horizontal distance of 10.5 m at an angle of descent of approximately 42°. Gliding ability has been subsequently confirmed (P. Agland, A. P. Mead, personal communications) and earlier reports provide some corroboration. Thus C. J. P. Ionides, quoted by Loveridge (1955), noted that *Holaspis* covers long distances in leaps between trees, and Laurent (1964) reports that local people in

northern Angola said that it can fly. In Cameroon, P. Agland saw lizards making glides of up to 30 m, sometimes at shallower angles than that observed by Schiøtz & Volsøe.

Little has been reported about the ecology of the four species of *Gastropholis*, largely because they are rarely observed and collected. Lang, quoted by Schmidt (1919), states that *G. echinata* is typically arboreal and was found in a rather moist, swampy portion of the Ituri Forest where the trees are covered in long moss. The lizards retreated into hollow trees and ate various hard-shelled beetles occurring on tree trunks. This species is perhaps mainly a canopy form. R. P. Lootens, quoted by Laurent (1956), found two specimens in a cavity in a branch that fell from the top of a tree.

It has also been suggested that *G. tropidopholis* is a canopy species (Laurent, 1958). H. Lang (Schmidt, 1919) found it in the same general situations as *G. echinata*. Although clearly arboreal, it came to the ground and basked on boulders in brooks. It was more sluggish than its congener but, when in danger, jumped from any height and dashed for the shelter of leaves or logs, sometimes running for 10 or 20 yards with the tail in the air.

Loveridge (1957) considered *G. prasina* a canopy form, although R. E. Moreau, who obtained the two specimens that Loveridge saw, knew of no evidence for this (personal communication). Tanga, the type locality of *G. prasina*, is in an area which had semi-evergreen coastal forest (R. R. Moreau, personal communication) and the juvenile Sokoke specimen was also seen in coastal forest where it was climbing on broad-leaved vegetation not far above the ground (K. Preston-Mafham, personal communication). J. Ashe (personal communication) has seen this species in forest near Watumu, in the same area. A captive specimen in his possession climbs well in vegetation, when the tail is put to constant use. This may be wound and twined around stems, occasionally leaving all four legs free, but is often used in conjunction with the hind legs so that the lizard can reach forward with the front ones. The tail is seldom wound in a very tight coil, except for the tip. No certain information appears to exist about the habits of *G. vittata*.

Although most are woodland species, at least some of the members of the Equatorial African group of lacertids bask in the sun. These include *Adolfus africanus* (Lang in Schmidt, 1919; Loveridge, 1942), *A. alleni* (Loveridge, 1936b; Coe, 1967), *Holaspis guentheri* (Barbour & Loveridge, 1928; Dunger, 1967; P. Agland, personal communication) and apparently *Gastropholis tropidopholis* (Lang in Schmidt, 1919).

Adaptive radiation

The members of the Equatorial African group of lacertids have a range of life modes. This radiation into different niches has been accompanied by morphological change, a proportion of which may be functionally associated with the problems of existence in those situations. The most primitive species, *A. jacksoni* is similar to many western Palaearctic lacertids assigned to *Lacerta* and *Podarcis*. However, this general resemblance is probably due to common ancestry rather than adaptation to its particular niche. Boulenger (1920) thought *A. jacksoni* has its nearest affinities to *Lacerta chlorogaster* of northern Iran and adjoining USSR, but close superficial similarity to this species, in such features as coloration, probably arises from convergence since they both occur on tree boles (see, for instance Droedov, 1964, for *L. chlorogaster*). *A. vauereselli* and especially *A. africanus* have a resemblance to some European species of *Algyroides*, particularly *Algyroides nigropunctatus*. This again may be partly

primitive and partly convergent. The two *Adolfus* occur on standing and fallen timber and forage among litter and it is probable that this is the original habitat of the *Algyroides* species concerned, although they are now most frequently observed in habitats modified by man (Arnold, 1973, 1987). Resemblance includes colour and pattern, general habitus, possession of large, blunt, keeled dorsal scales with smaller laterals and a pustulose scale surface on the dorsals. Most of these features may be essentially cryptic. *Adolfus africanus*, *Adolfus vauereselli*, and *Algyroides* also share relatively low numbers of presacral vertebrae (see Table 4 and Arnold, 1973), *Adolfus alleni*, the only member of the African Equatorial group to occur regularly outside forest, has lanceolate, strongly imbricate dorsal scales and overlapping ventrals. This scale configuration is frequent in another lacertids that, like *A. alleni*, live in low coarse or spiny vegetation or take refuge in it, such as members of *Psammodromus*, *Tropidosaurosa* and *Ophisops*, and appears to be protective (Arnold, 1973). The narrow, pale dorsolateral stripes found in *A. alleni* are also often associated with occupation of such vegetation, where they are frequently cryptic, resembling the light-coloured dead stems that are usually present.

Many of the unique morphological features of *Holaspis guentheri* appear to be related to its use of narrow crevices and ability to glide. As in species that utilise crevices in rock faces, such as *Lacerta oxycephala* (Arnold, 1973, 1987), the head and body are depressed, there is little scale imbrication and ossification of the skull is reduced (roofing bones thin, nasal openings large, cranial osteoderms including those in the palpebral region not or poorly developed). The premaxillary boss of *Holaspis* may be important in allowing it to push under loose bark and the modification of the scleral ring in which there are lacunae dorsally and ventrally may allow further flattening of the head. Low ossification should be advantageous for gliding in that body weight is reduced; as well as in the skull, ossification of the sternum is limited, so that there is a very large sternal fontanelle. Depression of the head and body are likely to increase their efficacy as an aerofoil; other features contributing to an effective lift surface are the flattened limbs and tail and the fringes of pointed scales on the tail and the hind toes. The body can also be laterally expanded to a striking degree (Dunger, 1967; P. Agland, personal communication). This radical change in form is apparently accomplished by forward rotation of the elongated dorsal ribs and the ability of the dorsolateral skin to stretch.

It is uncertain whether modifications for crevice use, which occur in a number of other lacertids, appeared first and preadapted *Holaspis* for gliding, but they are at least indicated in the related *Adolfus africanus* and *A. vauereselli*. In the terminology of Gould & Vrba (1982), if crevice modifications did arise first, these would be exaptations rather than adaptations to gliding.

Maynard Smith (1952) pointed out that in all groups of animals that fly, stable gliding and flight evolved before unstable flight. He argued that this was because stable flight was possible without the development of sophisticated neural control mechanisms necessary for successful unstable flight. The presence of a long aerofoil, largely comprising the tail, posterior to the centre of gravity, makes it certain that *Holaspis* is a stable glider and its main behavioural requirement is likely to be propensity to adopt and maintain a suitable posture with the underside downwards and the limbs spread. Again, this may involve little modification of previous abilities since observations suggest that many lacertids, even essentially ground dwelling ones, can adopt the relevant posture. A variety of lizards thrown upwards or dropped over a suspended sheet, so they landed without damage, adjusted their posture in the air and

descended belly downwards. They included specimens of *Acanthodactylus erythrurus*, *Algyroides nigropunctatus*, *Lacerta agilis*, *L. viridis*, *L. horvathi*, *L. mosorensis*, *L. oxycephala*, *Podarcis melisellensis*, *P. muralis* and *P. sicula*.

If the species of *Gastropholis* are indeed canopy or at least foliage dwelling forms, elongation of the body and tail could enhance movement and support in flimsy vegetation. The green coloration in most species is probably cryptic in foliage and the striated micro-ornamentation of the scales may contribute to the lack of reflection that Lang (in Schmidt, 1919) noted helped concealment in *G. tropidopholis*.

Gastropholis echinata is unique among lacertids in having a pad of long spiny scales on the upper surface of the proximal tail (Fig. 11). No observations exist on how this may be employed, but a circumstantial case can be made that it helps the lizard maintain its position on perpendicular stems and thin twigs, for instance when basking or waiting for passing prey. Many arboreal squamates habitually grip twigs or stems with their tails. This prehensility often involves applying the same longitudinal surface of the tail to the object gripped in a regular spiral of low pitch. Thus, some boids (*Corallus*, *Chondropython*) and vipers (*Bothrops schlegeli*), chameleons (*Chamaeleo*) and the skink, *Corucia*, apply the ventral surface of the tail, while colubrids like *Boiga* may use the lateral surface and some lizards, such as members of the gecko genus *Naultinus*, may employ both. *G. prasina* possibly uses the distal part of its tail in this way, but it and some other lacertids employ a different technique as well. This is seen in, for instance, the southeast Asian *Takydromus sexlineatus* and even in the European *Podarcis muralis* which only occasionally ascends vegetation. When climbing or perching on slender vertical or sloping stems, these lizards can maintain their position by twining the tail in a spiral of deep pitch and few turns around the stem (Fig. 12). In contrast to the first kind of prehensility described, the same longitudinal surface of the tail is not applied to the stem. In the individual of *Podarcis muralis*

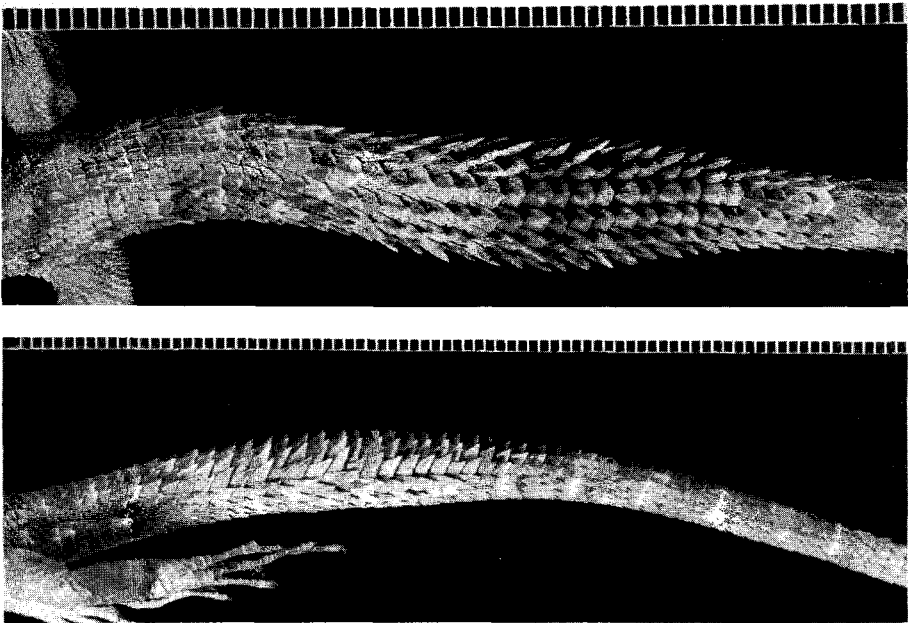


FIG. 11. Tail base of *Gastropholis echinata*: dorsal view (above) and lateral (below).

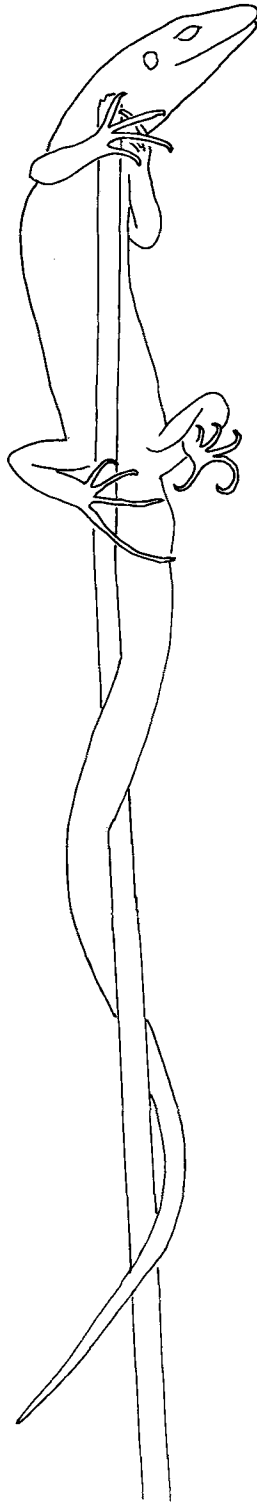


FIG. 12. *Podarcis muralis* from Boračko Jezero, Bosna-Hercegovina, Yugoslavia perching on upright stem.

shown, the face of the tail in contact with the stem changes. Starting from the base, the successive faces applied are right lateral, dorsal, left lateral, ventral, right lateral and dorsal. Activation of the combination of muscles that usually straighten the tail would cause the stem to be gripped firmly and prevent the lizard rotating around it. If *Gastropholis echinata* used its tail in this way when perching on upright stems, the dorsal spiny scales would be pressed obliquely downwards and inwards against the stem, presumably improving hold. The large, forwardly directed transverse vertebral processes present in the region of the pad may also be important in improving the action of the caudal muscles in this area and enhancing grip.

Twining the tail in a deep pitched spiral probably requires little, if any, initial morphological modification, for bending at each vertebral articulation is relatively modest and tends to be in only one main direction at each joint, either lateral or ventral. Use of the tail in a spiral of low pitch with only a single surface applied involves more bending per unit length and is often associated with substantial anatomic changes, such as shortening of the vertebrae and sometimes modification of the musculature so that it lies mainly in the plane of the usual direction of bending.

All *Gastropholis*, except *G. echinata*, are characterised by increase in the number of longitudinal rows of ventral body scales, which are also keeled and pointed. This produces an array of spines which is likely to enhance friction with flimsy vegetation, as occurs in grass dwelling forms, like many *Takydromus* species which have a similar scale arrangement.

Modifications apparently associated with life in the forest canopy have been described for the monitor, *Varanus prasinus*, by Greene (1986). Like most *Gastropholis*, this species is bright green with a relatively long body and a long tail which has some prehensibility. These features are shared by some or all members of the arboreal iguanid genus *Polychrus* (Greene, 1986), which like *Gastropholis*, has an elevated number of presacral vertebrae compared with most members of its family (Etheridge, 1959).

Material examined

The number of specimens examined of each taxon is given below. More details for the rarer species of *Gastropholis* appear above and a full list of material is deposited in the library of the Reptile Section of the British Museum (Natural History).

Adolfus africanus, 31; *A. alleni*, 72; *A. jacksoni*, 88; *A. vauereselli*, 11; *Gastropholis echinata*, 30; *G. prasina*, 2; *G. tropidopholis*, 7; *G. vittata*, 9; *Holaspis guentheri guentheri*, 29; *H. g. laevis*, 12.

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Natural History Congo Expedition of 1909–1915, which are reproduced here. C. J. Humphries and G. Underwood gave advice on computer processing of the data. A. d'A. Bellairs, R. C. Drewes, H. W. Greene and G. Underwood read the manuscript and provided useful comments.

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Addendum

Gastropholis prasina

An additional specimen of this very rare lizard has been lent to me by Dr K. M. Howell (KMH 3250). It comes from the Kiono Forest (6.13S 38.14E), Tanzania and is a male 102mm from snout to vent. Colouring is similar to that described on page 527, but the upper and posterior surfaces of the hind legs are greyish with small light spots. Scale counts are as follows: supratemporal scales 7/7, gular scales 28, number of dorsal scales in a transverse row at mid-body 32, number of ventral scales in longest transverse row 14, femoral pores (number on each side) 15/15.