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## Editorial: Garth Underwood – Dedication

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This issue, the last of the Zoology series of the *Bulletin of the Natural History Museum*, is dedicated to Dr Garth Underwood. Garth has had a long association with the Natural History Museum. In 1964, he was appointed Principal Research Fellow to work on snake systematics, a project which culminated in the modestly titled "A contribution to the classification of snakes" (Underwood, 1967). This book had a major impact on snake classification, pioneering the use of soft anatomy as a source of systematic characters. Its importance may be readily appreciated from the many references made to it in many of the papers in this special issue of the *Bulletin* (see especially Kochva in the introduction to his paper on burrowing asps, *Atractaspis*). In a more informal sense, Garth's association with the Natural History Museum started much earlier than 1964; a visit to the Museum in the late 1930's apparently gave him useful information for answering his Higher School Certificate papers in Zoology! Like many zoologists, an interest in natural history was something that was ingrained, and it seems that Garth always was seeking explanations for biological phenomena. His father, Leon Underwood, an eminent British sculptor and painter, dedicated a book called *Animalia*, subtitled *Fibs about Beasts* to Garth, showing him as a baby, thoughtfully looking at a frog. The book offers poetic or fanciful explanations about the animals within its pages, rather than scientific ones. The dedication

reads: "To Garth, For whom cleaving facts asunder fall, And fancy sheds a healing light on all". Garth, if not then, certainly now seeks more objective, scientific interpretations in the biological sciences, particularly of snake relationships.

Even a brief dedication such as this would be seriously deficient if it did not mention the contribution Garth has made to herpetology, not just in terms of his published work but through his encouragement and supervision of the studies of others. "A contribution to the classification of snakes" was a starting point; Garth has always sought new characters to shed new light on snake relationships, devised new ways of looking at data, and has never been afraid to revisit previous work to improve upon and revise earlier results. He has passed on these ideas to others; within the Museum alone he has supervised no less than 6 PhD's, most relating to snakes, but also encompassing frog and insect systematics. He has also run undergraduate and postgraduate courses in taxonomy, through times when systematics was less appreciated than formerly or even today.

Many people owe Garth a considerable debt of gratitude for his help, guidance and support. He has been an inspiration to generations of undergraduates, postgraduates and scientific colleagues worldwide; we hope he will be pleased with this token of our appreciation.

Editors for this issue:  
Barry Clarke and Mark Wilkinson

Sadly, Garth died on 15th October 2002 before this issue came out. He had seen or was aware of much of its contents.



# Hemipenial variation in the African snake genus *Crotaphopeltis* Fitzinger, 1843 (Serpentes, Colubridae, Boiginae)

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**SYNOPSIS.** Hemipenial variation within the six recognized species of the African snake genus *Crotaphopeltis* is described. The hemipenial ornamentation of the widely distributed species, *C. hotamboeia* and *C. hippocrepis*, seems fairly constant whereas the ornamentation of *C. degeni* and *C. tornieri*, species with disjunct distributions, displays relatively large intraspecific variation. In spite of the variation, the size and ornamentation of the hemipenes serve to distinguish between sympatric and parapatric species.

## INTRODUCTION

The various species within the African snake genus, *Crotaphopeltis* have been treated in a series of taxonomic papers (Rasmussen, 1985; 1993a; 1997; Rasmussen *et al.*, 2000). Hemipenes have been examined *in situ* and in everted or even in partly everted condition where possible. Recent collecting has increased the number of specimens with everted hemipenes. This provides a welcome opportunity for redescribing the hemipenes of the six recognized species. Further, differences between the hemipenes of the various isolated populations of *C. tornieri*, of *C. degeni*, and of the various populations of the widely distributed *C. hotamboeia* may provide an indication of the taxonomic status of some of the populations.

## MATERIAL AND METHODS

Specimens included in the present study are held in the collections of the following museums: The Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Museum of Comparative Zoology, Harvard (MCZ); Musée Royal d'Afrique Centrale, Tervuren (MRAC); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); National Museum of Natural History, Washington (USNM); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK); Zoological Museum, University of Copenhagen, Copenhagen (ZMUC).

In the following list the catalogue numbers and places of origin are given for each specimen of the six currently recognized *Crotaphopeltis* species:

*Crotaphopeltis barotseensis*. **BOTSWANA:** Okavanga Delta (ZMUC 631232).

*Crotaphopeltis braestrupi*. **SOMALIA:** Mareri, ca. 8 km SW of Gelib (CAS 153370, 153379).

*Crotaphopeltis degeni*. **CAMEROON:** Gueme (MRAC 73-15-R209). **ETHIOPIA:** Gambela (USNM 24389). **SUDAN:** Assalaya, 10 mls E. of Kosti (RMNH 24411, 25018). **TANZANIA:** Tumba,

Lake Rukwa (ZMUC 631233); Minziro Forest (ZMUC R631598, R631610, R631618, R631621). **UGANDA:** Kome Island, Victoria Nyanza (BMNH 1984.883).

*Crotaphopeltis hippocrepis*. **GHANA:** Legon (ZFMK 63880); Legon Hill (ZMUC R631238); Legon Road, Achimota (ZFMK 63775); Wa, Secondary School (ZFMK 63875, 63877).

*Crotaphopeltis hotamboeia*. **CONGO:** Tchissanga (ZMUC R631177). **GHANA:** Wa (ZFMK 63874). **KENYA:** Langata, NW of Nairobi (ZMUC R63984). **SOUTH AFRICAN REPUBLIC:** Cape Peninsula (ZMUC R63894); Tshaneni (ZMUC R63889). **SUDAN:** Talanga Forest (ZMUC R63980); Torit (ZMUC R63979). **TANZANIA:** Magombero Forest (ZMUC R63921); Msolwa area, Rubeho Mountains (ZMUC R631205–06, R631208–10); Rungwe Mountains (ZMUC R631264, R631266, and R631268). **ZAIRE:** 6 km NE of Kafumba, near Kikwit (ZMUC R631072).

*Crotaphopeltis tornieri*. **TANZANIA:** East Usambara Mountains: Amani (R631122–3); Kwamkoro (R631127). Rungwe Mountains: Rungwe Mission ZMUC R631257. Udzungwa Mountains: Kihanga River, Udzungwa Scarp Forest Reserve ZMUC R631269–70; Kilanzi-Kitungulu Forest Reserve ZMUC R631244–45, R631252–54, R631256. West Usambara Mountains: Mazumbai (ZMUC R63963, R631129, R631135, R631137, R631140, R631142–3, R631146–7, R631155).

Terminology follows Böhme (1988) and Ziegler & Böhme (1997). Preparation of the hemipenes of specimens previously preserved in alcohol was done according to the method described by Pesantes (1994) and Ziegler & Böhme (1997).

## RESULTS

*Crotaphopeltis barotseensis* (Fig. 1). *In situ* hemipenes extend to subcaudal scute no. 7–8 ( $\bar{x}=7.4$ ,  $n=5$ ) (Rasmussen, 1997). The only known everted hemipenes of this species have been prepared from a preserved specimen (ZMUC R631232). Consequently the organs are somewhat wrinkled, hardened and not completely distended.



**Fig. 1** *Crotaphopeltis barotseensis*, right hemipenis in sulcal, left hemipenis in asulcal view of ZMUC R631232.

Pedicle covered with tiny spines. Lower truncus covered with several somewhat enlarged spines, the most conspicuous on each side of the sulcus. Spines decrease in size towards the terminal somewhat calyculate apex. Sulcus spermaticus unforked, leading directly to the apex.

*Crotaphopeltis braestrupi* (Fig. 2). *In situ* hemipenes extend to subcaudal scute no. 15–23 ( $\bar{x}$ =18.4,  $n$ =61) and may be twice as long as in sympatric *C. hotamboeia* (Rasmussen, 1985). This distinctive difference is not reflected in the everted organs; however, the hemipenes of the present specimens (CAS 153370, 153379) are not entirely everted.

Pedicle covered with tiny spines except for a longitudinal depression on the outer asulcate surface that extends from the base of the pedicle to the lower truncus. Lower truncus covered with two to three slightly enlarged spines, one on either side of the sulcus and a less conspicuous one on the asulcate surface. Spines decrease in size towards the terminal somewhat calyculate apex. Sulcus spermaticus unforked, leading directly to the apex.

*Crotaphopeltis degeni* (Fig. 3). *In situ* hemipenes extend to subcaudal scute no. 7–11 ( $\bar{x}$ =8.4,  $n$ =35) (Rasmussen, 1997; Rasmussen *et al.*, 2000).



**Fig. 2** *Crotaphopeltis braestrupi*, asulcal view of right hemipenis of CAS 153379.



**Fig. 3** *Crotaphopeltis degeni*, asulcal view of hemipenes of ZMUC R631621.

In the specimens from Minziro Forest, Tanzania, with freshly but not completely everted hemipenes (ZMUC R631598, R631610, R631618, R631621) superficial genital morphology is as follows: Pedicel covered with tiny spines. Lower truncus somewhat constricted and with two distinctly enlarged spines: one outside the sulcus spermaticus and another on the inner truncal surface. Remaining spines slightly decreasing in size towards the apex. Sulcus unforked, running directly to the apex.

In the specimen from Lake Rukwa, Tanzania (ZMUC R631233) the right hemipenis was everted after fixation. The somewhat wrinkled, hardened and incompletely distended organ bears scarcely detectable, slightly enlarged spines on the lower truncus. In this specimen the sulcus is unforked, running directly to the apex, ending in a terminal extension. Tip of apex calyculate.

In contrast, in the incompletely everted hemipenes of the two specimens of *Crotaphopeltis degeni* from Sudan (RMNH 24411, 25018) the lower truncus bears a ring of several distinctly enlarged spines.

In the uneverted hemipenes of specimens from Ethiopia (USNM 24389), Uganda (BMNH 1984.883) and Cameroon (RGMC 73-15-R209) clearly enlarged lower truncal spines are discernible.

*Crotaphopeltis hippocrepis* (Fig. 4). *In situ* the hemipenes extend to subcaudal scute no. 8–12 ( $\bar{x}$  = 10.1,  $n$  = 38) (Rasmussen *et al.*, 2000).

Pedicel covered with tiny spines except for a longitudinal depression on the asulcate surface. Lower truncus with two distinctly



**Fig. 4** *Crotaphopeltis hippocrepis*, sulcal view of left hemipenis of ZFMK 63877.



**Fig. 5** *Crotaphopeltis hotamboeia*, asulcal view of hemipenes of ZMUC R631177.



**Fig. 6** *Crotaphopeltis hotamboeia*, asulcal view of hemipenes of ZMUC R631210.

enlarged spines on either side of the sulcus (ZFMK 63875, 63877, ZMUC R631238), each followed above by several (usually 1–3) enlarged spines, apically decreasing in size (see also Rasmussen *et al.*, 2000: fig. 3). Even in the only basally everted hemipenes of ZFMK 63775 and ZFMK 63880 these enlarged spines are easily recognizable. The remaining spines of truncus and apex are medium-sized, decreasing in size towards the apex which is calyculate terminally. Unforked sulcus spermaticus leading directly towards the apex, ending in a terminal extension.

*Crotaphopeltis hotamboeia* (Figs 5,6). *In situ* hemipenes extend to subcaudal scute no. 7–14 ( $\bar{x}$  = 10.1,  $n$  = 308).

Pedicel of the hemipenis of *C. hotamboeia* covered with tiny spines except for a longitudinal depression on the asulcate surface. Lower truncus with three distinctly enlarged spines, one on each side of the sulcus, the third on the asulcate surface (ZFMK 63874, ZMUC R63889, R63979–80, R631177, R631264, 631266, R631268). Even in the only basally everted hemipenes of ZMUC R63894, R63984, and R631072 these three enlarged spines are also easily detectable. Distal to the three enlarged spines the hemipenis is covered with medium-sized spines decreasing in size towards the apex. The very tip of the apex seems to be somewhat calyculate. Unforked sulcus is leading directly to the apex ending in a terminal extension.



Fig. 7 *Crotaphopeltis tornieri*, asulcal view of hemipenes of ZMUC R631147.

Contrary to this condition the hemipenes of ZMUC R631205–6 and R631208–10 (Msolwa area, Rubeho Mts., Tanzania) have, in addition to the three enlarged spines, a ring consisting of variously enlarged spines on the asulcate surface of the middle truncus. A similar condition was found in the hemipenes of ZMUC R63921 (Magombero Forest, ca. 50 km S Mikumi, Tanzania).

*Crotaphopeltis tornieri* (Fig. 7). *In situ* hemipenes extend to subcaudal scute no. 7–11 ( $\bar{x}=8.4$ ,  $n=27$ ) (Rasmussen, 1993a; unpubl.).

The pedicel of the hemipenis of *C. tornieri* is covered with tiny spines except for a longitudinal depression on the asulcate surface. Lower truncus usually with some enlarged spines. Distal to the enlarged spines, the spines become smaller towards the apex, which is terminally calyculate. Sulcus spermaticus is not forked and leads directly to the apex ending in a terminal extension.

In specimens from East and West Usambara Mountains the largest spine is on the outside of the lower truncus, the second largest on the asulcate surface. The spine ornamentation of the hemipenes of the West Usambara population was somewhat variable, in the hemipenes of ZMUC R63963 (Rasmussen, 1993: fig. 2) no distinctly enlarged spine could be found on the asulcate surface.

In some specimens (ZMUC R631245 and R631252) from Kilanzi-Kitungulu Forest Reserve, Udzungwa Mountains, the enlarged spine on the outside of the lower truncus is relatively small; furthermore an enlarged spine on the asulcate surface is scarcely detectable. In other specimens (ZMUC R631244, R631253–4 and R631256) from the same area, various enlarged spines are present on the lower truncus.

In specimens from Kihanga River, Udzungwa Scarp Forest Reserve (ZMUC 631269–70) and from Rungwe Mission, Mount Rungwe (ZMUC 631257), only the enlarged spine on the outside of

the lower truncus is easily seen. On the asulcate surface some enlarged spines are present.

## DISCUSSION

The hemipenial structures of *Crotaphopeltis* share several characters, e.g., pedicel largely covered with tiny spines, lower truncus with enlarged spines, spines decrease in size distally, apex calyculate, sulcus spermaticus unforked and leading directly to the apex. Regarding the simple and stout to elongate hemipenes within *Crotaphopeltis*, principally the differences in ornamentation of the (lower) truncus seem to offer a clue as to separate these taxa, in spite of the relatively large interspecific variation displayed.

*Crotaphopeltis barotseensis* principally has one moderate enlarged spine on each side of the sulcus in the hemipenes of the single specimen examined. The species has a restricted distribution in Central Southern Africa and is easily distinguished from sympatric *C. hotamboeia* by general morphology (Rasmussen, 1985) as well as hemipenial morphology.

Hemipenes of *Crotaphopeltis braestrupi* have two to three slightly enlarged spines on the truncus, one on each side of the sulcus and an inconspicuous one on the asulcate side. Comparing the hemipenes of *C. braestrupi* with those of sympatric *C. hotamboeia* from Kenya and Somalia, Rasmussen (1985) stated: 'The ornamentation is also very different. In *C. braestrupi* the hemipenis is covered with slender spines, of which three are somewhat enlarged. In *C. hotamboeia* the hemipenis is covered with stout spines of which three basal ones are strongly enlarged (Rasmussen, 1985: fig. 9).' It is difficult to judge the form of the variable spines (slender versus stout), which depend on the condition and the method of preparation of the hemipenes, but the three distinctly enlarged spines on the lower truncus are nonetheless characteristic of the hemipenes of *C. hotamboeia* across its entire distribution, i.e., Sub-Saharan Africa. Further studies are needed to show whether a separate taxon is justified for the specimens from Msolwa and Magombero Forest in Tanzania which, in addition to the three enlarged spines, have a ring consisting of some distinctly enlarged spines on the asulcate side of the hemipenes. External morphological investigations so far do not support such an assumption (Rasmussen, in prep.).

The hemipenes of *Crotaphopeltis degeni* usually bear two (specimens from Tanzania) to several enlarged truncal spines (specimens from Cameroon, Ethiopia, Sudan, Uganda). Concerning the truncal spines of the hemipenes of *Crotaphopeltis degeni* from Sudan Rasmussen (1997) stated, 'up to six enlarged, stout spines, one each side of the sulcus and two to four (usually three) more or less enlarged spines on the asulcate aspect of the organ'. The lower truncal spines of the hemipenis of a specimen from Lake Rukwa, Tanzania appear only slightly enlarged, most probably due to eversion after fixation. Rasmussen (1997) observed only two enlarged, proximal spines in the incompletely everted hemipenes of specimens from Kenya and Uganda. *Crotaphopeltis degeni* apparently has a disjunct distribution like that of *Causus resimus* (Spawls and Branch, 1995). Despite the intraspecific variation of this taxon it is easily distinguished from sympatric *C. hotamboeia* and parapatric *C. hippocrepis* by hemipenial morphology and as well as general morphology (Rasmussen *et al.*, 2000).

The hemipenes of *Crotaphopeltis hippocrepis* are characterized by the possession of two distinctly enlarged spines, each followed by a row of accessory spines decreasing in size apically. This unique ornamentation of the hemipenes seems fairly constant within the entire distribution area (West Africa) of *C. hippocrepis* and the species seems to be homogeneous (Rasmussen *et al.*, 2000).



In the northern part of its distribution (The Usambara Mountains) the hemipenes of *Crotaphopeltis tornieri* usually have two slightly enlarged spines, one on the outside of the truncus and one (rarely missing) on the asulcate side. Based on external morphology, Rasmussen (1993) found significant differences between the populations of *C. tornieri* from East and West Usambara Mountains. The present results of the genital investigation do not lend support to the recognition of different forms, nor do molecular (Gravlund, 2002) or microdermatoglyphic (Berggreen, 1996) studies. Accordingly, the differences found in numbers of ventral and caudal scutes between these areas are probably due to genetic drift in small, isolated populations.

Gravlund (2002) found significant differences between the molecular composition of the northern and southern populations of *C. tornieri* in the Eastern Arc. In particular, the population from the Rungwe Mountains is very different molecularly from those of the Udzungwa and the Usambara Mountains. The present study also shows slight hemipenial differences between these populations. In the hemipenes of the populations from Kihanga River (Udzungwa Scarp Forest Reserve) and the Rungwe Mountains only the enlarged spine on the outside of the truncus is visible. The picture, however, becomes blurred as hemipenes of specimens from Kilanzi-Kitungulu (Udzungwa Mountains) may have either a relatively small spine on the outside and likewise on the asulcate side or various enlarged spines on the truncus. Thus, the data on genital morphology indicate that the spine ornamentation of the lower truncus in the hemipenes of *C. tornieri* is variable even within single populations and with current knowledge should not be used for defining different taxa within the *C. tornieri* complex. This is in accordance with Berggreen (1996) who found some microdermatoglyphic variation within and between the various populations. The variation, however, was not population specific. *Crotaphopeltis tornieri* (*s.l.*) is restricted to the montane forest of the Eastern Arc of Tanzania and is easily distinguished from sympatric/parapatric *C. hotamboeia* from the lowland savanna.

Thus, irrespective of the fact that intraspecific variation may occur within the various species of *Crotaphopeltis*, the ornamentation of the lower truncus serves at least to distinguish between the males of sympatric or parapatric species. The length at least of the inverted hemipenes may also serve to distinguish between the species and so may the unique rows of accessory spines in the hemipenes of *C. hippocrepis*. Here, it is interesting to note, that the

pattern of the latter species is similar (Dowling, *in litt.*) to that of the sister-genus *Dipsadoboa* (Rasmussen, 1979), which is also characterized by similar, highly derived genital morphological features (Rasmussen, 1993b).

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# Review of the Dispholidini, with the description of a new genus and species from Tanzania (Serpentes, Colubridae)

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**SYNOPSIS.** The tribe Dispholidini (Bourgeois 1968) is reviewed, paying particular attention to dentition and visceral anatomy. A new genus and species, *Xyelodontophis uluguruensis*, is described from the Uluguru Mountains in Tanzania. All five genera have enlarged rear maxillary teeth. *Thrasops* seems to be basal. *Rhamnophis* shows the development of dagger-like teeth tapering from base to tip, then the other three genera appear to radiate, with *Xyelodontophis* having more derived dagger teeth broadest in the middle, while *Dispholidus* and *Thelotornis* seem to have independently developed enlarged grooved rear fangs.

*Thrasops schmidtii* is recognised as a relict evolutionary species. No subspecies of *Rhamnophis aethiopyssa* or *Dispholidus typus* are recognised, but the population of *Dispholidus* on Pemba Island probably represents an undescribed species.

## INTRODUCTION

From the time of Boulenger's catalogues (1893–96), it was customary to separate the aglyphous colubrid snakes (subfamily Colubrinae) from the opisthoglyphs (subfamily Dipsadomorphinae or Boiginae), see for example Loveridge (1957) and FitzSimons (1962).

Bourgeois (1968) erected a subfamily Dispholidinae, including the aglyphous genera *Thrasops* Hallowell 1857 and *Rhamnophis* Günther 1862, and the opisthoglyphous genera *Dispholidus* Duvernoy 1832 and *Thelotornis* A. Smith 1849. Subsequent authors have often treated *Rhamnophis* as a synonym of *Thrasops* (e.g. Hughes & Barry, 1969; Pitman, 1974; Spawls, 1978; Hughes, 1983; Trape & Roux-Estève, 1995; Chippaux, 1999) and many have considered these aglyphous snakes to be members of the tribe Philothamnini (e.g. Dowling & Duellman, 1978).

During a review of the genus *Thelotornis* in East Africa (Broadley, 2001), a snake from montane forest on the summit of the Uluguru Mountains was initially assumed to represent a new species. However, examination of its rear maxillary teeth showed that they were not the anticipated grooved fangs, but distinctive curved dagger-shaped teeth with sharp anterior and posterior ridges, which are widest midway along the tooth. To determine the relationships of this strange snake to the other taxa of the Dispholidini, its skull was prepared (after examination of the dental gland) and compared with skulls of the other genera. This prompted a review of the genera *Thrasops* and *Rhamnophis*, which appear to represent basal taxa of the Dispholidini. As the 'Dagger-tooth Vine Snake' of the Uluguru Mountains seems to be transitional between *Rhamnophis* and *Thelotornis*, but cannot be accommodated in any of the existing genera of the tribe Dispholidini, it is proposed to erect a new genus and species for it. In external appearance and scale counts it resembles *Thelotornis*, but it lacks the distinctive horizontal key-hole shaped pupil of that genus.

It is with pleasure that we dedicate this paper to Garth Underwood, in recognition of the major contributions that he has made to our understanding of African snakes.

## MATERIALS AND METHODS

This study is largely based on material available in the Natural History Museum of Zimbabwe and the Museum of Comparative Zoology, Harvard, with additional data derived from the literature. Unfortunately the collections in the Natural History Museum were not accessible. Loveridge's 1944 revisions of *Thrasops*, *Rhamnophis* and *Thelotornis* were based largely on scalation, supplemented by maxillary tooth counts and coloration of head and neck in the case of *Thelotornis*. We have emphasised the morphology of the rear maxillary teeth and skull, and have also used data from the visceral anatomy, using the Philothamnini as the outgroup for comparative purposes. Data for good series of *Philothamnus angolensis*, *Hapsidophrys lineatus* and *H. smaragdina* were available [Broadley (1966) provisionally synonymised *Gastropyxis* Cope 1860 with *Hapsidophrys* Fischer 1856, and this move is supported by the visceral data]. In the species accounts we have only presented chresonymies, full synonymies are included in the review of the East African *Thelotornis* (Broadley, 2001) and investigation of the variation in the wide-ranging genus *Dispholidus* awaits future workers!

In the description of the visceral anatomy, the mean value for most characters as % snout-vent length (SVL) is presented first, followed parenthetically by the range or midpoint (MP) value. When only the name of an organ is given, the value represents its length. Ratios of two visceral characters are presented in fractional notation. When only one value is given for a character, it is identical in the two specimens or differs by less than 0.1%.

The position of the umbilicus is determined by the most anterior ventral bearing a scar (the scar usually covers three ventrals and the umbilicus exited through the medial scute). The umbilical scar-vent interval is calculated by dividing the number of ventrals from the scar to the vent by the total number of ventral scutes.

Material for which skulls or viscera were examined is listed in appendices. Institutional abbreviations follow Leviton *et al.* (1985), with the addition of:

IRSL = Institut d'Recherche Scientifique, Lwiro, Democratic Republic of Congo (DRC); UNAZA = Université National du Zaïre, Kisangani, DRC; VW = Van Wallach dissection number (museum deposition of specimen unknown).

## CHARACTER ANALYSIS

**1. Rear maxillary teeth.** The three rear maxillary teeth of *Thrasops flavigularis* (type species) and *T. jacksonii* are enlarged and separated from the small anterior teeth by a diastema, they taper from base to tip and have slight ridges anteriorly and posteriorly (Fig. 1A, Group B dentition of Jackson & Fritts, 1995). The posterior ridge becomes blade-like in some genera, e.g. *Heterodon* (Kardong, 1979), *Thamnophis* (Wright, *et al.*, 1979) and *Stegonotus* (Jackson & Fritts, 1995).

The same teeth in *Rhamnophis aethiopyssa* (Fig. 1B) and *R. batesii* (Fig. 1C) are curved, with sharp anterior and posterior ridges, but not nearly as well developed as in the 'Dagger-tooth Vine Snake' of the Uluguru Mountains, in which the ridges are broadest midway along the tooth, which is leaf-shaped, narrowing at the base (Fig. 1F). In *Dispholidus* and *Thelotornis* the three greatly enlarged rear maxillary teeth are deeply grooved (Group D dentition of Jackson & Fritts, 1995), but these genera retain a strong ridge on the anterior face of the fangs. In *Thelotornis*, this ridge arises within the groove, so that the venom canal is divided, before petering out well before the fang tip (Fig. 1G, after Meier, 1981, fig 4). In *Dispholidus* on the other hand, the ridge runs along the anterior edge of the groove (Fig. 1H, after Meier, 1981, fig 2).

With regard to number of maxillary teeth, *Rhamnophis aethiopyssa* (16 to 20 + 3) resembles *Thrasops* spp. (17 to 18 + 3), but *R. batesii* (30 to 35 + 3, Fig. 1C) is divergent in this respect. The Dagger-tooth Vine Snake has 14 + 3, thus matching *Thelotornis* (11 to 16 + III) in actual tooth number. *Dispholidus* shows a marked reduction in number of anterior teeth to 4 to 8 + III. Counts of maxillary tooth sockets are much higher in the Philothamnini: 17–48 in *Philothamnus* and 20–33 in *Hapsidophrys*.

**2. Dental (Duvernoy's) gland.** This gland is small in *Thrasops* and *Rhamnophis* (Kochva, 1978), larger in *Thelotornis* (but smaller than the orbit), still larger in the Dagger-tooth Vine Snake (subequal to the orbit) and reaches its maximum development in *Dispholidus* (Kochva, 1978), with a large, purely serous, slightly branched, tubuloacinous Duvernoy's gland, the tubule walls highly folded, increasing the storage space within the gland (Taub, 1967), thus constituting a reservoir (Underwood, 1997). The mechanism of delivery of toxic dental gland secretions by low pressure systems has been demonstrated for *Boiga irregularis* (Kardong & Lavin-Murcio, 1993) and is effective regardless whether or not the teeth are grooved (Weinstein & Kardong, 1994).

**3. Skull.** The Dispholidini were first recognised (as a subfamily) by Bourgeois (1968) on the basis of their similar skull morphology (Fig. 2). She drew attention to the forked ectopterygoid, large optic fenestra and interorbital vacuity (also noted by Underwood, 1967). The ectopterygoid is shallowly forked in *Thrasops*, *Thelotornis* and the Dagger-tooth Vine Snake, but is very deeply forked in both species of *Rhamnophis* and in *Dispholidus*. Underwood (1967) noted the absence of a Vidian canal in the skulls of *Thrasops* and *Thelotornis*, but Vaeth (1982) found a short, but distinct, Vidian canal in the skulls of three *Thrasops jacksonii*.

**4. Pupil shape.** The pupil is round in *Thrasops* and *Rhamnophis* (Fig. 3) as in the Philothamnini, but in *Dispholidus* and the Dagger-

tooth Vine Snake it may be more pear-shaped, due to an anterior prolongation. *Thelotornis* is distinguished by its horizontal 'key-hole' shaped pupil (Fig. 4B-D).

**5. Visceral anatomy.** The Dispholidini can be characterized by the following visceral characteristics (Tables 2–4): umbilical scar-vent interval 8–12% total ventrals; hyoid short with posterior tips at 7–10% SVL, heart short, 1.5–3.1% (mean 2.4%); right systemic arch reduced to 0.20–0.40 left systemic arch diameter; liver narrow with midpoint at 43–46% SVL; gall bladder cranial of pancreas and spleen; testes normally unipartite but occasional specimens with bi- or tri-partite organs (the additional segments being small sections separated from the main body either posteriorly or anteriorly); kidneys compact but segmented (15–45 segments); no tracheal lung; trachea with narrow, well-separated cartilages that lack free tips, tracheal membrane expanded to 2.0–4.0 (mean = 2.9) times the circumferential width of the rings; weak development of the cardiac lung to midheart level; tracheal entry into right lung subterminal, right lung with small anterior lobe and small orifice; right lung elongate (69–70% SVL), extending to 94–97% body length, cranial vascular portion 0.15–0.25 lung length, usually with midventral avascular strip, caudal saccular portion long 0.75–0.85 lung length; faveolar parenchyma arranged in 2–3 tiers with pattern of transverse smooth muscle ribs enclosing rows of paired faveoli; semisaccular portion of lung short (0.10–0.20 vascular lung length) with abrupt termination of parenchyma along a transverse border.

The hemipenes of the genera *Thrasops*, *Dispholidus* and *Thelotornis* appear to be similar, being simple, capitate, with an undivided sulcus. There are large basal spines which diminish in size distally and are replaced by calyces on the distal cap (Bogert, 1940). The organs of the Dagger-tooth Vine Snake show little difference, the nude basal portion has four large hooks, the medial portion is spinose and the apical portion is calyculate. The hemipenes of *Rhamnophis* have not yet been described.

**6. Dorsal head coloration.** The development of complex head patterns may aid in species recognition. All four species of *Thrasops* have the head uniform olive when subadult, eventually becoming uniform black. *Rhamnophis batesii* has a uniform brown or black head, while that of *R. aethiopyssa* is green, with the shields margined with black. A somewhat similar black vermiculation on a yellow or green ground is found in males of some populations of *Dispholidus typus*, but many have no colour pattern. The Dagger-tooth Vine Snake has dark margins to the head shields and yellow labials. The four species of *Thelotornis* can be distinguished by the colour pattern of the head (Broadley, 2001). The top of the head is uniform green in *T. kirtlandii* (Fig. 4B), *T. usambaricus* and some *T. mossambicanus*, but blue-green with black and pink speckling in *T. capensis* (Fig. 4D). The temporals are uniform green in *T. kirtlandii* (Fig. 4B) and *T. usambaricus*, brown with black speckling in *T. mossambicanus* (Fig. 4C), and pink margined with black in *T. capensis* (Fig. 4D). The supralabials are uniform or with faint green or grey stippling in *T. kirtlandii*, but the other taxa have black spots, usually including a speckled black triangle on the sixth labial.

**7. Throat pattern.** All members of the Dispholidini (and some members of the Philothamnini) can inflate the throat in a threat display, reaching its maximum development in *Dispholidus*. Chippaux (1999, Pl. 17) illustrates this phenomenon in *Thrasops flavigularis*, where the black dorsum contrasts with the pale throat, but in *T. jacksonii* the throat often becomes entirely black. *Rhamnophis* has the dark green dorsal scales bordered with black, the throat is yellowish in *R. batesii* and green in *R. aethiopyssa*. *Dispholidus* comes in a wide range of colour patterns, but usually

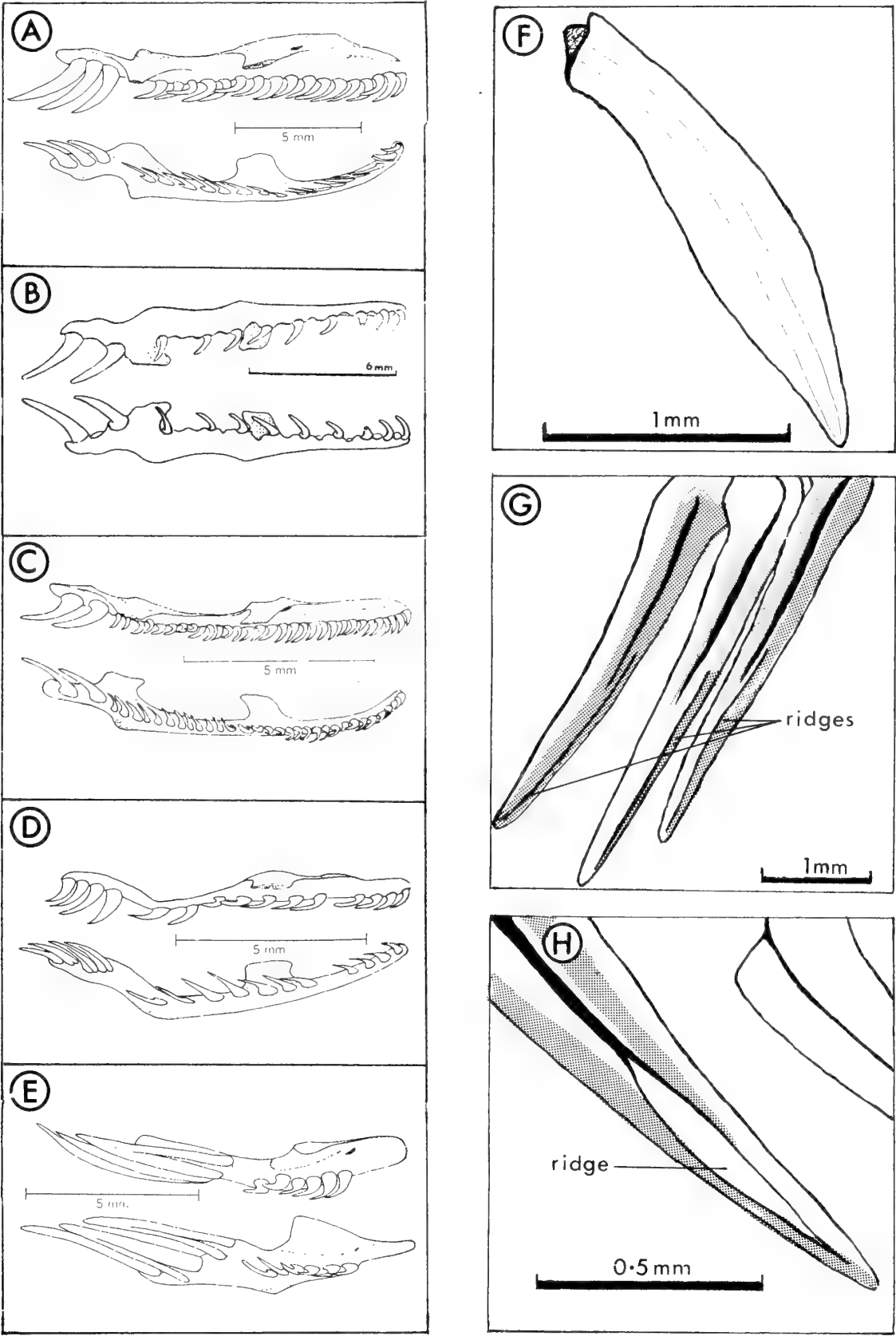


Fig. 1 Dentition: Left – maxillae of: A. *Thrasops flavigularis*; B. *Rhamnophis aethiopyssa*; C. *Rhamnophis batesii*; D. *Thelotornis kirtlandii*; E. *Dispholidus typus*. Right – teeth of: F. *Xyelodontophis uluguruensis*; G. *Dispholidus typus*; H. *Thelotornis kirtlandii*. (A, C, D, E after Chippaux, 1999; B after Bourgeois, 1968; F, G, H after Meir, 1981).

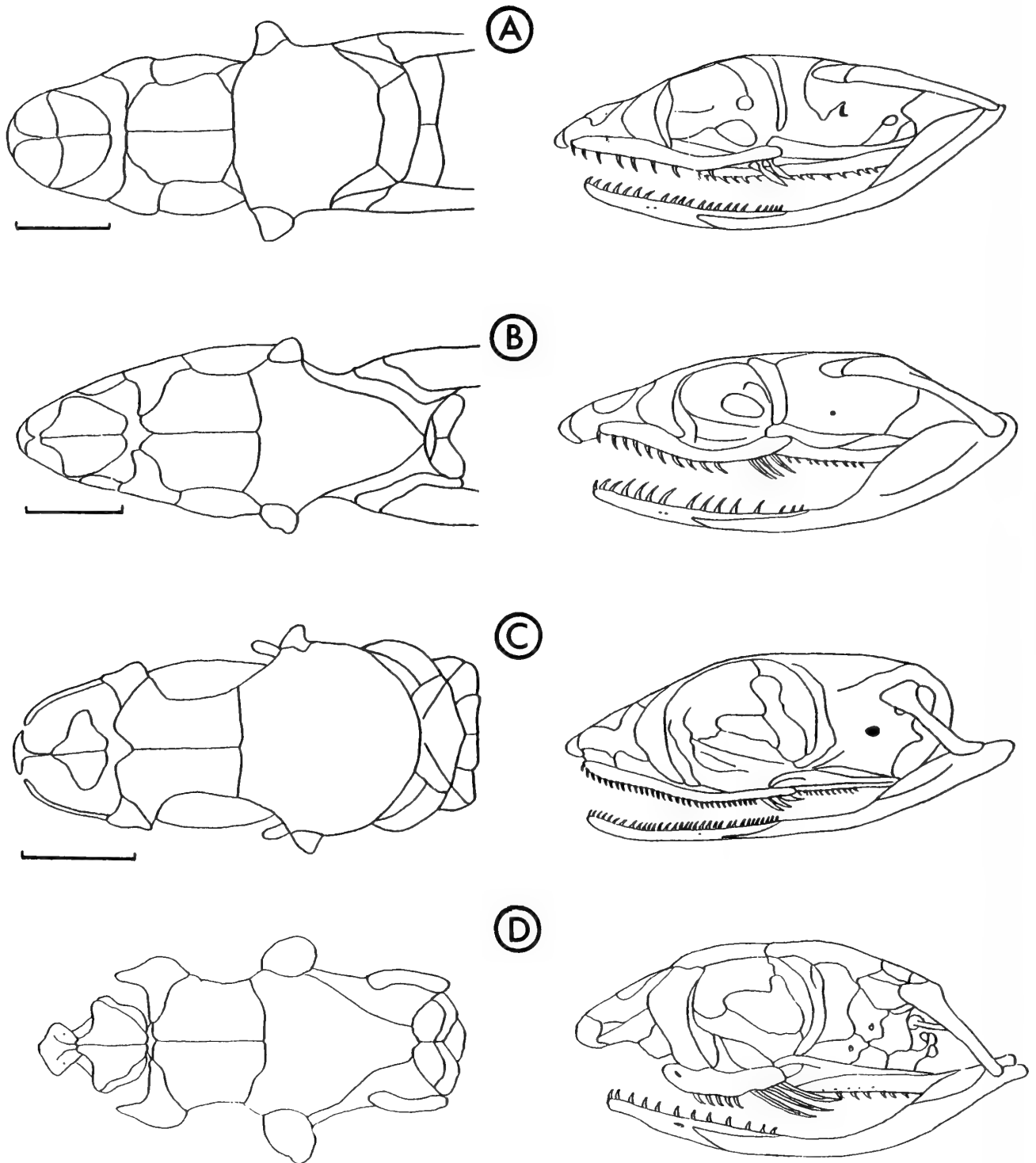


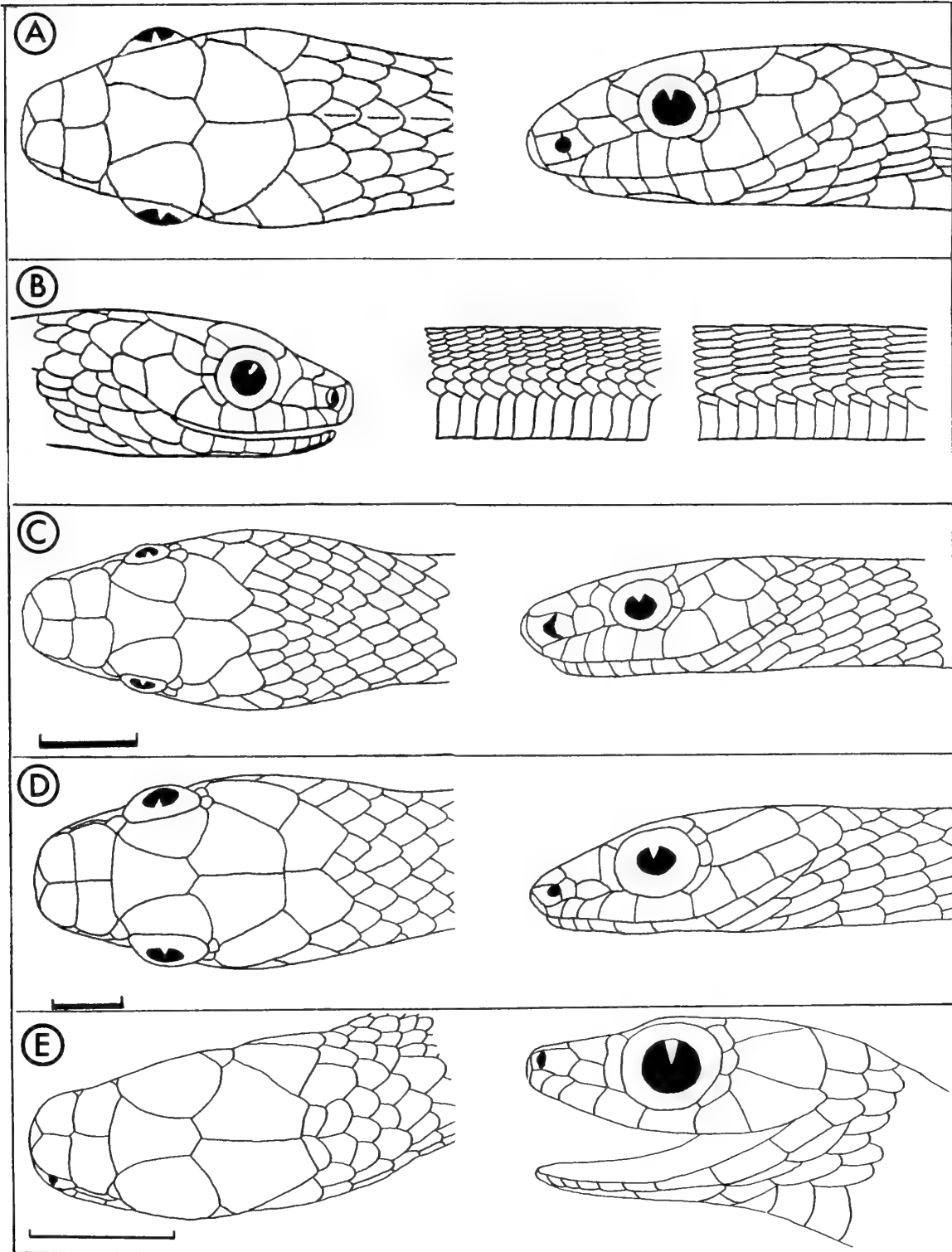
Fig. 2 Skulls of: A. *Xyelodontophis uluguruensis*; B. *Thelotornis mossambicanus*; C. *Rhamnophis batesii*; D. *Dispholidus typus*.

has a black spot on the side of the neck (Broadley, 1983, fig. 144), in this species the inflation may extend half way down the body. The inflated throat of *Thelotornis* is grey-white with distinctive black markings – crossbars in *T. kirtlandii*, chevrons in *T. usambaricus*, one or two elongate blotches in *T. mossambicanus* and two larger dorsally extensive blotches in *T. capensis*.

8. *Temporals and occipitals*. In *Thrasops* there are almost invariably 1 + 1 temporals and there are no enlarged occipital shields. In

*Rhamnophis* there is a single large temporal: *R. batesii* has four large occipitals, while *R. aethiopissa* has two very large ones. In *Dispholidus*, *Thelotornis* and the Dagger-tooth Vine Snake there are usually 1 + 2 temporals and three occipitals (or two separated by a smaller interoccipital). The Philothamnini tend to have more numerous temporals (1 + 1 up to 2 + 2 + 2) and no enlarged occipitals.

9. *Supralabials* (Table 1). *Thrasops* usually has 8 supralabials, the fourth and fifth entering the orbit. *Rhamnophis batesii* has 7 or 8, 4



**Fig. 3** Head shields of: A. *Thrasops flavigularis*; B. *Thrasops occidentalis*, with midbody scapulation to the right, compared with midbody scapulation of *T. flavigularis* on the far right (after Parker, 1940); C. *Thrasops jacksonii*; D. *Rhamnophis aethiopissa*; E. *Rhamnophis batesii*.

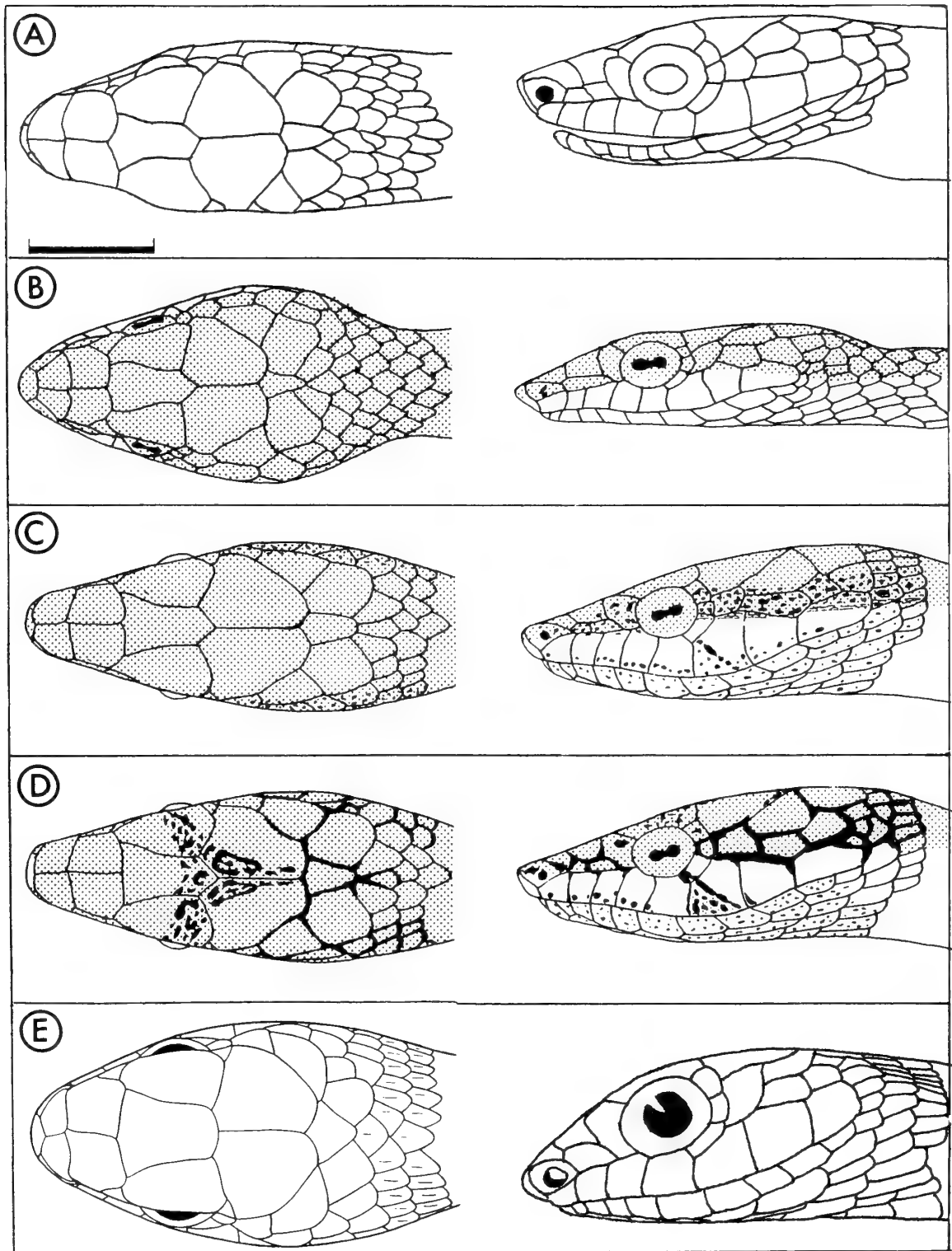


Fig. 4 Head shields of: A. *Xyelodontophis uluguruensis* (holotype); B. *Thelotornis kirtlandii*; C. *Thelotornis mossambicanus*; D. *Thelotornis capensis*; E. *Dispholidus typus*.



**Table 1** Dispholidini compared with Philothamnini: variation in midbody scale rows, ventrals, subcaudals and supralabials (rare variations in parentheses).

Taxon	midbody rows	ventrals	subcaudals	supralabials [in orbit]
<i>Philothamnus</i> spp.*	(13) 15	135–213	60–175	8/9 [4 to 6]
<i>Hapsidophrys</i> spp.**	15	150–176	90–172	8/9 [4 to 6]
<i>Thrasops flavigularis</i>	13 (15)	195–215	128–146	8 (9) [4,5 (5,6)]
<i>Thrasops occidentalis</i>	15 – 19 (21)	175–187	119–140	8 (7) [4,5 (5,6)]
<i>Thrasops jacksonii</i>	(17) 19 (21)	187–211	130–155	8 (9) [4,5 (5,6)]
<i>Thrasops schmidtii</i>	(16) 17 (19)	168–184	121–149	8 [4,5]
<i>Rhamnophis aethiopissa</i>	15 – 17 (19)	154–179	117–159	6 – 9 [3,4; 4,5; 5,6]
<i>Rhamnophis batesii</i>	13	163–179	91–114	7 – 8 [4,5; 5,6]
<i>Xyelodontophis uluguruensis</i>	19	168–169	?	8 [4,5]
<i>Thelotornis kirtlandii</i>	19	162–189	139–161	8 (7, 9) [4,5 (5,6)]
<i>Thelotornis usambaricus</i>	19	156–169	151–175	8 (9) [4,5 (3,4,5)]
<i>Thelotornis mossambicanus</i>	(17) 19 (23)	149–166	127–158	8 [4,5]
<i>Thelotornis capensis</i>	19	144–177	128–165	8 [4,5]
<i>Dispholidus typus</i>	(17) 19 (21)	164–201	104–142+ #	7 (3,4)

\*Data from Hughes (1985). \*\*Data from Chippaux (1999). #168 in D. 'pemba' (MCZ 45587).

& 5 or 5 & 6 entering orbit. The widespread *R. aethiopissa* is more variable, 6 to 9 labials, often with 3 & 4 entering orbit in southern and eastern populations. *Thelotornis* and the Dagger-tooth Vine Snake usually have 8 (4 & 5) and *Dispholidus* 7 (3 & 4).

**10. Dorsal scales** (Table 1). In *Thrasops* the dorsals are smooth in juveniles, the median rows keeled in adults, number of rows at midbody varies from 13–15 in *T. flavigularis* (which has the dorsals twice as long as the ventrals) to 17–21 (usually 19) in *T. jacksonii*. In *Rhamnophis* the dorsals are smooth, with the vertebral row enlarged, 13 rows in *R. batesii* and 15–19 rows in *R. aethiopissa*. The dorsals are feebly keeled and usually in 19 rows in *Thelotornis* and the Dagger-tooth Vine Snake, while *Dispholidus* usually has 19 rows of strongly keeled scales. In the Philothamnini there are usually 15 scale rows, which are usually smooth in *Philothamnus*, but keeled in *Hapsidophrys*.

**11. Ventral counts** (Table 1). The highest counts are found in *Thrasops flavigularis* and the lowest in *Thelotornis capensis*.

**12. Subcaudal counts** (Table 1). The lowest counts are found in *Rhamnophis batesii* and some populations of *Dispholidus typus*, while the highest are found in the two forest species of *Thelotornis*.

## SYSTEMATIC ACCOUNT

### *Thrasops flavigularis* (Hallowell)

Yellow-throated Bold-eyed Tree Snake

*Dendrophis flavigularis* Hallowell, 1852, *Proc. Acad. nat. Sci. Philadelphia*: 205. Type locality: 'Liberia', later corrected to Gabon.

*Hapsidophrys niger* Günther, 1872, *Ann. Mag. nat. Hist.* (4) **9**: 25. Type locality: Gaboon.

*Thrasops pustulatus* Buchholz & Peters, 1875, *Monatsb. Akad. Wiss. Berlin*: 199. Type locality: Mungo, Cameroon.

*Thrasops flavigularis* Bocage, 1895: 97; Bogert, 1940: 58; Loveridge, 1944: 132; Trape & Roux-Estève, 1995: 40; Chippaux, 1999: 95.

*Thrasops flavigularis flavigularis* Stucki-Stirn, 1979: 319.

*Thrasops flavigularis stimensis* Stucki-Stirn, 1979: 632.

**DIAGNOSIS.** Dorsal scales in 13–15 rows at midbody, the dorsals much longer than the ventrals; ventrals 191–214; subcaudals 128–146; usually 2 labials in contact with the lowest postocular; no enlarged occipitals.

**DESCRIPTION.** Supralabials 8 (rarely 9), fourth & fifth (rarely fifth & sixth) entering orbit; infralabials 9–12, the first 3–5 in contact with anterior sublinguals; preoculars 1 or 2; postoculars 3 (rarely 2), usually 2 labials in contact with the lowest; temporals 1 + 1; no occipitals. Dorsals in 17-15-13, 17-13-11, 15-13-13, 15-13-11 or 13-13-11 rows, feebly keeled in adults; ventrals 191–214; cloacal divided; subcaudals 128–146 pairs.

**COLORATION IN LIFE.** Subadults olive to dark brown above, head uniform, body mottled with black and yellow, the black being on the interstitial skin and bases of the scales, the yellow in the centres of the scales, the yellow spots very pronounced on the tail. Chin and throat yellow, rest of venter chequered black and yellow. Adults usually uniform black above, venter blackish, but throat usually yellow or brownish white.

**SIZE.** Largest ♂ (IFAN 687 – Sibiti, Congo-Brazzaville) 1514 + 586 = 2100 mm (Villiers, 1966); largest ♀ (AMNH 50573 – Metet, Cameroon) 1235 + 505 = 1740 mm (Bogert, 1940). Stucki-Stirn (1979) gives the maximum length as 240 cm.

**HABITAT.** Lowland forest.

**DISTRIBUTION.** Southwestern Nigeria, Bioko Island, Cameroon, Gabon, Congo-Brazzaville, extreme eastern Democratic Republic of Congo and northwestern Angola (Fig. 5).

### *Thrasops occidentalis* Parker

Western Bold-eyed Tree Snake

*Thrasops occidentalis* Parker, 1940, *Ann. Mag. nat. Hist.* (11) **5**: 273, fig. 1 & 2a. Type locality: Axim, Gold Coast [= Ghana]; Loveridge, 1944: 131; Cansdale, 1961: 31, Pl. vi, fig. 11 & 12; Hughes & Barry, 1969: 1018; Chippaux, 1999: 100.

**DIAGNOSIS.** Dorsal scales in 15–21 rows at midbody, the vertebral row widened; ventrals 175–187; subcaudals 119–140; 3 labials in contact with lowest postocular.

**DESCRIPTION.** Supralabials 8 (rarely 7 or 9), the fourth & fifth (rarely fifth & sixth) entering orbit; infralabials 8–10, the first 4–6 in contact with anterior sublinguals; preocular 1; postoculars 3, 3 labials in contact with the lowest; temporals 1 + 1; no occipitals. Dorsals in 15–21 rows at midbody, the median rows keeled in adults, smooth in juveniles; ventrals 175–187; cloacal divided; subcaudals 119–140 pairs.

**COLORATION IN LIFE.** Juveniles with head and neck olive, body

chequered in black and yellow above and below. Adults black above, chin and throat pale yellow, rest of venter dark olive.

SIZE. Largest ♂ (BMNH 66.1.28.6 – Sierra Leone, paratype) 670 + 495 = 1165 mm; largest ♀ (BMNH 1911.6.30.2 – Axim, Ghana, holotype) 682 + 403 = 1085 mm. Cansdale (1961) states that this species can exceed 210 cm.

HABITAT. Lowland forest.

DISTRIBUTION. Guinea east to southwestern Nigeria (Fig. 5).

### *Thrasops jacksonii* Günther

Jackson's Bold-eyed Tree Snake

*Thrasops Jacksonii* Günther, 1895, *Ann. Mag. nat. Hist.* (6) **15**: 528.  
Type locality: Kavirondo, Kenya.

*Rhmannophis jacksonii* Boulenger, 1896: 632.

*Thrasops Rothschildi* Mocquard, 1905, *Bull. Mus. natn. Hist. nat.* **11**: 287. Type locality: 'Afrique orientale anglaise'.

*Thrasops jacksonii jacksonii* Loveridge, 1936: 249, 1944: 134 & 1957: 264; Bogert, 1940: 58; Witte, 1953: 200; Laurent, 1956: 187, 354 & 1960: 46; Roux-Estève, 1965: 66, fig. 17; Villiers, 1966: 1739; Bourgeois, 1968: 124, 278, fig. 51; Pitman, 1974: 99, Pl. G, fig. 4; Spawls, 1978: 5; Broadley, 1991: 532; Hinkel, 1992: 319, Pl. 306; Trape & Roux-Estève, 1995: 40.

DIAGNOSIS. Dorsal scales in 19 (very rarely 17 or 21) rows at midbody; ventrals 187–214; cloacal divided; subcaudals 129–155; usually two labials in contact with lowest postocular.

VARIATION. Supralabials 8 (rarely 9, very rarely 7), fourth and fifth (rarely fifth and sixth) entering orbit; infralabials 9–13, the first 4–6 in contact with anterior sublinguals; preoculars 1–2 (rarely 3); postoculars 3 (very rarely 2 or 4), usually 2 labials in contact with lowest; temporals 1 + 1 (very rarely 1 + 2); no occipitals. Dorsals keeled in 19 (very rarely 17 or 21) rows at midbody; ventrals 181–214; cloacal divided; subcaudals 129–155 pairs.

COLORATION IN LIFE. Subadults dark olive above, mottled with black and buff posteriorly, greenish yellow below, becoming chequered black and yellow posteriorly. Adults uniform black above and below, or with the throat yellow or greyish. Iris of eye black.

SIZE. Largest ♂ (AMNH 12288) 1320 + 580 = 1900 mm, largest ♀ (AMNH 12290) 1550 + 610 = 2160 mm, both from the Ituri Forest, Orientale Province, D.R.C. (Schmidt, 1923). Pitman (1974) puts the maximum length at about 2300 mm.

HABITAT. Rain forest and gallery forests from about 200 m in the lower Congo region to 2400 m on Mount Elgon (Pitman, 1974).

DISTRIBUTION. From the lower Congo, east through the Congo basin to southern Central African Republic, southern Sudan, Uganda, western Kenya and northwestern Zambia (Broadley, 1991) (Fig. 5).

### *Thrasops schmidti* Loveridge

Schmidt's Bold-eyed Tree Snake

*Thrasops jacksonii schmidti* Loveridge, 1936, *Proc. Biol. Soc. Washington* **49**: 63. Type locality: Meru Forest, Mount Kenya, Kenya; 1944: 137 & 1957: 264; Spawls, 1978: 5.

DIAGNOSIS. Dorsal scales in 17 rows; ventrals 168–184; subcaudals 121–149; two labials in contact with lowest postocular.

DESCRIPTION. Supralabials 8, the fourth and fifth entering the orbit; infralabials 10–12, the first 4 or 5 in contact with anterior sublinguals; preocular 1; postoculars 3, the lowest in contact with 2

labials; temporals 1 + 1; no occipitals. Dorsals in 17 (rarely 19) rows at midbody, faintly keeled; ventrals 172–184; cloacal divided; subcaudals 121–147 pairs.

COLORATION IN LIFE. Subadult olive brown above, greyish white below, subcaudals grey. Adults uniform black.

SIZE. Largest ♂ (MCZ 9276 – Meru Forest, Kenya, holotype) 700 + 365 = 1065 mm; largest ♀ (NMK 1222 – Embu Forest, Kenya) 1200 + 455 = 1655 mm; largest unsexed (formerly NMK – Muthaiga, Nairobi, Kenya, paratype) 1671 + 584 = 2255 mm (Loveridge, 1923, 1936).

HABITAT. Montane forest.

DISTRIBUTION. Forests of the Kenya highlands from Mount Kenya south to Nairobi (Fig. 5).

REMARKS. *T. schmidti* is readily diagnosable on ventral counts and is separated from the population of *T. jacksonii* in the Kakamega Forest by 300 km, including the dry rift valley, so it is considered to represent an independently evolving taxon.

### *Rhmannophis aethiopissa* Günther

Splendid Dagger-tooth Tree Snake

*Rhmannophis aethiopissa* Günther, 1862, *Ann. Mag. nat. Hist.* (3) **9**: 129, Pl. x. Type locality: West Africa; Roux-Estève, 1965: 65, fig. 16; Chippaux, 1999: 97.

*Thrasops splendens* Andersson, 1901, *Bihang Till K. Svenska Vet.-Akad. Handl.* **27**(5): 11, Pl. 1, fig. 8. Type localities: Bibundi & Mapanja, Cameroon.

*Rhmannophis ituriensis* Schmidt, 1923, *Bull. Amer. Mus. nat. Hist.* **49**: 81, fig. 4. Type locality: Niapu, Belgian Congo [= D.R.C.]; Witte, 1941: 202.

*Rhmannophis aethiopissa elgonensis* Loveridge, 1929, *Bull. U. S. natn. Mus.* **151**: 24. Type locality: Yala (= Lukosa) River at the foot of Mount Elgon, Kenya; 1944: 129.

*Rhmannophis aethiopissa aethiopissa* Loveridge, 1944: 126; Perret, 1961: 136; Villiers, 1966: 1739; Stucki-Stirn, 1979: 335, figs.

*Rhmannophis aethiopissa ituriensis* Loveridge, 1944: 128; Laurent, 1956: 189, 355; 1960: 47 & 1964: 108; Bourgeois, 1968: 109, fig. 43–46; Broadley, 1991: 532.

*Thrasops aethiopissa elgonensis* Loveridge, 1957: 264; Pitman, 1974: 101, Pl. T, fig. 3; Spawls, 1978: 5.

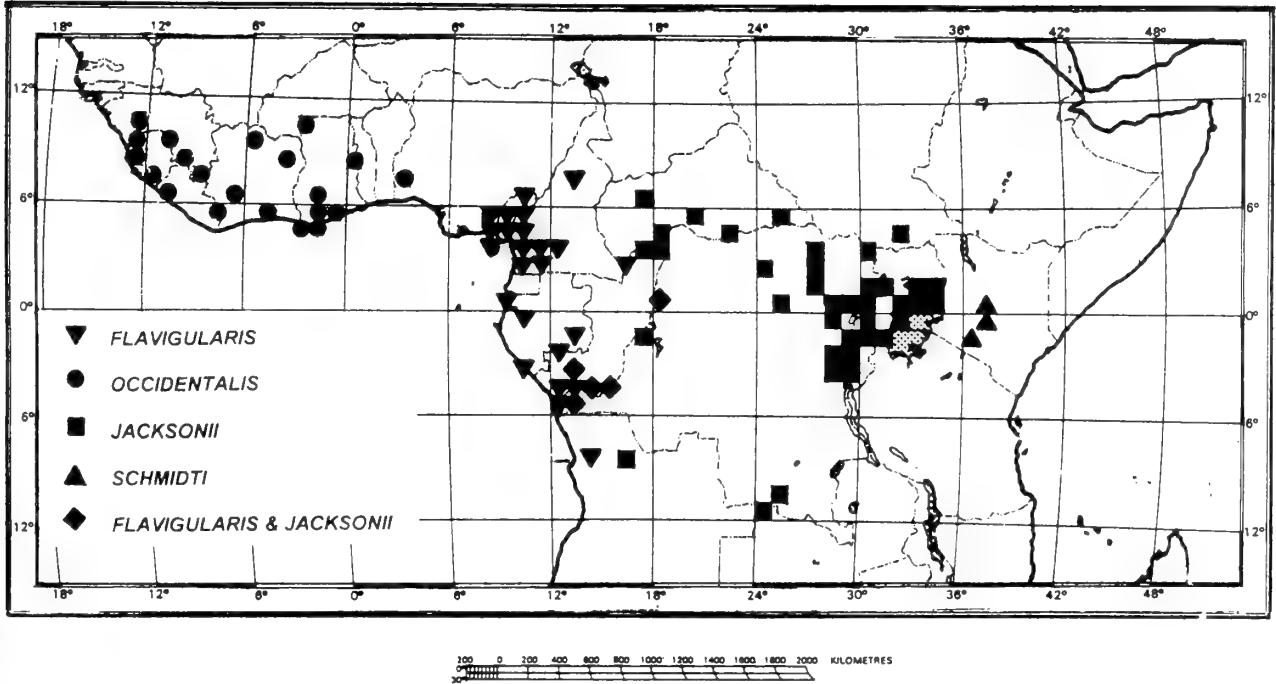
*Thrasops aethiopissa aethiopissa* Hughes & Barry, 1969: 1018; Trape & Roux-Estève, 1995: 40.

*Thrasops (Rhmannophis) aethiopissa* Hinkel, 1992: 144, Pl. 130.

DIAGNOSIS. Dorsal scales in 15–17 (rarely 19) rows at midbody, the vertebral row enlarged; ventrals 154–179; cloacal divided; subcaudals 117–159; two or three labials in contact with the lowest postocular; two large occipitals.

DESCRIPTION. Supralabials 6–9, the 3<sup>rd</sup> & 4<sup>th</sup>, 4<sup>th</sup> & 5<sup>th</sup> or 5<sup>th</sup> & 6<sup>th</sup> entering orbit; infralabials 7–11, the first 3–6 in contact with the anterior sublinguals; preocular 1 (very rarely 2); postoculars 2–3 (very rarely 4); a single temporal; two large occipitals (one longitudinally divided and the other semidivided in NMZB-UM 2548). Dorsals smooth, or vertebral and paravertebral rows keeled (Perret, 1961) in 15–17 (very rarely 13 or 19) rows at midbody (usually 17 rows in West Africa, Cameroon, Gabon and Central African Republic, 15 rows elsewhere); ventrals 154–179; cloacal divided; subcaudals 117–159 pairs, the lowest counts in Uganda and western Kenya.

**THRASOPS**



**RHAMNOPHIS & XYELEDONTOPHIS**

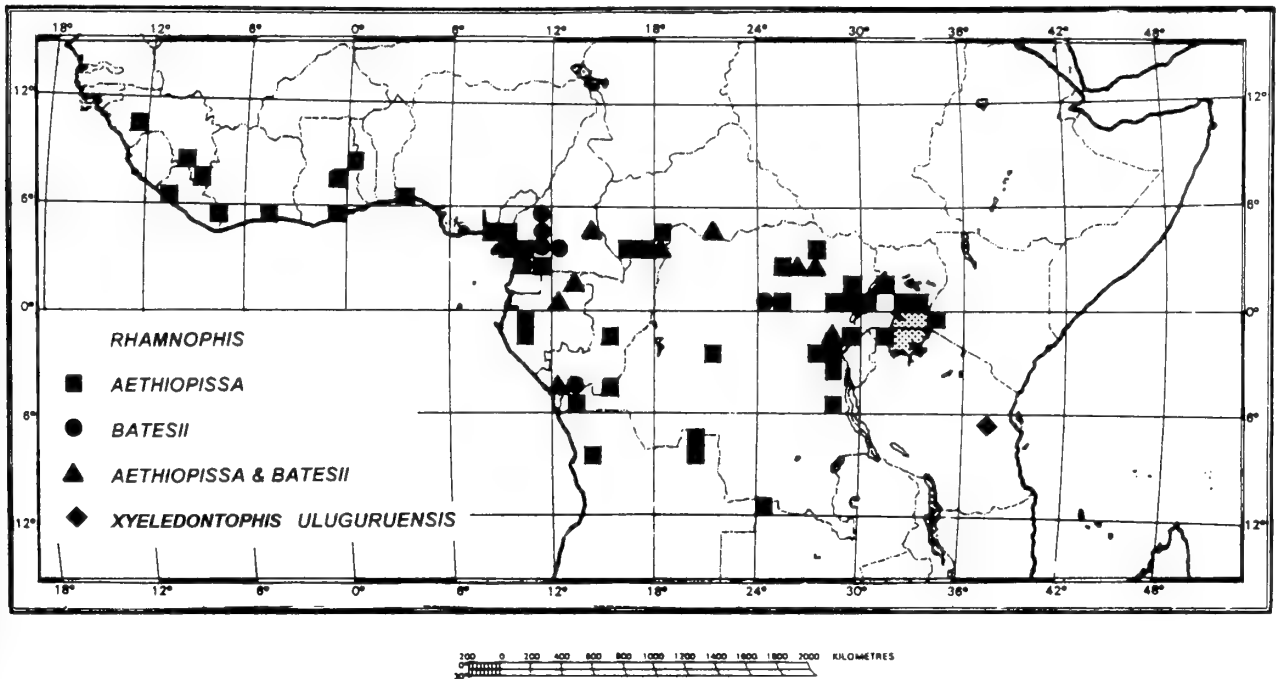


Fig. 5 Distributions of the genera *Thrasops* (upper), *Rhamnophis* and *Xyelodontophis* (lower).

**COLORATION IN LIFE.** Above, head olive-brown, uniform or posterior shields black-edged; body green with scales tipped or bordered with black; tail black with a green stripe on each scale row. Chin and throat yellow-green, rest of venter pale green, a dark median line on the subcaudals.

**SIZE.** Largest ♂ (MRAC 12257 – Kiroziret Forest, Kivu, D.R.C.) 948 + 509 = 1457 mm (Laurent, 1956); largest ♀ (NHRM 1979 – Bibindi, Cameroon, syntype of *T. splendens*) 950 + 520 = 1470 mm (Andersson, 1901).

**HABITAT.** Rain forest and gallery forest from sea level up to 2000 metres.

**DISTRIBUTION.** Guinea east to the Democratic Republic of the Congo, Rwanda, Uganda and western Kenya, south to northern Angola and northwestern Zambia (Broadley, 1991) (Fig. 5).

**REMARKS.** Roux-Estève (1965) placed *R. a. ituriensis* in the synonymy of the typical form and *R. a. elgonensis* hardly warrants subspecific recognition. Both subspecies were based on variable characters: the number of midbody scale rows, subcaudals and supralabials, and there are no major breaks in the distribution of the species.

### *Rhamnophis batesii* (Boulenger)

#### Spotted Dagger-tooth Tree Snake

*Thrasops batesii* Boulenger, 1908, *Ann. Mag. nat. Hist.* (8) 2: 93.

Type localities: Akok and Efulen, Cameroon; Trape & Roux-Estève, 1995: 40; Chippaux, 1999: 99.

*Rhamnophis batesii* Schmidt, 1923: 83, fig. 5; Loveridge, 1944: 125; Laurent, 1956: 355, Pl. xx, fig. 1; Perret, 1961: 136; Villiers, 1966: 1739; Stucki-Stirn, 1979: 339.

**DIAGNOSIS.** Dorsal scales in 13 rows at midbody, vertebral row enlarged; ventrals 163–179; cloacal entire; subcaudals 92–119; two labials in contact with lowest postocular.

**DESCRIPTION.** Supralabials 7 (rarely 6 or 8), the fourth & fifth (rarely third & fourth or fifth & sixth) entering orbit; infralabials 8 or 9, the first 4–6 in contact with anterior sublinguals; preocular 1 (rarely 2); postoculars 3 (rarely 2 or 4), 2 labials in contact with the lowest; a single temporal; 4 occipitals (3 in MRAC 19070 due to fusion of right hand pair; the median pair transversely divided in NMZB 13206). Dorsals smooth in 13-13-11 or 13-13-9 rows, vertebral row enlarged; ventrals 163–179; cloacal entire; subcaudals 92–123 pairs.

**COLORATION IN LIFE.** Dorsum pale violet-brown, many scales black at the base and along lower edge, giving a plaited effect to the supracaudals. Chin and throat cream, rest of venter pale green, with black labial sutures and numerous black spots or blotches on the venter.

**SIZE.** Largest ♂ (MCZ 38393 – Batouri District, Cameroon) 827 + 390 = 1217 mm; largest ♀ (BMNH —) 1450 + 350 = 1800 mm.

**HABITAT.** Rain forest between 400 and 1000 metres.

**DISTRIBUTION.** Cameroon, Gabon and Congo-Brazzaville, east through the Congo basin to the Orientale and Kivu Provinces of the D.R.C. (Fig. 5).

### *Xyelodontophis* gen. nov.

**DIAGNOSIS.** A member of the tribe Dispholidini, differing from the other genera in the development of strongly curved rear maxillary teeth, which have sharp flanges anteriorly and posteriorly and narrow at the base, hence the name *Xyelodontophis* = Dagger-tooth Snake. Both species of *Rhamnophis* also have 'dagger-shaped' rear maxillary teeth, but they are less well developed and the teeth taper from base to tip, while *Thelotornis* and *Dispholidus* have large deeply grooved rear fangs. The new genus agrees with *Thrasops* and *Thelotornis* in having a shallowly forked ectopterygoid bone, whereas *Rhamnophis* and *Dispholidus* have a deeply forked ectopterygoid. In general form and scalation the new snake agrees with *Thelotornis*, but it lacks the distinctive horizontal pupil of that genus.

### *Xyelodontophis uluguruensis* sp. nov.

#### Dagger-tooth Vine Snake

**HOLOTYPE.** NMZB 7443 (Figs 1f, 2a, & 4a) an adult female from Lupanga Peak, Uluguru Mountains, Tanzania (06° 52' S; 37° 43' E), collected by Jon Lovett in November, 1983 (KMH 2636). Named for the Uluguru Mountains, to which it is probably endemic.

**PARATYPE.** ZMB 48153, an adult male from Bondwa Peak, Uluguru Mountains (06° 54' S; 37° 40' E) at 1650 m, collected by D. Emmrich (DE 413) in November, 1989.

**DIAGNOSIS.** As for *Xyelodontophis* gen. nov.

**DESCRIPTION** (paratype variations in parentheses). Rostral feebly recurved onto upper surface of snout; very large nostril in a single nasal; loreals 2; preocular 1; postoculars 3; temporals 1 + 3; a pair of large occipitals behind the temporals, separated by elongate interparietal; supralabials 8, the fourth and fifth entering the orbit; infralabials 9, the first four or five in contact with the anterior sublinguals. Dorsals elongate, narrow, in 21-19-13 rows, moderately to feebly keeled, with single large apical pits; ventrals angular, but not keeled, 168 (169); cloacal longitudinally divided; subcaudals 132+ (18+), tail truncated. The paratype male has an umbilical scar on ventrals 147–149.

**COLORATION IN PRESERVATIVE.** Top of head brown, shields narrowly margined with black, labials, chin and throat immaculate. Body grey-brown, bases of scales (and interstitial skin anteriorly) black; venter uniform pale grey apart from some irregular brown margins to the free edges of the ventrals. The paratype male has the head and nape bronze, supralabials immaculate yellow, rest of dorsum black speckled with green and brown in life (Emmrich, pers. comm.); chin and throat yellow, rest of venter rapidly darkening to black with a few light markings.

**VISCERAL ANATOMY** (Tables 2–4). Umbilical scar-vent interval 11.6% VS (10.7–12.5%); peritoneum black; hyoid posterior tip 7.8% (7.6–8.1%); heart short 2.3% (2.0–2.6%), midpoint 25.2% (24.9–25.5%), junction of systemic arches ventrolateral and 0.71% (0.69–0.74%) heart length posterior to heart, right arch 0.33 diameter of left at junction; heart-liver gap 5.7% (5.5–5.9%), heart-liver interval 35.8% (34.3–37.2%); liver long 27.8% (26.4–29.2%) and narrow, midpoint 46.0% (45.7–46.2%), nearly contacting the gall bladder (liver-gall bladder gap 0.1% [0–0.2%]); liver-gall bladder interval 29.3% (28.3–30.4%), liver-kidney gap 28.0% (27.6–28.4%), liver-kidney interval 65.5%, liver length/right lung length ratio 0.40; gall bladder 1.4% (1.2–1.6%), midpoint 60.7% (59.9–61.5%), located anterior to the subequal pancreas 1.7% (1.5–1.9%) with small spleen (0.7%) attached cranially; gall bladder-gonad gap 10.7% (9.7–11.8%), gall bladder-gonad interval 23.0% (22.8–23.2%); gonads light yellow in color, right testis 4.8% (MP = 74.4%), left testis 4.1% (MP = 79.9%), total testis midpoint 77.4%; right ovary 5.3% (MP = 74.9%) with 6 small ova and 7 follicles, left ovary 4.9% (MP = 81.6%) with 5 small ova and 8 follicles, total ovary midpoint 78.0%, total gonad midpoint 77.7%; gonad-kidney gap 4.8% (4.4–5.3%); adrenal glands orange, very narrow and elongate, adjacent to posterior end of gonads, right adrenal 2.3% (2.2–2.5%), midpoint 75.4% (74.8–76.1%), left adrenal 2.6% (2.5–2.7%), midpoint 81.6% (81.2–82.1%), total adrenal midpoint 78.5% (78.4–78.6%); gall bladder-kidney gap 26.4% (26.3–26.5%), gall bladder-kidney interval 37.5% (36.3–38.8%); kidneys dark brown, segmented but compact with deep creases, right kidney 9.2% (8.0–10.4%) with 20 segments, midpoint 92.4%, right kidney length/liver length ratio 0.34; left kidney 7.0% (6.1–7.9%) with 21 segments,

**Table 2** Adult Dispholidini compared with Philothamnini: visceral characters as % snout-vent length

GS	n	U-V	Hy	HLG	HLI	L	LMP	LGBG	LGBI	GBMP	GBGG	GBKG	TGMP	GKI	TA	TAMP	TMP	RL	PT	LL
PA	55	8.6	8.1	7.3	29.0	18.8	42.8	3.5	24.2	56.6	11.7	23.9	79.7	23.7			13.7	76.9	95.5	1.4
HL	24	7.9	14.6	9.0	29.0	17.3	45.6	10.3	29.3	65.3	10.1	20.2	79.8	22.1			14.6	76.1	98.1	1.4
HS	30	6.8	11.4	8.8	29.3	17.7	46.6	5.6	29.5	66.2	17.0	22.1	83.2	20.0	1.2	84.7	15.1	78.4	97.9	0.8
TF	5	8.2	7.7	8.8	25.2	14.2	45.6	6.2	22.6	60.0	11.3	23.3	77.4	24.4	3.2	77.9	15.5	68.4	97.5	2.6
TJ	15	8.9	7.2	8.7	26.6	15.5	44.5	7.7	20.0	52.6	9.8	23.4	76.1	26.3	5.3	74.0	14.6	69.5	96.4	2.9
TO	2	7.8	6.7	9.9	26.0	14.0	43.9	7.5	23.0	59.2	8.8	25.1	76.1	28.2	2.6	75.8	14.1	71.9	97.6	5.3
TS	2	9.2	10.7	9.3	26.9	14.8	44.8	9.0	25.0	61.7	7.3	20.8	76.0	27.2	4.6	77.0	14.8	68.6	96.4	3.9
RA	12	7.4	10.2	7.4	27.1	17.4	44.0	5.3	24.4	58.8	12.5	27.3	79.0	25.3	3.9	79.6	14.5	69.3	96.3	1.2
RB	2	9.0	9.9	7.6	30.0	20.1	45.1	7.1	28.4	62.8	13.4	23.6	79.6	20.4	2.9	80.4	14.3	71.4	97.7	1.4
DT	12	10.1	9.0	7.3	29.0	19.0	44.1	7.2	27.5	61.7	7.7	18.8	77.0	35.1	2.9	69.7	14.2	70.5	96.3	2.3
TP	1	9.6	6.4	6.0	30.2	21.7	42.9	5.5	28.5	59.9	12.1	27.5	79.5	27.6	4.9	77.5	13.6	71.8	96.6	1.3
DC	4	11.4	8.2	7.1	31.9	22.3	44.2	7.8	31.8	64.0	8.2	18.6	78.6	23.4	3.0	79.9	13.6	71.0	96.1	1.3
TK	13	9.9	7.1	7.2	32.2	22.8	47.8	6.4	31.0	66.5	10.5	21.6	82.7	20.2	2.2	83.8	15.2	67.2	95.7	1.1
TM	5	9.4	7.2	6.9	36.3	26.9	45.7	4.5	33.3	64.6	9.3	19.3	80.5	21.9	2.5	81.6	13.4	72.5	96.9	1.5
TU	3	12.5	7.2	6.5	34.0	25.5	44.9	6.0	33.2	64.5	10.5	20.8	80.5	20.8	1.8	81.8	13.4	71.1	96.0	1.0
XU	2	11.6	7.8	5.7	35.8	27.8	46.0	0.1	29.3	60.7	10.7	26.4	77.7	25.4	4.9	78.5	13.8	68.6	93.4	1.4

(GS = genus/species: PA = *Philothamnus angolensis*, HL = *Hapsidophrys lineatus*, HS = *Hapsidophrys smaragdinus*, TF = *Thrasops flavigularis*, TJ = *Thrasops jacksonii*, TO = *Thrasops occidentalis*, TS = *Thrasops schmidtii*, RA = *Rhannophis aethiopsisa*, RB = *Rhannophis batesii*; DT = *Dispholidus typus*, DP = *Dispholidus 'pemba'*, TC = *Thelotornis capensis*, TK = *Thelotornis kirtlandii*, TM = *Thelotornis mossambicanus*, TU = *Thelotornis usambaricus*, XU = *Xyelodontophis uluguruensis*; n = sample size, UV = umbilical scar to vent as % total ventrals, Hy = hyoid posterior tip, HLG = heart-liver gap, HLI = heart-liver interval, L = liver length, LMP = liver midpoint, LGBG = liver-gall bladder gap, LGBI = liver-gall bladder interval, GBMP = gall bladder midpoint, GBGG = gall bladder-gonad gap, GBKG = gall bladder-kidney gap, TGMP = total gonad midpoint, GKI = gonad-kidney interval, TA = total adrenal length, TAMP = total adrenal midpoint, TMP = trachea midpoint, RL = right lung length, PT = right lung posterior tip, LL = left lung length).

**Table 3** Adult Dispholidini compared with Philothamnini: visceral characters as ratios

GS	R/LSA	K/L	RK/L	LK/RK	KOL	NTR	AL/LL	RB/LL	LB	SS/DV	V/S	LL/RL	LW/LL
PA	0.39	0.39	0.37	0.83	0.76	72	0.54	1.00	2.83	0.19	0.18	0.02	0.42
HL	0.36	0.68	0.67	0.83	0.80	75	–	0.41	0.53	0.14	0.17	0.02	0.30
HS	0.39	0.49	0.47	0.85	0.77	101	–	0.23	0.56	0.13	0.16	0.01	0.42
TF	0.33	0.88	0.66	0.83	0.38	90	0.31	0.13	0.60	0.09	0.25	0.04	0.21
TJ	0.41	0.70	0.57	0.75	0.40	92	0.36	0.21	0.67	0.10	0.23	0.04	0.22
TO	0.37	0.86	0.71	0.75	0.45	120	0.24	0.10	0	0.11	0.24	0.08	0.13
TS	0.20	0.93	0.82	0.78	0.50	89	0.13	0.11	0.50	0.10	0.26	0.06	0.29
RA	0.29	0.48	0.50	0.69	0.48	76	0.87	0.24	1.45	0.10	0.16	0.02	0.26
RB	0.22	0.48	0.46	0.81	0.76	79	1.00	0.19	1.67	0.13	0.15	0.02	0.35
DT	0.24	0.65	0.54	0.78	0.36	79	0.76	0.80	1.29	0.17	0.20	0.03	0.29
DP	0.25	0.41	0.33	0.74	0.40	99	0.90	0.21	4.00	0.21	0.15	0.02	0.30
TC	0.32	0.59	0.50	0.68	0.52	71	0.57	0.21	1.00	0.13	0.15	0.02	0.28
TK	0.26	0.37	0.37	0.74	0.55	75	0.54	0.19	2.7	0.14	0.15	0.01	0.25
TM	0.31	0.45	0.41	0.72	0.57	76	0.68	0.20	2.75	0.16	0.14	0.02	0.24
TU	0.38	0.43	0.39	0.79	0.63	71	0.79	0.17	3.00	0.14	0.12	0.01	0.39
XU	0.33	0.35	0.34	0.76	0.67	59	0.83	0.42	1.00	0.39	0.13	0.02	0.20

(genus/species acronyms as for Table 2, R/LSA = right systemic arch diameter/left systemic arch diameter, K/L = total kidney length/liver length, RK/L = right kidney length/liver length, RA/RK = right adrenal length/right kidney length, LK/RK = left kidney length/right kidney length, KOL = kidney overlap/total kidney length, NTR = estimated number of tracheal rings/10% SVL, AL/LL = anterior lobe length/left lung length, RB/LL = right bronchus length/left lung length, LB = mean number of cartilages in left bronchus (including bronchial ring), SS/DV = semisaccular lung/dense vascular lung, V/S = vascular lung/saccular lung, LL/RL = left lung length/right lung length, LW/LL = left lung width/left lung length).

midpoint 94.0%, left kidney length/liver length ratio 0.26; left kidney/right kidney 0.76, kidney overlap 0.67; kidney-vent interval 12.2% (11.6–12.8%), kidney-vent gap 2.5% (2.1–2.9%).

Trachea 25.1% (25.0–25.2%) with an estimated 149 rings (144–154) or 58.9 (58.6–59.2) per 10% SVL, trachea midpoint 13.8% (13.7–13.9%), tracheal rings narrow and well-separated from their neighbours, lacking free tips, tracheal membrane expanded to 3.5 times the tracheal ring circumference; tracheal lung lacking, only slight development of a cardiac lung (0.7%) anterior to the right lung; tracheal entry into right lung subterminal; right bronchus 0.3% with 3 cartilages; anterior lobe of right lung very short 1.0% (0.9–1.2%), its connecting orifice of moderate diameter; right lung 68.6% (66.0–71.2%), right lung midpoint 60.1% (59.1–61.2%), vascular portion of right lung 8.0% (7.2–8.7%) with three tiers of faveoli distributed dorsoventrally around inner lung circumference; vascular

lung lacking midventral avascular strip; faveolar pattern consists of transverse ribs enclosing transverse rows of paired diamond-shaped faveoli; vascular lung with semisaccular or sparse/dense vascular portion ratio 0.39 (0.35–0.42); saccular (avascular) lung 59.6% (58.0–61.3%), vascular lung/saccular lung ratio 0.13 (0.12–0.14), posterior tip of lung 93.9% (91.7–96.2%).

Left lung complex consists of an orifice at 26.3% (26.2–26.5%), a bronchus 0.1% with two rings in female (bronchus absent in male), and a vestigial lung 1.4% (1.1–1.6%). The left lung, with a left lung/right lung ratio of 0.02, supports a reticulated network of trabeculae and has a width/length ratio of 0.20 (0.15–0.25).

*Xyelodontophis*, while resembling *Thelotornis* in external morphology, is distinct from the latter genus in a number of internal characters: heart-liver gap, heart-liver interval, liver length, gall bladder midpoint, gall bladder-kidney gap, total gonad midpoint,

Table 4 Comparison of generic means for visceral characters

G	no.	Hy	HILG	HLI	L	LMP	LGBl	GBKg	KVI	TG	TGMP	GKG	TA	TMP	RL	PT	LL	RK/L	TK/L	A/K	L/R/L	NTR	TTR	SS/DV	U-V
Ph	12	13	7.2	30	20	44.6	30.2	22.8	12.4	8.5	79.7	1.5		15	77	94.8	1.0	0.52	0.56		0.28	70	180	0.19	7.7
Hy	2	13	8.9	29	18	46.1	29.4	21.2	11.9	6.2	80.9	1.8	1.2	15	77	98.0	1.1	0.57	0.58	0.08	0.23	80	219	0.17	7.2
Tr	4	8	8.7	25	14	43.3	23.4	22.1	20.5	3.7	76.7	2.8	3.8	14	70	96.5	3.0	0.68	0.85	0.23	0.22	93	252	0.10	7.8
Rh	2	11	7.5	28	18	44.4	24.9	26.2	13.0	3.7	77.3	4.3	3.8	15	69	96.3	1.2	0.53	0.60	0.22	0.36	77	212	0.12	9.0
Di	2	9	7.0	29	19	44.7	27.6	20.6	16.3	5.6	77.2	0.3	4.7	15	70	96.5	2.2	0.52	0.67	0.36	0.21	77	206	0.16	10
Th	4	8	6.9	31	23	44.4	32.0	20.3	13.6	6.0	81.0	4.6	2.5	14	69	96.0	1.2	0.41	0.46	0.21	0.39	74	191	0.14	10
Xy	1	8	5.7	36	28	46.0	29.3	26.4	12.2	9.6	77.7	4.8	4.9	14	69	93.9	1.4	0.34	0.35	0.39	0.81	59	149	0.39	12

(Ph = *Philothamnus*, Ha = *Hapsidophrys*, Tr = *Thrasops*, Rh = *Rhamnophis*, Di = *Dispholidus*, Th = *Thelotornis*, Xy = *Xyelodontophis*; G = genus, no. = number of species, measurements as % SVL; Hy = hyoid posterior tip, HILG = heart-liver gap, HLI = heart-liver interval, L = liver length, LMP = liver midpoint, LGBl = liver-gall bladder interval, GBKG = gall bladder-kidney gap, KVI = kidney-vent interval, TG = total gonad length (adults), TGMP = total gonad midpoint, GKG = gonad-kidney gap, TA = total adrenal length, TMP = total adrenal length, RL = right lung length, PT = right lung posterior tip, LL = left lung length, and as ratios: RK/L = right kidney length/liver length, TK/L = total kidney length/liver length, A/K = total adrenal length/total kidney length, L/R/L = liver length/right lung length, NTR = estimated number of tracheal rings/10% SVL, TTR = estimated total number of tracheal rings, SS/DV = semisacculus lung/dense vascular lung, UV = umbilical scar/vent interval as % total ventrals.

gonad-kidney interval, total adrenal length and midpoint, adrenal/kidney length ratio, total kidney/liver length ratio, number of tracheal rings, right bronchus/left lung ratio, semisaccular/dense vascular lung ratio, right lung posterior tip, left bronchus cartilages, and left lung width/length ratio. *Xyelodontophis* is also unique in differing from the rest of the Dispholidini in the means of the following characters: heart-liver interval, liver length, liver midpoint, liver-gall bladder gap, total gonad length, liver-kidney interval, gall bladder-kidney gap, total gonad length, right kidney and total kidney/liver length ratios, number of tracheal rings, semisaccular/dense vascular lung ratio, lack of ventral avascular strip in vascular lung, liver/right lung length ratio, and posterior tip of right lung.

In contrast to other Dispholidini, *Xyelodontophis* is most similar to *Thelotornis* in hyoid length, liver-gall bladder interval, and trachea midpoint; it is most similar to *Rhamnophis* and *Thelotornis* in total kidney midpoint, kidney-vent interval, and left lung length; it is most similar to *Dispholidus*, *Rhamnophis* and *Thelotornis* in total gonad midpoint; and it is most similar to *Dispholidus* in total adrenal length and adrenal/kidney length ratios.

**HEMIPENIS.** In the paratype male the single organs extend to the seventh subcaudal, the sulcus spermaticus is simple (on the left organ the sulcus lies on the medial side, on the right organ it lies on the lateral surface). In situ, the basal portion (2 subcaudals) is nude with four large hooks, the medial portion (2 sc) is spinose and the apical portion (2 sc) is calyculate. The sulcus is bordered by two basal hooks 5 mm long and the two largest hooks (7 mm) are on the ascalutate side. The calyces on the apex are smooth and form a network (with 1–2 mm cavities) very similar to the faveoli of the snake lung. The proximal 2–4 calyces are spinose with several tiny spinules on each calyx. The spines completely surround the organ and are arranged in 7–8 rows, increasing in size from distal (4 rows, 1 mm long) through medial (3 rows, 2 mm) to proximal (1 row, 3 mm); there are 7 large spines on the right organ and 8 on the left. The everted organ would probably show some resemblance to that of *Thelotornis kirtlandii* (Doucet, 1963: Fig. 40).

**SIZE.** Length 740 + 407+ mm (snout-vent 830 mm, tail truncated near base).

**DIET.** The holotype contained a recently swallowed leaf chameleon, *Rhampholeon uluguruensis*, an endemic species recently described from Bondwa Peak (Tilbury & Emmrich, 1996).

**HABITAT.** Montane evergreen forest. The habitat is described by Tilbury & Emmrich (1996).

**DISTRIBUTION.** Probably endemic to the Uluguru Mountains (Fig. 5).

***Thelotornis kirtlandii* (Hallowell) Forest Vine Snake**

*Leptophis Kirtlandii* Hallowell, 1844, *Proc. Acad. nat. Sci. Philadelphia*: 62. Type locality: Liberia, type ANSP 5271.

*Oxybelis Lecomtei* Duméril & Bibron, 1854, *Erpét. Gen.*, 7: 821. Type locality: Gabon.

*Tragophis rufulus* Duméril & Bibron, 1854, *Erpét. Gen.*, 7: 827. Type locality: Senegal.

*Oxybelis violacea* Fischer, 1856, *Abhand. Nat. Ver. Hamburg*, 3: 91, Pl. ii, fig. 7. Type locality: Edina, Grand Bassa County, Liberia.

*Dryiophis Kirtlandii* Bocage, 1895: 119 (part).

*Thelotornis kirtlandii* Schmidt, 1923: 112, Pl. xiv; Bogert, 1940: 69; Witte, 1953: 247, fig. 82; Laurent, 1964: 116.

*Thelotornis kirtlandii kirtlandii* Loveridge, 1944: 149 (part).

**DIAGNOSIS.** Top of head, including temporal region, uniform green;

neck with black crossbands; supralabials immaculate or with fine green or grey stipple; rostral and nasals strongly recurved onto top of snout; infralabials 7–11 (mode 9); ventrals 162–189; subcaudals 132–172.

**DESCRIPTION.** Rostral and anterior nasals recurved onto top of snout; a single loreal (in eastern populations); preocular 1; postoculars 3 (2 in two specimens from Digba through fusions with supraocular or fifth labial); temporals 1+2 (very rarely 1+1 or 2+2); supralabials 8 (rarely 9 or 10), the fourth and fifth (rarely fifth and sixth) entering the orbit; infralabials 7 to 11, the first 4 or 5 (very rarely 3) in contact with the anterior sublinguals. Dorsal scales feebly keeled in 19–19–13 rows (17 rows at midbody in four specimens from Kivu: Laurent, 1956, 1960); ventrals 164–179 in ♂♂, 164–189 in ♀♀; cloacal divided; subcaudals 135–157 in ♂♂, 138–165 in ♀♀.

**COLORATION.** Top of head uniform green, supralabials white, often with fine green or grey stipple; body mottled grey, green and brown, with black crossbars anteriorly (ZMUC R631282 lacks black markings on the neck), lighter below. The specimen illustrated by Hinkel (1992: fig. 129) appears to be uniform dark brown on top of the head, with heavy brown infuscation on the labials. This could be a captive specimen that has been exposed to strong sunlight, such a change has been observed in a captive *Thelotornis* at Watamu on the Kenya coast (S. Spawls, pers comm.).

**SIZE.** Largest ♂ (AMNH 12279 – Niangara, D.R.C.) 850 + 480 = 1330 mm, largest ♀ (ZMUC R631282 – Massisiswi, Udzungwa Mts, Tanzania) 1050 + 660 = 1710 mm.

**HABITAT.** Lowland forest in west and central Africa, relict populations in montane forests in Tanzania.

**DISTRIBUTION.** Islands of the Bijagós Archipelago, Guinea Bissau, east through forested areas of west Africa and the Congo basin to Uganda and southern Sudan, south to northern Angola, northwestern Zambia (Broadley, 1991) and south-central Tanzania (Rasmussen, 1997) (Fig. 6).

***Thelotornis usambaricus* Broadley Usambara Vine Snake**

*Thelotornis kirtlandii* (not Hallowell) Stejneger, 1893: 733.

*Thelotornis kirtlandii kirtlandii* (not Hallowell) Loveridge, 1944: 149 (part).

*Thelotornis capensis mossambicanus* (not Bocage) Broadley, 1979: 126 (part); Rasmussen, 1997: 138 (part).

*Thelotornis usambaricus* Broadley, 2001, *Afr. J. Herpetol.* 50 (2): 58. Type locality: Amani Nature Reserve, (Kwamkoro/Kwemsambia Forest Reserve), East Usambara Mountains, Tanzania. Holotype: NMZB 16182

**DIAGNOSIS.** Top of head, including temporal region, uniform green; neck with black chevrons; supralabials with scattered black spots, usually including a triangle on the sixth labial; rostral and nasals not, or only feebly, recurved onto top of snout; infralabials 9–13 (mode 11); ventrals 145–169; subcaudals 143–175.

**DESCRIPTION.** Rostral just visible from above; nasal entire; loreals 1 or 2; preocular 1; postoculars 3; temporals 1 + 2 (very rarely 1 + 3); occipitals 2, separated by a small interoccipital; supralabials 8 (very rarely 9), the fourth and fifth or third, fourth and fifth entering the orbit; infralabials 9 to 13, the first 4 or 5 in contact with the anterior sublinguals. Dorsal scales very feebly keeled, in 19–19–13 or 19–19–11 rows; ventrals 156–166 in ♂♂, 145–169 in ♀♀; cloacal divided; paired subcaudals 146–175 in ♂♂, 143–169 in ♀♀.

**COLORATION.** Top of head, including temporals, uniform green in

life, supralabials, chin and throat white or pale orange, with a few black spots and usually a speckled black triangle extending back from the eye through the lower postocular and sixth labial to the lip, a few black spots on posterior sublinguals and gulars; dorsum mottled brown, green and pale grey, three or four vague black chevrons on neck (more distinct in subadults); venter mottled pale brown and green.

SIZE. Largest ♂ (BMNH 1974.547) 640 + 454 = 1094 mm; largest ♀ (ZMUC R631310) 790 + 490 = 1280 mm, both from Amani.

HABITAT. Coastal forest.

DISTRIBUTION. The Usambara Mountains, with apparently relict populations on the lower slopes of other isolated mountains in the Eastern Arc chain and on the Kenya coast (Fig. 6).

*Thelotornis mossambicanus* (Bocage) Eastern Vine Snake

*Oxybelis Lecomtei* (not Duméril & Bibron) Peters, 1854: 623 (part).

*Thelotornis Kirtlandii* (not Hallowell) Peters, 1882: 131 (part), Pl. xix, fig. 2

*Dryiophis Kirtlandii* var. *mossambicana* Bocage, 1895, *Herp. Angola & Congo*: 119. Type locality: Manica, Mozambique. Lectotype MBL 1843 (destroyed).

*Thelotornis kirtlandii capensis* (not A. Smith) Mertens, 1937: 14.

*Thelotornis capensis* (not A. Smith) Bogert, 1940: 70 (part), fig. 11.

*Thelotornis capensis capensis* (not A. Smith) Laurent, 1956: 230 & 378.

*Thelotornis capensis mossambicanus* Broadley, 1979: 129.

*Thelotornis mossambicanus* Broadley, 2001: 60.

DIAGNOSIS. Top of head green to pale brown, uniform or speckled with black; temporals brown speckled with black; neck with black lateral blotch; supralabials with scattered black spots, including a triangle on the sixth labial; rostral and nasals not, or only feebly, recurved onto top of snout; infralabials 9–13 (mode 11); ventrals 144–172; subcaudals 123–167.

DESCRIPTION. Rostral and nasals barely visible from above; loreals usually 2 (rarely 1, very rarely 0 or 3); preocular 1; postoculars 3 (rarely 2 or 4); temporals 1 + 2 (very rarely 1 + 1, 1 + 3 or 2 + 2); supralabials 8 (rarely 9, very rarely 6 or 7), the fourth and fifth (rarely fifth and sixth, very rarely third and fourth, or third, or fifth only) entering orbit; infralabials 9–13, mode 11, the first 4 or 5 in contact with the anterior sublinguals; dorsal scales usually in 19–19–11 or 19–19–13 rows, very rarely 17, 21 or 23 rows at midbody (23 recorded by Rasmussen, 1997); ventrals 144–168 in ♂♂, 145–172 in ♀♀; cloacal divided; subcaudals 131–167 in ♂♂, 123–153 in ♀♀.

COLORATION. Crown of head uniform green or with a black speckled Y-shaped marking, or brownish, entirely speckled with black (the two extremes may occur within a population, as on Mafia Island); temporal region always brown, speckled with black; supralabials white spotted with black, including a triangle on sixth labial, chin and throat speckled with black; dorsum ash grey with diagonal rows of whitish blotches and flecks of brown and pink or orange, neck with one or two elongate black blotches; venter greyish, streaked with brown.

SIZE. Largest ♂ (MHNG 1376.34 – Newala, Tanzania) 910 + 525 + (tail truncated); largest ♀ (NMZB-UM 4157 – Mutare, Zimbabwe) 895 + 510 = 1405 mm, but MCZ 18476 from Zengeragusu, Tanzania, has a snout-vent length of 920 mm (tail truncated).

HABITAT. Savanna and coastal forest.

DISTRIBUTION. Southern Somalia south to central Mozambique at

about 22°30' S, west to the shores of Lake Tanganyika, Malawi and eastern Zimbabwe (Fig. 6).

*Thelotornis capensis capensis* A. Smith

Southeastern Savanna Vine Snake

*Thelotornis capensis* A. Smith, 1849, *Ill. Zool. S. Africa, Rept. App.*:

19. Type locality: 'Kaffirland and the country towards Port Natal', i.e. Durban (type lost).

*Thelotornis kirtlandii capensis* Loveridge, 1944: 154 (part).

*Thelotornis capensis capensis* Broadley, 1979: 126.

DIAGNOSIS. Top of head blue-green with pink and black speckling forming a 'Y' or 'T' marking, or speckling covering entire top of head; temporals pink margined with black; neck with black lateral blotches; supralabials with scattered black spots, including a triangle on the sixth labial; rostral and nasals not, or only feebly, recurved onto top of snout; infralabials 9–13 (mode 11); ventrals 144–164; subcaudals 127–155.

DESCRIPTION. Rostral and nasals barely visible from above; loreals usually 2 (rarely 1, very rarely 0 or 3); preocular 1; postoculars 3 (rarely 2 or 4); temporals 1 + 2 (very rarely 1 + 1 or 1 + 3); supralabials 8 (very rarely 7 or 9), the fourth and fifth (very rarely third & fourth, fifth & sixth or third, fourth and fifth) entering orbit; infralabials 9–13, mode 11, the first 4 or 5 (very rarely 3 or 6) in contact with anterior sublinguals; dorsal scales usually in 19–19–13 rows, rarely in 17 rows at midbody (15 rows only in TMP 45554); ventrals 144–160 in ♂♂, 148–162 in ♀♀; cloacal divided; subcaudals 133–155 in ♂♂, 127–147 in ♀♀.

SIZE. Largest ♂ (NMZB 6389 – Gwanda, Zimbabwe) 830 + 506 = 1336 mm; largest ♀ (TMP 5615 – Hectorspruit, Mpumalanga, South Africa) 911 + 455 = 1366 mm.

HABITAT. Savanna.

DISTRIBUTION. Southwestern Zimbabwe and southeastern Botswana, south through the northern provinces of South Africa and Swaziland to southern Mozambique and KwaZulu-Natal (Fig. 6).

*Thelotornis capensis oatesii* (Günther)

Oates' Savanna Vine Snake

*Oxybelis Lecomtei* (not Duméril & Bibron) Peters, 1854: 623 (part, Tete).

*Dryiophis oatesii* Günther, 1881, In *Oates' Matabeleland and the Victoria Falls*, App.: 330, Col. Pl. D. Type locality: Matabeleland (= western Zimbabwe), type BMNH 1946.1.9.76.

*Thelotornis Kirtlandii* (not Hallowell) Peters, 1882: 131 (part).

*Thelotornis kirtlandii capensis* Loveridge, 1944: 154 (part).

*Thelotornis capensis* (not A. Smith) Witte, 1953: 249, fig. 82.

*Thelotornis kirtlandii oatesii* Loveridge, 1953: 277.

*Thelotornis capensis oatesii* Laurent, 1956: 231, fig. 35

DIAGNOSIS. Top of head blue-green with pink and black speckling forming a 'Y' or 'T' marking; temporals pink margined with black; neck with black lateral blotches; supralabials with scattered black spots, including a triangle on the sixth labial; rostral and nasals not, or only feebly, recurved onto top of snout; infralabials 9–13 (mode 11); ventrals 150–177; subcaudals 126–168.

DESCRIPTION. Rostral and nasals barely visible from above; loreals usually 2 (rarely 1, very rarely 0); preocular 1; postoculars 3 (rarely 2, very rarely 1 or 4); temporals 1 + 2 (very rarely 1 + 3 or 1 + 1); supralabials 8 (rarely 7, very rarely 9), the fourth and fifth (very rarely third & fourth, fifth & sixth, third, fourth & fifth, or third, or



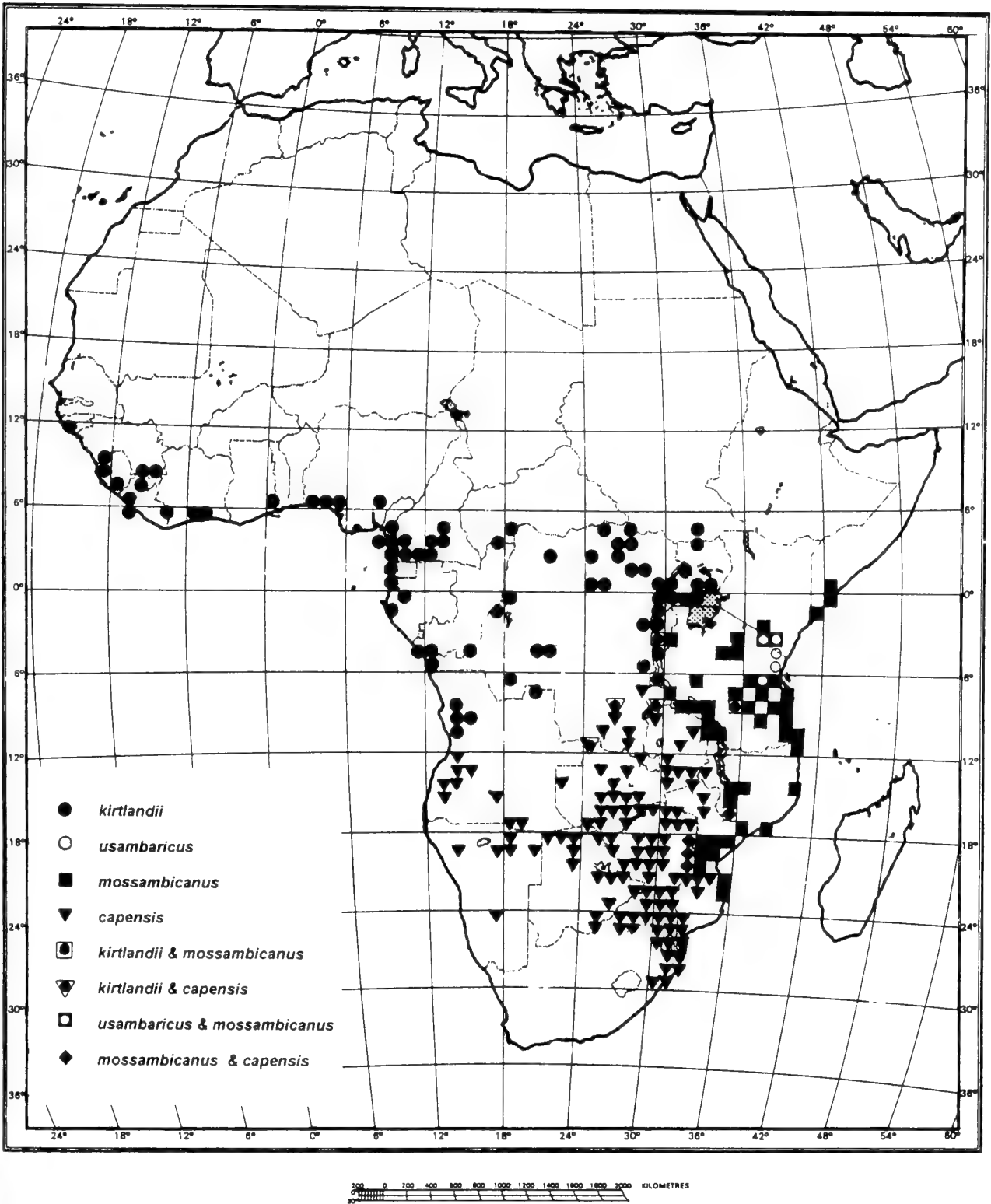


Fig. 6 Distribution of the genus *Thelotornis*.

fourth only) entering orbit; infralabials 9–13, mode 11, the first 4 or 5 (rarely 3) in contact with anterior sublinguals; dorsal scales usually in 19–19–11 or 19–19–13 rows, very rarely 17 rows at midbody; ventrals 150–177 in ♂♂, 153–177 in ♀♀; cloacal divided; subcaudals 132–173 in ♂♂, 126–168 in ♀♀.

SIZE. Largest ♂ (NMZB 3828 – Mtorashanga, Zimbabwe) 1062 + 620 = 1682 mm; largest ♀ (NMZB 3600 – Lake Kariba, Zimbabwe) 975 + 560 = 1535 mm, but NMZB-UM 1061 from Shurugwe, Zimbabwe, has a snout-vent length of 1050 mm (tail truncated).

HABITAT. Savanna.

DISTRIBUTION. Southern Angola and northern Namibia, west through northern Botswana, Zambia and southeast Katanga (D.R.C.) to Zimbabwe, western Mozambique and Malawi (Fig. 6).

### *Dispholidus typus* (A. Smith) Boomslang

*Bucephalus typus* A. Smith, 1828, *South African Commercial Advertiser* 3 (144): 2, col. 4. Type locality: Eastern districts of South Africa; 1829, *Zool. Journ.*, 4: 441 (*B. typicus*).

*Bucephalus Jardineii* A. Smith, 1828, *South African Commercial Advertiser* 3 (144): 2, col. 4. Type locality: Cape Town, South Africa; 1829, *Zool. Journ.*, 4: 422.

*Bucephalus gutturalis* A. Smith, 1828, *South African Commercial Advertiser* 3 (144): 2, col. 4. Type locality: Forests of the eastern districts of South Africa; 1829, *Zool. Journ.*, 4: 442.

*Bucephalus Bellii* A. Smith, 1828, *South African Commercial Advertiser* 3 (144): 2, col. 4. Type locality: Eastern districts of South Africa; 1829, *Zool. Journ.*, 4: 442.

*Dispholidus Lalandii* Duvernoy, 1832, *Ann. Sci. Nat. (Paris)* 26: 150. Type locality: Cape of Good Hope.

*Dendrophis colubrina* Schlegel, 1837, *Essai Phys. Serp.* 2: 238, Pl. ix, fig. 14–16. Type locality: Ronsbosch, [Western] Cape Province, South Africa.

*Bucephalus viridis* A. Smith, 1838, *Illus. Zool. S. Africa, Rept.*: Pl. iii. Type locality: Old Latakoo [Northern Cape Province], South Africa.

*Bucephalus capensis* A. Smith, 1841, *Illus. Zool. S. Africa, Rept.*: Pl. x–xiii. Type locality: Cape Province, South Africa; Bocage, 1895: 121.

*Dendrophis pseudodipsas* Bianconi, 1848, *Nuovi Ann. Sci. Nat. (2)* 10: 108, Pl. iv, fig. 2 & 1850. *Spec. Zool. Mosamb.* 40, Pl. iv, fig. 2. Type locality: [Inhambane] Mozambique. Holotype: Bologna 100296.

*Thrasops jacksonii mossambicus* Mertens, 1937, *Abhand. senckenberg. naturf. Ges.*, No. 435: 13. Type locality: Cheringoma Farm, Inhaminga, Mozambique. Holotype SMF 22246.

*Dispholidus typus kivuensis* Laurent, 1955, *Revue Zool. Bot. Afr.* 51: 127. Type locality: Uvira, Kivu, Congo Belge [= D.R.C.]. Holotype MRAC 17505.

*Dispholidus typus punctatus* Laurent, 1955, *Revue Zool. Bot. Afr.* 51: 129. Type locality: Dundo, Angola. Holotype MRAC 17395.

*Dispholidus typus occidentalis* Perret, 1961, *Bull. Soc. neuchateloise Sci. nat.* 84: 138. Type locality: Cameroon, no type designated.

DIAGNOSIS. Dorsal scales strongly keeled in 19 (rarely 17 or 21) rows at midbody; ventrals 164–201; anal divided; subcaudals 94–142.

DESCRIPTION. Supralabials 7 (rarely 8 or 6), the third and fourth (rarely 5<sup>th</sup> & 6<sup>th</sup>) entering orbit; lower labials 8–13, the first 3–6 in contact with anterior sublinguals; preocular 1; postoculars 3 (very rarely 2 or 4), the lower in contact with two labials; temporals 1 + 2 (very rarely 1 + 1, 1 + 3, 2 + 1, 2 + 2 or 2 + 3); three enlarged

occipitals, the middle one subtriangular. Dorsals strongly keeled in 19 (rarely 17 or 21) rows; ventrals 164–201; cloacal divided; subcaudals 94–142 pairs.

COLORATION IN LIFE. Juveniles are speckled dark grey-brown above, with paired blue spots on some adjacent scales that become visible when the skin is stretched, the lower scale rows are grey and the venter is white, heavily stippled with dark red-brown. The head is brown above, the labials and chin white, sometimes with some black spots, and the throat is bright yellow. The iris of the eye is bright green. The juvenile coloration is gradually lost as the snake approaches one metre in length and there is great variation in adult colour pattern.

Males are usually green, with or without black-edged scales, females usually olive or brown above, paler below. This sexual dimorphism in colour pattern does not always apply, for example green females are not uncommon in Mozambique and KwaZulu-Natal, while in southwestern Zimbabwe some males are olive-brown above and duck-egg blue below. In East Africa a uniform black phase may occur in either sex. In the Eastern Cape Province (the 'type locality') males are usually black above, each scale and head shield with a green or yellow spot, venter yellow-green, each ventral bordered with black, but in the southwestern Cape the dorsum is uniform black and the venter yellow. In the western form described as *D. t. punctatus* Laurent, the males are black above, each scale or head shield with an orange spot, ventrals violet edged with black. Females are usually red-brown above, paler below.

SIZE. Largest ♂ (NMZB 3947 – Mutoko, Zimbabwe) 1290 + 530 = 1820 mm; largest ♀ (NMZB 3820 – Makote, Newala, Tanzania) 1447 + 475 = 1922 mm (tail tip truncated). C.J.P. Ionides recorded a brown male from Tanzania that measured 2134 mm (Pitman, 1974).

HABITAT. Savanna.

DISTRIBUTION. Senegal east to the Horn of Africa, south to the southwestern Cape, excluding areas of rain forest, grassland and desert.

REMARKS. The data for the solitary specimen examined from Pemba Island, Tanzania (MCZ 45587), confirm the long held opinion of Barry Hughes that this population is taxonomically distinct: he will describe it when he has access to more material. The subspecies described by Laurent (1955) were based on male coloration and subcaudal counts, but there is clinal variation in both characters. The species needs to be reviewed, using material from throughout its extensive range.

### Key to the genera and species of Dispholidini

- 1a. Nasal divided; rear maxillary teeth not grooved ..... 2
- 1b. Nasal entire; enlarged grooved fangs on posterior maxilla ..... 8
- 2a. Head elongate with two loreals in tandem; temporals 1+2; maxillary teeth 17, the last three enlarged and dagger-shaped .....  
..... *Xyelodontophis uluguruensis*
- 2b. Head short with single loreal; temporals 1+1 or one only; maxillary teeth 20–38, the last three enlarged ..... 3
- 3a. Vertebral scale row enlarged; a single temporal; 2 or 4 enlarged occipitals ..... 4
- 3b. Vertebral scale row not enlarged; 1+1 temporals; no enlarged occipitals ..... 5
- 4a. Cloacal shield entire; midbody scale rows 13; occipitals 4 .....  
..... *Rhamnophis batesii*

- 4b. Cloacal shield divided; midbody scale rows 15–19; occipitals 2 ..... *Rhamnophis aethiops*
- 5a. Dorsal scales twice as long as lower row of laterals and ventrals; midbody scale rows 13 (rarely 15) ..... *Thrasops flavigularis*
- 5b. Dorsal scales subequal in length to the ventrals; midbody scale rows 15–19 (rarely 21) ..... 6
- 6a. Three supralabials in contact with lower postocular ..... *Thrasops occidentalis*
- 6b. Two supralabials in contact with lower postocular ..... 7
- 7a. Midbody scale rows usually 19; ventrals 187–214 ..... *Thrasops jacksonii*
- 7b. Midbody scale rows usually 17; ventrals 168–184 ..... *Thrasops schmidtii*
- 8a. Head elongate; pupil horizontal, keyhole shaped; eight supralabials, fourth and fifth entering orbit ..... 9
- 8b. Head short; pupil round or pear-shaped; seven supralabials, third and fourth entering orbit ..... *Dispholidus typus*
- 9a. Top of head, including temporal region, uniform green; black crossbands or chevrons on neck; habitat forest ..... 10
- 9b. Top of head uniform green or black speckled, temporal region always brown, speckled with black, or pink, shields margined with black; neck with black lateral blotches; habitat usually savanna ..... 11
- 10a. Rostral and nasals strongly recurved onto top of snout; infralabials 7–11, mode 9; supralabials immaculate or with fine green or grey stipple ..... *T. kirtlandii*
- 10b. Rostral and nasals not, or only slightly, recurved onto top of snout; infralabials, 9–13, mode 11; supralabials with scattered black spots, usually including a triangle on the sixth labial ..... *T. usambaricus*
- 11a. Top of head bright green to pale brown, uniform or speckled with black; temporals brown speckled with black ..... *T. mossambicanus*
- 11b. Top of head blue-green with pink and black speckling forming a 'Y' or 'T' marking, or speckling covering entire top of head; temporals pink margined with black ..... *T. capensis*

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## Appendix 1. Material for which skulls were prepared:

*Dispholidus typus* (NMZB-UM 3058; NMZB 922, 1350, 1658, 3322, 10870, 13378); *Rhamnophis aethiopissa* (NMZB 10793, 16726); *Rhamnophis batesii* (NMZB 13206); *Xyelodontophis uluguruensis* (NMZB 7443 – holotype); *Thelotornis capensis* (NMZB-UM 88, 16199, 17922); *Thelotornis kirtlandii* (NMZB 32185); *Thelotornis mossambicanus* (NMZB-UM 3058; NMZB 11390); *Thelotornis usambaricus* (NMZB 15629); *Thrasops flavigularis* (NMZB 16725); *Thrasops jacksonii* (NMZB 10717).

## Appendix 2. Material examined internally:

*Dispholidus typus* (BMNH 1979.205; FMNH 58379; IRSL 2 unnumbered; IRSNB 13281a–b, MCZ 18223, 32475, 32478, 53458, 53730–31, 55250, 55255, 67927), *Dispholidus* 'pemba' (MCZ 45587), *Hapsidophrys lineatus* (BMNH 1979.165–67; IRSL 15 unnumbered; SDSU unnumbered; UNAZA 4 unnumbered; VW 1010), *Hapsidophrys smaragdinus* (BMNH 1979.157–59; FMNH 179036; IRSL 14 unnumbered; MZUSP 8159; PEM 3363, 3403; UNAZA 4 unnumbered; VW 907, 1012, 1026, 1068, 1099), *Philothamnus angolensis* (IRSL 23 unnumbered; MZUSP 8174–75, 8177; NMV D55548; PEM 3382–83; SDSNH 63865–66; UF 52485, 80395–99, 80671; UNAZA 4 unnumbered; VW 1086, 1197, 1211, 1254, 1429–30, 1451, 1745, 1986–87, 1990, 2226; ZRC 2.3427), *Philothamnus bequaerti* (MCZ 47846), *Philothamnus carinatus* (UNAZA 2 unnumbered), *Philothamnus dorsalis* (UNAZA 2 unnumbered), *Philothamnus heterodermus* (UNAZA 1 unnumbered), *Philothamnus heterolepidotus* (LSUMZ 40781), *Philothamnus hoplogaster* (BYU 30895), *Philothamnus macrops* (MCZ 23244), *Philothamnus nitidus* (UNAZA 1 unnumbered), *Philothamnus occidentalis* (VW 6360), *Philothamnus punctatus* (MCZ 52666), *Xyelodontophis uluguruensis* (NMZB 7443; ZMB 48153), *Rhamnophis aethiopissa* (IRSL 6 unnumbered; MCZ 13607, 258900, 38392, 48343, 178494; SDSNH 63873; SDSU unnumbered), *Rhamnophis batesii* (IRSNB 2813; MCZ 13604, 38393), *Thelotornis capensis* (FMNH 191163; MCZ 41963, 44581, 69036; ZMB 23526), *Thelotornis kirtlandii* (FMNH 205972, 214828; IRSL 1 unnumbered; IRSNB 5370, 5371a–b, 6451, 6454; MCZ 22523, 49687, 49734, 51835; SDSU unnumbered; ZMB 21627), *Thelotornis mossambicanus* (FMNH 248040; MCZ 51628, 56922; ZMB 16783, 28001), *Thelotornis usambaricus* (MCZ 23349; ZMB 16786, 21130), *Thrasops flavigularis* (MCZ 8776–77; MHNG 967.20, 1520.68, 1520.75, 1520.78), *Thrasops jacksonii* (BMNH 1979.190–91; UF 52476; MCZ 25954; MZUSP 8178–79; UNAZA 5 unnumbered; VW 1077, 1083, 1230, 1232, 1965, 2350), *Thrasops occidentalis* (MCZ 55232; UG C34P12), *Thrasops schmidtii* (MNHN 1940.197, 1974.1; NRM 2297b).

# On the African leopard whip snake, *Psammophis leopardinus* Bocage, 1887 (Serpentes, Colubridae), with the description of a new species from Zambia

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**SYNOPSIS.** An examination of scalation and dentition of specimens in Brussels (IRSN), Tervuren (MRAC) – mostly Bredo collection, and London (BMNH) from Angola, Congo-Kinshasa and Zambia suggests the existence of a species which is neither *P. sibilans leopardinus* of which the type is from Namibia, nor *P. 'sibilans' [mossambicus]* of Congo-Kinshasa and Zambia, but a new species previously unnamed.

## INTRODUCTION

Bocage (1887:206) described from Catumbela, Angola a *Psammophis* (MBL 1798, now destroyed) with a striking reticular pattern on the neck and anterior part of the body as a variety of *Psammophis sibilans*, a taxonomic treatment later followed by Broadley (1977). More recently Brandstätter (1995, 1996: Fig. 4) has recognised *P. sibilans* as occurring no further south than the northern part of Tanzania and has treated Bocage's variety as *P. brevirostris leopardinus*, following an earlier practice by Broadley (1971). He has followed Broadley (op. cit.) in assigning to this subspecies Zambian specimens showing the same reticular pattern on the neck. However, such a pattern occurs sporadically elsewhere, as in West African specimens of *P. sibilans* (BMNH 1930.6.5.8 from Mogonori, Ghana; 1956.1.5.87 from Ikoyi, Lagos, Nigeria; CM 24636 from Accra; MNHN 1985.442–3 from Ghana; ZMH R04466 from Gana Gana or Segbana, Niger Delta, Nigeria: these have neck bars sometimes interconnected as in *leopardinus*). Dependence on pattern for identification in a genus whose species are notorious for their variability is unconvincing. In an attempt to find other, more reliable criteria by which to distinguish species of *Psammophis*, total tooth counts were undertaken and revealed significant differences between specimens of '*leopardinus*' from Angola and those from Zambia. Secondly, the Zambian specimens are often of a colour pattern rarely met with elsewhere during the study of several thousand specimens from all parts of Africa and the Middle East. Thirdly, the ventral and subcaudal counts of the Zambian specimens are lower than those from neighbouring localities in Zambia and Congo-Kinshasa. Fourthly, a SEM micrograph of a dorsal scale of a specimen from Ikelenge (Brandstätter, 1995: Fig. 39) differs considerably from those of species assigned to the *P. sibilans* complex. For these reasons, it is thought necessary to coin a new name for the Zambian specimens.

## SYSTEMATICS

*Psammophis zambiensis* sp. nov.      Zambian Whip Snake

*Psammophis sibilans*, not Linnaeus 1758, Pitman, 1934: 297 (part, Chimikombe specimens only).

*Dromophis lineatus*, not Dumeril & Bibron, Laurent 1956:247 Kundelungu male & female.

*Psammophis ? sibilans* Broadley & Pitman 1960: 445

*Psammophis brevirostris leopardinus* Broadley 1971:88; Brandstätter, 1995: 53, Fig. 39 and 1996: 48 (Zambian specimens only); Haagner *et al.* 2000:16.

*Psammophis sibilans leopardinus* (Zambian specimens) Broadley 1977:18

*Psammophis brevirostris leopardinus* Brandstätter 1996:48 (Zambian specimens only)

**HOLOTYPE.** BMNH 1959.1.1.81 supposedly from 'Abercorn' (now Mbala) area of Zambia, part of the H.J. Bredo collection, sent on from Brussels, but likely to be from Mweru-Wantipa – see discussion (Figs 1–3).

**PARATYPES.** IRSN 2561,2565–6 of same origin, BMNH 1932.9.9.132–3 from Chimikombe at 4500 ft. (= Chimilombe, Solwezi District); NMZB 10635–6, 10736, 10757 from Ikelenge (Broadley 1991:529); IRSN 2562 from Mambwe; IRSN 2567 and PEM 1438/12 from Mporokoso District (probably Mweru-Wantipa); IRSN 2563 from Mweru-Wantipa, and IRSN 2564 from an unknown source in Zambia; MRAC 18622–3 SERAM, Kundelungu Plateau 1750 m, Congo-Kinshasa (Laurent 1956:247 as *Dromophis lineatus*).

All specimens, except two (BMNH 1932.9.9.132–3) are female; Haagner *et al.* (2000) have listed two more males as '*P. brevirostris leopardinus*'.

**DIAGNOSIS.** Often distinguished by a combination of the reticular body pattern of *leopardinus* but lacking the higher tooth counts of the latter (Table 1.). A detailed description of colouration, based on 5 specimens, is given by Broadley & Pitman (1960:445) but can be summed up by saying that they are greenish rather than the usual khaki-brown and the scales heavily edged in black. Unlike associated specimens of '*P. sibilans*' the vertebral 'chain' is more like a stripe, the lighter marking on each vertebral scale being more of a line than a spot; and behind the eyes the head is crossed by three transverse light bars – a common feature in many *Psammophis* spp. but these are narrow, as in *P. angolensis* or *Dromophis lineatus*. Smaller specimens (e.g. Fig. 2–3) are more distinctly marked with greater contrast around the body. As Haagner *et al.* (2000) have

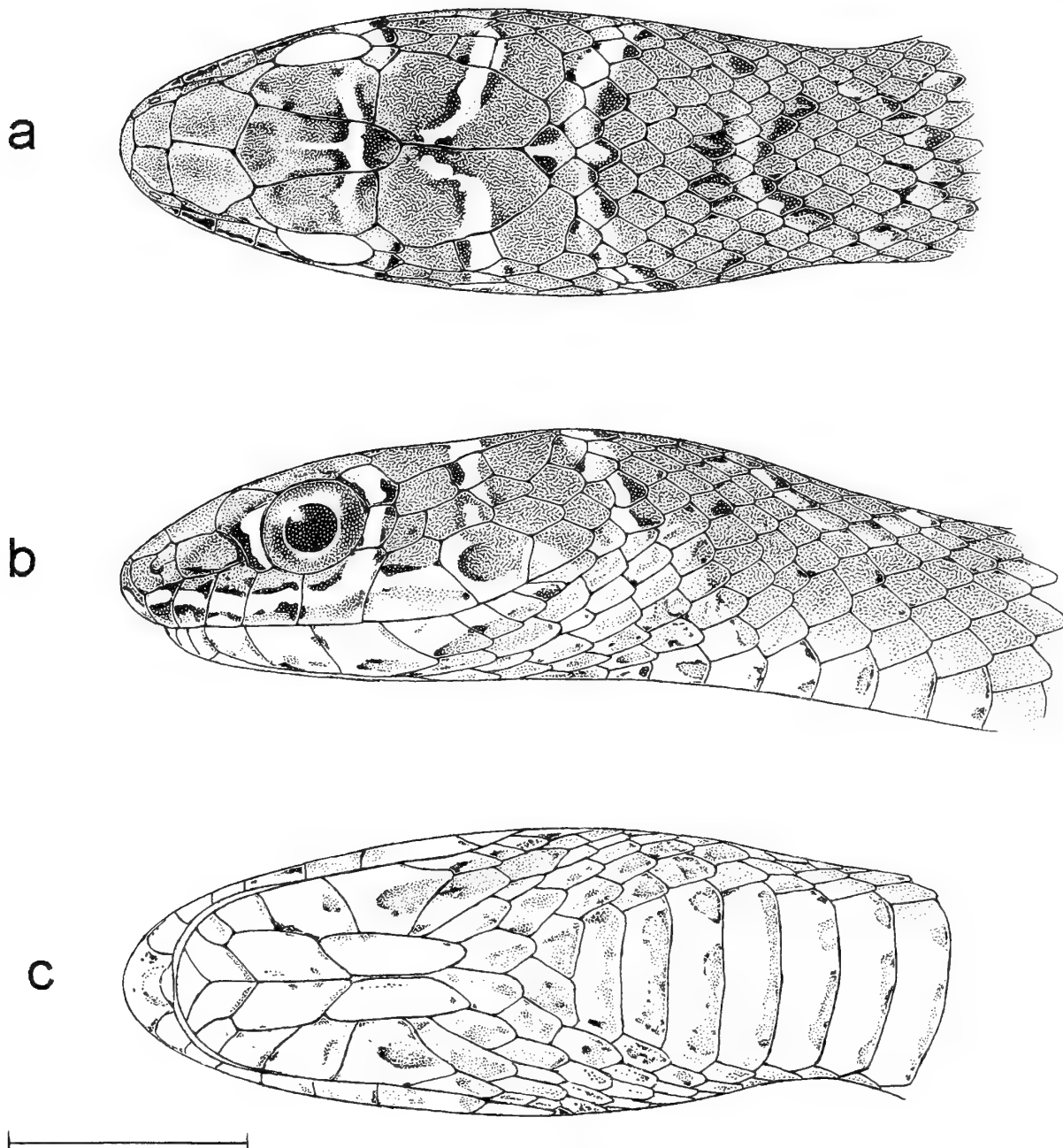


Fig. 1 Head of *P. zambiensis* (adult holotype, BMNH 1959.1.1.81) seen in (a) dorsal, (b) lateral and (c) ventral views.

Table 1 Dentitions – left/right sides.

species	museum no.	max.pre-2F	post.dentary	palatine	pterygoid
<i>leopardinus</i> (Namibia)	1937.12.3.166	5/5	23/24	11/9	23/18
<i>zambiensis</i>	1959.1.1.81	4/3	17/14	9/8	17/14
<i>zambiensis</i>	10636	–/3	14/13	8/9	13/12
<i>zambiensis</i>	10736	4/4	15/14	8/9	16/15
<i>zambiensis</i>	10521	3/3	15/15	8/8	16/16
<i>zambiensis</i>	10522	3/3	13/–	9/8	15/14
<i>zambiensis</i>	10523				
<i>zambiensis</i>	18622	3/3	16/16	7/8	14/15
<i>zambiensis</i>	18623	4/4	17/15	8/9	17/18
<i>zambiensis</i>	1932.9.9.132	3/3	17/19	9/9	17/16
<i>zambiensis</i>	1932.9.9.133	3/3	20/20	8/8	19/18
<i>zambiensis</i>	1953.1.2.15	3/3	17/18	8/8	18/18
<i>sibilans</i>	1953.1.2.14	3/3	19/18	8/8	16/15?

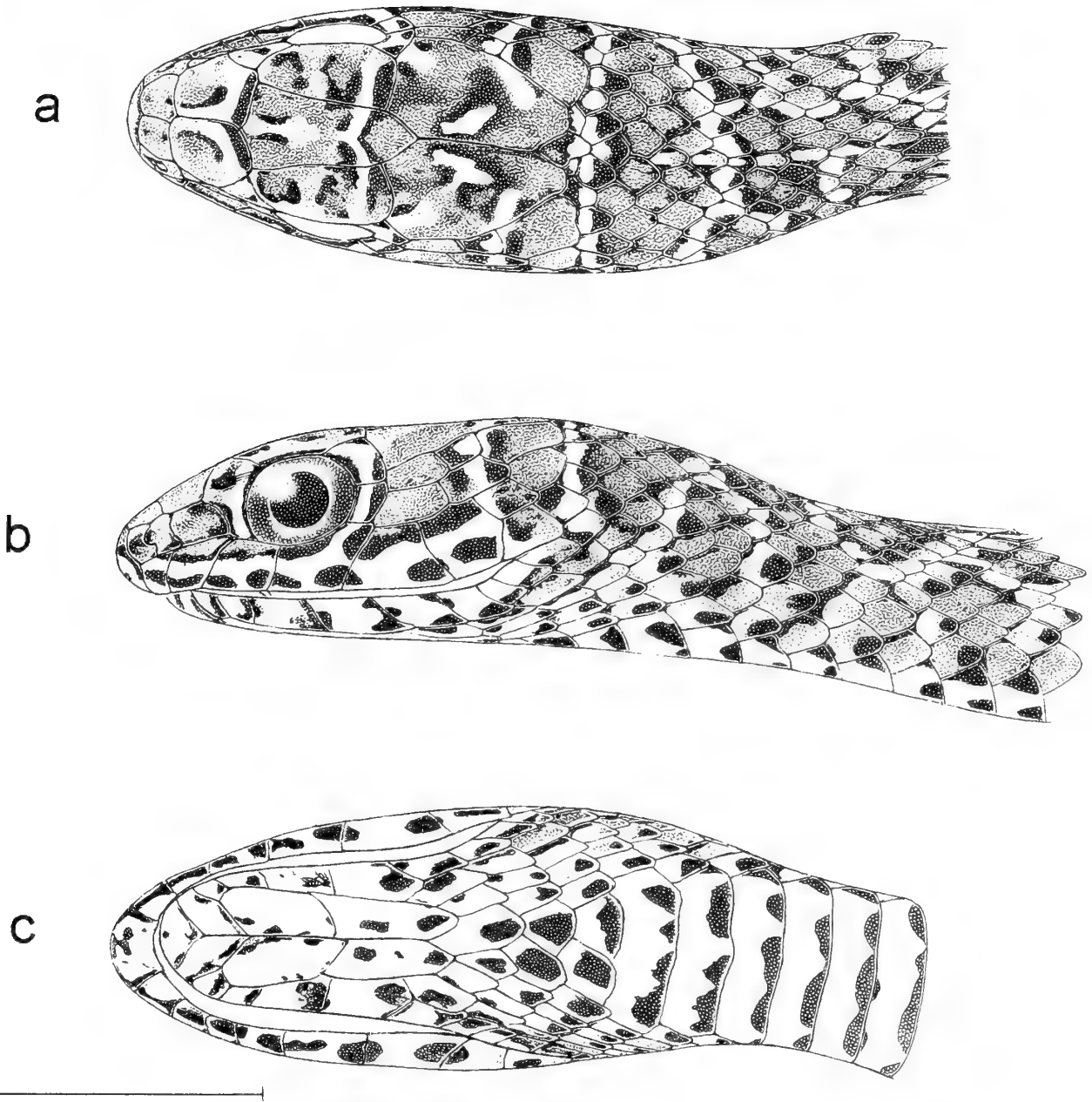


Fig. 2 Head of juvenile paratype *P. zambiensis* (IRSN 10523) seen in (a) dorsal, (b) lateral, and (c) ventral views.

noticed, the reticular neck pattern is not always present and these specimens are distinguished from '*sibilans*' by their lower ventral counts and usually by lower subcaudal counts (Table 2).

Brandstatter (1995: Fig. 39) has provided a SEM micrograph of a dorsal scale from a *P. zambiensis* paratype NMZB 10636, and the micro-ornamentation resembles that of *Dromophis lineatus* (his Fig. 83) more than any species of the *P. sibilans* complex.

**HABITAT.** Unfortunately, no field notes are available for this species, but the fact that many specimens appear to have originated from the Mweru-Wantipa suggests that it requires a marshy habitat like *Dromophis lineatus*, with which it is sympatric in this area (Broadley & Pitman, 1959). In the Ikelenge area there are many suitable dambos and one local specimen had eaten an *Eumecia anchietae*, a large skink that frequents such places (Broadley, 1991). The

Sanolumba snake had eaten a ranid frog (Haagner *et al.*, 2000).

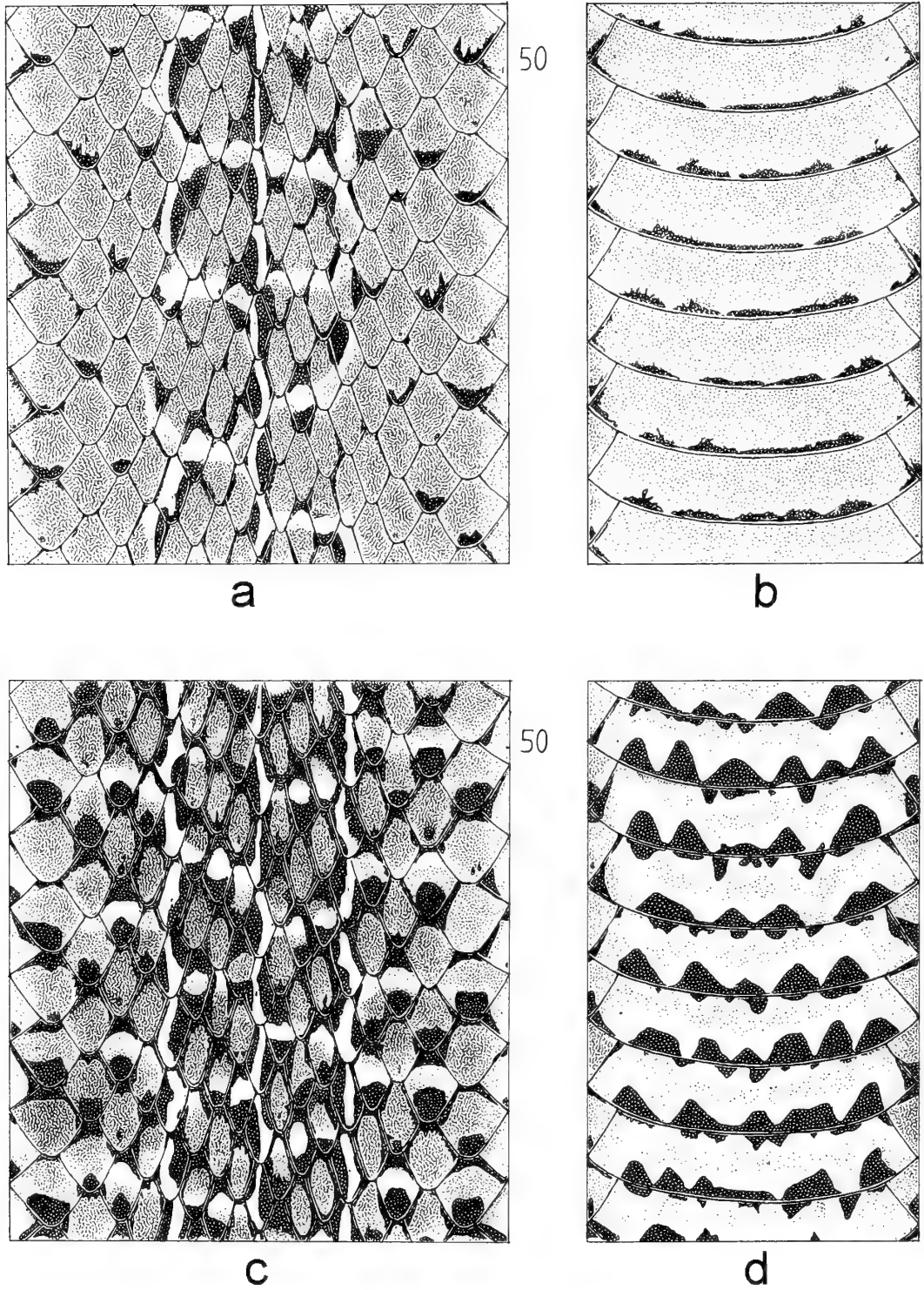
#### OTHER SPECIES AND SOURCES OF DATA

*Psammophis leopardinus* [only those with numbers seen by BH, those without numbers DGB data or from publications].

ANGOLA – Bella Vista MCZ; Caconda MBL  $\times 8$ ; Capelongo AMNH  $\times 6$ ; Catengue SMF  $\times 2$ ; Catumbela MBL lectotype, destroyed; Iona TM; Luanda USNM; Lobito Bay AMNH R50612–3, R50617–8, and  $\times 5$ ; Oncocua, 37 km NE on way to Otchinzau TM; NAMIBIA – Swakop-Tal, Namib Desert BMNH 1937.12.3.166.

*Psammophis* '*sibilans*', currently treated as *P. mossambicus*.

CONGO-KINSHASA – Kambore MRAC 2017; Kansenia MRAC 7002, 7639; Kapanza MRAC 9649–50; Kapiri MRAC 7027, 7056–



**Fig. 3** Stretches of the body of *P. zambiensis* between ventral scales 50 and 57 seen in dorsal and ventral views. (a, b) Adult holotype (BMNH 1959.1.1.81); (c, d) juvenile paratype (IRSN 10523).



**Table 2** Scale counts (sample size)

species	M ventrals	F ventrals	M subc.	F subc.
'leopardinus'	151–71 (9)	151–74 (20)	79–104 (4)	80–105 (10)
'leop.' refined	151–65 (8)	151–67 (16)	79–104 (4)	80–105 (8)
'zambiensis'	148–61 (5)	149–65 (17)	80–90 (3)	75–86 (9)
'sibilans'	167–77 (32)	167–77 (19)	89–103 (26)	781–100(12)

N.B. The *P. 'leopardinus'* data is for Angolan specimens and from Broadley (pers. com.): I suspect that specimens of another species are included and *P. 'leop. refined'* has the data of that species removed. The *P. 'sibilans'* (currently treated as *P. mossambicus*) data is from Zambian specimens so called by Broadley (1971:88) although he has since referred them to *P. phillipsi* (Broadley 1983) and later *P. mossambicus* (Broadley, in prep.), and from Haagner et al (2000) who treat their specimens as *P. mossambicus*. The *P. zambiensis* data incorporates that of *P. 'brevirostris leopardinus'* from Haagner et al. (2000).



**Fig. 4** Brandstätter's (1996, fig. at p. 48) map of the occurrence of *Psammophis brevirostris leopardinus*.

9, 7061; Kapolowe MRAC 9970; Kasai MRAC 968; Kasenyi IRSN 6861; Lofoi MRAC 598; Lubumbashi [as Elizabethville] IRSN 6310; MRAC 7661, 8378–9, 9397–8; Lukafu MRAC 7187, 71199–201, 7217; Luluaborg St Joseph MRAC 2627–9; Luebo MRAC 2996; Lukonzolwa MRAC 2165; Lusambo MRAC 16378, 16381; Merode MRAC 3113; Moero Lake Region MRAC 15323; Musosa IRSN 4780–1; Niambi to Baudouinville MRAC; Pweto MRAC 252, 260, 1980, 1999, 2027; Sandoa MRAC 7935, 7941, 7967–9, 8271–2, 9854; Tembwe MRAC 4186, 4216, 4237–8;

MALAWI – Chitipa (as Fort Hill) BMNH 97.6.9.135–6; Chiromo BMNH 1959.1.3.37; Chiromo, 20 km N of Mangochi (as Fort Johnston); Fort Johnston BMNH 1926.5.8.49; Kasungu AMNH; Kondowe (=Livingstonia Mission) to Karonga BMNH 97.6.9.132–4; Nkhotakhota (as Kota Kota) BMNH 96.12.12.19; Mkanga BMNH 1959.1.3.38; Mlanje River AMNH; × 2; Mtimbuka AMNH × 4; Mulanje Mt. AMNH; Nchisi AMNH × 2; Nkahta Bay to Ruarwe

BMNH 97.6.9.131 (Boulenger 1897:801); Zomba BMNH 93.10.26.57, 94.2.13.12 (Günther 1894:618, Boulenger 1896:164,l,m), 1933.4.5.2; Zomba Mt BMNH 1948.1.2.28.

NAMIBIA – Old Sangwali (Broadley 1983; Barts & Haacke 1997).

TANZANIA – Ipiama ZMB 16984; Kingani, nr Dunda ZMB 172777, 17338; Zimba ZMB 23476;

ZAMBIA – IRSN 8834,b–c, 10520, Broadley & Pitman 1960; ZFMK 18904; Barotseland MNHN 1921.533; Buleya IRSN 8802 (Bulaya of Broadley & Pitman 1960); Chipangali UM; Chisi Lake (Broadley & Pitman 1960); Chunga, Kafue N.P. UM; Dumdumwensi UM 20841; Fort Manning BMNH 1962.497; Ikelenge × 2 (Broadley 1991 as *P. phillipsii*); Kabinda BMNH 1932.9.9.130; Kabwe (as Broken Hill) BMNH 1932.5.3.95–100, 1932.9.9.134–8, 1936.3.6.34, 1959.1.1.96; Kalabo FMNH, UM; Kaputa IRSN 8805,a, Broadley & Pitman 1960); Kasama IRSN 8832, Broadley & Pitman 1960; Lachisi IRSN 8830; Lealui MNHN 20.104, 21;533; Lusaka, 100 km SW of ZFMK 18904; Makupa IRSN 8835,a,b; Mambwe IRSN 8804, 8828–9, Broadley & Pitman 1960; Maskie's, Namwala District BMNH 1932.5.3.95–8, 1932.5.3.101; Mbala (as Abercorn, Broadley & Pitman 1960) BMNH 1959.1.1.81, 1959.1.1.96; IRSN 8798a–e – 803,a, 8799a–b, 8800–1, 8806–27, 8836–8, 8839 (Broadley & Pitman 1960 as *Psammophis subtaeniatus sudanensis*); Mkanda UM; Mporosoko IRSN 8803a–b (Mporokoso of Broadley & Pitman 1960); Msoro UM (Wilson 1965); Mukopa (Broadley & Pitman 1960); Muswema IRSN 8833, Broadley & Pitman 1960; Mweru–Wantipa IRSN 8831, Broadley & Pitman 1960; Namantombwa Hill, Mumbwa UNZA; Nchelenge, Luangwa Valley BMNH 1932.12.13.231; Ngoma, Kafue N.P. UM; Nsangu BMNH 1932.9.9.131; Sayiri UM (Wilson 1965); Serenje BMNH 1953.1.2.13–6; Yacobi Village, Luangwa Valley LACM;

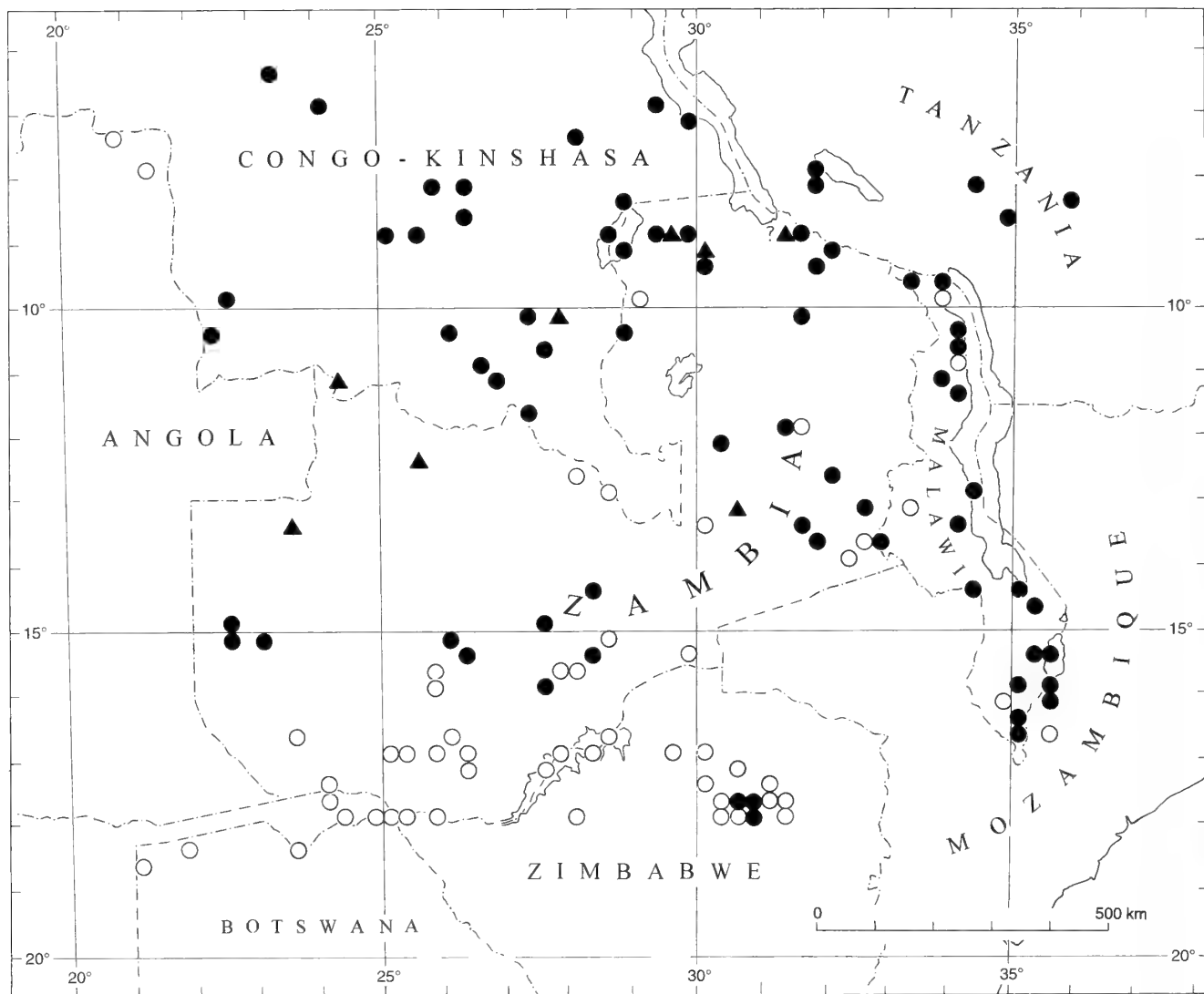
ZIMBABWE – Bari, Chikwakwa UM; Bulawayo UM × 3; Elim Mission, Inyanga UM; Harare (as Salisbury) NMK; Harare (as Salisbury), Borrowdale Brook UM × 2; Inkomo UM; Mabalauta UM; Mazoe (Broadley 1959) BMNH 1902.2.12.96–7; Mondoro UM; Odzi UM × 2; Rugare, Inyanga UM; Umsweswe Bridge, Gatooma UM; Umtali UM × 3 (Broadley 1959) BMNH 1954.1.3.23–4; Vumba Mt UM × 2; Wankie N.P., main camp UM × 2.

*Psammophis zambiensis* (other, non-type specimens)

ZAMBIA – Ikelenge NMZB 10636, and × 2; PEM × 7; Mbala (as Abercorn, Broadley & Pitman 1960) IRSN 10521–2; Mbala area (as 'Abercorn' but see Discussion); BMNH 1959.1.1.81; Mporosoko (Broadley & Pitman 1960 as Mporokoso) IRSN 10523; PEM × 2 (Haagner et al 200); Sakeji School PEM × 6 (Haagner et al., 2000).

## DISCUSSION

The many names by which Zambian *P. 'sibilans'* has been known (see above under synonymy) is an indication of the uncertainty which attends identification of specimens of this species complex. The very distinctive colouration of some specimens of *P. zambiensis* attracts attention but it is not reliable in separating this species from other(s) with which it may be sympatric. A letter from Desmond Vesey-FitzGerald to Donald G. Broadley (Broadley, pers. comm.), dated 29 Sept. 1959, suggests that the source of 'Abercorn' specimens is to be doubted: 'I would guess that all these snakes may have come from Mweru-Wantipa in Mporokoso District, where Bredo would have been collecting in the 1943/44 period.' Vesey-FitzGerald (1958) collected long series of *P. sibilans* [= *P. mossambicus*] in



**Fig. 5** Map of area of sympatry between *P. sibilans*\* (O, literature ref. which may include *zambiensis*; ● specimen seen by BH or DGB and *P. zambiensis* ▲ specimens seen). Many records taken from Broadley (1983:146, map 36 of *P. 'phillipsii'*), others from an as yet unpublished, revised map (DGB in prep.) which we have been privileged to see. Localities listed by country and quarter degree square (without 'se' prefix); sources indicated when locality is a map plot without name. For locality data see Appendix 1.

Abercorn [= Mbala] District, but none had either the characteristic pattern or low ventral counts of *P. zambiensis*. However, he did record one snake from Chinsali (10.32 C1) with only 160 ventrals and 90 subcaudals, which may have been a *P. zambiensis*, but it was apparently not preserved. Only by collecting data on a large number of specimens can the limits of variability become known and consistent differences in meristic data become apparent.

*P. zambiensis* and *P. sibilans*\* appear to be sympatric at Mbala (Abercorn) (Fig. 3, se08.31C4) but all of the *P. zambiensis* specimens so attributed are likely from Mweru-Wantipa (see above), so that true sympatry may occur only at Mporokoso (se09.30), Ikelenge (se11.24a2) Serenje (se13.3061) and near Mchinji (13.32d4). The co-occurrence over such a large distance – more than 600 km from Ikelenge to Mweru Wantipa without more instances of sympatry suggests the occupation of different habitats.

*P. zambiensis* seems to be distinct from *P. leopardinus* to the south and *P. sibilans*\* (or '*phillipsii*') to the north; the true identity of the

latter can become clearer only after analysis of specimens from the whole of the Congo Basin and West Africa.

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## Appendix 1

**ANGOLA** – 17.19d3 DGB in prep. **BOTSWANA** – 18.21b4 DGB in prep.; c1 DGB in prep. **CONGO-KINSHASA** – 06.23a4 Merode; 06.24c3 Kapanza; 06.29c4 Tembwe; 07.28a3 Kiambi; 07.29 Niambi to Baudouinville; 07.29b2 Baudouinville; 08.25c3 Kamina; 08.26a2 Kikondja. 08.26c2 Nyonga; 08.28b4 Pweto; 08.28d3 Lukonzolwa.; 09.22d3 Sandoa; 09.28b2 Moero Lake region; 10.22a4 Dilolo; 10.26a3 Kansenia; Kapiri; 10.26d3 Kambove; 10.27 Katanga; 10.27a2 Lofoi; 10.27d1 Lukafu; 10.27d2 SERAM, Kundelungu; 10.28b3 Kasenga; 11.26b2 Kapolowe; 11.27c2 Lubumbashi [as Elizabethville] 11.24b1 Sanolumba; **MALAWI** – 09.33c2 Chitipa (as Fort Hill); 09.33d1 Misuku Hills; 09.33d4 Karonga (Pickersgill

& Watson 1998); 10.34a3 Nyungwe; 10.34c1 Kondowe (= Livingstonia Mission); 10.34c3 Nchenachena; 11.33b2 Rumpi; 11.34a3 Nkhata Bay to Ruarwe; 12.34c4 Nkhotakhota (as Kota Kota); 13.32a2 Kasungu; 13.34a3 Nchisi Mt.; 14.34a4 Dedza; 14.35a3 Mtimbuka; a4 Mangochi (as Fort Johnston); 15.35a4 Zomba; b3 Mchenga; c3 Limbe (Sweeney 1961:147); d3 Mlanje Mt.; 16.34b2 Likabula R., Mt Mlanje; 16.35a3 Broadley (1983, as *P.phillipsii*); b1 Broadley (1983 as *P.phillipsii*); c1 Chiromo (Broadley 1983 as *P.phillipsii*); Makanga. **MOZAMBIQUE** – 16.31b1 DGB in prep.; 17.35d3 Broadley (1983); 18.33a3 Broadley (1983); 18.34a4 Broadley (1983); 18.35b4 Broadley (1983); **NA-MIBIA** – 17.24c1 DGB in prep.; c2 DGB in prep.; c4 DGB in prep.; d4 DGB in prep.; 17.25c3 DGB in prep.; 18.23b3 Old Sangwali; **TANZANIA** – 07.31d4 Zimba; 08.31b2 Milepa; 08.35b4 Uzungwa (as Udzungwa Mts); 09.33d2 Ipiama. **ZAMBIA** – 08.29c4 Mukupa Katandula; 08.29d3 Lake Chisi, Mweru-Wantipa; 08.29d4 Kaputa; 08.31c4 Mbala (as Abercorn); 09.28b2 Molo; 09.29c3 Kawambwa; 09.30a3 Mporokoso; 09.31b2 Mambwe; 10.30c3 Luwingu District; 10.31a2 Kasama; 10.31b1 Nchelenge; 11.24a2 Ikelenge; Sakeji School; 11.31c4 Mpika; Nsangu R.; 12.26b3 Chimilombe (as Chimikombe); 12.27b4 Chingola (Haagner *et al.*, 2000); d1 Lufwanyama Farm (Haagner *et al.*, 2000); d2 Musenga (Haagner *et al.*, 2000); 12.28c3 Kitwe (Haagner *et al.*, 2000); d3 Ndola (Johnsen, 1962); 12.28c1 24 km W of Mufulira (Johnsen, 1962); 12.30a2 Kabinda, Lukulu R.; 12.32c1 Yakobe (as Yacobi), Luangwa Valley; 12.33a3 Lundaz (Wilson, 1965); 12.34c4 Kota Kola; 13.24c1 Kabompo.; 13.25b4 Kasempa; 13.28a2 8km W. of Luanshya.; 13.30a2 DGB in prep.; a3 Katete (Wilson, 1965); b1 Serenje – *P. zambiensis* sympatric with *P. 'sibilans'*; 13.31d2 Msoro; b3 Nsangu River, W of Lavushi River; 13.32a3 Chikowa (Wilson, 1965); b1 Chipangali (Wilson, 1965); b3 DGB in prep.; c2 Kalichero (Wilson, 1965); c4 Sayiri (Wilson, 1965); d1 Chipata (Wilson 1965, as Fort Jameson); d2 Mkanda; d4 near Mchinji (as Fort Manning); 13.33a2 Kasanga; 14.22d3 Kalabo; 14.27c3 Mumbwa; 14.28a4 Kabwe (as Broken Hill); 14.30d1 Kacholola; 15.22b1 Buleya; b4Ndau School; 15.23a1 Lealui; 15.25d4 Ngoma, Kafue N.P.; 15.26a1 Chunga, Kafue N.P.; c2 Maskies; Fort Manning (Wilson, 1965); 15.27d3 100 km SW of Lusaka; d4 Mazabuka.; 15.28a4 Lusaka; b3 50 km E. of Lusaka; c2 Balmoral, (Peirce, 1984; Norton & Peirce, 1985) Chilanga; 15.29c2 DGB in prep.; d2 DGB in prep.; 16.23d1 Kachola (Wilson 1965, as Kacholola); 16.25c3 Machife Forest Station.; c4 Mulanga; d4 Katanda; 16.26c1 Dumdumwensi; c4 Kasusu; 16.27c3 Nansi Farm; d4 Chezia confluence, Kariba Lake; 17.24a3 Katima Mulilo; a4 Wenela base, Caprivi; 17.26a2 Kalomo; c4 DGB in prep.; d4 Ihaha; 17.27b1 Kariba lake, Lulongwe confluence; 18.21b4 Broadley (1983); c1 Broadley (1983); 18.23b3 Old Sangwali; **ZIMBABWE** – 16.28c4 Lake Kariba, Bumi confluence; d1 Kariba lake, Sanyati basin; 16.29d3 DGB in prep; 16.30b4 Mzarambanitam; c3 Salator Farm, Mkanguru; 16.31d3 Mt Darwin (Broadley, 1959); 17.28c3 Sengwa R.; 17.30a1 DGB in prep.; a3 Sinoia (Broadley, 1959); b1 Msitkwe R., Mutorashanga; c1 Selukwe; c2 Broadley (1983); c3 Kutama (Broadley, 1959); c4 Broadley (1983); d1 Inkomo, d2 Mazoe (Boulenger 1910; (Broadley, 1959); Mt Hampden (Broadley, 1959); d3 Norton (Broadley, 1959); d4 Hunyani (Broadley, 1959); 17.31a3 Broadley (1983); c1 Harare (as Salisbury, Broadley 1959); Borrowdale Brook; c2 Bari, Chikwakwa; c3 Harare (as Salisbury, Boulenger 1910); c4 Melfort (Broadley, 1983); 17.32a3 5 km W of Mutolo Broadley (1983); d2 Elim Mission, Inyanga; d3 Maristvale, Nyanga (Broadley 1983); d4 Nyamaropa, Nyanga (Broadley, 1983); 18.26c4 Broadley (1983); d2 Broadley (1983); 18.27c2 Broadley (1983); 18.32b4 Broadley (1983).



# Morphological variation and the definition of species in the snake genus *Tropidophis* (Serpentes, Tropidophiidae)

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**SYNOPSIS.** Historically, the definition of species in the Neotropical snake genus *Tropidophis* has been difficult because of intraspecific variation in scalation and a paucity of specimens of most taxa. There were 13 species recognized at the time of the last review in 1960, but additional species have since been discovered and a taxonomic review and update is needed. Data on morphological variation are presented here and used to clarify the status of the described taxa. Because many taxa are allopatric with their closest relatives, it is necessary to make decisions as to their status as species or subspecies. As a gauge of species status in the genus, character divergence in ten pairs of closely related sympatric species was examined. Typically, such species are differentiated by two non-overlapping colour pattern differences, often in combination with a diagnostic (non-overlapping) or overlapping difference in scalation. Using this criterion, seven taxa previously considered as subspecies are here elevated to species status, whereas seven other taxa are retained as subspecies, although in some cases they are allocated to different species. As a result, the genus *Tropidophis* is considered here to comprise 29 species, 26 of which are West Indian and 15 of those are restricted to Cuba.

## INTRODUCTION

*Tropidophis* are typically small, stout-bodied snakes of the family Tropidophiidae that occur in South America and the West Indies. This family is a member of the primitive snake Infraorder Henophidia (Underwood, 1967). As recognized here, there are 29 valid species of *Tropidophis* and all but three occur in the West Indies, where Cuba (15 species) is the centre of diversity (Table 1). They are nocturnal and feed mostly on sleeping lizards (especially *Anolis*), but also on frogs (especially *Eleutherodactylus*); other nocturnal snakes may impinge on *Tropidophis* ecologically. All are viviparous and most are terrestrial, although several Cuban species are arboreal and gracile in habitus. They exhibit a diversity of colour patterns that include spots (mostly), bands (saddles), and stripes. They have the unusual ability of being able to change their colouration, physiologically (Hedges, Hass & Maugele, 1989). Typically they are paler when active (at night) and dark while inactive. Species distributions tend to be greatly restricted, with species endemic to single islands or island banks, and often to small areas on an island. However, species density can be high, and as many as six species are sympatric in some areas of Cuba.

Historically, the taxonomy of *Tropidophis* has been difficult to study because of small numbers of specimens and a paucity of diagnostic characters. For example, two of the earliest described species, *T. maculatus* and *T. pardalis*, have been confused repeatedly. Boulenger (1893) and Stull (1928) commented on the confusion of these species by Cope (1868), whereas Schwartz and Marsh (1960) later commented on their confusion by Stull! Most of these early problems in *Tropidophis* taxonomy stemmed from the use of characters later found to be unreliable, such as the keeling of scales or hemipene morphology. It was not until Schwartz and Marsh (1960) assembled a large number of specimens and collected extensive data on proportions, scalation and pattern that the systematics of this genus became reasonably well known. Although it was a large study, it was not comprehensive because it omitted species related to

*T. melanurus* and those placed by Schwartz (1957) in the *semicinctus* group. However, their success was in recognizing the utility of colouration and pattern characters, and that species diagnosis in this genus often requires consideration of multiple characters, some of which may not be individually diagnostic.

This is not a comprehensive revision of the genus but rather a taxonomic update, motivated by the many changes that have occurred since that last major review (Schwartz & Marsh, 1960) and the need to summarize what is known of morphological variation in the genus. Another motivation is to address a recurring problem in the systematics of this group: determining the species status of allopatric populations and taxa. In the process, taxa previously considered as subspecies are here elevated to species status, some are assigned to different species, and others are left unchanged.

## MATERIALS AND METHODS

The data presented herein are almost entirely from the literature, or were used in published studies (but not necessarily published in the form here). Most derive from the raw data sheets of the late Albert Schwartz, used primarily in several publications (Schwartz, 1975; Schwartz & Garrido, 1975; Schwartz & Henderson, 1991; Schwartz & Marsh, 1960; Schwartz & Thomas, 1960; Thomas, 1963). Schwartz's Cuban specimens are in the American Museum of Natural History and his other material is almost entirely in the collection of the Museum of Natural History, University of Kansas. In addition to those data, I have included data from specimens I and colleagues have collected during the last two decades of field work, and which, for the most part, formed the basis of several published studies: (Hedges, Estrada & Diaz, 1999; Hedges & Garrido, 1992; Hedges & Garrido, 1999; Hedges & Garrido, 2002; Hedges, Garrido & Diaz, 2001). This material is in the National Museum of Natural History (Smithsonian) and in Cuban collections (National Museum of Natural History, Havana; Institute of Ecology and Systematics,

**Table 1** Species, species groups, and distributions of snakes of the genus *Tropidophis*.

Species	Species Group	Distribution
<i>T. battersbyi</i> Laurent	taczanowskyi	South America
<i>T. bucculentus</i> Cope	melanurus	Navassa Island
<i>T. canus</i> Cope	melanurus	Bahamas
<i>T. caymanensis</i> Battersby	melanurus	Grand Cayman
<i>T. celiae</i> Hedges, Estrada, and Díaz	melanurus	Cuba
<i>T. curtus</i> Garman	melanurus	Bahamas
<i>T. feicki</i> Schwartz	maculatus	Cuba
<i>T. fuscus</i> Hedges and Garrido	pardalis	Cuba
<i>T. galacelidus</i> Schwartz and Garrido	pardalis	Cuba
<i>T. greenwayi</i> Barbour and Shreve	haetianus	Turks and Caicos
<i>T. haetianus</i> Cope	haetianus	Hispaniola
<i>T. hardyi</i> Schwartz and Garrido	pardalis	Cuba
<i>T. hendersoni</i> Hedges and Garrido	pardalis	Cuba
<i>T. jamaicensis</i> Stull	jamaicensis	Jamaica
<i>T. maculatus</i> Bibron	maculatus	Cuba
<i>T. melanurus</i> Schlegel	melanurus	Cuba
<i>T. morenoi</i> Hedges, Garrido, and Díaz	maculatus	Cuba
<i>T. nigriventris</i> Bailey	pardalis	Cuba
<i>T. pardalis</i> Gundlach	pardalis	Cuba
<i>T. parkeri</i> Grant	melanurus	Little Cayman
<i>T. paucisquamis</i> Müller	taczanowskyi	South America
<i>T. pilsbryi</i> Bailey	pardalis	Cuba
<i>T. schwartzi</i> Thomas	melanurus	Cayman Brac
<i>T. semicinctus</i> Gundlach and Peters	maculatus	Cuba
<i>T. spiritus</i> Hedges and Garrido	pardalis	Cuba
<i>T. stejnegeri</i> Grant	jamaicensis	Jamaica
<i>T. stullae</i> Grant	jamaicensis	Jamaica
<i>T. taczanowskyi</i> Steindachner	taczanowskyi	South America
<i>T. wrighti</i> Stull	pardalis	Cuba

Havana). In nearly all cases, museum numbers and localities of those specimens are listed in the publications and therefore are not repeated here.

In some cases, summary data presented in the tables of Schwartz and Marsh (1960) do not agree with those in the raw data sheets or with data mentioned in the text of Schwartz and Marsh, presumably because of typographical errors in their tables. Some of the data presented later in Schwartz and Henderson (1991), such as the ventral range of *T. canus* and caudal range of *T. maculatus*, appear to be derived from those typographical errors. Although these errors are minor, the summary data presented in this paper were taken directly from Schwartz's raw data sheets, to avoid any confusion, and supplemented with additional data. Also, some characters were not scored by Schwartz in some species (e.g., parietal contact in *T. feicki*, *T. melanurus*, *T. semicinctus*, etc) or at all (e.g., ratios of eye length to head width and head width to neck width, and aspects of colour pattern). In those cases, specimens at hand were examined to fill in the gaps. I have examined preserved material of most taxa, and have observed and collected 12 of the species: *T. canus*, *T. feicki*, *T. fuscus*, *T. greenwayi*, *T. haetianus*, *T. maculatus*, *T. melanurus*, *T. pardalis*, *T. pilsbryi*, *T. stejnegeri*, *T. stullae*, and *T. wrighti*.

Because this is not a comprehensive revision, there was no attempt to survey all collections for holdings of *Tropidophis* or to examine all available material. It is anticipated that such an undertaking will be attempted in the future.

## RESULTS AND DISCUSSION

The conclusion of this taxonomic update is the recognition of 29 species of *Tropidophis* (Table 1). This is an increase of about six species over the number recognised earlier this year (Hedges &

Garrido, 2002). The difference involves the elevation of some taxa previously considered as subspecies. Below, I discuss the utility of different characters used, my reasoning in determining species boundaries, and the taxonomic issues involved in each geographic area. The phylogeny and biogeography of species in this genus, using DNA sequence data, is discussed elsewhere (S. B. Hedges, S. C. Duncan, A. K. Pepperney, in preparation). The species group status (Table 1) is based on that work, but otherwise the focus of this current assessment is the definition of species boundaries, not phylogenetic relationships.

## Characters

Variation in 20 characters among the 29 species of *Tropidophis* is shown in Tables 2–4. They are grouped into those involving proportions (Table 2), scalation (Table 3), and pattern and coloration (Table 4). In general, sexual dimorphism in *Tropidophis* is not pronounced and therefore data from both sexes can be combined, with the exception of body size, which shows slight differences. Characters that I have found to be of limited value have been eliminated. These include four that are commonly scored in snake systematics: upper and lower labials and the pre- and postoculars. All four are variable within species and in almost all cases, not diagnostic. Upper labials are usually 9–10 and lower labials usually 9–12 in all species. In *T. melanurus* and some related species, labial counts tend to be higher, although even in those cases there is often overlap. There is usually one preocular and 2–3 postoculars in *Tropidophis*, although some species occasionally have two preoculars and as many as 4 postoculars; however, variation in ocular scales does not appear to be of taxonomic utility. Examples of exceptions, as noted by Schwartz and Marsh (1960), are *T. pardalis* (usually 2 postoculars) and *T. maculatus* (usually 3 postoculars), although such differences are rarely diagnostic. Stull (1928) considered the forking of the hemipenis (bifurcate versus quadrifurcate) to be a diagnostic character but Schwartz and Marsh (1960) could not identify any species or specimens with a quadrifurcate condition. Also, such a character would not be very useful in this group because of limited material and scarcity of specimens with properly everted hemipenes.

Schwartz scored several other characters in *Tropidophis*, but I have also found them to be of limited value in diagnosing taxa. In the case of relative tail length (Schwartz & Marsh, 1960), it is useful in distinguishing *T. canus* from *T. curtus* (see below) but otherwise is difficult to score because of tail damage in some specimens, and overlapping of ratios. The colour of the tail tip (pale versus dark) was useful in distinguishing Cayman Islands *Tropidophis* from *T. melanurus* (Thomas, 1963), and other trends are noticeable, but differences between juveniles and adults, and intraspecific variability, make it a less useful character.

Now considering the 20 tabulated characters, maximum snout-vent length (SVL) is useful because some species differ greatly in body size, and most individuals encountered are adults. Two ratios (Table 2) that I have found to be of utility are eye length/head width (i.e., relative size of the eye) and head width/neck width (i.e., distinctiveness of the head). Both ratios are larger in the arboreal species *T. feicki*, *T. semicinctus*, and *T. wrighti*, and in another gracile Cuban species (*T. fuscus*) that is possibly arboreal (Hedges & Garrido, 1992). Unfortunately, both show variation within species and sample sizes still are small.

Despite the intraspecific variability in the scale characters (Table 3), some are useful when considered simultaneously with other characters. Ventral and midbody scale row counts are perhaps the most useful whereas caudal counts and posterior scale row counts are the least useful. Contact of the two parietal scales can be

**Table 2** Variation in proportions of snakes of the genus *Tropidophis*.

Species	Max. SVL (mm)		Eye diameter/ head width	Head width/ neck width	Sample size <sup>1</sup>	References <sup>2</sup>
	males	females				
<i>T. battersbyi</i>	na <sup>3</sup>	na	na	na	1	1
<i>T. bucculentus</i>	360	596	0.19–0.24 (2)	1.50–1.55 (2)	4	2–5
<i>T. canus</i>	363	338	na	na	20	2, 6
<i>T. caymanensis</i>	470	438	0.26 (1)	1.59 (1)	13	2–3, 7
<i>T. celiæ</i>	na	344	0.28 (1)	1.31 (1)	1	8
<i>T. curtus</i>	357	354	0.25 (1)	1.35 (1)	93	2–3, 6
<i>T. feicki</i>	411	448	0.28–0.32 (4)	1.76–2.24 (4)	29	2–3, 9
<i>T. fuscus</i>	287	304	.30–.33 (2)	1.83–1.99 (2)	8	10–11
<i>T. galacelidus</i>	187	405	0.28 (1)	1.45 (1)	6	2–3, 6, 12
<i>T. greenwayi</i>	313	301	0.23 (1)	1.35 (1)	16	2–3, 6
<i>T. haetianus</i>	534	552	0.22–0.25 (8)	1.28–1.52 (8)	158	2–3, 6, 13
<i>T. hardyi</i>	303	334	0.26–0.31 (2)	1.30–1.49 (2)	8	2–3, 6, 12
<i>T. hendersoni</i>	302	315	0.28 (1)	1.45 (1)	1	14
<i>T. jamaicensis</i>	338	306	0.20–0.21 (3)	1.47–1.54 (3)	23	2–3, 6
<i>T. maculatus</i>	327	347	0.23–0.32 (5)	1.30–1.92 (5)	25	2–3, 6
<i>T. melanurus</i>	770	957	0.21–0.26 (8)	1.28–1.77 (8)	100	2–3, 15
<i>T. morenoi</i>	na	295	0.24–0.27 (2)	1.39–1.52 (2)	2	16
<i>T. nigriventris</i>	184	227	na	na	4	2, 6, 12
<i>T. pardalis</i>	264	287	0.24–0.27 (4)	1.26–1.63 (4)	161	2–3, 6
<i>T. parkeri</i>	422	512	0.24 (1)	1.95 (1)	21	2–3, 7
<i>T. paucisquamis</i>	101	283	0.24–0.28 (3)	1.53–1.71 (3)	3	2–3
<i>T. pilsbryi</i>	295	260	.24–.25 (2)	1.59–1.62 (2)	8	2–3, 6, 10
<i>T. schwartzi</i>	385	321	na	na	17	2–3, 7
<i>T. semicinctus</i>	383	408	0.30–0.34 (2)	1.70–1.88 (2)	26	2–3, 9
<i>T. spiritus</i>	320	372	0.24–0.37 (4)	1.35 (1)	4	17
<i>T. stejnegeri</i>	395	529	0.22–0.28 (3)	1.39–1.48 (3)	23	2–3, 6
<i>T. stullæ</i>	260	248	0.23–0.25 (3)	1.78–1.86 (3)	4	2–3, 6
<i>T. taczanowskyi</i>	305 <sup>4</sup>	243	0.27–0.30 (2)	1.46–1.51 (2)	3	3, 10, 18
<i>T. wrighti</i>	330	323	0.32–0.34 (7)	1.77–2.24 (7)	17	2–3, 9

<sup>1</sup>number of specimens used for most measurements and counts, unless otherwise indicated in parentheses.

<sup>2</sup>primary sources of the data reported in this and other tables: 1 (Laurent, 1949), 2 (Albert Schwartz, unpublished data), 3 (S. B. Hedges, unpublished data), 4 (Thomas, 1966), 5 (Bailey, 1937), 6 (Schwartz & Marsh, 1960), 7 (Thomas, 1963), 8 (Hedges *et al.*, 1999), 9 (Schwartz, 1957), 10 (Hedges & Garrido, 1992), 11 (Ansel Fong, unpublished data), 12 (Schwartz & Garrido, 1975), 13 (Schwartz, 1975), 14 (Hedges & Garrido, 2002), 15 (Schwartz & Thomas, 1960), 16 (Hedges *et al.*, 2001), 17 (Hedges & Garrido, 1999), 18 (Stull, 1928).

<sup>3</sup>data not available

<sup>4</sup>sex not determined

diagnostic in some comparisons (Hedges & Garrido, 2002), but problems arise in how different people score the character (e.g., when an interparietal is present and scales barely touch). As already noted, the keeling of the dorsal scales is often variable within species. Many species have weakly keeled scales that are noticeable only above the vent region and are difficult to score consistently, and depend sometimes on condition of preservation. However, some species consistently have smooth scales and others (e.g., *T. melanurus*) have distinctly keeled scales.

Colour and pattern variation (Table 4) has been important in *Tropidophis* taxonomy, in part because the snakes are frequently spotted and this provides yet additional characters to count. In fact, Schwartz and Marsh (1960) considered coloration and pattern to be the most reliable characters, in combination with scalation, for 'separating and combining' taxa. Except for *T. feicki*, which has crossbands, most species have 2–12 rows of body spots. I have used the Schwartz and Marsh (1960) methods of scoring body spots and spot rows. Spot rows include those on the dorsum and venter, all around the body (both sides) whereas body spots are counted along one row of spots (usually just to one side of middorsal region) from behind the head to just above the vent. Typically, the largest and most distinctive spots are those near the middorsal region. This reaches an extreme in species of the *melanurus* group where some individuals have only those two spot rows present, resulting in widely varying row counts (e.g., 2–10). Occipital spots sometimes fused to form a white neckband, are diagnostic of several species (e.g., *T. celiæ*, *T. galacelidus*, *T. pilsbryi*, *T. stejnegeri*) and are

common in others (e.g., *T. pardalis*).

The dorsal ground colour of most species is a shade of brown or grey, and often variable within species. I once collected two specimens of *T. pilsbryi* in the same rock pile in Cuba, and was initially misled into thinking they were different species because one was brown and the other grey. On the other hand, *T. stullæ* is consistently pale tan and differs from the other two Jamaican species, which are darker. Also, two boldly spotted species that occur sympatrically in western Cuba can be distinguished by, among other things, their dorsal ground colour: greyish pink in *T. feicki* and yellow to orange in *T. semicinctus*. Although most species are spotted, those in the *melanurus* group often have narrow lateral stripes as well as a middorsal stripe. The absence of middorsal spot contact occurs in two related species, *T. maculatus* and *T. semicinctus*, and the two Bahaman species *T. canus* and *T. curtus* are united by the presence of an anteriolateral (face and neck) stripe. Ventral pattern is diagnostic for *T. nigriventris* (almost completely dark) and in several species that lack a ventral pattern, but otherwise most have different degrees of spotting and flecking.

## Species boundaries

Most taxonomists discern the presence of sympatric species by covariation of multiple characters from individuals of a single locality, indicating lack of gene flow between the species. For example, in a series of dark and pale snakes found together, two species would be indicated if all of the dark snakes also had small

**Table 3** Variation in scalation of snakes of the genus *Tropidophis*. (Numbers and character states in brackets represent rare or infrequent occurrences; Y = yes, N = no; other notation as in Table 2.

Species	Ventrals	Caudals	Dorsal scale rows			Parietal contact	Keel-dorsals
			Anterior	Midbody	Posterior		
<i>T. battersbyi</i>	200	41	21	23	17	N	N
<i>T. bucculentus</i>	183–186	28–32	24–25	25–27	17–19	N	Y
<i>T. canus</i>	170–183	29–35	21[20,22,23]	23[22]	16–21	N/Y	Y[N]
<i>T. caymanensis</i>	183–200	33–38	23–27	23[25]	17[19]	N	N/Y
<i>T. celiae</i>	203	30	25	27	19	Y	N
<i>T. curtus</i>	146–173	22–37	19–27	23–25	17–22	N[Y]	Y[N]
<i>T. feicki</i>	217–235	34–41	23–25[19,21]	23–25	17–19	N/Y	N
<i>T. fuscus</i>	160–185	30–36	21–24	23	15–19	N	Y
<i>T. galacelidus</i>	177–186	29–35	25–27	25–27	19–20	N	Y
<i>T. greenwayi</i>	155–165	26–30	23–25	25–27	17–19	Y	N
<i>T. haetianus</i>	170–194	27–39	23–27	25–27[23,29]	17–19[21]	Y[N]	N
<i>T. hardyi</i>	153–172	31–48	20–24	23–25	18–20	N/Y	N/Y
<i>T. hendersoni</i>	190	33	23	25	19	N	Y
<i>T. jamaicensis</i>	167–181	28–36	23–27	25–29	15–23	N/Y	N
<i>T. maculatus</i>	189–208	28–40	22–25	25[23]	17–21	N/Y	N/Y
<i>T. melanurus</i>	188–217	31–44	24–27[19]	27–29	17–21	N	Y
				[24,25,26,30]	[16,22,23,24]		
<i>T. morenoi</i>	198–199	42–44	23	23	17	N	N
<i>T. nigri-ventris</i>	144–150	25–26	23–25	23–25	18–22	N	N
<i>T. pardalis</i>	140–157	23–34	21,23	23,25	17–21[16]	N/Y	N[Y]
			[19,22,24,25]	[21,22,24]			
<i>T. parkeri</i>	199–212	33–41	25[23,24]	27[25,26]	17[18,19]	N	Y
<i>T. paucisquamis</i>	170–178	37–40	21	21	17	Y	N
<i>T. pilsbryi</i>	160–169	26–31	22–25	23–25	17–21	N	N/Y
<i>T. schwartzi</i>	191–205	31–39	25	25[26]	17[15]	N	Y
<i>T. semicinctus</i>	201–223	33–41	21,23[22,24,25]	25[21–24]	17–20	N/Y	N
<i>T. spiritus</i>	183–200	35–39	21–23	23	17	N	N
<i>T. stejnegeri</i>	181–190	30–38	25–27[23]	25,27[26]	17–19	N/Y	Y
<i>T. stullae</i>	166–170	31–34	25	25	16–19	N	N
<i>T. taczanowskyi</i>	149–160	25–27	23–25	23	19–21	Y	Y
<i>T. wrighti</i>	192–215	36–45	21–23	21–23	17[16,18,19]	N	N

heads and fewer spots than the pale snakes (thus, body colour would be covarying with head size and spot number). In the case of allopatric populations, it is typically assumed that character differences similar to or greater than observed between sympatric species indicate that the two forms are different species. Thus, the 'yardstick' used for assessing allopatric populations is character divergence between closely related, sympatric species. This is the principle that I use here in assessing species status within *Tropidophis*. It is a practical species concept but is based on the observation that species are reproductively isolated from each other, as noted by Darwin (1859) and later articulated by Mayr (1942) as the *biological species concept*.

The reason that a particular degree of differentiation is necessary, rather than a minimal diagnostic difference, concerns the 'reality' of species in evolution. Almost all species are fragmented (structured) to some degree, and many populations can be diagnosed by one or a few nucleotide differences or minor morphological differences. However, through time, such populations frequently combine and separate again as part of the reticulate nature of gene flow and evolution within species. It is only those populations that have differentiated sufficiently, genetically and/or morphologically, and presumably reflecting a length of time, that evolve reproductive isolation from other populations. Thus, to assign species status to diagnosable, but ephemeral, populations during one slice of time is arbitrary from an evolutionary standpoint. Although Frost and Hillis (1990) recommended abandoning the use of quantitative criteria (molecular and morphological) for discerning species status of allopatric populations, they did not propose anything to replace that procedure and thus few have heeded their recommendation.

Sympatric species of *Tropidophis* occur only in Cuba. In western Cuba, the following six species have been found in the general region of Canasí, Habana Province: *T. celiae*, *T. feicki*, *T. maculatus*, *T. melanurus*, *T. pardalis*, and *T. semicinctus*. In central Cuba, the following six species have been found in the vicinity of the Trinidad mountains: *T. galacelidus*, *T. hardyi*, *T. melanurus*, *T. pardalis*, *T. semicinctus*, and *T. spiritus*. In eastern Cuba, the following four species are known from the region of Baracoa, Guantánamo Province: *T. fuscus*, *T. melanurus*, *T. pilsbryi*, and *T. wrighti*. To identify the level of character divergence associated with species differentiation in *Tropidophis*, I now focus on four clusters of sympatric species, each of which are members of the same species group: (1) *feicki/maculatus/semicinctus*, (2) *celiae/melanurus*, (3) *pardalis/galacelidus/hardyi*, and (4) *fuscus/wrighti/pilsbryi*.

In cluster (1), *T. maculatus* and *T. semicinctus* are closest relatives according to DNA sequence evidence (S. B. Hedges, S. C. Duncan, A. K. Pepperney, in preparation) and are distinguished primarily by colour pattern: the number of body spots (no overlap) and number of spot rows (no overlap). All scale counts in those two species overlap, although *T. semicinctus* tends to have a higher number of ventrals. In the case of *T. feicki* and *T. maculatus*, there are non-overlapping differences in ventral counts, body spots, and spot rows. Considering *T. feicki* and *T. semicinctus*, the ground colour and spot rows are non-overlapping, and the ventral counts are different but overlap slightly.

In cluster (2), *T. celiae* and *T. melanurus*, which are close relatives according to DNA sequence evidence, completely overlap in all scale counts, although parietal contact might be considered diagnostic if there were more than one specimen of *T. celiae*. Otherwise,



**Table 4** Variation in pattern and colouration of snakes of the genus *Tropidophis*. (Numbers and character states in brackets represent rare or infrequent occurrences; Y = yes, N = no; other notation as in Table 2.

Species	Body spots	Tail spots	Spot rows	Occipital spots	Dorsal ground colour	Dorsal pattern	Anterio-lateral	Stripe	Mid-dorsal spot contact	Ventral pattern
<i>T. battersbyi</i>	na	na	6	na	Pale brown	spots	N	na	na	spotted
<i>T. bucculentus</i>	48-54	5-7	6	N	pale ashy brown	spots and stripes	N	N	Y	spotted or not
<i>T. canus</i>	43-59	3-7	6,8[7,9]	N	pale greyish yellow	spots and stripes	Y	N	Y	speckled
<i>T. cymmanensis</i>	48-61	5-9	2-10	N	pale grey and cream	spots and stripes	N	Y	Y	speckled
<i>T. celiae</i>	60	12	6	Y	pale tan	spots	N	Y	Y	none
<i>T. curtus</i>	38-90	2-13	10[8,9,11,12]	N	greyish brown	spots and stripes	Y	N/Y	Y	spotted or not
<i>T. feicki</i>	17-26	2-6	1	N	grey or pink	saddles	N	N	Y	none
<i>T. fuscus</i>	43-52	na	6-8	N/Y	dark brown	spots	N	N	Y	spots
<i>T. galacelidus</i>	44-50	4-9	10	Y	grey	spots	N	N/Y	Y	spots
<i>T. greenwayi</i>	27-49	3-6	10[8]	N	dark brown	spots and broken lines	N	N	Y	spots
<i>T. haetianus</i>	36-61	0-13	8-10[6]	N	brown or tan	spots	N	N	Y	none or stippled
<i>T. hardyi</i>	32-44	4-6	6-8	N	medium brown	spots	N	N	Y	spotted
<i>T. hendersoni</i>	48-52	7-8	10	Y	tan	spots	N	N	Y	unpatterned
<i>T. jamaicensis</i>	38-54	4-10	6-10	N	chocolate brown	spots	N	N	Y	spots
<i>T. maculatus</i>	35-55	4-11	8-10	N	red or reddish tan	spots	N	N	N	spots
<i>T. melanurus</i>	47-54 (20)	5-7 (3)	2-10	N	tan or brown	spots and stripes	N	Y	Y	stippling
<i>T. morenoi</i>	38-39	4-8	6	N	whitish beige	narrow bands	N	N	Y	spots
<i>T. nigriventris</i>	37-46	4-5	8	N	Brown	spots	N	N	Y	dark brown
<i>T. pardalis</i>	25-42	3-7	6[8]	N/Y	tan to brown	spots	N	N	Y	spots
<i>T. parkeri</i>	40-62	4-6[8]	2-10	N	pale grey and tan	spots and stripes	N	Y	Y	speckled
<i>T. paucisquamis</i>	25-26	0	6-8	na	Brown	spots	N	N	na	spots and bands
<i>T. pilsbryi</i>	36-48	4-8	8-10	Y	grey or brown	spots	N	N	Y	spots
<i>T. schwartzi</i>	49-64	5-9	2-10	N	pale grey and cream	spots and stripes	N	Y	Y	speckled
<i>T. semicinctus</i>	18-29	3-9	2	N	yellow to orange	spots	N	Y	N	none
<i>T. spiritus</i>	36-42	3-6	6	N	greyish tan	spots	N	N	Y	spots
<i>T. stepnegeri</i>	36-57	4-11	8-10	Y	Yellowish grey	spots	N	Y	Y	spots
<i>T. stullae</i>	43-54	5-8	10[4]	N	pale tan	spots	N	Y	Y	spots
<i>T. taczanowskyi</i>	na	0	8	N	brownish violet	spots and stripes	N	N	na	spots and bands
<i>T. wrighti</i>	21-37	3-6	4	N	white or tan	spots	N	N	Y	spots

about the only characters that distinguish these two species are body size and aspects of coloration (e.g., neckband in *T. celiae* and higher number of body spots). In case the reader is wondering, the presence of enlarged ova in the small holotype of *T. celiae*, and details of the pattern, indicate it is not a juvenile *T. melanurus* (Hedges *et al.*, 1999).

In cluster (3), there are no molecular data available for *T. galacelidus* and *T. hardyi* to confirm their species group association with *T. pardalis*. However the association is supported by the fact that there are no diagnostic (non-overlapping) scale or pattern characters that distinguish *T. hardyi* and *T. pardalis*. This problem was noted in the original description (Schwartz & Garrido, 1975). However, *T. hardyi* has a higher number of ventrals, even though overlapping with *T. pardalis*, and it is a larger species with a distinctly smaller head. The latter character caused Schwartz and Garrido to associate (as a subspecies) *T. hardyi* with the small-headed *T. nigriventris*. The third sympatric species of this trio, *T. galacelidus*, can be distinguished from the other two species by its higher number of ventrals, dorsal spots, and spot rows (all non-overlapping).

In the case of cluster (4), DNA sequence evidence place all three together as close relatives. *Tropidophis fuscus* and *T. pilsbryi* have no completely diagnostic scale differences, although the combination of ventral scale counts and midbody scale rows will distinguish the species. Also, *T. fuscus* has a more gracile body shape. The third species, *T. wrighti*, is diagnosed from the other species by its higher ventral counts, and fewer dorsal spots and spot rows (all non-overlapping).

To summarize, of the ten combinations of closely related, sympatric species, nearly all were distinguished by at least two non-overlapping differences in colour pattern, or (less frequently) body proportions. In addition, there was usually one other difference (either non-overlapping or overlapping) in scalation. More distantly related species of *Tropidophis* often have two (or more) non-overlapping differences in scalation, in addition to any other differences. This suggests a temporal sequence in character differentiation, with colour pattern and body proportion differences accruing first, followed by scalation differences. Ideally, one would like to use molecular data as well for assessing differentiation, although tissue samples still are not yet available for many taxa. Using this morphological criterion for assessing species status in *Tropidophis*, I will now review the current status of the taxa in this genus.

## Hispaniola

Only one species (*T. haetianus*), with three subspecies, occurs on Hispaniola: *T. h. haetianus* (most of island), *T. h. hemerus* (distal portion of the Tiburon Peninsula in Haiti) and *T. h. tiburonensis* (extreme eastern portion of the Dominican Republic). Although Schwartz and Marsh (1960) and Schwartz (1975) have considered the Jamaican taxa to be subspecies of *T. haetianus*, genetic evidence has shown that they are more closely related to the Cuban species (Hass, Maxson & Hedges, 2001) and thus are removed from *T. haetianus* (see below). Also, the Cuban specimens of *T. haetianus* discussed by Schwartz and Marsh (1975) and Schwartz and Garrido (1975) have been removed from that species and assigned to a new species, *T. hendersoni* (Hedges & Garrido, 2002). Because the subspecies of Hispaniolan *T. haetianus* are parapatric and apparently intergrade (Schwartz, 1975), and because their character differentiation is less than that of sympatric species, I suggest retaining their current taxonomic status as subspecies. It is possible that genetic studies in the future may further clarify their status. Thus, *T. haetianus* is confined to Hispaniola and contains three subspecies.

## Navassa Island

Four specimens of *T. bucculentus* are known from this small island between Hispaniola and Jamaica, but apparently no snakes have been seen in over 100 years and thus the species is considered extinct (Powell, 1999). Since it was described by Cope (1868), there has been considerable confusion as to its species status and relationship with other species. Most who have examined the type series, including me, have noted a resemblance to *T. melanurus* (Thomas, 1966), although Stull (1928) instead considered it a subspecies of *T. pardalis*. There is no overlap in ventral counts between *T. bucculentus* and *T. melanurus*, and almost no overlap in caudal counts. Although there appear to be pattern differences between the two species, the single specimen in the Academy of Natural Sciences (Philadelphia) differs from the other three specimens (National Museum of Natural History, Smithsonian) in terms of ventral pigmentation (Bailey, 1937). Based on the diagnostic scalation differences alone, I would consider *T. bucculentus* as a valid species. The unusual geographic location of a species with apparent Cuban affinities, on Navassa Island, is remarkable. With the exception of the anole (*Anolis longiceps*), other species on Navassa have affinities with nearby Hispaniola (Powell, 1999; Thomas, 1966), which is logical based on the westerly direction of ocean currents. However, the eastern tip of Cuba is further east than Navassa, and ocean currents flow southerly through the Windward Passage separating Cuba and Haiti. Dispersal on those currents is thus possible and is the most likely explanation for the origin of *T. bucculentus* (and *A. longiceps*) on Navassa and possibly the gecko *Sphaerodactylus notatus* on the Morant Cays southeast of Jamaica. The locally changing direction of water currents during a hurricane may also have aided in the dispersal of these taxa.

## Cuba

With 15 described species, Cuba is the hot spot of species diversity in the genus. Recently, two subspecies described by Schwartz and Garrido (1975) were elevated to species status and a new species was described from eastern Cuba (Hedges & Garrido, 2002). Character differences among many of the Cuban species have been discussed above (see 'Species Boundaries'), and I consider all 15 species to be valid. Also, I am aware of material that likely represents additional, undescribed species. Undoubtedly, more species will be discovered.

Two remaining taxa are considered subspecies of *T. melanurus*: *T. m. dysodes* and *T. m. eriksoni* (Schwartz & Thomas, 1960). The former is known from three female specimens from near La Coloma, Pinar del Rio Province, and the latter is restricted to Isla de Juventud. These taxa differ from *T. m. melanurus* primarily in size of the dorsal spots and in having bolder, darker colouration, with *T. m. dysodes* having the darkest pigmentation of the three subspecies. The ventral counts of *T. m. eriksoni* are low for the species, but there is considerable overlap with the other two taxa. Considering that there are no diagnostic differences in body proportion or scalation, and the colouration differences, although real, are not as trenchant as those distinguishing sympatric, closely related species (e.g., *T. maculatus* and *T. semicinctis*), I am inclined to leave their status as subspecies unchanged until additional data warrant a reconsideration.

## Jamaica

The three Jamaican taxa, originally described as full species, are closer to Cuban taxa than to *T. haetianus* based on immunological data (Hass *et al.*, 2001) and DNA sequence data (S. B. Hedges, S. C. Duncan, A. K. Pepperney, in preparation). However, they form a

single genetic and morphological group (*jamaicensis* group), and are distinguished morphologically from the Cuban species at the species level, although they are closest to species of the *pardalis* group. The question then remains as to whether they should be treated as a single species (*T. jamaicensis*) or three separate species: *T. jamaicensis*, *T. stejnegeri*, and *T. stullae*. However, using the morphological criterion for species status, I recommend the latter. Each of these three taxa can be diagnosed based on scalation, body proportions, and colour pattern, and they are as different from each other as sympatric species in Cuba. In body size, *T. stejnegeri* (529 mm SVL) is considerably larger than *T. stullae* (260 mm SVL), with *T. jamaicensis* (338 mm SVL) being intermediate in size. Ventral counts of *T. stejnegeri* do not overlap with those of *T. stullae*, and counts of *T. jamaicensis* are nearly completely non-overlapping with the other two taxa. *Tropidophis stejnegeri* has keeled scales and occipital spots whereas the other two taxa are smooth scaled and lack occipital spots. Additionally, dorsal ground colours differ, being yellowish-grey (*T. stejnegeri*), chocolate brown (*T. jamaicensis*) and pale tan (*T. stullae*). A middorsal stripe is present in *T. stejnegeri* and *T. stullae* but absent in *T. jamaicensis*. The head of *T. stejnegeri* is pointed but that of *T. stullae* is distinctly squared-shaped.

### The Bahamas Bank

Six taxa are currently recognized from the Bahamas Bank: *Tropidophis canus androsi* Stull (Andros Island), *T. c. barbouri* Bailey (central Bahamas, from Eleuthera to Ragged Island), *T. c. canus* Cope (Great Inagua), *T. c. curtus* Garman (New Providence, Bimini Islands, and Cay Sal Bank), *T. g. greenwayi* Barbour and Shreve (Ambergris Cay), and *T. g. lanthanus* Schwartz (Caicos Islands). Schwartz and Marsh (1960) considered all except the last two to be subspecies of a single species (*T. canus*) and that arrangement has since been followed. However, it is worth reviewing morphological variation in *T. canus* in the context of our current understanding of species definitions in the genus. Recent evidence from DNA sequences has shown that *T. greenwayi* is most closely related to *T. haetianus* (Hispaniola) and unrelated to the complex currently considered under *T. canus*.

Among the four subspecies of *T. canus*, *T. c. canus* stands out both morphologically and geographically. It is isolated in the south, being separated from the northern taxa by islands apparently lacking *Tropidophis*: Crooked, Acklins, Mayaguana, and Little Inagua. It has a higher number of ventrals (170–183). One specimen (1%) of the northern group has 173 ventrals; all others have fewer than 168 ventrals. Anterior and midbody scale rows in *T. c. canus* typically are 21–23 whereas they are typically 23–25 in the northern taxa, although there is some overlap. The tails of *T. c. canus* are distinctly shorter, averaging 11% (9.4–12.1), compared with 13% (11.0–15.2) in the northern taxa. Rows of body spots number 6–8 in *T. c. canus* whereas they are typically 10 or more in the northern taxa; overlap consists of nine specimens (10%) of northern taxa with eight rows and two (2%) with nine rows, and one (5%) *T. c. canus* with nine rows. This degree of difference is the same or greater than that seen between sympatric species of *Tropidophis* in Cuba, and therefore the northern taxa should be removed from *T. canus*.

The status of the three northern Bahaman taxa is problematic at this time. Clearly there is geographic variation among these forms. For example, *androsi* tends to have a higher number of ventral scales than the other two taxa, although there is considerable overlap with *barbouri* and some with *curtus*. Within one taxon (*curtus*), snakes from Bimini are distinctly larger than those from New Providence. Both Bailey (1937) and Schwartz and Marsh (1960) noted very little

difference, overall, between *barbouri* and *androsi*. When considering the ‘species boundary’ characters noted above, there is insufficient justification at present to recognize these taxa as distinct species. Additional specimens and genetic analyses will be necessary to better resolve geographic variation in northern Bahaman *Tropidophis*. Until then, I suggest here that *androsi* and *barbouri* be recognized as subspecies of *T. curtus*: *T. curtus androsi* (new combination) and *T. curtus barbouri* (new combination).

*Tropidophis greenwayi lanthanus* is a subspecies found in the Caicos Islands and is distinguished by coloration difference from the nominate subspecies on nearby Ambergris Cay (Schwartz, 1963). However, the difference concerns ‘interspace stippling’ and not actual numbers of spots or spot rows. There are no diagnostic scale count differences, and the presence of two postoculars in the two known specimens of *T. g. greenwayi* is not remarkable because half of the specimens of *T. g. lanthanus* also have two postoculars, at least on one side of the head. More material of *T. g. greenwayi* is needed, in addition to genetic analyses, before the species status of *T. g. lanthanus* can be accurately assessed. I suggest that the latter taxon continue to be recognized as a subspecies.

Thus, *Tropidophis* of the Bahamas Bank are placed here in three species: *T. greenwayi* (Turks and Caicos), *T. canus* (Great Inagua), and *T. curtus* (northern and central Bahamas). The question as to whether some Bahaman species also occur in Cuba has been raised in the past, primarily because of two old specimens (Schwartz & Marsh, 1960). The first is the type of *T. curtus*, purportedly from ‘Cuba’ (Garman, 1887). However, morphologically it agrees with snakes from New Providence, Bahamas, and the specimen number (MCZ 6114) is close to other numbers in that collection from New Providence. Also, the origin of the specimen was investigated and found to be ‘without definite history’ (Stull, 1928). Thus, I agree with Stull in considering this specimen to be from New Providence. The other specimen is AMNH 2946 from ‘Nuevitas, Cuba’ (no other information). As noted by Schwartz and Marsh (1960) it agrees in morphology with snakes here considered as *T. curtus*. Although they considered the provenance of the specimen to be correct, partly because of the confusion surrounding the holotype, I raise the question here that it also may be an error. The specimen number is close to several *T. curtus* from Andros Island (AMNH 2925–2927) apparently cataloged at about the same time and its scale counts fall within the range of counts of snakes from that island. Thus I consider the range of *T. curtus* to be restricted to the Bahamas.

### The Cayman Islands

Currently there are three subspecies of *T. caymanensis* recognized from the Cayman Islands (Thomas, 1963) and they differ in scale row counts, ventral counts, and colour pattern. Each is endemic to a single island, and there is no evidence of intergradation. At the time they were last reviewed (Thomas, 1963), a more conservative definition of species boundaries in the genus prevailed. Although no new material has been examined here, the level of differences seen among these taxa would suggest that they are distinct species. *Tropidophis caymanensis* (Grand Cayman) is distinguished from *T. parkeri* (Little Cayman) by its lower anterior and midbody scale rows (23–25 versus 25–27), lower number of ventrals (183–200 versus 199–212), and a larger, darker cephalic pattern. *Tropidophis caymanensis* is distinguished from *T. schwartzi* (Cayman Brac) by its larger body size (maximum SVL = 470 mm versus 385 mm), lower anterior scale rows (23 versus 25), lower, albeit overlapping, number of ventrals (183–200,  $\bar{x}$  = 192, versus 191–205,  $\bar{x}$  = 198), fewer tail spots (4–8, mode = 6 versus 5–9, mode = 8) and a larger, darker, cephalic pattern. *Tropidophis parkeri* is distinguished from

*T. schwartzi* by its higher midbody scale rows (27 versus 25), higher number of ventrals (199–212,  $\bar{x}$  = 203 versus 191–205,  $\bar{x}$  = 198), and a larger, darker cephalic spot (Thomas, 1963).

## South America

Although Stull (1928) and Schwartz and Marsh (1960) attempted to relate one or more of the South American taxa to West Indian species groups, I do not envision a close relationship. For example, the keeling of the dorsal scales in *T. taczanowskyi* is greater than I have seen in any West Indian taxon. In the case of *T. paucisquamus*, the low number (21) of midbody scale rows and a distinctive pattern of middorsal stripe and blotches is not like any West Indian species, as noted by Schwartz and Marsh (1960). The only known specimen of *T. battersbyi* has been described only as having six rows of spots, including two rows on the venter (Laurent, 1949; Pérez-Santos & Moreno, 1991). The fact that the venters of *T. paucisquamus* and *T. taczanowskyi* have both been described as consisting of black and yellow spots and bands (Stull, 1928) is noteworthy; such a pattern and colouration is not known in West Indian taxa. This might also suggest a relationship at least between these two species. Molecular phylogenetic evidence (S. B. Hedges, S. C. Duncan, A. K. Pepperney, in preparation) places *T. paucisquamus* outside of the West Indian clade, reinforcing the morphological distinction. Examination of additional specimens, and genetic data from *T. battersbyi* and *T. taczanowskyi*, are needed to clarify the relationships of these South American species. Until then, available evidence supports the placement of the South American species in a separate species group (*taczanowskyi* group).

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# *Atractaspis* (Serpentes, Atractaspididae) the burrowing asp; a multidisciplinary minireview

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**SYNOPSIS.** The family Atractaspididae is a highly modified derivative of a lineage that apparently arose early in the history of 'colubroid' snakes, and its taxonomy and relationship with other ophidian groups is still uncertain. Snakes of the genus *Atractaspis* have a characteristic venom apparatus, including the structure and function of the striking unit and of the venom glands. The composition of their venom is also unique in containing several low-molecular weight components, the sarafotoxins, which affect the cardiovascular system and are similar to the mammalian endothelins.

## Dedication

This paper is dedicated to Dr. Garth Underwood on the occasion of the 35<sup>th</sup> anniversary of his classic 'Contribution to the Classification of Snakes' (1967), about which one may say:

**This is a small book by a great man!**

And also – (ז, ה, ו, ט) **מכאן שהחזיק מועט את המרובה**

**A little that contains a lot** (Theodor & Albeck, 1996)

## HISTORY

There are not many snake species that posed problems from the very beginning of their discovery; one of the most prominent ones is certainly that which we now call the genus *Atractaspis* of the family Atractaspididae (Fig. 1).

The first two specimens of *Atractaspis* were described by Reinhardt in 1843 as *Elaps irregularis*, a species that he considered to be extremely abnormal because of the presence of only a few, very small teeth. On the basis of squamation, Underwood inferred that at least one of the specimens was *A. dahomeyensis*. The genus *Atractaspis* was established by Smith in 1848 for the South African species *bibroni* and since then it was variously considered as a separate family, as a subfamily of the family Viperidae, and finally as a genus within the Viperinae.

Already Haas (1931), on the basis of the pattern of the head musculature, was unhappy with the inclusion of *Atractaspis* in the Viperidae, but it was not until 1961 that Monique Bourgeois, studying at the Université Officielle du Congo à Lubumbashi, came out with a challenging question: *Atractaspis* – a misfit among the

Viperidae? This short note was followed by a detailed study suggesting the establishment of a separate subfamily for a group of opisthoglyphous colubrids together with *Atractaspis* (Bourgeois, 1968).

Underwood (1967) lists a long series of skeletal and other anatomical characters in which *Atractaspis* differs from the Viperidae and states: '*Atractaspis* differs so widely from the other vipers that I have no doubts about reviving a separate family group taxon to receive it' (p. 103). This he did after a detailed analysis that resulted in the resurrection of the subfamily Atractaspidinae (Gunther, 1858); and, finally, the establishment of a separate family, Atractaspididae, for the approximately 15 species of *Atractaspis* together with some African colubrid genera (Underwood & Kochva, 1993).

## TAXONOMY

Recently several suggestions concerning the taxonomy and relationship of the *Atractaspis* species have been raised, mainly dealing with the question of which additional genera should be included in the family Atractaspididae and with which, if any, larger clades they should be grouped (Gravlund, 2001). Underwood himself (personal communication) is now reconsidering the composition of the family Atractaspididae in order to decide which genera, in addition to *Atractaspis*, should be included in it. However, no one is now questioning the separate status of the genus *Atractaspis*, and its apparent distinction from the other venomous snake families is widely, though not unanimously, agreed upon. *Atractaspis* thus certainly deserves the rank of a family of its own; this may also include some rear-fanged snakes that are apparently harmless as far as humans are concerned.



**Fig. 1** *Atractaspis engaddensis* in a combined defensive/offensive position. Note the arched neck and the beginning of the coiled body with exposed tip of the tail.

## DISTRIBUTION

The distribution of the *Atractaspis* species is unique (Fig. 2), starting from the Cape of South Africa, through the entire breadth of central Africa and along the Rift Valley to Arabia, Sinai, Jordan and Israel, reaching its northernmost border at Mount Gilboa (Al-Oran & Amr, 1995; Kochva, 1998).

It is in Israel that the last species of *Atractaspis* was found and described. It was first recorded by Aharoni in 1945 as *Atractaspis aterrima* and later described as a new species, *Atractaspis engaddensis*, by Haas in 1950. *A. engaddensis* is very similar to the Arabian *A. microlepidota andersoni* (Gasperetti, 1988), but a decision on the exact status of the two will have to await further information on the distribution of *Atractaspis* forms in the Arabian Peninsula as well as on the toxicity and composition of their venoms (see also Al-Sadoon *et al.*, 1991; Al-Sadoon & Abdo, 1991; Schätti & Gasperetti, 1994).

## BEHAVIOUR

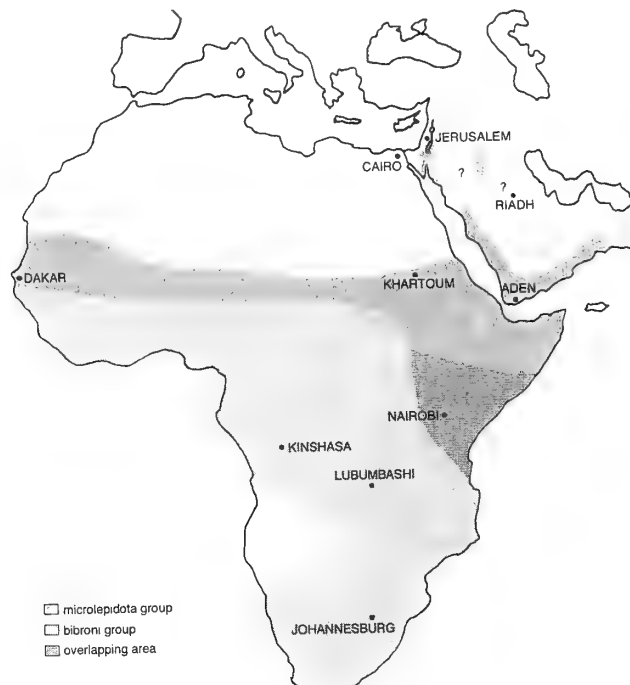
Species of the genus *Atractaspis* are desert-dwelling, fossorial snakes, whose behaviour and natural history are not well known. The Israeli species, *A. engaddensis*, is mostly found in the Negev desert and Dead Sea area, but it also extends to the Judean desert and along the Jordan Valley up to Mount Gilboa (Fig. 2).

*A. engaddensis* feeds mainly on skinks, but also on lizards and geckoes that are caught at night above or below ground, beneath stones or other objects. In captivity, it also accepts baby mice and rats. *A. microlepidota* feeds on other snakes such *Typhlops* and *Leptotyphlops*, amphibians and small mammals, mostly rodents (Scortecci, 1939; Greene, 1997). In a four-year field study carried out by Akani *et al.* (2001) in south-eastern Nigeria, it was found that *A. irregularis* fed mainly on rodents, while *A. aterrima* and *A. corpulenta* ate lizards, skinks and snakes.

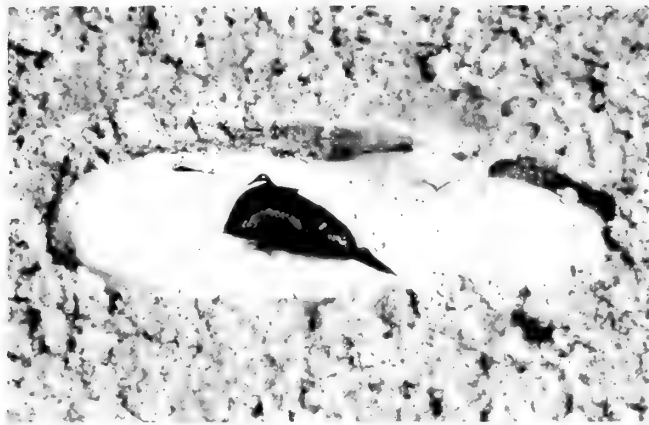
The swallowing behaviour of *Atractaspis* may be influenced by its nearly vestigial teeth. As described for *A. bibroni*, it is characterised by a rather inefficient transport mechanism in which the snake forces its head over the prey with lateral rotations around a vertical axis, rather than with the 'pterygoid walk' used by other snakes. This can be considered to be an adaptation towards feeding in narrow spaces and explained by the lack of connection between the pterygoid and palatine bones that are separated by a wide gap bridged by a ligament (Deufel & Cundall, 2000; MS; see also Underwood and Kochva, 1993).

*A. engaddensis* lays 2–3 elongated eggs during the months of September–November and hatching occurs after about 3 months (Fig. 3).

An interesting behavioural feature of this snake is its threat posture during which it presses its head to the ground while arching its neck (Fig. 1). This may turn either into a strike or into what appears to be a defensive display mechanism (Greene, 1979; 1997; Golani & Kochva, 1993). The snake forms a tight coil with the head hidden underneath the body and the wriggling tail is exposed above



**Fig. 2** Distribution map of *Atractaspis* species with the southern African *bibroni* group and the northern *microlepidota* group reaching the region of Mount Gilboa (after Underwood & Kochva, 1993; Joger, 1997).



**Fig. 3** Hatching of *Atractaspis engaddensis*.

the coil so as to mimic the head (Fig. 4). The tail ends in a sharp tip that the otherwise immobile snake uses for poking when grasped at the posterior end of the body (Fig. 5). This behaviour may be mistaken for a genuine strike with the fang and deter any potential predator. Should that not suffice, there is always the hidden head that can be produced quickly from underneath the body coils and inflict a real, painful and dangerous strike.

## VENOM APPARATUS

The venom apparatus of *Atractaspis* has not been dealt with in great detail beyond the general statement that the maxillary/fang unit is similar to that of vipers. This similarity is, however, superficial as the articulation between the prefrontal and maxilla in *Atractaspis* is in the form of a ball and socket articulation, which is more restricted in its movements, but apparently stronger (Pasqual, 1962). This condition may be important for the peculiar striking of these snakes, which is performed with one fang at a time while the mouth remains almost entirely closed (Fig. 6). Striking in this manner may be considered as a special adaptation for fossorial snakes that feed in narrow burrows underground.

The venom fangs are relatively long and canaliculate and possess a blade-like ridge near the orifice of the fang (Kochva & Meier, 1986), which may increase the wound and cause additional tissue damage during the strike, thus facilitating the spread of venom. Analyses of films taken during a strike through plastic sheathings show first the establishment of a firm contact of the head with the substrate, followed by the erection of the fang and piercing of the substrate by arching, lateral bending and downward rotation of the head (Fig. 6). Ejection of the venom is performed while the fang moves backward, further cutting through the surface (Golani & Kochva, 1988).

The venom glands have a distinctive structure with secretion tubules arranged concentrically around the main lumen (Fig. 7). Unlike the viperids and elapids, there are no differentiated mucous accessory glands, but mucous cells are found in each of the secretion tubules close to the central lumen (Kochva *et al.*, 1967). As in the other families of venomous snakes, there are species (the *microlepidota* group, Underwood & Kochva, 1993) with elongated venom glands that reach far beyond the corner of the mouth (Kochva, 1959). The compressor muscle accompanies the gland along its entire length and probably squeezes it during the strike so as to increase the pressure in the central lumen and push the venom through the venom duct, fang canal and into the wound. The species with short glands (the *bibroni* group) have a short, but thicker compressor.

In a 756 mm long *A. engaddensis* the right gland reached the 30<sup>th</sup> ventral and was 70 mm long, while in *A. microlepidota* it may reach one third of the body length – more than 300 mm in a specimen of 900 mm (Scortecci, 1939). The left gland is usually longer than the right gland in both species and it is sometimes twisted along its longitudinal axis (Fig. 8).

## VENOM

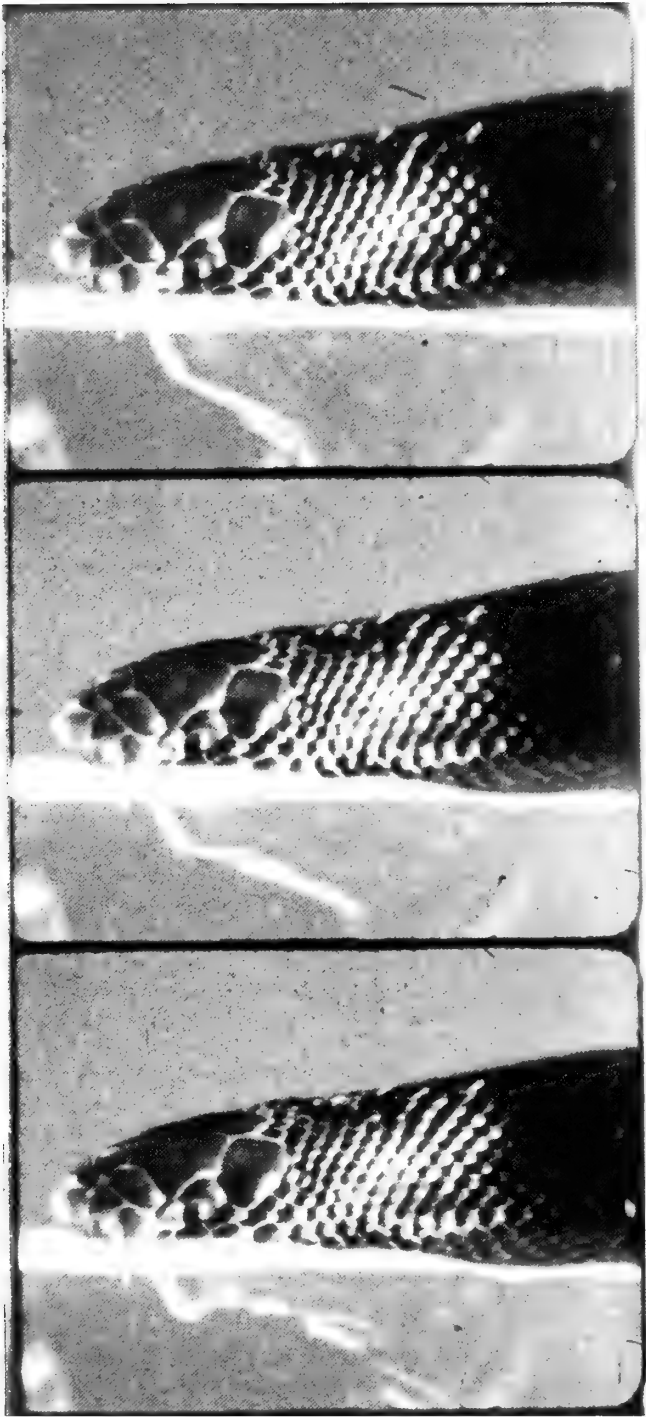
The venom of *Atractaspis* remained unknown for a long time, probably because not many serious bites were reported until now and it was thus ignored by toxinologists. In addition, the venom is very difficult to obtain not only because of the relative paucity of specimens collected, but also because of the difficulty in extracting



**Fig. 4** Defense mimicry posture by *Atractaspis engaddensis*, with hidden head and exposed tail.



**Fig. 5** Tail poking by *Atractaspis engaddensis*.

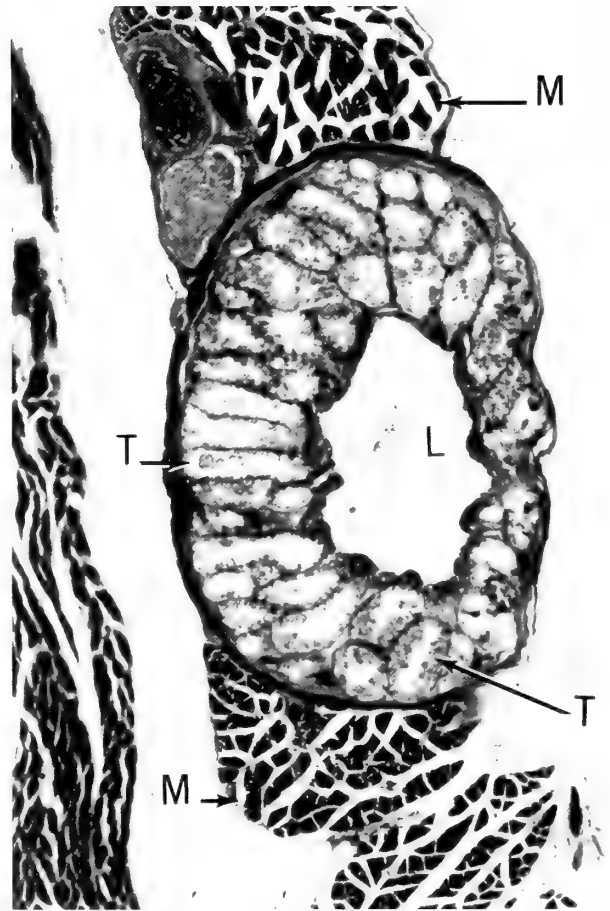


**Fig. 6** Striking sequence by *Atractaspis engaddensis*; sequence from film (see text).

it from the glands. *Atractaspis*, with its spade-shaped head, cannot be milked the way other venomous snakes are; a special method had to be devised as shown in Figure 9.

Even today the biochemistry and pharmacology of the venom are known for only a few species, with almost all the information available originating from research with the venom of *A. engaddensis*.

The toxicity of the venom varies among the species tested, the most potent venom being that of *A. engaddensis*, exceeding by 40 times or more that of some other species (Table 1). It contains a set



**Fig. 7** Venom gland of *Atractaspis engaddensis*, cross section: M = compressor muscle, L = lumen of venom gland, T = secretion tubules.

of enzymes not unlike those of other venomous snakes, a quite powerful hemorrhagin and a group of low-molecular weight toxins, the sarafotoxins, named after the Hebrew name of *A. engaddensis* – Saraf. When the venom was first fractionated by molecular sieving on a Sephadex G-50 column, 7 protein peaks were obtained. The first two contained high-molecular weight proteins with a hemorrhagic factor and the enzyme L-amino acid oxidase; the third peak showed phospholipase A<sub>2</sub> activity and peaks 5 and 6 contained very low molecular weight peptides, which made up 40% of the venom proteins and were highly toxic in i.v.-injected mice (Kochva *et al.*, 1982). These fractions were further purified resulting in several toxins characterised as sarafotoxins (SRTX), which showed

**Table 1** Toxicity of *Atractaspis* venoms, sarafotoxins, and mammalian endothelins in mice. LD<sub>50</sub> (ng/g b.w.)

<i>A. bibroni</i>	500
<i>A. dahomeyensis</i>	2000
<i>A. microlepidota</i>	>2000
<i>A. micropholis</i>	>3000
<i>A. engaddensis</i>	75
Sarafotoxin-a	10
Sarafotoxin-b	10
Sarafotoxin-c	300
Sarafotoxin-d/e	>2000
Endothelin-1	15
Endothelin-3	30



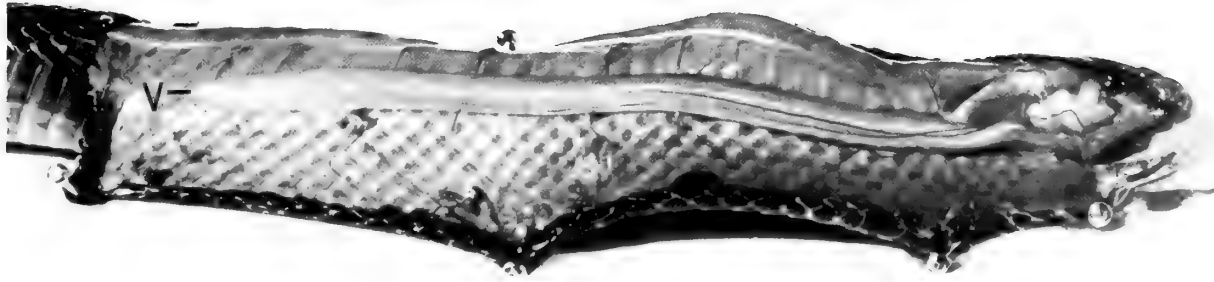


Fig. 8 Elongated venom glands of *Atractaspis engaddensis*: V = venom gland.



Fig. 9 Venom extraction from *Atractaspis engaddensis* using a piece of tubing for safety and a parafilm-covered lid for the collection of venom.

a high degree of structural homology amongst themselves and with a group of active peptides that were isolated from mammalian endothelium, the endothelins (Fig. 10). The sarafotoxins and endothelins are also similar in their pharmacological activity and are

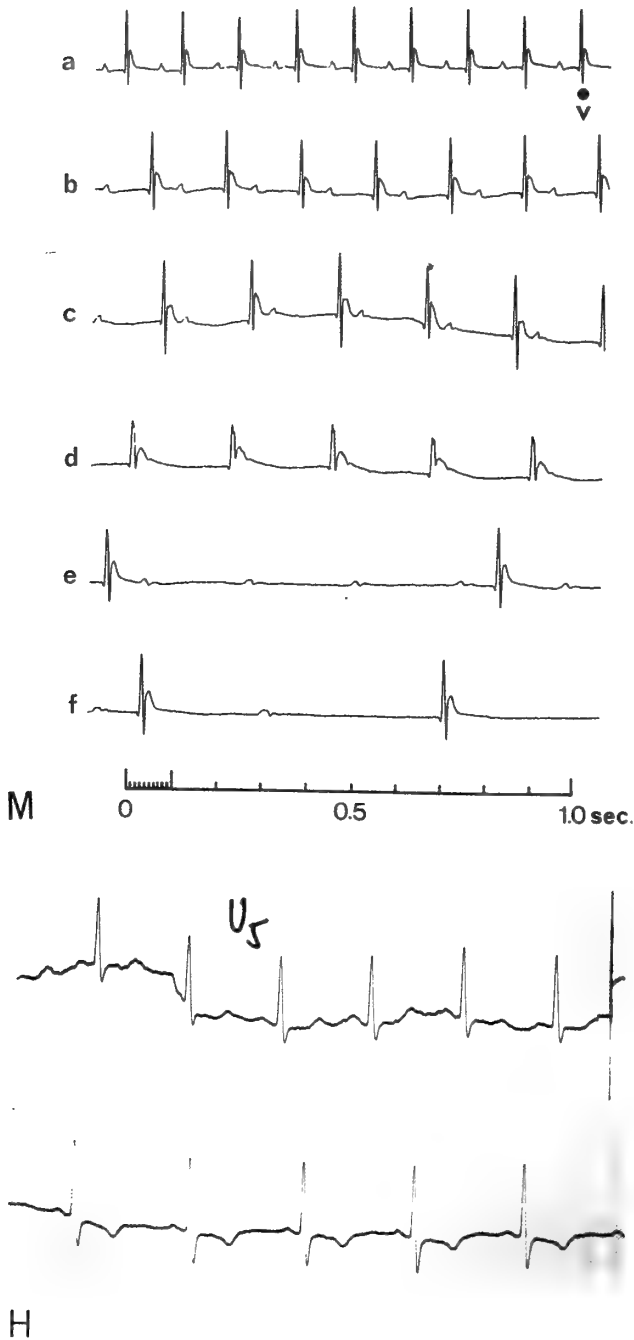
composed of 21 amino acid residues, with two disulphide bridges between Cys 1–15 and 3–11 (Yanagisawa *et al.*, 1988; Takasaki *et al.*, 1988; Wollberg *et al.*, 1990; Kochva *et al.*, 1993). Another member of the sarafotoxin/endothelin family, bibrotoxin, was isolated from the venom of *A. bibroni*. It differs from SRTX-b in only one amino acid substitution and induces vasoconstriction in rat aorta (Becker *et al.*, 1993). The venom of *A. m. microlepidota* contains a series of peptides with a somewhat higher molecular weight that are composed of 24 amino acids (Ducancel *et al.*, 1999) and are apparently less toxic than SRTX-a or b.

The sarafotoxins and endothelins are now synthesised by pharmaceutical companies and are widely used in both basic and applied research, both clinical and industrial, in the field of cardiology and in blood pressure studies (Ducancel *et al.*, 1999; Yaakov *et al.*, 2000).

The various sarafotoxins (and endothelins) differ in their activity and toxicity, the most potent ones being SRTX-a and SRTX-b (Table 1), which exert a strong influence on the cardiovascular system (Wollberg *et al.*, 1988). SRTX-b shows three, apparently separate, effects on the heart: 1) positive inotropicity, which is manifested by an increased contractility in isolated hearts and heart muscles and in *in vivo* injected mice with sublethal doses of the

1	5	10	15	20	
Cys-Ser-Cys-Lys-Asp-Met-Thr-Asp-Lys-Glu-Cys-Leu-Asn-Phe-Cys-His-Gln-Asp-Val-Ile-Trp					SRTX-a
Cys * Cys * * * Ser * * * Cys * * * Cys * * * * * * * *					SRTX-a1
Cys * Cys * * * * * * * * Cys * Tyr * Cys * * * * * * *					SRTX-b
Cys * Cys * * * Ser * * * * Cys * Tyr * Cys * * * * * * *					SRTX-b1
Cys * Cys-Ala * * * * * * * * Cys * Tyr * Cys * * * * * * *					BTX
Cys-Thr-Cys-Asn * * * * * Glu * Cys * * * Cys * * * * * * *					SRTX-c
Cys-Thr-Cys * * * * * * * * Cys * Tyr * Cys * * Gly-Ile * * *					SRTX-d/e
Cys * Cys-Asn * Ile-Asn * * * * Cys Met Tyr * Cys * * * * * *					Asp-Glu-Pro <i>A. microlepidota</i>
Cys * Cys-Ser-Ser-Leu-Met * * * Cys-Val-Tyr * Cys * Leu * Ile * * *					ET-1
Cys * Cys-Ser-Ser-Trp-Leu * * * Cys-Val-Tyr * Cys * Leu * Ile * * *					ET-2
Cys * Cys-Asn-Ser-Trp-Leu * * * Cys-Val-Tyr * Cys * Leu * Ile * * *					VIC
Cys-Thr-Cys-Phe-Thr-Tyr-Lys * * * Cys-Val-Tyr-Tyr-Cys * Leu * Ile * * *					ET-3
Cys * Cys-Ala-Thr-Phe-Leu * * * Cys-Val-Tyr * Cys * Leu * Ile * * *					ET-trout (1999)
1	5	10	15	20	

Fig. 10 Amino acid sequences of sarafotoxins and endothelins: BTX = bibrotoxin, ET = endothelin, SRTX = sarafotoxin, VIC = vasoactive intestinal contractor.



**Fig. 11** ECG recording after *Atractaspis engaddensis* envenomation. M = mouse: v = venom injection; b – f: 120 – 600 seconds after venom injection. H = human: upper trace – at admission to the hospital; lower trace – 24 hours after the bite (see text).

toxin; 2) direct effect of the toxin on the cardiac conducting system; and 3) cardiac ischemia, which is caused by constriction of the coronary blood vessels. The latter two cause severe A–V block, which may lead to cardiac arrest. The cardiotoxic effects are manifested by marked changes in the ECG, in both human victims and in mice injected with either SRTX-b or whole venom (Fig. 11). These changes include an increase in amplitude of the R- and T-waves, a prolongation of the P–R interval, ‘dropped beats’ and complete A–V block and cardiac arrest. In addition, SRTX-b causes contraction

of other blood vessels and may be considered as one of the most potent vasoconstrictors.

In human patients too, cardiotoxic symptoms and a rise in blood pressure were observed, but were considered as secondary developments of some kind of neurotoxic effects. However, neither presynaptic nor postsynaptic neurotoxicity was observed in laboratory tests with nerve-muscle preparations using whole *A. engaddensis* venom (Weiser *et al.*, 1984); SRTX does show specific binding to different isolated regions of brain preparations, with the highest binding capacity found in the cerebellum, choroid plexus and hippocampus (Ambar *et al.*, 1988), but its function there is not known.

In human bites by *A. engaddensis* and *A. irregularis*, some of which were extremely severe, changes in the ECG were observed (Fig. 11), including S–T elevation or depression, flattening of the T-waves and prolonged P–R intervals pointing to myocardial ischemia and atrioventricular conduction abnormalities (Chajek *et al.*, 1974; Warrell, 1995; Kurnik, *et al.*, 1999). The transient atrioventricular block that developed in a 17-year old boy bitten on his left foot was considered to be a secondary complication of the bite (Alkan and Sukenik, 1974), rather than a direct influence of the toxins on the heart.

The other systemic symptoms, which may develop within minutes, include fever, nausea, general weakness, sweating, pallor, fluctuations in the level of consciousness and a rise in blood pressure (Doucet & Lepesme, 1953; Chajek *et al.*, 1974; Kurnik *et al.*, 1999).

Most bites were on the fingers and the local effects were demonstrated mainly by gross oedema of the hand that extended up to the forearm and shoulder (*A. irregularis* – Doucet and Lepesme, 1953; *A. corpulenta* – Gunders *et al.*, 1960; *A. microlepidota* – Warrell *et al.*, 1976) and by blistering and serous vesicles that appeared at the site of the bite and underwent hemorrhagic transformation (Fig. 12; Kurnik *et al.*, 1999). In some previously reported cases (Chajek *et al.*, 1974; Chajek & Gunders, 1977), local necrosis developed that required surgical intervention including amputation. In two cases, one by *A. bibroni*, the other by *A. engaddensis*, the bitten finger partially or fully recovered within a month, but tenderness of the bitten site remained for a long time (Stewart, 1965; Kurnik *et al.*, 1999).

Although the bites by several species of *Atractaspis*, such as *A. dahomeyensis*, *A. aterrima*, *A. corpulenta* and *A. bibroni* were mild (Warrell *et al.*, 1976; Tilbury & Branch, 1989), *A. engaddensis*, *A. irregularis* and perhaps other species should be regarded as dangerous



**Fig. 12** Bitten index finger showing hemorrhagic transformation of serous vesicles.



**Fig. 13** Ridges on the teeth of *Pachyrhachis problematicus* (arrow).

mainly because of their influence on the cardiovascular system, which may lead to death. Only a very small number of lethal cases has been recorded until now, perhaps a total of five, three by *A. microlepidota* (one adult man and two girls aged 4 and 6), one by *A. irregularis*, an adult man, and one unknown (Corkill *et al.*, 1959; Warrell *et al.*, 1976). Despite the fact that *A. engaddensis* has one of the most potent venoms known, all patients bitten by this species finally recovered, one probably due to ‘the immediate and energetic treatment he received’ (Chajek *et al.*, 1974). Most recently (July, 2002) a forty-six-year-old man was bitten on the inner aspect of the right thumb while trying to catch an *Atractaspis engaddensis* near his home in the Judean Desert, some 15 km north west of Jericho. He was taken to the hospital where he arrived after about 40 minutes in serious condition. Resuscitation failed and he was pronounced dead after about 45 minutes (Nadir & Stalnikowicz, personal communication). This is the first death by an *Atractaspis engaddensis* bite in Israel. Another recent case, from Saudi Arabia, involved a two-year-old-girl who died within one hour after being bitten on the foot by what was identified as *A. microlepidota engaddensis*. The region where the bite occurred, at Diriyah near Riyadh, Saudi Arabia, is a

new distribution record for *engaddensis* (Al-Sadoon & Abdo, 1991; see also Al-Sadoon *et al.*, 1991; Gasperetti, 1988; Joger, 1997; Schätti & Gasperetti, 1994).

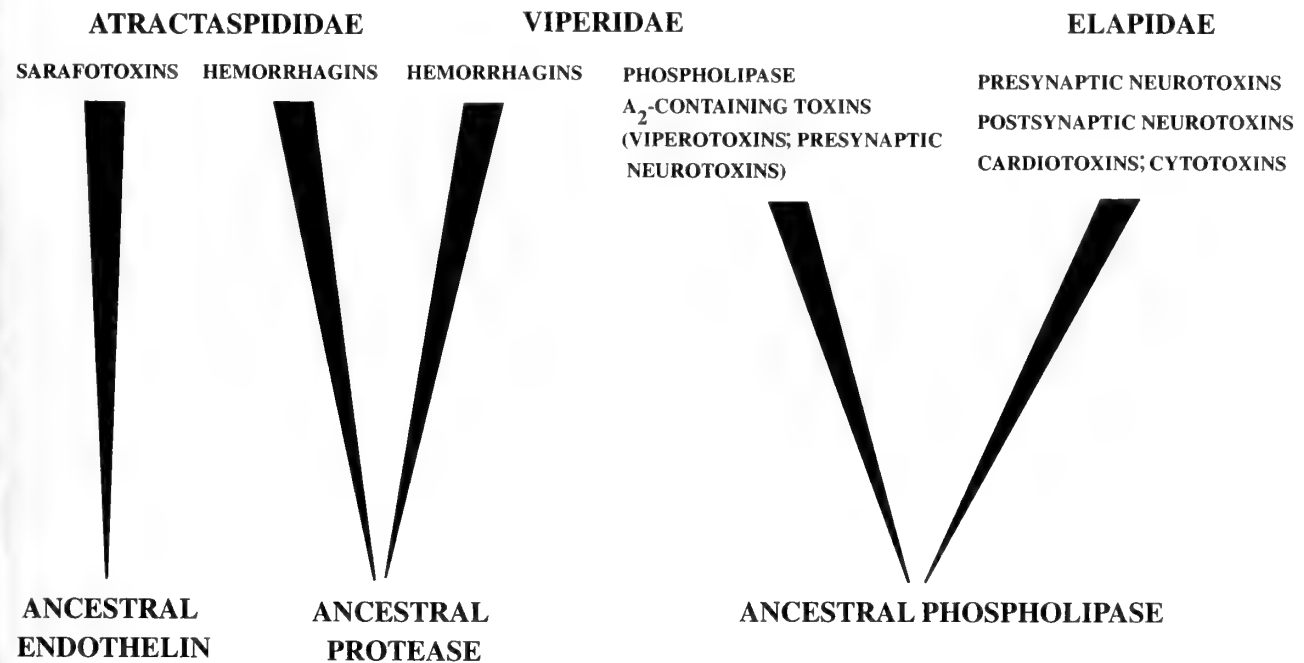
It should be pointed out that the toxicity of the venom of certain species, such as *A. microlepidota*, may vary according to distribution, causing death in certain cases (see above) or containing less potent toxins in others (above and Table 1).

As with other venoms, snakes and some mammals are also resistant to *Atractaspis engaddensis* venom, including the local mongoose (*Herpestes ichneumon*, Bdolah *et al.*, 1997). At least in one instance, it was found that a mongoose (*Paracynictis selousi*) fed on a specimen of *A. bibroni* (Greene, 1997).

There is no antiserum available against any of the *Atractaspis* species.

**EVOLUTION**

The discussion of snake origin and evolution has been recently revived by a new and renewed examination and analysis of the fossils discovered by Haas (1979; 1980a; 1980b) at an Upper Cretaceous site north of Jerusalem. While the debate on the ecological origin (marine or terrestrial) and the relationships of these specimens (mosasauroid or macrostomatan) is still going on (Lee & Caldwell, 1998; Greene & Cundall, 2000; Tchernov *et al.*, 2000), Rieppel & Zaher (2001) have recently concluded that ‘*Pachyrhachis* is neither a basal snake, nor a link between snakes and mosasauroids, but shows macrostomatan affinities instead’. *Pachyrhachis* possesses ridges or cutting edges on its teeth (Rieppel & Kearney, 2001; Fig. 13) and the teeth of another fossil, *Haasiophis*, have still to be further investigated in detail. Should furrows or any other suggestive structures be found, they could be taken as plausible signs for the existence of some kind of glands that might have secreted active substances, even before the appearance of caenophidian snakes.



**Fig. 14** Schematic representation of the possible origin of some major snake venom toxins from enzymatic precursors (partly after Strydom, 1979).

It has been suggested that a system that produced active substances with the means of introducing them into the prey probably lay at the foundation of the major radiations of higher snakes (Underwood & Kochva, 1993). This system underwent further evolution in the Atractaspididae (mainly *Atractaspis*), Viperidae, Elapidae and several lineages of 'Colubridae'.

Some of the active substances were probably enzymatic in nature and related to enzymes secreted by evolutionarily 'older' glands, such as the pancreas. Indeed, phospholipases found in the venom of Elapidae, for instance, show sequence homology with the enzymes secreted by the mammalian pancreas. Some of the ancestral enzymes developed into toxins, such as hemorrhagins and neurotoxins, with or without loss of enzymatic activity (Fig. 14; Strydom, 1979; Kochva, 1987).

Hemorrhagins are found in two families (Viperidae and Atractaspididae); presynaptic neurotoxins in two (Elapidae and Viperidae); and two families each possess a specific and unique group of toxins – postsynaptic neurotoxins in elapids and sarafotoxins in *Atractaspis*.

The hemorrhagin found in the venom of *Atractaspis* is neutralised by antibodies against *Vipera palaestinae* venom (Ovadia, 1987) and may thus be related to viperid hemorrhagins, originating from some kind or kinds of protease. The presynaptic and postsynaptic neurotoxins, as well as the cytotoxins and cardiotoxins, apparently originate from phospholipase-like molecules. The enzyme phospholipase A<sub>2</sub> may be part of the presynaptic neurotoxins and its enzymatic activity may still be essential for its toxicity. The postsynaptic neurotoxins, the cytotoxins and the cardiotoxins apparently underwent major changes including loss of enzymatic activity, chain shortening and gain of neurotoxicity (Strydom, 1979).

The sarafotoxins are structurally very similar to the endothelins, which are evolutionarily highly conserved, and are found in all vertebrates, as well as in some invertebrate groups. It should be emphasised, however, that the genes of the mammalian endothelins were found on three separate chromosomes, whereas the sarafotoxin genes seem to be located on the same chromosome. The organisation of the SRTX genes of both *A. engaddensis* and *A. m. microlepidota* and their precursors are also different from those of the endothelins and may have evolved separately (Ducancel *et al.*, 1993; 1999).

There is, of course, a great deal of information still missing, but the evolution of the sarafotoxins and of some of the other snake venom toxins and their use in feeding and defense may best be defined as exaptations; these are features that once had different functions but are now used in a new role that enhances the fitness of their bearers (Gould & Vrba, 1982).

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# Origin and phylogenetic position of the Lesser Antillean species of *Bothrops* (Serpentes, Viperidae): biogeographical and medical implications

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**SYNOPSIS.** We use mitochondrial DNA sequences to infer the origin and phylogenetic position of the Lesser Antillean species of the pitviper genus *Bothrops*, *B. caribbaeus* and *B. lanceolatus*. The two species form a monophyletic group, which in turn forms the sister clade to the *Bothrops asper-atrox* complex. High levels of sequence divergence among the Caribbean species, and between them and the nearest mainland relatives, suggest a relatively ancient origin of these snakes. The hypothesis that the Lesser Antillean *Bothrops* are the result of a recent colonisation event from within the South American *B. atrox* complex is rejected, as is the hypothesis that they were introduced to their island habitats by aboriginal humans. The high level of morphological apomorphy displayed by *B. lanceolatus* suggests a stepping-stone colonisation, St. Lucia being colonised first and then Martinique from St. Lucia. The medical implications of these findings are discussed: a recent case of envenoming from Saint Lucia suggests that *Bothrops caribbaeus* causes the same thrombotic syndrome of envenoming as *B. lanceolatus*.

## INTRODUCTION

The genus *Bothrops* Wagler, 1824 contains most of the pitviper fauna of South America. The genus (including the arboreal species sometimes assigned to *Bothriopsis*) contains approximately 36 species, with a wider variety of body shapes and natural history traits than in any other New World pitviper genus. This greater diversity has been ascribed to the fact that *Bothrops* was the first group of pitvipers to reach the South American continent, thus giving ample opportunity for adaptive radiation (Wüster *et al.*, in press).

Two species of *Bothrops* occur in the Lesser Antilles: *Bothrops caribbaeus* (Garman, 1887) on St. Lucia, and *Bothrops lanceolatus* (Lacépède, 1789) on Martinique. The status and origin of these forms has been the subject of much debate. Long considered to be conspecific with *Bothrops atrox*, *B. lanceolatus* was revalidated by Hoge (1952), and the validity of *B. lanceolatus* and *B. caribbaeus* confirmed by Lazell (1964). This latter interpretation has been followed by most authors since then (e.g., Campbell & Lamar, 1989). However, Sandner Montilla (1981, 1990) regarded the Lesser Antillean *Bothrops* as conspecific with each other, as well as with mainland *Bothrops asper* and the northern Venezuelan populations of the *B. asper-atrox* complex.

The origin of the Antillean *Bothrops* has been the subject of much speculation and mythology. This includes popular tales that the

snakes were originally introduced by Carib Indians in their attempts to gain control of the islands from resident Arawaks (Dowling, 1965), and the notion that dispersal from the South American mainland is common and ongoing (Sandner Montilla, 1981).

The reptile fauna of the Lesser Antilles is primarily the result of long-distance dispersal by individual species, as these islands have not been linked to the South American mainland or any other landmass at any time in their history (Thorpe *et al.*, in press; Malhotra and Thorpe 1999). This means that some species present in these islands represent long-standing endemic lineages (Thorpe *et al.*, in press; Malhotra and Thorpe 2000), whereas others appear to be the result of relatively recent dispersal events from well-defined source populations or taxa in South America, as is the case for the genus *Corallus* (Henderson & Hedges, 1995).

Compared to morphological data, molecular markers such as mitochondrial DNA (mtDNA) sequence data have the advantage that they can give an estimate of phylogeny reasonably free of the confounding effects of differing natural selection pressures on the external phenotype. Moreover, molecular sequence data also have the advantage that they can give at least an approximate estimate of times of divergence between lineages, although the interpretation of molecular clocks is subject to various analytical and empirical problems (Hillis *et al.*, 1996).

Several recent mtDNA-based phylogenetic analyses of the genus *Bothrops* have included the Antillean species. Salomão *et al.* (1997,



PLATE 1

*Bothrops caribbeus* © R.S. Thorpe

1999), using 580 b.p. of cytochrome *b* sequence, found *B. caribbaeus* and *B. lanceolatus* to be sister species of the South American populations of the *B. atrox* complex. However, the study included only a limited sampling of South American members of the *B. atrox* complex, and did not include representatives of *B. asper* from Central America.

The aim of this paper is to explore in more depth the origin of the Antillean *Bothrops*, and its implications for other fields, using an expanded dataset of more sequence information from a larger number of potentially related species.

## MATERIALS AND METHODS

We obtained tissue (ventral scale clippings or tail tips) and/or blood samples from species representing the principal clades within the genus *Bothrops* (including *Bothriopsis*), as well as the closely related *Bothrocophias* – see Wüster *et al.* (in press). We also included samples of the *B. asper-atrox* complex from around the coast of South and Central America, as these have been considered to be potential founder populations from which the ancestor of Antillean *Bothrops* could have arisen. For outgroup rooting, we used sequences of *Bothrops alternatus* and *Bothrocophias microphthalmus*. Two regions of the mitochondrial DNA molecule were amplified using the polymerase chain reaction (PCR): a 767 base pair (bp) section of the gene for cytochrome *b* (*cytb*), and a 900 bp region of the gene for NADH dehydrogenase subunit 4 (*ND4*). Details of primers and laboratory protocols are given in Pook *et al.* (2000).

Sequences were aligned by eye against published *Bothrops* sequences (Puerto *et al.*, 2001). In order to test for the presence of saturation of certain categories of substitution, we calculated Tamura–Nei distances between all samples. This takes into account deviations from equal base compositions and differences in substitution rates among nucleotides. We then plotted unadjusted *p*-distances for transitions and transversions, and for the three codon positions separately, against Tamura–Nei distances. A decline in the rate of accumulation of individual categories of substitution with increased Tamura–Nei distances indicates saturation of that substitution category.

We checked all sequences for insertions, deletions or the presence of stop codons. Any of these would have indicated that the sequences represent nuclear insertions of the mitochondrial genes (Zhang and Hewitt, 1996). The sequence data were assayed for the presence of a significant phylogenetic signal by means of the *gI* tree skewness



*Bothrops lanceolatus* © D. Warrell

statistic (Hillis and Huelsenbeck, 1992), calculated from 100,000 trees randomly generated by PAUP\* 4.0b8 (Swofford, 2001). Sequence divergences between clades were estimated using the program Phyltest (Kumar, 1996).

We analysed our sequence data using both maximum parsimony (MP) and maximum likelihood (ML) as optimality criteria. Using multiple optimality criteria should identify those parts of a phylogenetic tree that are supported independently of the optimality criterion used. Such nodes should inspire greater confidence than nodes that are unstable and vary depending on method of analysis. All analyses were carried out using the program PAUP\* 4.0b8 (Swofford, 2001).

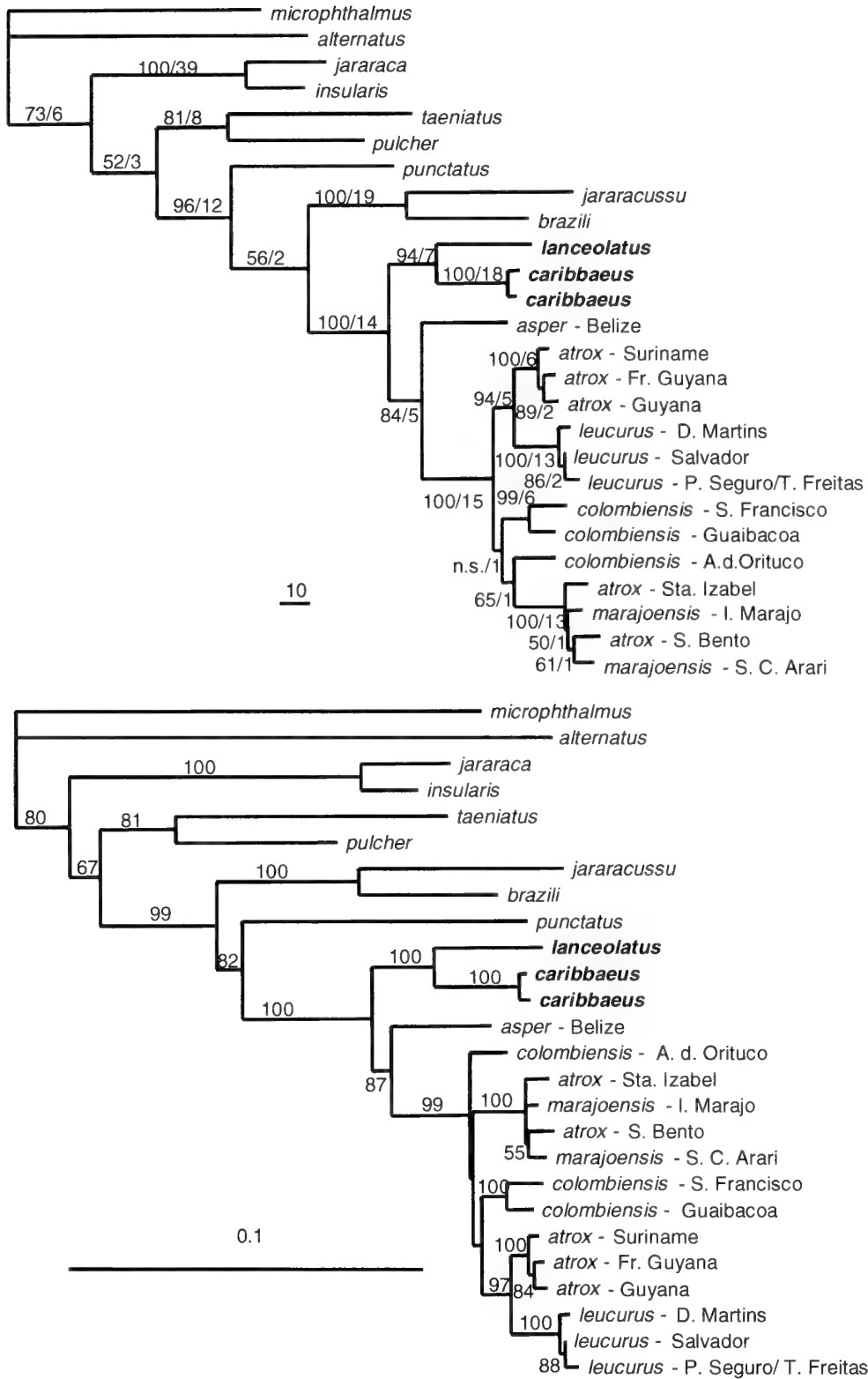
For MP analyses, we selected *Bothrops alternatus* and *B. microphthalmus* as outgroups. We employed the heuristic search algorithm of PAUP\* 4.0b8, using TBR branch swapping and 100 random addition sequence replicates. The analysis was carried out on the unweighted data only.

The extent to which individual nodes on the tree were supported by the data was assessed using bootstrapping and Bremer (1994) branch support. Non-parametric bootstrap was implemented using heuristic searching, 1000 replicates, TBR branch swapping and 10 random-addition-sequence replicates per bootstrap replicate. Bremer branch support for individual nodes was calculated through the use of the converse constraint option of PAUP\*.

For ML analyses, we identified the most appropriate model of sequence evolution through the use of the MODELTEST software (Posada & Crandall, 1998). A first ML search was run, using heuristic searching, a neighbour-joining starting tree and TBR branch swapping, and the sequence evolution parameters identified by the Modeltest software. These parameters were then re-estimated from the resulting ML tree, and a further search run using these re-estimated parameters. This was repeated until further estimates yielded no further changes of parameter values or tree likelihood scores. Bootstrap analysis involved 100 replicates, using NJ starting trees and NNI branch swapping.

An important consideration of any proposed scientific hypothesis is whether the data supporting it can reject alternative hypotheses with statistical significance. In other words, do the data allow us to reject the null hypothesis that differences in tree optimality between the optimal tree and trees consistent with alternative hypotheses are due to random chance? In the case of the Antillean *Bothrops*, we tested the following alternative phylogenetic hypotheses: (i) non-monophyly of the Antillean *Bothrops*, i.e., the Antillean populations of *Bothrops* result from separate colonisation events; (ii) non-





**Fig. 1** Maximum parsimony (top) and maximum likelihood (bottom) estimates of the phylogeny of *Bothrops*. In the MP tree, numbers before the slash refer to bootstrap support, numbers after the slash indicate Bremer support. In the ML tree, numbers on nodes indicate bootstrap support.

monophyly of the *B. asper-atrox* complex, i.e., that the Antillean populations originate from within the *B. asper-atrox* complex; (iii) non-monophyly of the South American *B. atrox* complex, i.e., that the Antillean species originate from within the cis-Andean *B. atrox* complex, paralleling the phylogeography of *Corallus* (Henderson & Hedges, 1995); and (iv) monophyly of *B. caribbaeus*, *B. lanceolatus*, *B. asper* and northern Venezuelan populations of the *B. asper-atrox* complex to the exclusion of the cis-Andean *B. atrox* complex, as implied by the classification of Sandner Montilla (1990). We used Wilcoxon signed-ranks (WSR) tests (Templeton tests – Templeton, 1983) to compare the optimal MP tree and MP trees depicting alternative hypotheses, and Shimodaira–Hasegawa (SH) tests (Shimodaira & Hasegawa, 1999) to compare the corresponding ML trees.

## RESULTS

We aligned a total of 1401 b.p. of mtDNA sequence information (ND4: 693 b.p.; *cytb*: 708 b.p.). The sequences included no indels or stop or other nonsense codons, and contained the usual bias towards transitions and substitutions concentrated into third codon positions typical of mitochondrial DNA. We conclude that our sequences represent mtDNA rather than nuclear insertions. Samples are listed in Appendix 1. The 100,000 random trees generated a skewness statistic of  $g_1 = -0.599403$ , rejecting the null hypothesis that the data contain no significant phylogenetic signal ( $P < 0.01$ ; Hillis and Huelsenbeck, 1992).

Levels of sequence divergence among the taxa included ranged from 0.3% to 13.65% (unadjusted p-distance). *Bothrops caribbaeus* and *B. lanceolatus* differ from each other by 4.3%, and from the *B. asper-atrox* group by an average of 5.77% and 6.15% respectively, with an average divergence of 5.9% when the Antillean haplotypes are treated as a single clade. Levels of sequence divergence within the *B. asper-atrox* clade range from 0.3% to 5.5%

The MP analysis resulted in a single most parsimonious tree of 1030 steps (CI 0.5398; HI 0.4602; RI 0.6465). In this tree, the two Antillean taxa formed a clade, which in turn forms the sister clade of all samples of the *Bothrops asper-atrox* complex (Fig. 1).

The MODELTEST software identified the GTR+I+G model, a submodel of the general time-reversible model (Yang *et al.*, 1994) as optimal for the data at hand. A ML tree was constructed using the parameters calculated by MODELTEST, and the parameters were recalculated from the resulting tree, and used in a further ML search, which resulted in a tree with the likelihood score  $-\ln(L) = 6652.69122$ .

Further estimates of sequence evolution parameters did not result in any change of parameter values or tree likelihood score (Fig. 1). The MP and ML trees differ only in branching order within the cis-Andean *B. atrox* complex, and in the relative position of the *B. jararacussu-brazili* clade and *B. punctatus*.

The results of our tests of alternative tree topologies are shown in

Table 1. Neither the WSR nor the SH test significantly reject the possibility that the two Antillean species may be the result of separate colonizations of the Lesser Antilles, although the result of the SH test was almost significant. They do, however, significantly reject the hypothesis that the Antillean species originate from within the cis-Andean radiation of the *B. asper-atrox* complex, and also reject Sandner Montilla's suggestion of conspecificity between *B. lanceolatus*, *B. caribbaeus*, *B. asper* and northern Venezuelan *Bothrops*, to the exclusion of other South American populations of the *B. atrox* group.

## DISCUSSION

Our results confirm the position of the Antillean species of *Bothrops* as the sister clade of the *Bothrops asper-atrox* complex, as suggested by Salomão *et al.* (1997, 1999) and Wüster *et al.* (1997, 1999). The monophyly of the Antillean taxa is supported by high bootstrap and Bremer support values, although a tree supporting this arrangement is not significantly longer than the optimal tree constrained not to include this clade.

The high level of sequence divergence between the Antillean *Bothrops* and their mainland relatives (5.9%) is consistent with a lineage split dating back to the Miocene or earliest Pliocene. Wüster *et al.* (in press) suggested a rate of sequence evolution for *cytb* and ND4 of between 0.66 and 1.4% My<sup>-1</sup> in Neotropical pitvipers. This would date the timing of the split between the Antillean *Bothrops* clade and the *B. asper-atrox* clade at 4.2–8.9 Mya, i.e., the late Miocene or earliest Pliocene. Similarly, the split between *B. caribbaeus* and *B. lanceolatus* (sequence divergence: 4.3%) can be dated to 3.1–6.5 Mya. Hedges (1996) estimated the divergence of the *B. asper-atrox* complex to have taken place within the last 4 My, and assumed dispersal to the Antilles to have taken place during that timeframe, whereas our data suggest a slightly earlier lineage split. In any case, it can be concluded that the two Antillean *Bothrops* species represent two relatively old, independent lineages. Obviously, in view of the errors inherent in any attempt at molecular clock usage, these estimates should be treated as approximations rather than exact timings.

The notion that these populations are the result of a recent dispersal event from within South America, as is the case in West Indian *Corallus* (Henderson & Hedges, 1995), is refuted by both tree topology and statistical tree comparison tests. Equally, the notion that the presence of these snakes in the Lesser Antilles is the result of a primitive form of biological warfare among aboriginal people (Dowling, 1965) will have to be abandoned, despite its romantic appeal.

The colonisation sequence of the two species can be resolved from morphological data, particularly scalation. In terms of dorsal and ventral scale counts, *B. caribbaeus* is indistinguishable from many populations of the *B. asper-atrox* complex. On the other hand,

**Table 1** Differences in tree length or likelihood, statistics, and their significance, between the most parsimonious or the most likely trees, and trees constrained to be compatible with alternative phylogenetic or biogeographical hypotheses.

	d(steps)	Wilcoxon signed-ranks – z	P	Shimodaira–Hasegawa d(lnL)	P
Non-monophyly of <i>B. caribbaeus</i> and <i>B. lanceolatus</i>	7	1.4000	0.1615	15.05075	0.054
Non-monophyly of <i>B. asper-atrox</i> complex	5	1.1471 – 1.5076	0.1317–0.2513	3.15866	0.181
Non-monophyly of cis-Andean <i>B. atrox</i> complex	15	2.4019	0.0163*	20.06423	0.018*
Monophyly of <i>B. caribbaeus</i> , <i>B. lanceolatus</i> , <i>B. asper</i> and northern Venezuelan populations	18	2.9200 – 3.0870	0.002 – 0.0035*	24.34213	0.005*

*B. lanceolatus* has higher ventral and dorsal scale row counts than practically all populations of the *B. jararacussu-punctatus-atrox* clade. This suggests that the extreme scale counts found in *B. lanceolatus* represent an autapomorphy compared to *B. caribbaeus* and mainland *Bothrops*. This makes a hypothesis of dispersal from the mainland to St. Lucia, and then a further dispersal event to Martinique, more parsimonious than dispersal to Martinique followed by further dispersal to St. Lucia. Since St. Lucia lies between South America and Martinique, this scenario is also more geographically parsimonious than the alternative. The slightly greater length of the branch leading to *B. lanceolatus* is also consistent with this hypothesis (De Salle & Templeton, 1988; Thorpe *et al.*, 1994).

An understanding of the phylogenetic position of *Bothrops caribbaeus* and *B. lanceolatus* may also have implications for their venom composition and the treatment of snakebite in the Caribbean. *Bothrops lanceolatus* envenoming has been documented to produce a unique syndrome different from that of other species of *Bothrops*. In addition to local symptoms such as pain, swelling, bleeding at the site of the bite, ecchymosis and necrosis, which are common to most crotaline envenomings, the systemic bothropic syndrome observed in Central and South America is characterised by the development of consumption coagulopathies and spontaneous systemic bleeding, depending on venom components which affect clotting factors as well as haemorrhagins which damage vascular endotheliums (Barrantes *et al.*, 1985; Kamiguti *et al.*, 1991). On the other hand, apart from similar local signs, the severity of systemic envenoming by *Bothrops lanceolatus* in Martinique was correlated with the development of multiple cerebral infarctions and/or other major vessel occlusion that may appear within 8 hours to 7 days after the bite in approximately 30 to 40% of cases (Thomas *et al.*, 1995, 1998). Infarctions can develop in patients who present initially with signs of moderate envenoming with normal blood clotting and low serum levels of venom antigens. The infarction process can involve several small vascular territories altogether, and is associated with the development of an isolated thrombocytopenia. Bogarin *et al.* (1999) demonstrated that *Bothrops lanceolatus* venom, obtained from 20 specimens collected at different locations in Martinique, is devoid of thrombin-like enzymes and of *in vitro* coagulant and defibrinating activities, and is not coagulant when added to human citrated plasma, even at concentration as high as 100 µg/mL. These data suggest that thromboses observed in human *B. lanceolatus* envenoming result from a toxin-linked vasculitis process rather than from a systemic procoagulant effect. However, the exact thrombogenic mechanism responsible for these thromboses remains unexplained.

The monophyly of *Bothrops lanceolatus* and *B. caribbaeus* leads to the prediction that these snakes may share venom properties, which may in turn be of importance for the treatment of patients bitten by these snakes. In particular, do bites by *B. caribbaeus* result in a similar thrombotic syndrome as observed in *B. lanceolatus*? *Bothrops caribbaeus* envenoming was poorly documented until now. However, the case of a 32 year old man who was bitten in Saint Lucia and who subsequently developed multiple cerebral infarctions in the anterior and posterior cerebral artery territories was recently published (Númeric *et al.*, 2002). The clinical presentation of this patient was identical to that of patients bitten by *Bothrops lanceolatus*. Thus, envenomings from these two species develop a unique systemic thrombotic syndrome, which differs fundamentally from the defibrination and bleeding syndrome that characterizes all other *Bothrops asper-atrox* complex envenomations. This example suggests that, at least in some cases, an understanding of the phylogeny of medically important snakes can help predict the syndrome of envenoming to be expected from a hitherto undocumented species.

Our results also have implications for the conservation of the Antillean *Bothrops*. Our data show that both *B. caribbaeus* and *B. lanceolatus* represent relatively old, independent evolutionary lineages, and not recent offshoots of widespread South American taxa. Conservation policy on their respective islands needs to take this into account. Although Lazell (1964) described both *B. lanceolatus* and especially *B. caribbaeus* as common (and Dowling, 1965, reported similar experiences for the latter), more recent workers have reported these snakes to be harder to find (Powell & Wittenberg, 1998). These observations indicate that *B. caribbaeus* and *B. lanceolatus* may have suffered a decline in population numbers over the last few decades, and that a reassessment of their conservation status should be a priority.

Finally, this paper also represents an opportunity to clarify some confusion surrounding the nomenclature and synonymy of the Caribbean *Bothrops*. As noted by Hoge & Romano Hoge (1978/79) and subsequent authors, the St. Lucian lancehead was described under several different names by Gray (1842). Species of *Bothrops* described by Gray (1842) include *B. cinereus* ('America'), *B. sabinii* ('Demerara'), and *B. subscutatus* ('Demerara'). Gray (1849) also described *B. affinis* ('Demerara' and 'Berbice').

The types of *B. sabinii* and *B. subscutatus* were the specimens collected by Capt. (later Col.) Sabine discussed by Underwood (1993), and are unquestionably assignable to *B. caribbaeus* (Underwood, 1993; pers. obs.), of which the names *B. subscutatus* and *B. sabinii* therefore represent senior synonyms. However, the precedence of Garman's well-established name *B. caribbaeus* over Gray's disused names was formally established by Wüster (2000).

The female type specimen of *Bothrops cinereus*, considered *incertae sedis* by Peters & Orejas-Miranda (1970) and conspecific with *B. caribbaeus* by Hoge & Romano Hoge (1978/79) and Powell & Wittenberg (1998), has 31 scale rows at midbody and 224 ventral scales. These counts are consistent with *B. lanceolatus*, but not with *B. caribbaeus*; *B. cinereus* is thus a junior synonym of *B. lanceolatus*. The syntypes of *B. affinis* are assignable to *B. atrox*, and are consistent with Guyanan populations of that species based on both scalation (24–27 dorsal scale rows, 189–200 ventrals) and colour pattern.

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## Appendix 1

Origin and vouchers of samples sequenced in this study. Institutional Codes for vouchers: IB = Instituto Butantan, São Paulo, Brazil, Herpetological Collection. FHGO = Fundación Herpetológica Gustavo Orcés, Quito, Ecuador. INHMT = Instituto de Higiene y Medicina Tropical ‘L. Izquieta Pérez’, Guayaquil, Ecuador. ROM = Royal Ontario Museum, Toronto. WW = Wolfgang Wüster collection. Collection numbers refer to preserved specimens unless otherwise stated. Photographs and/or morphological data for many unvouchered specimens are available from the first author.

*Bothrocophias microphthalmus*: ECUADOR: Zamora Chinchipe: Cuenca del Río Jamboe: Pumbami. FHGO 2566. *Bothrops alternatus*: BRAZIL: Paraná: Pinhão. IB 55314. *B. asper*: Belize: Mile 38, Western Highway. WW 264. *B. atrox*: BRAZIL: Pará: Santa Isabel. WW 735. Maranhão: São Bento: WW 723. FRENCH GUYANA: Mana. WW 554. GUYANA: NorthWest District: Baramita. ROM 22848. SURINAME: Coronie District: 7.5 km E. Totness. WW 537. *B. brazili*: ECUADOR: Morona Santiago: Macuma. FHGO 982. *B. caribbaeus*: SAINT LUCIA: Grande Anse. WW 144 WW 148. *B. colombiensis*: VENEZUELA: Guárico: Altagracia de Orituco. WW 74. Falcón: San Francisco. J.L. Yrausquin, live coll. Guaibacoa. J.L. Yrausquin, live coll. *B. insularis*: BRAZIL: São Paulo: Ilha da Queimada Grande. Released after sampling. *B. jararaca*: BRAZIL: Paraná: Piracuará. WW 926. *B. jararacussu*: BRAZIL: São Paulo: Cananéia. IB 55313. *B. lanceolatus*: MARTINIQUE. Not vouchered. *B. leucurus*: BRAZIL: Bahia: Porto Seguro. IB 55480–1; Salvador. IB 55478. Espírito Santo: Domingos Martins. IB 55557. *B. marajoensis*: BRAZIL: Pará: Ilha de Marajó: 10 km NW Camará. WW 80. Santa Cruz do Arari: WW 943. *B. pulcher*: ECUADOR: Zamora Chinchipe: Estación Científica San Francisco. FHGO live coll. 2142. *B. punctatus*: ECUADOR: Pichincha: Pedro Vicente Maldonado. FHGO live coll. 2166. *B. taeniatus*: ECUADOR: Morona Santiago: Macuma. FHGO 195.

# A contribution to the systematics of two commonly confused pitvipers from the Sunda Region: *Trimeresurus hageni* and *T. sumatranus*

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**SYNOPSIS.** The systematics of two Southeast Asian green pitviper species, *Trimeresurus hageni* and *T. sumatranus*, are investigated by canonical variate analysis. Preliminary results reveal two morphological forms corresponding to mainly *T. hageni* in West Malaysia, Thailand and Singapore and *T. sumatranus* in Borneo. Allopatric populations of both taxa are examined from Sumatra. Geographic variation is present in both species, which are distinguished mainly by head scalation, but also by colour and pattern.

## INTRODUCTION

*Trimeresurus sumatranus* (Raffles, 1822) and *T. hageni* (Lidth de Jeude, 1886) are closely related species, occupying low elevations in undisturbed forests and having largely overlapping ranges. The systematics of these species and their precise distribution is an area of long-standing confusion. Many workers assign both species to *T. sumatranus* by default (Tweedie, 1983; Lim, 1991; Jintakune, 1995; David and Vogel, 1996) and the status of *T. hageni* has been in dispute since its initial description (Lidth de Jeude, 1886; Lidth de Jeude, 1890; Boulenger, 1896; Brongersma, 1933).

*T. hageni* was described as a separate species from *T. sumatranus* on the basis that only one or two supralabial scales are in contact with the subocular (compared with three in *T. sumatranus*), and the dark edges on head and body scales and dorsal cross-bands that are characteristic of *T. sumatranus* are not present (Lidth de Jeude, 1886). The species' distribution is widely debated, but specimens from south Thailand, West Malaysia and Singapore are normally assigned to *T. hageni*, and specimens from Borneo are normally assigned to *T. sumatranus* (David and Vogel, 1996; Cox *et al.*, 1998; Stuebing and Inger, 1999), but see Dring (1979) who placed specimens in the NHM collections from West Malaysia, southern Thailand and Sarawak in *T. sumatranus*. Both species are thought to occur on Sumatra and surrounding islands (Brongersma, 1933; Dring *et al.*, 1989; Cox *et al.*, 1998).

There have been few attempts to resolve the systematics of *T. hageni* and *T. sumatranus* since their initial description; these have been based on small sample sizes and a traditional character-by-character approach (Boulenger, 1896; Brongersma, 1933). Given the levels of geographic, ontogenetic and sexual variation usually present in viper species (Wüster *et al.*, 1992; Malhotra and Thorpe, 1997), the systematics of these taxa is best approached using modern statistical methods based on a broad range of morphological characters. In this paper, we present preliminary results from an ongoing investigation of the systematics and interrelationships of *T. hageni* and *T. sumatranus*.

## MATERIALS AND METHODS

We examined 78 specimens from museum collections in the United States, Europe and Malaysia (Figure 1). A total of 93 characters

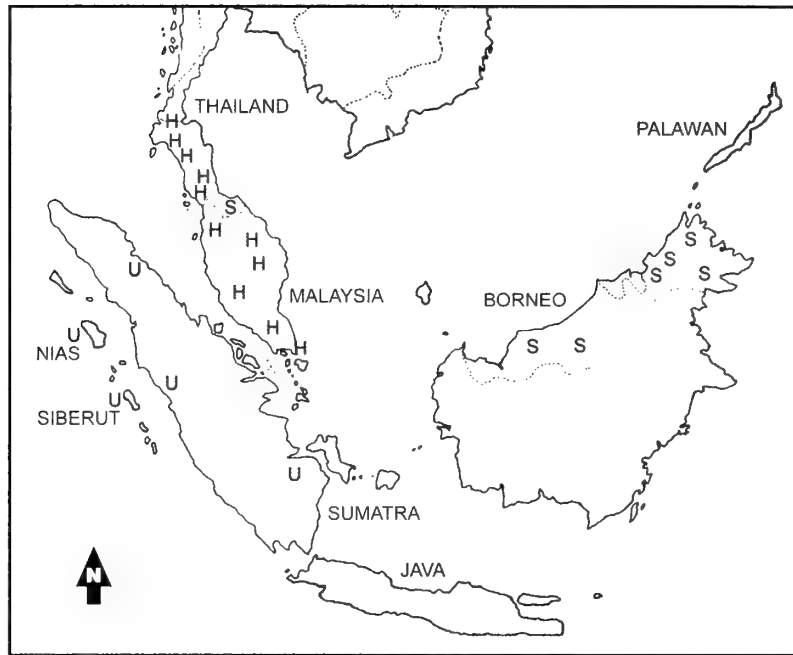
relating to scalation, colour and pattern were recorded for each specimen. Ventral scales were counted from head to vent, with the first ventral identified according to the method of Dowling (1951). The positions of scale reductions along the body (recorded as the number of the ventral or subcaudal scale opposite which it was situated) were transformed to percentage ventral scale (%VS) or caudal scale (%CS) position, in order to compensate for variation in ventral and subcaudal scale number. Male and female specimens were treated separately in all analyses to avoid bias caused by sexual dimorphism.

Specimens were grouped by locality into operational taxonomic units (OTUs). Two groups dominated the analysis, one was comprised of specimens from Thailand, West Malaysia and Singapore, and another was comprised of specimens from Borneo (Sabah and Sarawak). These groups were shown to be monophyletic by molecular analysis (unpublished data), which revealed a clear distinction between western specimens that lacked dorsal cross-bands and had at most two supralabials connected to the subocular scale, and eastern specimens that had dorsal cross-bands and had three supralabials in contact with the subocular scale. Molecular data was not available for specimens from Sumatra, and these were grouped individually to avoid combining sympatric species in one OTU.

Each OTU was checked prior to further analysis using Principal Component Analysis, which does not require that individuals be assigned groups prior to the analysis. The integrity of the OTUs was confirmed with the exception of one specimen from Betong (south Thailand), which had dark banding and in the PCA ordination was closest to the Borneo OTU. In subsequent analysis this specimen was grouped separately from the other western specimens. The OTUs used and their sample size for each sex is listed in Table 1.

Variation between OTUs was tested for individual characters by means of one-way analysis of variance (ANOVA). Only characters showing significant between-OTU variation were used in subsequent analyses. These are presented in Table 2.

Canonical variate analysis (CVA) was used to investigate patterns of geographic variation between OTUs. This method maximises the separation between groups relative to variation within groups. It is a standard multivariate method and has been applied successfully to numerous models of geographic variation in reptiles (Wüster *et al.*, 1992; Thorpe *et al.*, 1994; Daltry *et al.*, 1996).



**Fig. 1** Geographic origin of specimens used in multivariate analysis. S = *Trimeresurus sumatranus*; H = *Trimeresurus hageni*; U = unidentified specimens. Shading represents the known distribution of *T. hageni* and/or *T. sumatranus*.

**Table 1** List of OTUs and sample size for each sex.

OTU	Sample Size	
	Males	Females
Thailand, West Malaysia, Singapore	16	15
North Sumatra 1 (Medan)	1	1
North Sumatra 2 (Medan)	0	1
Central Sumatra 1 (Padang)	1	1
Central Sumatra 2 (Padang)	0	1
South Sumatra 1 (Palembang)	0	1
Nias	1	10
Siberut	3	3
East Malaysia	4	18
Betong (south Thailand)	1	0
Total	27	51

### Museum Acronyms

BMNH	The Natural History Museum, London, formerly the British Museum (Natural History), London
FMNH	Field Museum of Natural History, Chicago
IMR	Institute of Medical Research, Kuala Lumpur
KSP	Sabah Park Zoological Museum, Mount Kinabalu National Park, Sabah
MCZ	Museum of Comparative Zoology, Harvard
MHNG	Museum d'Histoire Naturelle de Geneva, Switzerland
NMBA	Naturhistorisches Museum Basel, Switzerland
NMW	Naturhistorisches Museum Vienna, Austria
QSMI	Queen Saovabha Memorial Institute, Bangkok
PH	Perhelitan, Kuala Lumpur
ZRC	Raffles Museum of Biodiversity Research, National University of Singapore, Singapore

### RESULTS

The CVA of males shows clear separation along the first canonical variate of specimens normally assigned to *T. hageni* from Thailand,

West Malaysia and Singapore and those normally assigned to *T. sumatranus* from East Malaysia. The Siberut and the single specimens from Nias and northern Sumatra are closest to the mainland *T. hageni* population. The specimens from Betong, Thailand and central Sumatra are closest to the Borneo OTU, but are well differentiated on CV2.

Analysis of females also shows strong differentiation between the Thailand, West Malaysia and Singapore OTU and the Borneo OTU. The Siberut and Nias specimens are phenotypically close to *T. hageni* from Thailand, West Malaysia and Singapore. Specimens from north and south Sumatra are also closely affiliated to this mainland population. The specimens from central Sumatra are closest to the Borneo population along CV1, although are clearly differentiated on CV2.

CVA analysis can be used to identify the characters that account for most variation between groups. In both sexes scalation characters were more important in distinguishing between the taxa than were characters relating to colour and pattern. The most important character is the fifth supralabial scale, which meets the subocular scale in *T. sumatranus* and in *T. hageni* is separated from the subocular by one scale. Also important is the frequent presence of an internasal scale in *T. sumatranus*, which is usually lacking in *T. hageni*. In addition, *T. sumatranus* has fewer supralabial scales and fewer scales between supraoculars than *T. hageni*. Our work verifies two of the original diagnostic characters used by Lidth de Jeude (1886) who described *T. hageni* as a distinct species that lacks dorsal cross-bands and has fewer supralabial scales in contact with the subocular scale. However, we did not find dark edging on head and body scales to be a valid diagnostic character on the basis that *T. hageni* specimens from Nias have very strong dark edges on their head and body scales.

### DISCUSSION

The results of this preliminary analysis reveal a major phenotypic

**Table 2** Characters used for multivariate analysis of *T. sumatranus* & *T. hageni*.

Characters	Males	Females
1. No. of ventral scales	—	*
2. No. of subcaudal scales	—	*
3. %VS position of reduction from 21 to 19 body scale rows	*	*
4. %VS position of reduction from 19 to 17 body scale rows	—	*
5. %DV position of reduction from 19 to 17 body scale rows	—	*
6. %VS position of reduction from 17 to 15 body scale rows	*	*
7. %CS position of reduction from 14 to 12 tail scale rows	—	*
8. %DV position of reduction from 14 to 12 tail scale rows	—	*
9. %CS position of reduction from 10 to 8 tail scale rows	—	*
10. %DV position of reduction from 10 to 8 tail scale rows	—	*
11. %CS position of reduction from 8 to 6 tail scale rows	*	*
12. %CS position of reduction from 6 to 4 tail scale rows	—	*
13. No. of supralabial scales	*	*
14. No. of sublabial scales	*	*
15. No. of scales bordering the supraocular scales	*	*
16. Minimum no. of scales separating the supraocular scales	*	*
17. Maximum no. of scales separating the supraocular scales	*	*
18. No. of internasal scales	*	*
19. No. of scales separating the fourth supralabial scale from the subocular scale	*	*
20. No. of scales separating the fifth supralabial scale from the subocular scale	*	*
21. No. of scales contacting the suboculars, excluding the preoculars and postoculars	*	*
22. Average no. of scales between the first ventral scales and the anterior genial scales	<	*
23. No. of scales between the last sublabial scales and first ventral scales	*	*
24. Presence of stripe on dorsal scale row one	*	—
25. No. of scale rows involved in stripe	*	—
26. Presence of postocular stripe	—	*
27. No. of scale rows involved in postocular stripe	—	*
28. Presence of dark edging on body scales	*	*
29. No. of bands on body	*	*
30. Mean no. of scales of three half bands on body	—	*
31. Mean no. of scales between three half bands on body	—	*
32. Presence of dark edging on head scales	*	*

\* indicates significance value  $p < 0.05$  (ANOVA).

division in both sexes. This corresponds to *T. sumatranus* in Borneo, central Sumatra and southern Thailand and *T. hageni* in southern Thailand, West Malaysia, Singapore, north Sumatra, south Sumatra, Nias and Siberut. The species are best distinguished by head scalation, but can also be identified by colour and pattern.

Geographic variation is also present at the intra-specific level. The Siberut and Nias specimens show stronger differentiation in males than in females. Their phenotypic similarity to mainland *T. hageni* is based mainly on scalation characters. Moreover, on the basis of colour and pattern, the Nias population is quite distinct with head and body scales strongly edged in black. Nias was last connected to Sumatra in the geologically recent past (c. 18,000 years ago), whereas Siberut has been isolated for around one million years (Dring *et al.*, 1989). The extent to which these populations have diverged from the mainland population will be investigated using molecular methods and may lead to taxonomic revisions.

Sumatran populations are represented by few specimens, but these exhibit the same general pattern in males and females: *T. sumatranus* from central Sumatra appear to be strongly differentiated from the Borneo OTU, whereas *T. hageni* from north and south Sumatra are only weakly differentiated from the mainland OTU. This pattern will be tested when additional data becomes available. An analysis of the phylogenetic relationships of these populations, using mitochondrial sequence data, is also underway and should help to clarify their status.

**ACKNOWLEDGEMENTS.** We thank our collaborators at the University of Science, Malaysia, and in particular Dr. Shahrul Anuar. We also thank the staff and curators of the following institutions for allowing us access to their

specimens: BMNH, FMNH, IMR, KNP, MCZ, MHNG, NMBA, NMW, PH, QSMI, ZRC. This study was supported by the Natural Environment Research Council studentship to KLS (NER/S/A2000/03695), the Leverhulme Trust (F/174/I and F/174/O), the Wellcome Trust (057257/Z/99/Z and 060384/Z/00/Z), and the Darwin Initiative (162/6/65) with additional support for fieldwork from the Linnaean Society of London, Side, Bonhote, Omer-Cooper and Westwood Fund.

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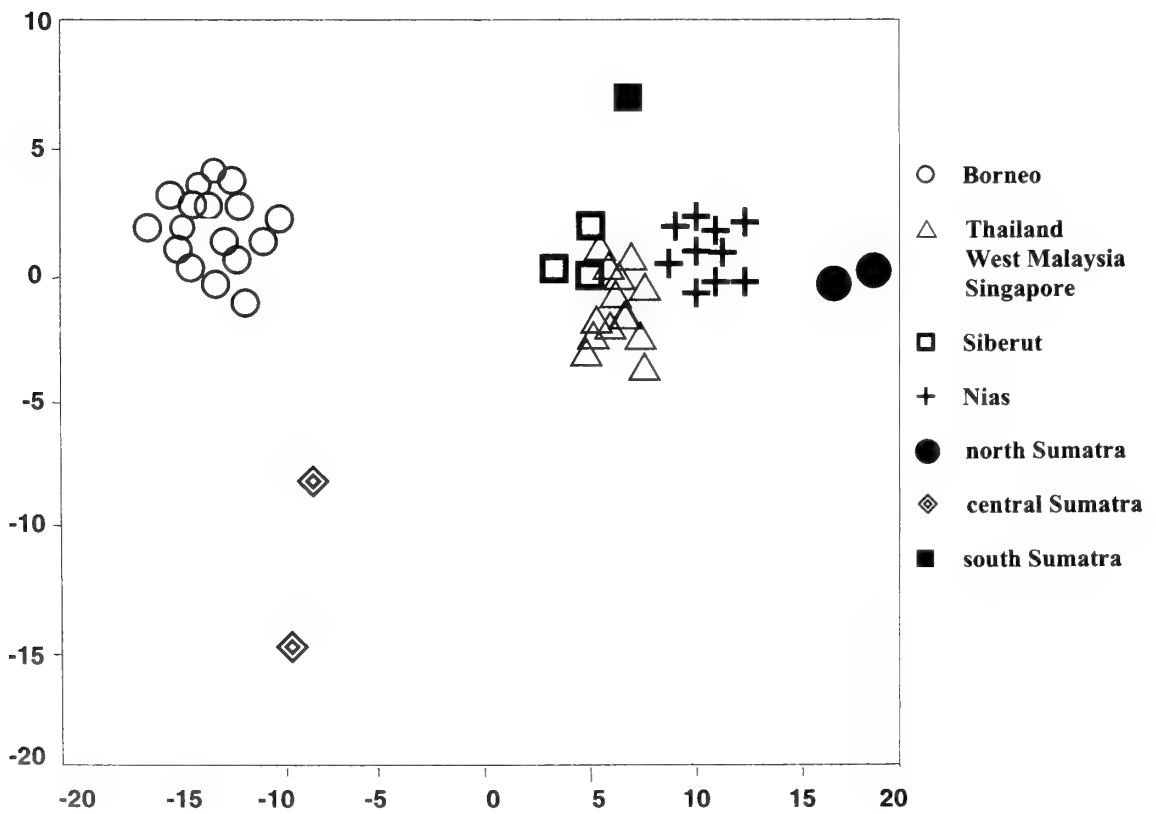
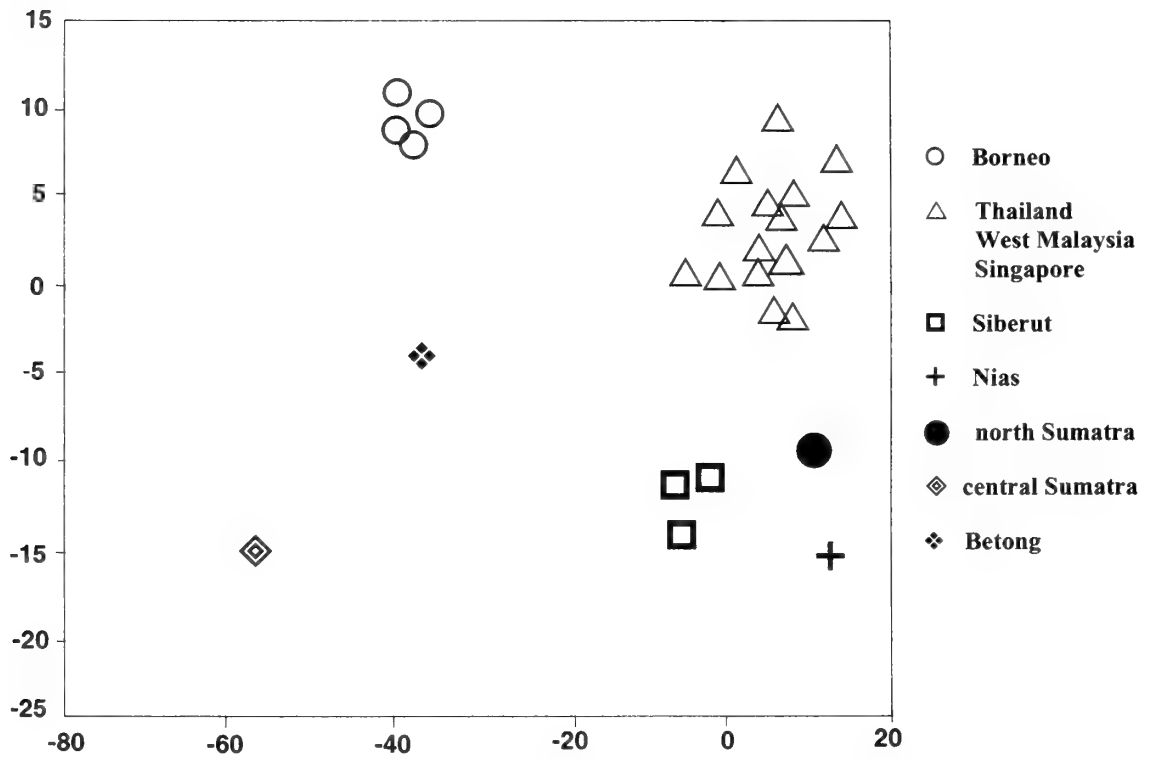


Fig. 2 Canonical Variate Analysis of *T. hageni* and *T. sumatranus* populations (top = males; bottom = females).



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## Appendix 1 Specimens used in morphological analysis

MUSEUM/FIELD REF	LOCALITY	SEX
QSMI	Pangna, Thailand	M
QSMI 11190	Krabi, Thailand	M
MHNG 2072.87	Surat Thani, Thailand	M
MHNG 2072.89	Surat Thani, Thailand	M
MHNG 1403.95	Singapore	M
MCZ 132799	Kuala Lumpur, W. Malaysia	F
PH	Krau WR, W. Malaysia	F
PH	Tapa, W. Malaysia	F
PH	Selangor, W. Malaysia	F
PH no.79	Kuala Jasin, W. Malaysia	F
PH no.134	Ulu Gombak, W. Malaysia	F
FMNH 183787	Janda Baik, W. Malaysia	F
FMNH 183788	Ulu Gombak, W. Malaysia	M
FMNH 143948	Selangor, W. Malaysia	M
FMNH 138690	Kapit District, Sarawak	F
FMNH 138689	Kapit District, Sarawak	F
FMNH 148829	Kapit District, Sarawak	F
FMNH 148830	Kapit District, Sarawak	F
FMNH 138687	Kapit District, Sarawak	F
FMNH 239948	Kota Mardu, Sabah	F
FMNH 239959	Mendolong, Sabah	F
FMNH 243943	Mendolong, Sabah	F
FMNH 230064	Danum Valley, Sabah	F
FMNH 230063	Danum Valley, Sabah	F

FMNH 239952	Tenom, Sabah	F
FMNH 239950	Tenom, Sabah	F
FMNH 239958	Tenom, Sabah	F
FMNH 239957	Tenom, Sabah	F
FMNH 239947	Kota Mardu, Sabah	M
FMNH 138688	Kapit District, Sarawak	M
NMBA 9179	Nias, Indonesia	M
NMBA 5108	Palembang, Sumatra	F
NMBA 22401	Pangna, Thailand	M
NMW 28160.4	Nias, Indonesia	F
NMW 28160.3	Nias, Indonesia	F
NMW 28160.2	Nias, Indonesia	F
NMW 28160.1	Nias, Indonesia	F
NMW 28157.1	Nias, Indonesia	F
NMW 28156.1	Nias, Indonesia	F
NMW 23909.2	Medan, Sumatra	M
NMW 28159.4	Medan, Sumatra	F
NMW 23909.3	Medan, Sumatra	F
NMW 28159.2	Padang, Sumatra	F
NMW 23909.4	Padang, Sumatra	F
NMW 28159.1	Padang, Sumatra	M
NMW 28158.1	Kedah, W. Malaysia	F
NMW 28158.2	Kedah, W. Malaysia	F
BMNH 1936.9.12.3	Betong, Thailand	M
BMNH 1884.1.8.47	Nias, Indonesia	F
BMNH 1884.1.8.46	Nias, Indonesia	F
BMNH 1884.12.31.13	Nias, Indonesia	F
BMNH 1884.12.31.14	Nias, Indonesia	F
BMNH 1977.1237	Siberut, Indonesia	M
BMNH 1979.267	Siberut, Indonesia	F
BMNH 1979.268	Siberut, Indonesia	M
BMNH 1978.1879	G.Mulu, Sarawak	F
BMNH 1880.9.10.7	Singapore	F
BMNH 1936.9.12.5	Kuala Teku, W. Malaysia	M
BMNH 1967.2290	G.Benom, W. Malaysia	M
KSP 04361	Kota Mardu, Sabah	F
KSP 04362	Bukit Tawau, Sabah	F
IMR 103649	Bukit Lakai, W. Malaysia	F
IMR 104270	Simpang, W. Malaysia	F
IMR 104271	Ulu Gombak, W. Malaysia	F
IMR 105684	Ulu Gombak, W. Malaysia	F
IMR 95995	Simpang, W. Malaysia	M
ZRC 2.2938	Siberut, Indonesia	M
ZRC 2.2937	Siberut, Indonesia	F
ZRC 2.2936	Siberut, Indonesia	F
KLS 01129	Poring, Sabah	M
KLS 01119	Poring, Sabah	M
KLS 0008	Endau Rompin NP, W. Malaysia	F
KLS 0199	Perak, W. Malaysia	M
AFS 9815	Songkhla, Thailand	M
AFS 97b20	Satun, Thailand	F
AFS 0005	Kuala Lumpur, W. Malaysia	F

AFS/KLS indicate wild caught specimens examined under anaesthesia.



# Underwood's classification of the geckos: a 21<sup>st</sup> century appreciation

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**SYNOPSIS.** The publication in 1954 of Underwood's 'On the classification and evolution of geckos' was the first comprehensive attempt to understand the systematics, evolution and biogeography of this group of lizards. Combining the use of the exploration of novel characters with a global overview of geckos, Underwood erected hypotheses of relationship and patterns of distribution. In the 48 years since that landmark publication much has changed, but much has stayed the same. Underwood's division of geckos into four major clusters is still recognised today, although the sphaerodactyls are now regarded as a group derived from within the gekkonines, and the diplodactylines have been diminished by the removal of several genera and their placement in the gekkonines. The framework that Underwood established has resulted in generic and/or species level phylogenies being generated for the eublepharids, some sphaerodactyls, the carphodactyline diplodactylines and some clusters within the gekkonines. The latter group, because of its size, has remained intractable to detailed systematic analysis at the generic level, although the recognition of many discrete monophyletic clusters within the Gekkonidae (the Gekkoninae of Underwood) holds out the possibility that greater levels of intergeneric resolution are close to realisation.

Underwood's initial approach to the systematic analysis of geckos was distinguished by its use of novel characters of the visual system that led to new insights. It is possible that the next breakthrough in higher level systematic analysis of geckos may again come from the exploitation of new character sources. Some examples of these possibilities are discussed.

## INTRODUCTION

'[We] would like to make a distinction between *how* [Dr. Underwood] thought about the classification of [gekkotans] and *what* he thought, since in [our] view how a man thinks is far more important than what he thinks ... [we] suggest that *how* [Underwood] thought about classification survives untarnished to this day. Does *what* he thought about it bear critical scrutiny nearly fifty years later?' With these words (bracketed modifications aside) Garth Underwood (1971a) began his *A Modern Appreciation of Camp's 'Classification of the Lizards'*. Nearly 50 years after its publication we here consider Underwood's classification of the Gekkota, its central position in the study of these lizards, its influence on subsequent work in the field and how its conclusions have been modified over the intervening decades. This work was Underwood's first substantial contribution to squamate evolution, preceding other major contributions to the systematics of pygopods (Underwood, 1957) and snakes (Underwood, 1967) and establishing the way he was to think about and employ character analysis in approaches to what had previously been regarded as rather intractable problems.

Garth Underwood was interested in both the theory and practice of systematics and also in the evolutionary morphology of the organisms that he chose as the subjects of his systematic analyses. He was bold in embracing novel sources of data for his systematic analyses, put forward hypotheses of relationship in the hopes that they would be scrutinised and evaluated by others, and frequently returned to systematic problems that he had already published some years earlier to bring fresh insights and approaches. Specimens always figured prominently as a primary source of inspiration and new data.

A comparison of the lizard families recognised by Boulenger (1885), Camp (1923), and most modern workers (e.g., Macey *et al.*, 1997; Harris *et al.*, 1999) reveals almost no discrepancies. The gekkotan lizards, however, are an exception. Until the middle of the 20<sup>th</sup> century, lizard systematists variously recognised the Eublepharidae and Uroplatidae as entities distinct from the Gekkonidae. Different classificatory schemes reflected not only different interpretations of characters, but alternative views of the systematic meaning of novel morphologies. For most of the time after the description of the first gecko genera by Laurenti (1768), gecko systematics was dominated by alpha systematic treatments and the allocation of newly discovered species to an ever growing number of genera, defined chiefly by externally discernible digital features. This reliance on digital characters as almost the sole determinant of affinity resulted in the widespread recognition of composite genera constituted by digitally convergent taxa. Further, the focus on foot structure did little to resolve higher order relationships among gekkotans, as the digital characters then recognised suggested many discrete clusterings of species, but provided few putative links between them.

Garth Underwood was led to the topic of gecko classification, which he (1954:469) characterised as 'far from stable', through his research on the reptilian eye. His earlier work on retinal morphology (Underwood 1951a) and pupil shape (Underwood 1951b) had both highlighted the distinctiveness of the gecko eye and suggested that ophthalmological characters could be of use in the resolution of higher order relationships among the many gecko genera. Underwood's optimism that the eye could provide useful characters was bolstered by the then recent work of Bellairs (1948), who had conclusively demonstrated that the true eyelids of the eublepharid geckos were primitive to the derived condition of a well-developed

brille and lack of moveable lids typical of other geckos. Further, Walls (1942) and Prince (1949) had examined the eyes of some geckos in their broader ophthalmological treatments, suggesting avenues for further research.

Walls' (1942) comprehensive treatment of the vertebrate eye led Underwood to hypothesise that this organ system could yield useful and stable associations of characters. The general recognition of the retinal characteristics of the eyes of geckos as evidence of secondary nocturnality, and a preliminary survey (Underwood 1951b) of the form of the pupil suggested that a more intensive survey of pupil form may provide a means by which gekkonids could be subdivided into more manageable and meaningful subsets reflective of their evolutionary history. Underwood (1954) set himself the task of surveying a moderately comprehensive collection of preserved geckos at the Museum of Comparative Zoology, Harvard University, and to analyse the resulting data. He used these data to erect the first modern generic level analysis of gekkotan relationships. He recognised potential problems with character state interpretation caused by state of preservation and the limitations of a single-character classification, but nonetheless regarded pupil character states to be sufficiently discrete for the purpose of establishing a workable classification of geckos, which would be subject to modification as additional data became available. Werner (1977) later demonstrated that pupil shape and dilation change with differing light levels, and these observations have helped refine Underwood's (1954) initial conclusions (see below).

## UNDERWOOD'S CLASSIFICATION OF THE GECKOS

Underwood (1954) recognised three families of gekkotan lizards. The Eublepharidae was characterised by true eyelids, the lack of a spectacle and vertical pupils reflective of the nocturnal adaptations of the family. The five genera he included were those subsequently placed by Kluge (1967a) in his Eublepharinae, and by Kluge (1987) and Grismer (1988) in the Eublepharidae. [Note: The current allocation of taxa employed in this article is based upon Kluge, 2001]. Underwood (1954) considered *Aeluroscalabotes* as the most primitive member of the family. It has subsequently been regarded as the sister group of all remaining eublepharids (Grismer, 1988).

Underwood's Sphaerodactylidae was supported by the presence of a round, diurnal-type pupil (or elliptical or straight vertical pupil in some cases), the existence of a fovea, and the presence of a spectacle. He included five genera therein, corresponding to Kluge's (1967a) Sphaerodactylinae and later Sphaerodactylini (Kluge 1987, 1995).

All remaining genera were placed in the Gekkonidae, characterised by a spectacle and lack of a fovea. Pupil shape was variable. Within the Gekkonidae he recognised two subfamilies, the Diplodactylinae and the Gekkoninae. The former had vertical pupils with straight margins, or circular pupils. He included 22 genera in this group. Among them are all of the genera now assigned to the Diplodactylinae by Kluge (1967a) except for *Eurydactylodes*, *Pseudothecadactylus*, and *Crenadactylus*. Underwood had doubts about the placement of the first of these genera (see below), specimens of which he had not examined himself, and changed its allocation the following year (Underwood 1955). *Crenadactylus ocellatus* was examined but was included with *Phyllodactylus* in the Gekkoninae by Underwood (1954). The Diplodactylinae was subsequently retained by Kluge (1987) and Bauer (1990a), although its affinities with the Pygopodidae were uncertain (see below).

Stephenson and Stephenson (1956) regarded New Zealand geckos (*Hoplodactylus* and *Naultinus*) as the most primitive forms on the basis of Underwood's (1955) revised view that amphicoelous vertebral centra are primitive within lizards and within the Gekkota. Furthermore, Stephenson (1960) rejected Underwood's (1954) ophthalmological division of the Gekkonidae into two subfamilies as it was inconsistent with osteological characters, but neither Underwood nor Stephenson 'correctly' placed all Australian genera.

Also included in Underwood's Diplodactylinae were several genera not now regarded as closely allied to the Australo-Pacific diplodactylines: *Aristelliger*, *Chondrodactylus*, *Colopus*, *Gymnodactylus*, *Palmatogecko*, *Phelsuma*, *Ptenopus*, *Rhoptropella*, *Rhoptropus*, *Saurodactylus*, and *Teratoscincus*. Four of these, *Chondrodactylus*, *Colopus*, *Rhoptropus*, and *Palmatogecko*, share many features in common with each other and with *Pachydactylus* (placed by Underwood [1954] in the Gekkoninae). Kluge (1967a) moved these taxa to the Gekkoninae, and Russell (1972) and Haacke (1976) established the affinities of these forms as part of the *Pachydactylus* group (see below).

Two other taxa, *Rhoptropella* and *Phelsuma*, have also been regarded as being closely related to one another (see below). Both of these genera, as well as all remaining ones, were moved to the Gekkoninae by Kluge (1967a) and have remained there since, with *Teratoscincus* as the sister group of all other gekkonines. The affinities of *Gymnodactylus* have remained problematic (Abdala 1988, 1996; Abdala and Moro 1996), as have those of *Aristelliger* (Russell and Bauer 1993), and *Ptenopus* (Bauer 1990b), whereas *Saurodactylus* has been considered allied to the sphaerodactyline lineage (Kluge 1995). Underwood's *Phyllurus* also included within it a species now assigned to the gekkonine genus *Nactus*.

The Gekkoninae were characterised by *Gekko*-type pupils or secondarily circular pupils. Underwood's (1954) Gekkoninae, although lacking the taxa mentioned above (and with the addition of *Eurydactylodes*, and *Crenadactylus* as *Phyllodactylus ocellatus*) otherwise included all of the genera placed in the group by Kluge (1967a). This grouping also included *Uroplatus*, which by virtue of a large suite of autapomorphic features had been accorded separate familial status by many previous workers (see Bauer and Russell 1989 for a review). In this regard, Underwood's (1954) results were similar to those of Wellborn (1933), who had based her conclusions on osteological data. Underwood did not rely entirely on the pupil character, however, as *Lygodactylus*, with round pupils, was placed in the Gekkoninae on the basis of other (digital) similarities with *Hemidactylus*.

Nine genera were not assigned to family or subfamily by Underwood. Five of these were unplaced due to lack of material. The remaining four were taxa with round pupils that were regarded as secondarily diurnal gekkonids, but which Underwood considered, on the basis of existing data, could not be allocated to one or the other of his two subfamilies. Of the latter, one genus, *Ancylodactylus*, has been synonymized with another, *Cnemaspis*. The other two were *Quedenfeldtia* and *Pristurus*. Of the genera not examined, *Ceramodactylus* has since been subsumed in *Stenodactylus*, and *Dravidogecko* has been synonymized with *Hemidactylus*.

Underwood also recognised some instances of convergence among geckos. Specifically he addressed the allocation of species of leaf-toed geckos (then chiefly distributed in *Diplodactylus* and *Phyllodactylus*), and bent-toed geckos (then mostly placed in *Gymnodactylus*). Among the leaf-toed geckos, pupil shape suggested the transfer of several species of African *Diplodactylus* to *Phyllodactylus*. These geckos are now regarded as members of the genus *Urocotyledon* (Kluge, 1983) and are, as Underwood indicated, correctly assigned to the Gekkonidae rather than the Diplodactylidae.

*Diplodactylus*, as recognised by Underwood, corresponds to two currently recognised genera, *Diplodactylus* and *Strophurus*. His reconstituted *Phyllodactylus* included forms now placed in that genus as well as *Asaccus*, *Afrogecko*, *Euleptes*, *Christinus*, *Crenadactylus*, *Paroedura* and *Urocotyledon* (based on his list of specimens examined). He also separated *Narudasia* from *Quedenfeldtia*, and divided the then cosmopolitan *Gymnodactylus* into four genera: *Gymnodactylus* (restricted to South America), *Phyllurus* (corresponding to the current *Phyllurus* and *Saltuarius*, but also including the species *vankampeni*, now allocated to the gekkonine genus *Nactus*), *Cyrtodactylus* (including representatives of *Cyrtodactylus*, *Geckoella*, *Tenuidactylus*, *Mediodactylus*, *Nactus*), and *Wallsaurus* (the latter now synonymized with *Homonota*, a genus listed as unexamined by Underwood).

## STEPS TOWARDS FURTHER SYSTEMATIC RESOLUTION

Underwood's (1954) classification provided a springboard for subsequent systematic work on geckos. The four large units he established were 'corrected' by Kluge (1967a), but remained as the chief elements in Kluge's higher order treatment of the group. Moffat (1973) generally accepted Kluge's (1967a) allocation of genera to subfamilies but disagreed with his methodology and his pattern of subfamilial relationships.

### Eublepharidae

The most stable unit has been the Eublepharidae. This group was retained intact by Kluge (1967a), although reduced to subfamilial rank. All subsequent researchers have accepted the monophyly of this group and more recent treatments have reflected the phylogenetic position of the Eublepharidae as the sister-group of all other gekkotans by again according it familial rank (e.g. Grismer 1988). Further, patterns of relationship within the eublepharids have been established at the generic and species levels (Grismer, 1988, 1991, 1994; Grismer *et al.*, 1999; Ota *et al.*, 1999). In this instance, Underwood (1954) chiefly used primitive features in diagnosing the family (e.g. true eyelids present, etc.) but subsequent research has identified numerous synapomorphies that support the reality of this monophyletic unit (Grismer, 1988; Ota *et al.*, 1999).

### Sphaerodactylidae

The Sphaerodactylidae of Underwood has remained unchanged in terms of generic content. Kluge (1967a) recognised the group as a subfamily and considered it to be highly derived, in contrast to Underwood (1954), who interpreted it as a primitively diurnal group and a relatively early offshoot of the gekkotan lineage. Subsequently Kluge (1987) demonstrated that sphaerodactyls are derived from within gekkonines, confirming their monophyly while obviating their recognition as a higher order group, as such recognition would render the Gekkoninae paraphyletic. This arrangement also received support from reproductive characters including the restriction of the calcareous eggshell to gekkonines and sphaerodactylines (Bustard 1968; Werner 1972). Kluge (1995) later conducted an explicit investigation of the phylogeny of the sphaerodactyls, yielding a fully resolved generic level pattern for the group. Kluge (1995) regarded the gekkonine *Pristurus* as the immediate sister group of the sphaerodactyls and considered *Quedenfeldtia*, *Cnemaspis*, *Narudasia* and *Saurodactylus* as other appropriate outgroup taxa for his analysis (see below). Of these outgroup genera, Underwood

examined material of only *Narudasia* and *Saurodactylus*. Species level analyses within individual sphaerodactyl genera are ongoing and have been attempted for the largest genus, *Sphaerodactylus* (Hass 1991, 1996).

### Diplodactylinae

The composition of the Diplodactylinae has changed most significantly. Kluge (1967a, b) removed a large number of genera from this group to the Gekkoninae, leaving only forms with parchment-shelled eggs in his Diplodactylinae, and provided a generic level hypothesis of relationships among the remaining forms. Bauer (1990a) erected a species level hypothesis of relationships among the Carphodactylini, one of two tribal groups established by Kluge (1967a). Additional hypotheses at the species level have been presented by Good *et al.* (1997) and Vences *et al.* (2001). The Diplodactylini, also established by Kluge (1967a), has yet to be investigated phylogenetically at the species level, although Kluge (1967b) erected a generic level hypothesis of relationships and King (1987b) suggested a species level phylogeny of *Diplodactylus* based on several karyotypic characters. Underwood (1954) had purged the genus *Diplodactylus* of two taxa with *Gekko*-type pupils, rendering a cluster of taxa still accepted as monophyletic. However, he retained in *Phyllodactylus* the species *ocellatus*, which has since been recognised as a diplodactyline and placed in the genus *Crenadactylus*.

Although the content of Underwood's (1954) Diplodactylinae as a whole has changed little, argument persists over patterns of internal relationship. In particular, the monophyly of the Carphodactylini has been called into question (Donnellan *et al.* 1999) and the relationship of New Zealand taxa has also been re-evaluated (Chambers *et al.* 2001). King (1987b) and King and Mengden (1990), based on chromosomal data, argued that *Oedura* was more closely allied to the Carphodactylini than to other Diplodactylini, and that pygopods are also allied to the carphodactylines. Donnellan *et al.* (1999), based on molecular data (12SRNA, c-mos), regarded the Diplodactylini, including *Oedura*, as monophyletic, but suggested that the Carphodactylini is paraphyletic. They found pygopods to be the sister group of all Diplodactylines.

Patterns of relationship within the Diplodactylinae have further been complicated by the recognition that pygopods are more closely related to this group (or some component thereof) than to other gekkotans (Kluge 1987). On this basis, Kluge (1987) recognised a redefined Pygopodidae for the group that includes diplodactyline geckos plus pygopods. Good *et al.* (1997), based in part on arguments presented by Bauer (1990a), proposed an alternative higher level scheme, recognising the Diplodactylidae as a family level group. Based on the patterns of relationship retrieved by Donnellan *et al.* (1999), the Diplodactylidae and Pygopodidae are sister taxa.

As mentioned above, the genus *Eurydactylodes* proved particularly problematic to Underwood (1954) and he only included it in his Diplodactylinae in the following year (Underwood, 1955). For a variety of reasons, this genus has continued to be enigmatic, exhibiting an odd mosaic of characteristics. Although *Eurydactylodes* appears to be a member of a monophyletic New Caledonian carphodactyline radiation (Bauer 1990a), it possesses a number of features that are problematic and, at least superficially, link it to other groups of geckos. One such feature is the tail-squirting apparatus. Members of this genus have caudal glands that secrete a sticky substance as a defensive mechanism. Such mechanisms have been widely reported in arthropods (Deslippe *et al.* 1996), and amphibians (Arnold 1982), but among amniotes have been noted only for geckos of the Australian diplodactyline genus *Strophurus* (Rosenberg

and Russell 1980) and *Eurydactylodes* (Böhme and Sering 1997). Although the secretion has not been characterised, it is likely similar to that of *Strophurus* spp., which is proteinaceous (Rosenberg *et al.* 1984) and is effective in deterring at least some small predators, such as spiders, which become entangled in the secretion (Minton 1982). However, both the anatomy of the gland and the ejection mechanism of secretion differ between the two gecko genera, suggesting that the apparatus in convergent (Böhme and Sering 1997). *Eurydactylodes* is also convergent with *Strophurus* in its bright yellow-orange mouth coloration. Most geckos have unpigmented buccal linings.

*Eurydactylodes* also shares some features with gekkonid geckos. Most notable is the presence of extracranial endolymphatic sacs in the neck region, especially in juveniles and reproductive females. These calcium-storing structures frequently form conspicuous bulges on the necks of gekkonids, but in diplodactylids are intracranial and contain little calcium. *Eurydactylodes* is an exception in that very large sacs are often present, in some individuals artificially increasing the apparent size of the head (Bauer 1989). Perhaps related to this, the eggshells of *Eurydactylodes*, although similar in most regards to those of typical carphodactylines, are covered by a calcified outer surface (Bauer and Sadlier 2000), which otherwise typifies gekkonids (Bustard, 1968; Werner, 1972).

## Gekkoninae

The Gekkoninae was the most heterogeneous and unwieldy of Underwood's higher order groups and it has remained largely intractable to this day. Indeed, as a result of the resolution of the content of the Diplodactylinae, the Gekkoninae has grown significantly. Further, the vast majority of all new or resurrected genera since 1954 are gekkonines. Underwood (1954) initiated the process of dismantling some of the larger gekkonid genera that he recognised as polyphyletic assemblages of digitally convergent taxa. In particular he addressed the composition of *Phyllodactylus* and *Gymnodactylus*, two of the largest and most cosmopolitan taxa.

Subsequent reduction of *Phyllodactylus* occurred with the removal of *Crenadactylus* and its shift to the Diplodactylinae (Dixon and Kluge 1964), and the placement of several geographically coherent gekkonine leaf-toed forms into *Paroedura* (Dixon and Kroll 1974), *Asaccus* (Dixon and Anderson 1973), *Urocoryledon* (Kluge 1983), and *Christinus* (Wells and Wellington 1983). All remaining Old World leaf-toed geckos were removed from the now strictly American *Phyllodactylus* by Bauer *et al.* (1997), who erected *Haemodracon*, *Dixonius*, *Afrogecko*, *Cryptactites* and *Goggia*, and resurrected *Euleptes*. Nussbaum *et al.* (1998) further provided a new generic name for the elongate-bodied leaf-toed geckos of Madagascar, *Matoatoa*. Arnold and Gardner (1994) also provided a species level phylogeny for *Asaccus*, using a variety of Old and New World leaf-toed geckos as outgroup taxa, but without explicit justification. Both these authors and Nussbaum *et al.* (1998) suggested that at least some phyllodactyl taxa might be closely related.

A similar dismantling of *Gymnodactylus* was begun by Underwood (1954), who removed *Phyllurus* to the Diplodactylinae and recognised the genera *Gymnodactylus*, *Cyrtodactylus* and *Wallsaurus* for a subset of the naked-toed geckos. Subsequently Golubev and Szczerbak (1981) and Szczerbak and Golubev (1984) divided the Old World forms placed by Underwood in *Cyrtodactylus*, which they regarded as polyphyletic, into several genera, including the Palearctic *Tenuidactylus*, *Cyrtopodion*, *Mesodactylus*, *Carinatio-gecko*, *Mediodactylus* and *Asiocolotes*. Tropical forms were divided into *Cyrtodactylus*, *Geckoella* and *Nactus* (Kluge 1983).

The effect of these actions has been to dismantle several larger, clearly polyphyletic groups and to instead recognise a larger number

of smaller, but putatively monophyletic, genera. The problem remains, however, that relationships among these genera are poorly resolved. While the identification of monophyletic units is a necessary first step in the resolution of gekkotan relationships, the increase in the number of such units increases the sampling required in order to erect a hypothesis of relationship across all members of the group. This has been the major stumbling block in the phylogenetic interpretation of the Gekkoninae: any attempt to resolve relationships among some subset of genera of necessity requires an analysis of virtually all other genera. The sheer diversity of the group has been an impediment to its resolution.

Despite the difficulty of determining relationships among gekkonines, some clusters of genera that appear to be monophyletic have been identified. These groups are chiefly those that share highly distinctive and generally restricted derived conditions. Thus, such groups have typically been identified on the basis of information intrinsic to themselves rather than on the basis of outgroup comparison. Indeed, when outgroup analysis has been attempted, the choice of outgroup has been based on geography (e.g., Joger 1985; Bauer 1990b; Abdala 1996; Macey *et al.* 2000) or on some preconceived notion of similarity, usually based on digital anatomy (e.g., Arnold and Gardner 1994; Macey *et al.* 2000). Chromosomal characteristics of gekkonids are highly heterogeneous (King 1987c), but such variation may occur within genera and thus has contributed little to the resolution of higher order relationships.

One of the most substantially supported subgroups of gekkonines is the *Pachydactylus* group. This is a cluster of genera sharing the unique feature of hyperphalangy of digit I of both the manus and pes. The group includes the chiefly Mediterranean genera *Tarentola* and *Geckonia* and the southern Africa forms *Pachydactylus*, *Rhoptropus*, *Chondrodactylus*, *Colopus*, and *Palmatogecko*. Underwood (1954) recognised the relationship of all of these except *Pachydactylus* itself, placing them in the Diplodactylinae and identifying a peculiar pupil shape, the *Rhoptropus*-type, that all shared. Several species of *Pachydactylus* (e.g., *P. austeni*, *P. kochi*) are strikingly similar, even in external appearance, to *Colopus* and *Palmatogecko*. By chance, however, Underwood's (1954) list of taxa examined reveals that he did not examine any of these species. Hyperphalangy had previously been identified in some members of the group by Wellborn (1933), but her sampling was inadequate to highlight the potential phylogenetic value of the feature. Russell (1972, 1976) and Haacke (1976) recognised the significance of hyperphalangy and argued convincingly that this was evidence of the relatedness of these taxa. Virtually all subsequent workers (Bauer 1990b, 2000; Kluge and Nussbaum 1995; Lamb and Bauer 2002; but see Joger 1985) have agreed that these seven genera (including collectively approximately 80 species) form a monophyletic group. With closely related taxa thus identified, species level phylogenies have been possible within constituent genera (e.g., *Rhoptropus*: Bauer and Good 1996, Lamb and Bauer 2001; *Pachydactylus*: Lamb and Bauer 2000, 2002).

Other clusterings, although less well investigated, have also been proposed, although not necessarily tested. The *Gekko* group, consisting of *Gekko*, *Gehyra*, *Hemiphyllodactylus*, *Lepidodactylus*, *Luperosaurus*, *Perochirus*, *Pseudogekko*, and *Ptychozoon*, all share similarities of digital structure (Kluge 1968; Russell 1972, 1976) and are probably a monophyletic group, although particular patterns of intergeneric relationship remain untested.

The large and heterogeneous genus *Hemidactylus* seems to be related to a number of much smaller genera that are also similar digitally, and are united by synapomorphies of size and shape of the intermediate phalanges (Russell, 1977a). *Dravidogekko*, for example, has been synonymized with *Hemidactylus* on the basis of digital

morphology (Bauer and Russell 1995). In addition, *Cosymbotus*, *Briba* and *Teratolepis* are also very similar and are almost certainly share a common ancestry with *Hemidactylus*, or are derived from within it.

Bauer (1990b) found some evidence for the recognition of a Madagascan radiation including several genera of leaf and fan-toed geckos including *Uroplatus*, *Ebenavia* and *Paroedura*. Kluge and Nussbaum (1995) did not retrieve identical patterns of relationship, but these genera nonetheless grouped closely when only Afro-Malagasy geckos were included in the analysis. An expanded Indian Ocean lineage, including these taxa plus *Ailuronyx*, *Blaesodactylus*, *Homopholis*, and *Geckolepis* was retrieved by Bauer (1990b), although not by Kluge and Nussbaum (1995).

Another putatively monophyletic group is the *Lygodactylus* complex (Pasteur 1964), which includes two additional genera, at least one of which, *Millotisauros*, is probably derived from within *Lygodactylus* (Pasteur, 1995; Krüger, 2001). *Lygodactylus* itself clustered with *Phelsuma* in analyses constrained to include only Afro-Malagasy genera (Bauer 1990b; Kluge and Nussbaum 1995). Krüger (2001) also clustered *Lygodactylus* and *Phelsuma* together.

Although some genera have been revised at the alpha level, and numerous new taxa have been erected, most revisions have merely proposed species groups, without providing explicit hypotheses of relationship (e.g. Pasteur 1964; Brown and Parker 1977; Nussbaum and Raxworthy 2000). These, like many of the other groups, share digital similarities and geographic cohesiveness. Among those genera for which some idea of relationships exist, there are several for which species level phylogenies have been proposed, including *Uroplatus* (Bauer and Russell 1989) and *Gehyra* (selected species only; King 1979, 1983).

*Rhoptropella* has been associated with several different genera by different authors. Russell (1977b) used digital morphology to argue that it was in fact a *Phelsuma*, with no direct affinities to *Rhoptropus*, with which it had previously been associated (e.g. Boulenger 1885). Russell and Bauer (1990) found additional support for this from histological investigations and Good and Bauer (1995) presented allozyme evidence for *Rhoptropella*'s links to *Phelsuma*. Both Bauer (1990b) and Kluge and Nussbaum (1995) found the two genera to be sister taxa when a generic analysis was conducted. Rösler (2001), discussing pholidosis, also concluded that *Phelsuma* and *Rhoptropella* are sister taxa. Röhl (1999), however, using ophthalmological and digital surface data, interpreted it as displaying features of both *Rhoptropus* and *Phelsuma*, which, if true, could suggest affinities between the chiefly African *Pachydactylus* group and the putatively monophyletic Indian Ocean complex. A variety of character types also suggest that *Bogertia* and *Thecadactylus* may be allied (Russell and Bauer 1988; Abdala and Moro 1996).

*Cnemaspis*, *Narudasia*, *Quedenfeldtia*, *Saurodactylus* and *Pristurus* have been proposed as gekkonine taxa basal to the sphaerodactyl lineage (Arnold 1993; Kluge 1995), demonstrating the paraphyly of the Gekkoninae. Although Kluge (1995) did not claim any specific relationships among these taxa, his analysis did yield patterns in which *Pristurus* was the sister group of the sphaerodactyls, and *Narudasia*, *Saurodactylus* and *Cnemaspis* formed a clade. Arnold (1993) advocated the pattern (((*Pristurus*, *Quedenfeldtia*) sphaerodactyls) *Saurodactylus*) *Narudasia*). Behavioural apomorphies unique to this cluster were documented by Rösler and Wranik (2001), who noted reproductive morphological apomorphies shared by *Quedenfeldtia* and the sphaerodactyls to the exclusion of *Pristurus*. Arnold (1993) provided a species level phylogeny for *Pristurus*. The African members of this group were also clustered together in an analysis of Afro-Malagasy taxa by Kluge and Nussbaum (1995). Röhl and Schwemer (1999) identified a

unique crystallin ligand common to several of these taxa (plus *Lygodactylus*), that they interpreted as synapomorphic. This was subsequently found in *Cnemaspis* (Röhl, in press), but whether this indicates affinity or convergence among secondarily diurnal forms remains to be determined.

The naked-toed geckos have proved especially difficult to deal with. Szczerbak and Golubev (1984, 1986) provided evidence of relationship among some Palearctic forms, such as *Tenuidactylus*, *Mediodactylus*, *Asiocolotes*, and *Cyrtopodion*. Macey *et al.* (2000) found evidence for the monophyly of *Cyrtopodion* and *Mediodactylus* and hypothesized relationships among a small number of species in each group. The generic allocation of certain Himalayan members of the group has proved especially problematic (Khan 1993; Khan and Rösler 1999).

Another group of naked-toed geckos including *Agamura*, *Bunopus*, *Alsophylax*, *Crossobamon*, *Microgecko*, and *Tropicolotes* has been even less well investigated (Leviton and Anderson 1972; Szczerbak and Golubev 1977; Golubev 1984; Golubev and Szczerbak 1985). The New World naked toed forms, *Gymnodactylus* and *Homonota*, have been included in analyses by Abdala (1996) and Abdala and Moro (1996) but these investigations included only South American gekkonines. Abdala (1988) also provided a species level phylogeny for *Homonota* (see also Vanzolini 1968).

While some degree of resolution for the gekkonine taxa outlined above has been reached, certain other gekkonines remain enigmatic and without any sound indication of affinities. *Teratoscincus* is highly unusual in its morphology, and appears to be the sister group of all remaining gekkonines (Kluge 1987). A species level phylogeny for this group has been generated (Macey *et al.* 1999). *Stenodactylus* has sometimes been considered to be allied to *Teratoscincus* (Kluge 1967a; Kluge and Nussbaum 1995), but its position remains equivocal (Arnold 1980).

Another perplexing padless genus is *Ptenopus*, a southern African endemic. Both Bauer (1990b) and Kluge and Nussbaum (1995) found little evidence for particular affinities, and constrained or retrieved a basal placement among African gekkonines. *Ptenopus* possesses a large number of autapomorphic traits (Haacke 1975; Rittenhouse *et al.* 1998; Russell *et al.* 2000). This mirrors the situation that plagued analyses of *Uroplatus* in that many features segregate these geckos from other taxa, but those traits that are shared are chiefly primitive ones.

Four pad-bearing genera, which appear unrelated to one another and have no obvious affinities to previously discussed groups, are also problematic. These are *Afroedura*, *Aristelliger*, *Calodactylodes*, and *Paragehyra*. *Paragehyra* was long known from a single specimen of a single species, but a second species was recently discovered (Nussbaum and Raxworthy 1994). The availability of additional material allowed the relationships of the genus to be investigated in more detail, but this has not yielded any definitive statements about its position within the Gekkoninae (Kluge and Nussbaum 1995), although Nussbaum and Raxworthy (1994) noted the similarity of the digits of this form to those of another enigmatic taxon, the West Indian *Aristelliger*.

Russell (1972) grouped *Afroedura* and *Calodactylodes* in the same digitally defined cluster. Loveridge (1944) had initially segregated *Afroedura* from the Australian *Oedura*, and this was reflected in Underwood's (1954) placement of the genera in different subfamilies. Some question as to the distinctiveness of these taxa remained, however, until Cogger (1964) conducted detailed osteological comparisons. Despite some similarities in digital design, Russell and Bauer (1989) concluded that *Calodactylodes* and *Afroedura* were more likely convergent than related. Bauer and Das (2000) noted some superficial similarity and geographic proximity

to *Asaccus*, but again concluded that the relationships of *Calodactylodes* were obscure.

*Aristelliger* was one of the taxa regarded as enigmatic by Underwood (1954). He placed it in the Diplodactylinae and regarded it as an archaic form, possibly unable to compete with the gekkonines, which he regarded as more derived. Indeed, he regarded it as being a basal gekkonid, retaining oil droplets in the eyes and displaying vertebral amphicoely. In part, Underwood's (1954) assessment of this genus may have been influenced by the fact that he was, at the time, based in the West Indies and had more information about it than most other geckos, and certainly more than any that he also placed in the Diplodactylinae. *Aristelliger* has been employed in a variety of evolutionary (Hecht 1952) and morphological (Ruibal and Ernst 1965) studies, probably because of ease of availability. These studies, however, have helped little to clarify the position of the taxon. Although it has rather complex external digital structure, anatomically it reveals a quite simple architecture. Thus more detailed studies of the digits (Russell 1976, 1979; Russell and Bauer 1990, 1993) have not assisted in placing it with other genera that typically show a more complex anatomy.

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## BIOGEOGRAPHIC AND EVOLUTIONARY IMPLICATIONS OF UNDERWOOD'S CLASSIFICATION OF THE GECKOS

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Underwood (1954) pioneered a comprehensive approach to gecko systematics. As a result of this, he was faced with issues of biogeography and evolution that begged an explanation. For geckos, this was essentially uncharted territory and the recognition of clusters, especially within his Gekkoninae, generated new biogeographic and evolutionary problems. Chief among these was the need to explain the biogeography and evolution of his Diplodactylinae. This proved especially challenging because, as noted above, this cluster of taxa later proved to be the least stable of Underwood's (1954) proposed units.

Underwood (1954) interpreted eublepharids, with their scattered distribution, as an ancient radiation with its own specialisations, chiefly to arid conditions, rather than as a cluster of relicts. He viewed the eublepharids as the primary, ancient Northern Hemisphere radiation of the Gekkota.

The sphaerodactylids were biogeographically non-problematic as all occur in the New World. Underwood (1954) viewed them as an early New World offshoot of the Gekkota, based on his belief that they were primitively diurnal, retaining certain plesiomorphic lacertilian ophthalmological features. Kluge's (1967) demonstration that the sphaerodactyls are derived from within the gekkonines, and subsequent recognition of secondary diurnality in the sphaerodactylines (Röll, in press) has resulted in a reinterpretation of sphaerodactyl biogeography and evolutionary history, with north African affinities being supported by more recent systematic investigations (Arnold, 1993; Kluge, 1995).

Underwood (1954) undertook to explain the distribution of the Diplodactylinae which, in his view, included a large core of Australo-Pacific taxa, but also genera from Africa and the Americas. He noted that no genus occupied more than one continent and that most genera had rather limited or patchy distributions. Only *Aristelliger* and the New Zealand taxa did not co-occur with Gekkonines. He felt that ovoviviparity might explain their ability to survive in New Zealand. In the case of *Aristelliger*, he noted that its occurrence was basically complementary to that of gekkonines, and suggested that it may have formerly had a broader distribution but had subsequently

withdrawn in the face of competition with gekkonine geckos. He viewed the gekkonines as a more modern, expanding group that was displacing diplodactylines from areas of previous occupancy. He regarded New Caledonia as marking the periphery of the range of the gekkonines, with *Lepidodactylus* and *Eurydactylodes* being relatively recent invaders into diplodactyline (*Rhacodactylus* and *Bavayia*) territory. He believed that *Phelsuma*, being chiefly insular, diurnal, and arboreal, was ecologically segregated from the gekkonines with which it co-occurs. He regarded its occurrence in mainland East Africa as a recent event. Its arrival on islands of the Indian Ocean was hypothesised to be as a nocturnal stock, an offshoot of the southern African cluster of diplodactylines, with a subsequent change in life style enabling it to coexist with gekkonines. He regarded most continental diplodactylines as being terrestrial, with arboreal forms being peripheral.

The foregoing rather tortuous scenario developed by Underwood (1954) to account for diplodactyline biogeography and evolution was the direct result of the recognition of, as it was formulated at the time, a polyphyletic assemblage. Removal of *Aristelliger*, *Phelsuma* and a variety of other taxa (see above) from the Diplodactylinae (Kluge, 1967) and inclusion of *Eurydactylodes* within it (Underwood, 1955) rendered biogeographic and evolutionary consideration of the remaining diplodactylids more tractable (Bauer, 1990a), but left the Gekkonidae (Underwood's Gekkoninae) yet more unwieldy. That some gekkonine genera were present on multiple continents suggested to Underwood (1954) that this was the dominant group. He recognised four major digital morphologies among gekkonines, and believed that each had reached most areas of the world and that most had radiated in situ in each area, giving rise to numerous regionally endemic genera. Thus, while expansion was an important theme in the evolution of gekkonines, there was significant within-region evolution as well. These ideas were obviously heavily influenced by those of Darlington (1948) and by the idea of competitive exclusion (a more ecological than historical view). He noted the waif dispersal capabilities of some geckos and opined that this complicated the picture of dispersal via land bridges that served as his main paradigm. The issue of waif dispersal, though recognised as being restricted to certain taxa, remains to this day as a confounding factor in the interpretation of the evolution of gekkonid spatial patterns.

Further systematic consideration (see above) has resulted in an increased complement of gekkonid genera, but has also resulted in some level of internal resolution, which, in turn, has influenced some aspects of biogeographic interpretation. For many regions, local radiations of monophyletic clusters of genera have been recognised, but resolution of pattern between these clusters remains poorly understood.

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## CONCLUSIONS

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Underwood's (1954) systematic, biogeographic and evolutionary considerations of geckos marked the first attempt to comprehensively assess this circumglobal and highly diverse cluster. His analyses brought some degree of order to a previously very poorly understood set of problems, and his choice of ophthalmological characters as those of primary consideration resulted in the establishment of a basic pattern that has survived to the present in modified form. Although Underwood (1968, 1970, 1971b, 1977a,b) revisited the gekkotan eye repeatedly, the promise of phylogenetic utility originally held out by ophthalmological data has not, until recently, been pursued. Röll (1995, 1997, 1999) and Röll and Schwemer (1999) have demonstrated that many diurnal geckos are



unable to modify pupil shape and instead regulate light through absorbance by crystallins in the lens. Although Röhl and Schwemer (1999) assumed that the use of particular crystallins was likely to have evolved only once, there is no evidence that all diurnal gekkonids are allied (e.g. *Phelsuma* + *Lygodactylus* and *Sphaerodactylus* + *Quedenfelia* + *Narudasia* + *Saurodactylus*; Kluge and Nussbaum 1995). This avenue of approach, however, suggests that at the anatomical and molecular level, data from the visual system may yet be of significance in assisting in the resolution of pattern between nocturnal and secondarily diurnal clusters of gekkonids (including sphaerodactyls).

Despite attempts to move away from digital architecture as a primary means of identifying suprageneric clusters, this has continued to play a role and has been instrumental, by way of examination of internal architecture, in assisting in the circumscription of a number of apparently monophyletic assemblages (Russell, 1976). Pedal anatomy remains a primary determinant of generic allocation and a major clue to potential higher order relationships (e.g., Nussbaum and Raxworthy 1994).

Changes in generic alignment and more modern views of plate tectonics have necessitated a rethinking of Underwood's (1954) biogeographic hypotheses. Essentially the eublepharids appear to represent an ancient Laurasian radiation, in keeping with Underwood's (1954) ideas. The remaining gekkotans are now regarded as being of Gondwanan origin and to consist of an essentially east Gondwanan diplodactylid radiation and a west Gondwanan gekkonid radiation, with the latter having given rise, in turn, to the New World sphaerodactyls.

Interpretation of patterns of relationship must now deal with the recognition that the age of the Gekkota is much greater than was believed in 1954 and that many genera might be quite ancient. Hence, generic body plans may have been established for very long periods, making them rather discrete from one another and rendering it difficult to erect hypotheses of relationship. Even among the sphaerodactyls, generic differentiation is estimated to have occurred as much as 40 million years ago (Hass 1991). King (1987a, 1987b), on the basis of chromosomal and immunological data correlated with tectonic history of the Australian region, estimated a minimum divergence of 66 my between the two major clades of diplodactylines, and at least 120 my for the origin of the gekkotans.

Despite the magnitude of the problem, only patterns of relationship within the rather amorphous Gekkonidae (Underwood's Gekkoninae) remain relatively unassailed. Even here, however, large, circumglobal unwieldy genera have been broken into smaller, more geographically circumscribed taxa and there is now an opportunity to begin to make inroads into the determination of the patterns of interrelationship of suprageneric clusters of gekkonid taxa. This may best be broached by taking exemplars, appropriately selected (Bininda-Emonds *et al.* 1998) from the putative clusters and the enigmatic genera, and investigating a combination of morphological and molecular data. Given the magnitude of the problem, this will be an iterative process and will necessitate frequent cross-checking within and between clusters. The boldness of Garth Underwood's approach will have to be adopted in selecting novel sources of data to allow new approaches to be taken and insights to be revealed.

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# The skull of the Uropeltinae (Reptilia, Serpentes), with special reference to the otico-occipital region

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**SYNOPSIS.** The skull anatomy of uropeltines is reviewed, and new data is presented on the highly derived otico-occipital region. A phylogenetic analysis of uropeltine interrelationships using parsimony is performed using characters derived from skull structure. The basal position of the genus *Melanophidium* is confirmed; *Pseudotyphlops* is a relatively derived uropeltine, in spite of its relatively large size. The monophyly of the genera *Melanophidium* and *Rhinophis* requires further testing.

## INTRODUCTION

Uropeltinae (Nopcsa 1923. The name is here used as by Kluge 1991, Fig. 4; see also Cundall *et al.* 1993) remain an enigmatic group of basal alethinophidian snakes. This is largely due to their burrowing habits and restricted distribution, and the consequent scarcity of material available in public repositories. We have studied the uropeltine skulls from the collections of The Natural History Museum, London, which permitted us to review the highly derived skull structure in this monophyletic clade of snakes.

The first detailed description of a uropeltine skull was given by Baumeister (1908) in a monograph on the genus *Rhinophis*. Peculiarities of the cranio-vertebral joint in the group were dealt with by Williams (1959), Underwood (1967), and Hoffstetter & Gasc (1969). Some aspects of the skull of uropeltines were described by Rieppel (1977, 1978, 1983), Bellairs & Kamal (1981), and Wever (1978), but none of these studies addressed details of the morphology of the otico-occipital complex. The lower jaw of uropeltines was described by Rieppel & Zaher (2000). In their detailed analysis of the cranial anatomy and phylogenetic relationships of *Anomochilus*, Cundall & Rossman (1993), and Cundall *et al.*, (1993), comment on various aspects of the skull structure of uropeltines, and their functional as well as phylogenetic significance. In particular, Cundall & Rossman (1993; see also Cundall & Greene 2000) recognized a fundamentally different design of skull adaptation to burrowing habits in scolecophidians and uropeltines (Fig. 1). The phylogenetic relationships of uropeltines within snakes were discussed in cladistic terms by Cundall *et al.* (1993), Scanlon & Lee (2000), and Tchernov *et al.*, (2000). Only one study has appeared so far that dealt with uropeltine interrelationships, based on microcomplement fixation techniques (Cadle *et al.* 1990). In this paper, we review the skull anatomy of uropeltines, adding new detail to previous descriptions (Rieppel 1977, 1978) and providing new data on the detailed morphology of the otico-occipital complex. These morphological characters are used in a phylogenetic analysis of uropeltine interrelationships, which will be compared to the results obtained by Cadle *et al.* (1990). This study is presented in honor of Dr. Garth Underwood, who more than 20 years ago introduced the senior author to the study of the skull of 'henophidian' snakes.

## MATERIAL EXAMINED

The present study is based on the investigation of the skull of the following taxa (generic names used in the manuscript refer only to the specimens here listed), arranged as outgroup taxa and in-group (uropeltine) taxa.

### Institutional abbreviations

BMNH, British Museum (Natural History), now The Natural History Museum; FMNH, Field Museum of Natural History, now The Field Museum.

Outgroup taxa: *Anilius scytale* (FMNH 35683); *Cylindrophis maculatus* (BMNH 1930.5.8.48); *Cylindrophis ruffus* (FMNH 179033); *Boa constrictor* (FMNH 22435, 22438); *Calabaria reinhardtii* (FMNH 31372); *Candoia aspera* (FMNH 13915); *Candoia b. australis* (FMNH 22997); *Lichanura roseofusca* (FMNH 31565); *Python molurus* (FMNH 223198); *Tropidophis pardalis* (FMNH 233).

In-group taxa: *Melanophidium punctatum* (BMNH 1930.5.8.119); *Melanophidium wynaudense* (BMNH 1930.5.8.124–125); *Platyplecturus madurensis* (BMNH 1930.5.8.111); *Plecturus perroteti* (BMNH 1930.5.8.105); *Pseudotyphlops philippinus* (BMNH 1978.1092); *Rhinophis drummondhayi* (BMNH 1930.5.8.67–68); *Rhinophis sanguineus* (BMNH 1930.5.8.59); *Teretrurus rhodogaster* (BMNH 1930.5.8.98); *Uropeltis woodmansoni* (BMNH 1930.5.8.73–74);

### Abbreviations used in the figures

**ang**, angular; **bo**, basioccipital; **com**, compound bone; **d**, dentary; **ec**, ectopterygoid; **f**, frontal; **ls**, laterosphenoid; **m**, maxilla; **n**, nasal; **oc**, otic capsule; **op-ec**, opisthotic-exoccipital; **p**, parietal; **pl**, palatine; **pm**, premaxilla; **po.vc**, posterior opening of Vidian canal; **prf**, prefrontal; **pro**, prootic; **pro.c**, prootic canal; **pro.r**, preorbital ridge; **pt**, pterygoid; **q**, quadrate; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **tr.f.r**, transverse frontal ridge; **v**, vomer; **II**, optic foramen; **V<sub>2</sub>**, trigeminal foramen (maxillary branch); **V<sub>3</sub>**, trigeminal foramen (mandibular branch); **VII**, facialis foramen; **X**, jugular foramen; **XII**, hypoglossal foramen.

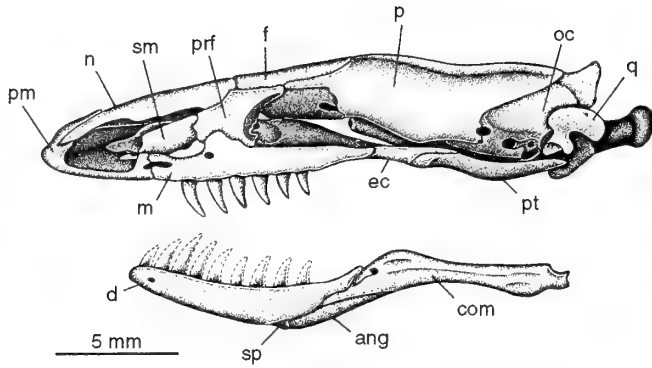


Fig. 1 The skull and mandible of *Pseudotyphlops philippinus* (BMNH 1978.1092) in left lateral view.

## GENERAL ASPECTS OF THE SKULL

The premaxilla of uropeltines is characterized by a single premaxillary foramen (Fig. 2). The vomerine processes of the premaxilla meet the vomer in a well-defined contact. The premaxilla of uropeltines shows characteristic variation within the group (Rieppel 1977; Cundall & Rossman 1993). The anterior margin of its transverse process is more or less evenly rounded in *Melanophidium*, which correlates with a gentle anteromedial curvature of the anterior end of the maxilla (Fig. 2A). The two bones closely approach each other, or barely establish contact. This genus therefore retains a plesiomorphic configuration of the snout, which is also inferred to be present in *Platyplecturus* (the specimen BMNH 1930.5.8.111 lacks the premaxilla, but retains the maxilla which shows an anteromedially curved anterior end), and which represents a condition similar to that seen in *Anomochilus* (Cundall & Rossman 1993). The other uropeltines have a similar premaxilla, which carries an anteriorly projecting, bipartite rostrum. The straight 'transverse' processes point posterolaterally, and meet the straight maxilla

in a shizarthrosis (Cundall & Rossman 1993; Fig. 2B–E). These two elements define the lateral margins of the strongly 'telescoped' (Haas 1930), i.e., tapering and pointed snout (see also Cundall & Rossman 1993, Fig. 25B).

The maxilla of basal alethinophidians carries an anterior medial process (Rieppel 1977; Scanlon & Lee 2000), which is particularly well developed in uropeltines, where it participates in the formation of a broadly overlapping contact between maxilla, premaxilla, and vomer. In *Melanophidium*, the anterior medial process of the maxilla is not engaged in any such contact, but freely underlaps the septomaxilla. In *Pseudotyphlops*, the anterior medial process of the maxilla overlaps a medially extending horizontal flange of the transverse process of the premaxilla in a complex, interlocking premaxillary – maxillary contact (Fig. 2B, D–E). *Rhinophis* and *Uropeltis* are unique in that the anterior medial process of the maxilla forms a well-defined sutural contact with an anterior lateral process of the vomer in front of the opening for Jacobson's organ.

The medial or choanal processes of the palatines of uropeltines are broad, arching over the choanal tubes and projecting ventrally again medial to the choanal tubes. Their ventral tips are embraced anteriorly by the posterior ends of the vomers, as is also the case in other basal alethinophidians (Cundall & Rossman 1993; Cundall *et al.* 1993; Rieppel 1983; Fig. 2, 3). The parasphenoid forms a sagittal interchoanal process that lies between the choanal processes of the palatines, as is also the case in *Anomochilus* and *Cylindrophis* (Cundall & Rossman 1993; Cundall *et al.* 1993). The dorsal lamina of the nasal is variously developed in uropeltines, but tends to be relatively broad and notched anterolaterally in species with a rounded snout, but slender and tapering to a fine tip in species with a strongly telescoped snout.

The snout complex is suspended from the rest of the skull at the naso-frontal joint (see Rieppel 1978, for details) and through the link provided by the prefrontal (Fig. 3). The maxilla of uropeltines carries a well-developed ascending process that is in a firm planar (i.e., not interdigitating) contact with the prefrontal. Medial to the ascending process, the superior alveolar nerve canal is open dorsally in uropeltines, appearing as a groove on the dorsal surface of the

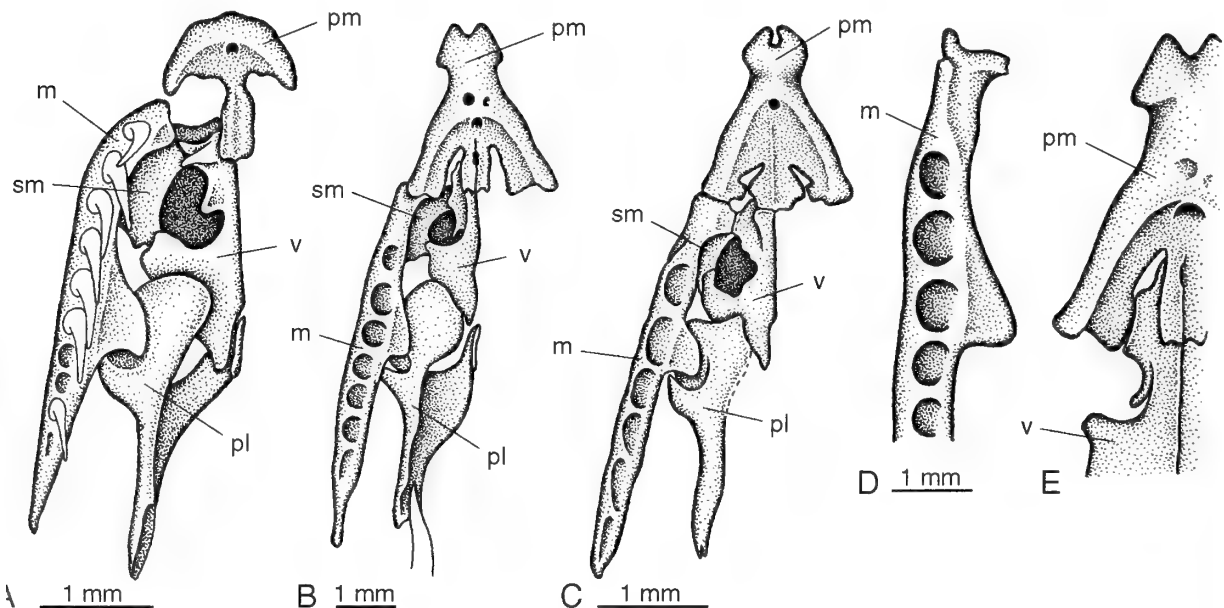


Fig. 2 A–E The palate in uropeltine snakes. A, *Melanophidium wynaudente* (BMNH 1930.5.8.124); B, *Pseudotyphlops philippinus* (BMNH 1978.1092); C, *Rhinophis sanguineus* (BMNH 1930.5.8.59); D–E, *Pseudotyphlops philippinus* (BMNH 1978.1092).

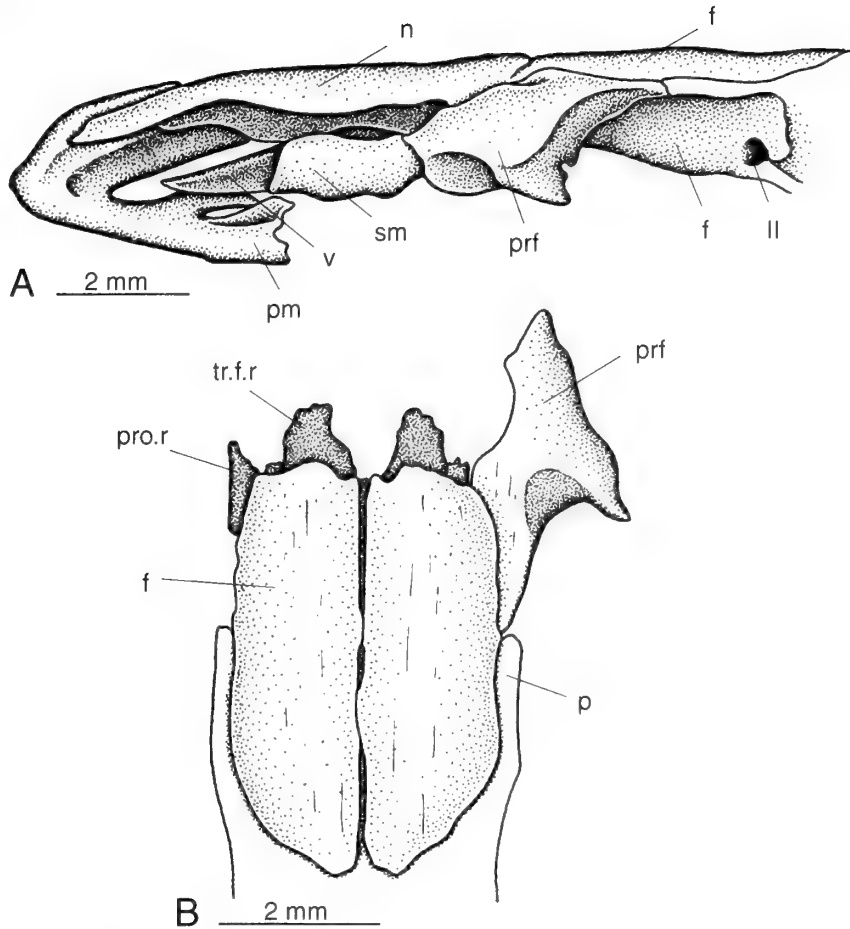


Fig. 3 The snout complex of *Pseudotyphlops philippinus* (BMNH 1978.1092).

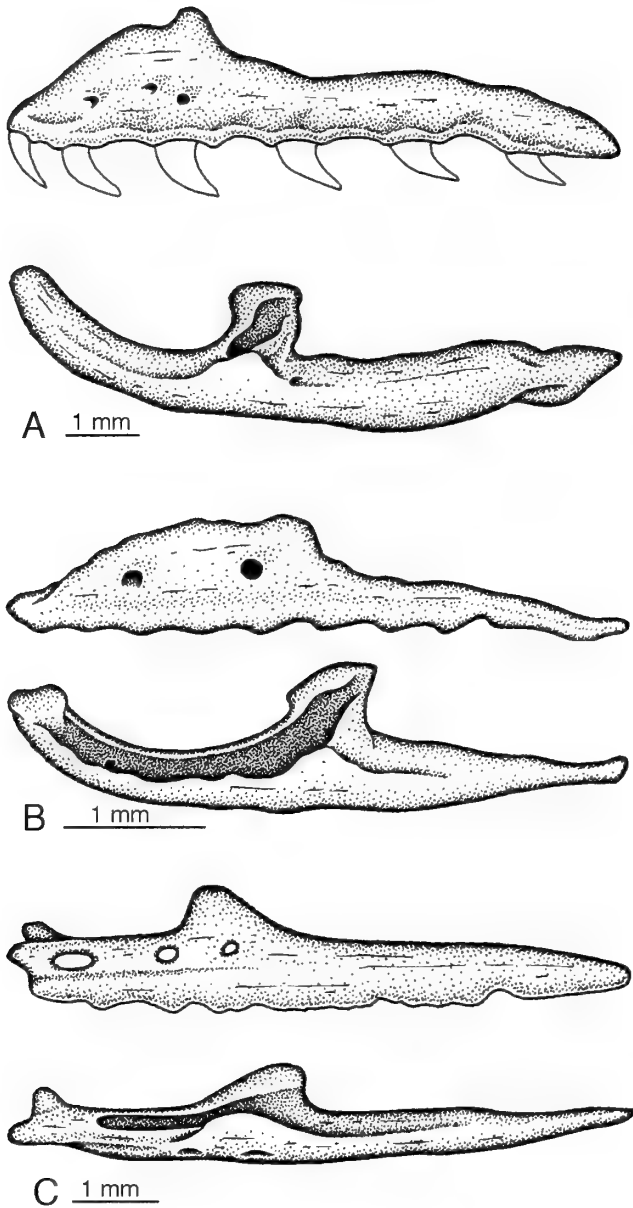
maxilla, a unique condition among snakes (Fig. 4). The suspension of the snout complex from the braincase is more elaborate in uropeltines than it is in other basal alethinophidians (Rieppel 1978).

The parietal of uropeltines forms distinct anterolateral, i.e., supraorbital processes which may or may not contact the prefrontal (Fig. 3). In *Cylindrophis maculatus* and in *Anomochilus* (Cundall & Rossman 1993), as well as in *Melanophidium punctatum*, the supraorbital process of the parietal participates in the suspension of the prefrontal. In other uropeltines, the contact between parietal and prefrontal may be reduced or absent, due to a relatively shorter supraorbital process of the parietal (this character is bilaterally variable in the skull of *Platyplecturus*). The optic foramen is located between the frontal and parietal in *Melanophidium* and *Platyplecturus*, but within the frontal in *Plecturus*, *Rhinophis*, and *Uropeltis* (Underwood, 1967: 64). In *Pseudotyphlops* (Fig. 3A) and *Teretrurus*, the optic foramen is a slit-like opening in the posterior margin of the frontal. The parietal carries a low sagittal crest in the relatively large *Pseudotyphlops* (Fig. 5C). In the other species with smaller skulls, such a sagittal crest is at best very faintly developed in the posterior part of the parietal (Fig. 5A–B). In some uropeltines such as *Rhinophis* and *Uropeltis* (Fig. 5B), the parietals are not completely fused in their posterior part. A supratemporal is absent in uropeltines, and the quadrate is suspended from the otic capsule in a relatively low position. The suprastapedial process of the quadrate is very elaborate in uropeltines, and as in *Anomochilus* (Cundall & Rossman 1993), it exceeds the shaft of the quadrate in length.

In *Anomochilus*, the anterior end of the edentulous palatine shows

some elaboration into a broader structure that receives the medial (palatine) process of the maxilla in a deep facet (Cundall & Rossman 1993, Fig. 2B). In uropeltines, the anterior process of the palatine is modified to form a broad wing which establishes a broad ventral overlap with the posterolateral part of the vomer, and which receives the well developed medial process of the maxilla in a deeply recessed lateroventrally facing facet (Fig. 2). The infraorbital nerve (maxillary division of the trigeminal nerve) pierces the bottom of this recessed facet to become the superior alveolar nerve. The morphology of the palatine in *Anomochilus* is intermediate between that of *Cylindrophis* on the one hand, and that of uropeltines on the other (Cundall & Rossman 1993). Palatine teeth are absent in *Anomochilus* and uropeltines with the exception of *Melanophidium wynaudente*. The ectopterygoid and pterygoid are reduced in uropeltines (and even more so in *Anomochilus*: Cundall & Rossman 1993), and the pterygoid is edentulous.

The para-basisphenoid is relatively broad in uropeltines, gradually becoming narrower anteriorly and tapering to a pointed tip between the choanal processes of the palatines. The ventral surface of the para-basisphenoid is distinctly convex in *Pseudotyphlops* resulting in the formation of ventrolateral ridges. These are at best weakly, or only very faintly, developed in other, smaller, species with a para-basisphenoid that has a flat or even slightly convex ventral surface. Along the lateral edge of the para-basisphenoid the ossified crista trabecularis ends behind the anterior margin of the laterally descending flange of the parietal in most taxa except for *Teretrurus* and *Rhinophis drummondhayi*, where it ends at the anterior margin of the



**Fig. 4** A–C A, The left maxilla of *Cylindrophis maculatus* (BMNH 1930.5.8.48) in lateral and dorsal views; B, The left maxilla of *Melanophidium wynaudense* (BMNH 1930.5.8.124) in lateral and dorsal views; C, The left maxilla of *Pseudotyphlops philippinus* (BMNH 1978.1092) in lateral and dorsal views.

laterally descending flange of the parietal. In *Rhinophis sanguineus* and *Uropeltis*, the crista trabecularis extends further anteriorly and terminates below the optic foramen that is located in the frontal. In front of the ossified crista trabecularis, the cartilaginous trabecula cranii is embedded in all taxa in a deep furrow located between the lateral margin of the parasphenoid and the ventrally projecting margin of the frontal. Tiny fontanelles may persist along the line of fusion of the basisphenoid and basioccipital in *Rhinophis* and *Uropeltis*.

## THE OTICO-OCCIPITAL COMPLEX

The otico-occipital complex is here considered to include the prootic, opisthotic-exoccipital, supraoccipital, and basioccipital. These brain-

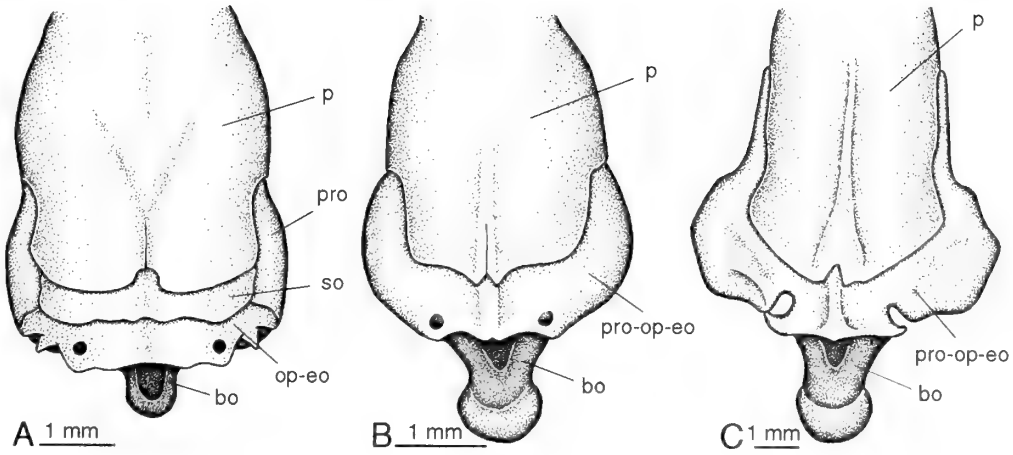
case elements show a variable degree of fusion with each other among the specimens examined (Fig. 6). All braincase elements except the opisthotic and exoccipital remain separate from one another in *Melanophidium*. All braincase elements are fused with one another in *Plecturus*, *Pseudotyphlops*, *Rhinophis* and *Uropeltis*, but the basioccipital remains separate from the basisphenoid in *Teretrurus*. The exoccipitals and basioccipital are always fused in the occipital condyle. The stalk of the occipital condyle is short in *Melanophidium*, *Platyplecturus*, and *Teretrurus*, but distinctly elongated in the other taxa investigated, such that the depression of the basioccipital housing the brainstem is exposed in dorsal view (Fig. 5). The exoccipitals define the dorsal margin of the foramen magnum, and their posterolateral corners are either deeply notched, or perforated by a foramen.

A laterosphenoid is always present in uropeltines, but while it remains a relatively narrow element in *Melanophidium* (Fig. 6A–B) and *Pseudotyphlops* (Fig. 6C), it becomes distinctly broadened in the other taxa investigated.

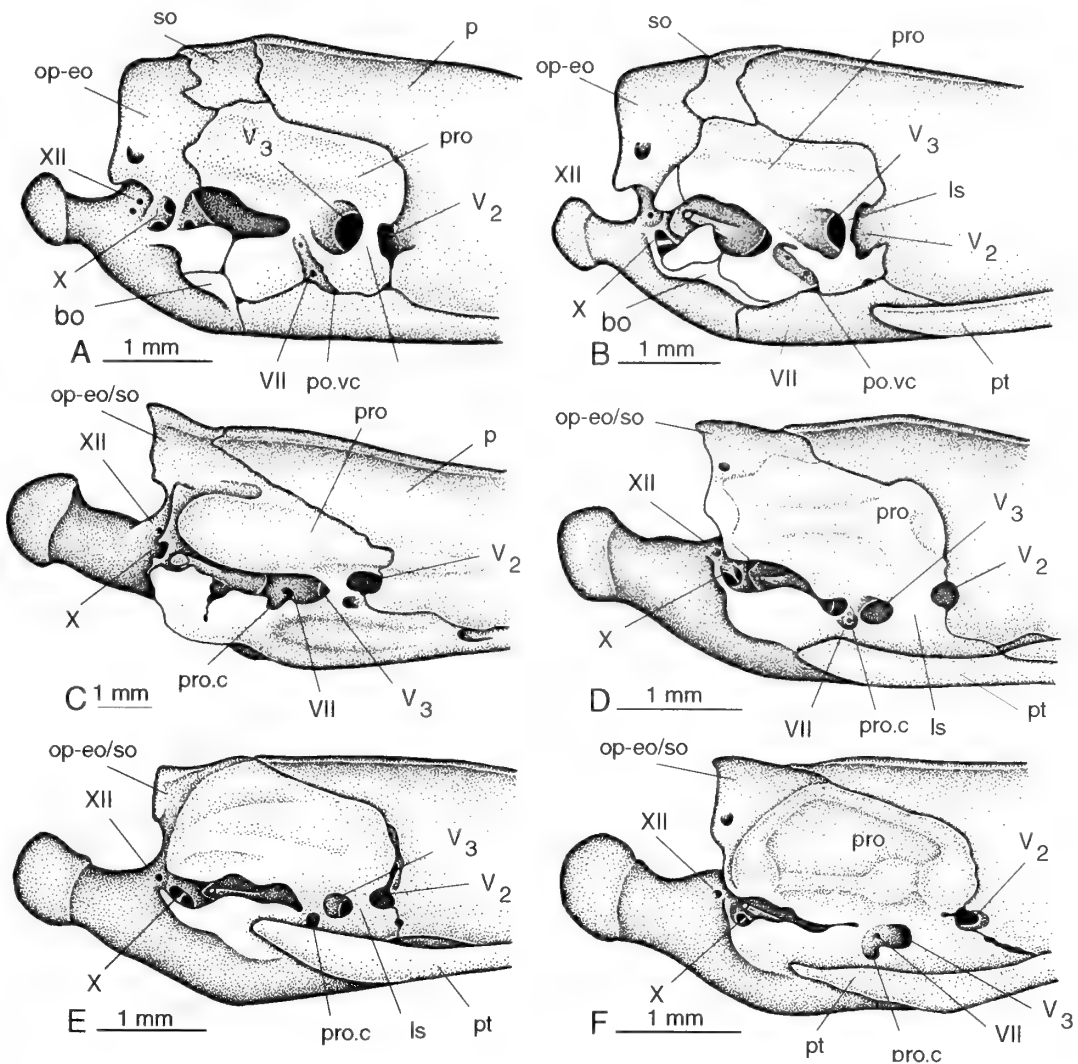
The plesiomorphic condition of the posterior opening of the Vidian canal and its relation to the facial nerve branches is exemplified by *Melanophidium* among uropeltines (Fig. 6A–B). The hyomandibular and palatine branches of the facial nerve exit from separate foramina opening into an obliquely oriented recess located on the prootic closely behind the foramen for the mandibular branch of the trigeminal nerve in *Melanophidium punctatum* (Fig. 6A), and incompletely separated from the posterior margin of the mandibular branch foramen in *Melanophidium wynaudense* (Fig. 6B). The recess housing the facialis foramina becomes deeper ventrally, as it connects with the posterior opening of the Vidian canal that is located on the prootic – basisphenoid suture. This condition is closely comparable to that in *Cylindrophis* and *Anomochilus* (Cundall & Rossman 1993), except that the posterior opening of the Vidian canal is located more (*Anomochilus*: Cundall & Rossman 1993, Fig. 4) or less (*Cylindrophis maculatus*) below the prootic – basisphenoid suture. In *Pseudotyphlops* (Fig. 6C) and *Rhinophis sanguineus* (Fig. 6F), the palatine branch of the facial nerve enters directly into a canal within the prootic which connects ventrally with the Vidian canal, and which opens dorsally within the posteriorly expanded recess of the mandibular branch foramen. This prootic canal appears to be a modification of the condition observed in *Melanophidium* by the lateral closure of the prootic recess that houses the facialis nerve foramina. In *Pseudotyphlops* and *Rhinophis sanguineus* the Vidian canal retains no separate posterior opening; the internal carotid enters directly into the opening of the prootic canal. In all other taxa investigated (e.g., *Uropeltis*, Fig. 6D; *Rhinophis drummondhayi*, Fig. 6E), the palatine branch of the facial nerve enters again a prootic canal which is completely separated from the mandibular branch foramen however, and which opens anteroventral to the anterior corner of the juxtastapedial recess. The internal carotid enters the prootic canal on its way to the sella turcica. The anterior opening of the Vidian canal lies on the suture between para-basisphenoid and parietal in front of the dorsolateral wings of the para-basisphenoid (McDowell 1967).

The juxtastapedial recess is well developed in uropeltines, which all except *Pseudotyphlops* share with *Anilius* and *Cylindrophis* the presence of a fenestra pseudorotunda (Rieppel 1979a). The shaft of the stapes is directed posterolaterally as it connects with the elongated suprastapedial process of the quadrate via the stylohyal (Rieppel 1980; see also Wever 1978). As in scolecophidians and basal alethinophidians, the juxtastapedial recess is open posteriorly, and the jugular foramen is exposed in lateral view (Tchernov *et al.* 2000; Fig. 6). The posteroventral corner of the crista circumfenestralis is enlarged to form a gliding surface for the quadrate ramus of the





**Fig. 5** A–C The otico-occipital region of uropeltine snakes in dorsal views. **A**, *Melanophidium wynaudente* (BMNH 1930.5.8.124); **B**, *Uropeltis woodmansoni* (BMNH 1930.5.8.73); **C**, *Pseudotyphlops philippinus* (BMNH 1978.1092).



**Fig. 6** A–F The otico-occipital region of uropeltine snakes in right lateral views. **A**, *Melanophidium punctatum* (BMNH 1930.5.8.119); **B**, *Melanophidium wynaudente* (BMNH 1930.5.8.124); **C**, *Pseudotyphlops philippinus* (BMNH 1978.1092); **D**, *Uropeltis woodmansoni* (BMNH 1930.5.8.73); **E**, *Rhinophis drummondhayi* (BMNH 1930.5.8.67–68); **F**, *Rhinophis sanguineus* (BMNH 1930.5.8.59).

pterygoid in *Melanophidium* (Fig. 6A–B) and *Pseudotyphlops* (Fig. 6C), a surface that is ‘rounded off’ to a variable degree in smaller species, and reduced in *Rhinophis drummondhayi* (Fig. 6E). By the fact that the braincase elements remain separate in *Melanophidium*, it is possible to ascertain that the prootic, opisthotic-exoccipital, and basioccipital contribute to this enlarged posteroventral part of the crista circumfenestralis. In the plesiomorphic condition, the juxtastapedial recess is wide open laterally (*Cylindrophis*, *Anomochilus*; Cundall & Rossman 1993), and such is also the case in *Melanophidium* (Fig. 6A–B), *Platyplecturus* and *Teretrurus*. In other uropeltines, the lateral opening of the juxtastapedial recess is closed to a narrow slit, most extremely so in *Uropeltis* (Fig. 6D) and *Rhinophis* (Fig. 6E–F), where the dorsal and ventral lips of the crista circumfenestralis closely approach each other, or may even establish a restricted contact with each other. Never is the juxtastapedial recess fully closed laterally, however, as is the case in *Liotyphlops* (Haas 1964), typhlopids and leptotyphlopids (Rieppel 1979b). The jugular foramen is internally subdivided in most uropeltines (except in *Pseudotyphlops*, *Teretrurus* and *Uropeltis*), and it is located either behind the juxtastapedial recess (plesiomorphic), or in the posteroventral corner of the latter (in *Platyplecturus*, *Plecturus*, *Teretrurus* and *Uropeltis*). The exoccipital is pierced by two hypoglossal foramina in *Melanophidium punctatum* (Fig. 6A), but by a single, enlarged hypoglossal foramen in the other taxa investigated.

## PHYLOGENETIC INTERRELATIONSHIPS

Recent cladistic analyses hypothesized that *Anomochilus* is the sister-group of uropeltines (Scanlon & Lee 2000; Tchernov *et al.* 2000), and *Cylindrophis* is the sister-group of uropeltines plus *Anomochilus* (Tchernov *et al.* 2000; see also McDowell 1987; Cundall *et al.* 1993, osteological data only). The addition of soft anatomy characters by Cundall *et al.* (1993) resulted in a different

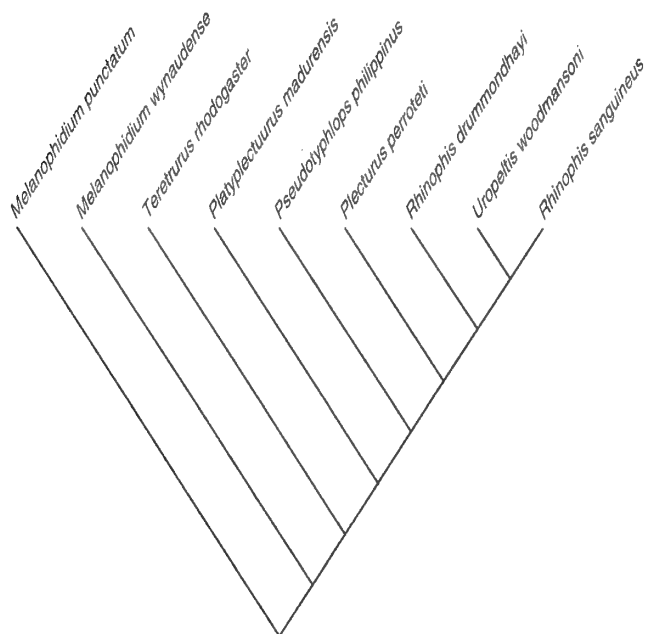


Fig. 7 The phylogenetic interrelationships of Uropeltinae. See text for further discussion.

Table 1. The data matrix used in the analysis of the phylogenetic interrelationships of Uropeltinae. Character definitions are given in Appendix I.

	12345	67891	11111	11112	22222	22223	333	
			0	12345	67890	12345	67890	123
<i>Melanoph. punctatum</i>	00000	01000	00000	00022	11111	11111	111	
<i>Melanoph. wynaudente</i>	00100	00000	00000	10022	11111	11111	111	
		1						
<i>Platyplecturus</i>	01100	00111	12011	10122	11111	11121	111	
		1						
<i>Uropeltis</i>	11111	20111	12110	11222	11111	11121	111	
<i>Teretrurus</i>	10100	11110	12001	10222	11111	11121	111	
<i>Rhinophis drum.</i>	11111	11111	12110	11222	11111	11121	111	
<i>Rhinophis sang.</i>	11111	20111	11110	11222	11111	11121	111	
<i>Plecturus</i>	11101	00111	12110	11122	11111	11121	111	
		1						
<i>Pseudotyphlops</i>	11100	01111	01101	11222	11111	11121	111	
<i>Anomochilus</i>	00100	01000	00000	00011	11111	11120	000	
<i>Cylindrophis</i>	00000	00000	00000	00010	00001	11110	000	
		1	1					
<i>Anilius</i>	00000	00000	00000	00000	00000	00010	000	

cladogram, which still reproduces the monophyly of Alethinophidia and Macrostromata respectively, but which shows anilioids (Rieppel 1977, 1988) to be paraphyletic. The sound transmitting apparatus was found to be ‘similar’ in *Typhlops* and *Rhinophis* by Wever (1978: 705), but a sister-group relationship of scolecophidians and uropeltines has so far never been recovered through cladistic analysis of morphological data (Cundall *et al.* 1993; Kluge, 1991; Scanlon and Lee 2000; Tchernov *et al.* 2000), and it was specifically rejected by Cadle *et al.* (1990; see also Cundall & Rossman 1993).

Previous work (Tchernov *et al.* 2000), and the description of the uropeltine skull presented above, allows the delimitation of 33 phylogenetically potentially informative characters (Appendix I and Table 1) for an analysis of uropeltine interrelationships. Given the currently controversial relationships of *Anilius* and *Anomochilus* relative to uropeltines, these two taxa together with *Cylindrophis* were used as paraphyletic outgroup in the analysis of uropeltine in-group relationships (characters 25 through 28 are uninformative using this rooting procedure, and were ignored in the analysis). The analysis was performed using PAUP version 3.1.1. (Swofford 1991, Swofford & Begle 1993). All multistate characters were unordered, and the branch-and-bound search option was implemented. Character optimization is based on the DELTRAN routine.

A single most parsimonious tree was obtained (TL = 49; CI = 0.796; RI = 0.877) with fully resolved uropeltine relationships. Given the scarcity of characters, it is not surprising that some nodes among uropeltines are rather poorly supported (with the minimal decay index or Bremer support index [Bremer 1988]: +1). Nevertheless, the tree (Fig. 7) suggests some interesting preliminary results.

The basal position of *Melanophidium* among uropeltines was expected (Rieppel 1977; McDowell 1987), and is reproduced here. However, there is a signal for paraphyly of the genus *Melanophidium*. *Melanophidium wynaudente* appears to be more closely related to other uropeltines than it is to *Melanophidium punctatum* (decay index: +1) on the basis of the presence of a single (enlarged) hypoglossal foramen behind the jugular foramen (16[1]; ci=1). Evidently, the monophyly of the genus *Melanophidium* must be tested by the addition of other characters, including soft anatomy, because the result obtained here may be nothing more than the reflection of the fact that as coded, *Melanophidium punctatum* is plesiomorphic relative to all other uropeltines in all characters that

are informative for the analysis of uropeltine interrelationships (unfortunately, *Melanophidium* was not included in the analysis performed by Cadle *et al.* [1990]).

The genera *Teretrurus*, *Platyplecturus*, *Pseudotyphlops*, *Plecturus*, *Uropeltis*, and *Rhinophis* form a monophyletic clade that is very strongly supported on the basis of 7 characters (decay index: +6). This represents a strong corroboration of the basal position of the genus *Melanophidium* (unequivocal synapomorphies are designated with an asterisk): \*8(1), supraoccipital fused to opisthotic – exoccipital; \*9(1) prootic fused to opisthotic – exoccipital; 11(1) laterosphenoid broad (reversal implied); 12(2) palatine branch of facial nerve enclosed in prootic canal which is separate from mandibular branch foramen; 15(1) jugular foramen single (reversals implied); 18(2) posteroventral process of dentary absent (reversal implied); 29(2) gliding surface for pterygoid posteroventral to juxtastapedial recess ‘rounded off’ (reversal implied). The monophyly of all uropeltines except *Melanophidium* is the most strongly supported clade on the basis of this data set.

Within that clade, *Platyplecturus* is the sister-taxon of a clade that includes (*Pseudotyphlops* (*Plecturus* (*Rhinophis*, *Uropeltis*))) on the basis of 2 characters (decay index: +1): \*2(1) nasals narrow anteriorly, gradually tapering to pointed tip; \*10(1) basioccipital fused to basisphenoid. *Pseudotyphlops* is the sister-taxon of a clade that includes (*Plecturus* (*Rhinophis*, *Uropeltis*)) on the basis of three characters (decay index: +1): 1(1) transverse process of the premaxilla points posterolaterally, and meets the straight maxilla in a shizarthrosis (convergent in *Teretrurus*); \*13(1) narrow lateral opening of the juxtastapedial recess; \*17(1) stalk of the occipital condyle elongated. *Plecturus* shares with the (*Rhinophis*, *Uropeltis*) – clade three characters (decay index: +2): 5(1) optic foramen fully enclosed by frontal; 14(1) jugular foramen recessed within posteroventral corner of juxtastapedial recess; 15(0), jugular foramen internally subdivided (reversal).

The clade that includes *Rhinophis* and *Uropeltis* (decay index: +1) is diagnosed by a well-defined buttressing contact between the processus medialis anterior of the maxilla and an anterior lateral process of the vomer (\*4 [1]). Interestingly, there is a signal for the paraphyly of the genus *Rhinophis*, because *Rhinophis sanguineus* appears to be more closely related to *Uropeltis* than to *Rhinophis drummondhayi* on the basis of two characters (decay index: +1): 6(2) crista trabecularis ends in front of lateral fronto-parietal suture; 7(0) supraorbital process of parietal does not contact prefrontal (reversal).

## DISCUSSION AND CONCLUSIONS

The monophyly of Uropeltinae has not previously been questioned (Rieppel 1977; Cadle *et al.* 1990; Cundall *et al.* 1993; Scanlon & Lee 2000; Tchernov *et al.* 2000) and is here corroborated by six unequivocal synapomorphies (decay index: +3): \*19(2), exoccipitals and basioccipital fused in occipital condyle; \*20(2), anterior dentigerous process of palatine modified into expanded lamina; \*30(1), occipital condyle modified as described by Williams (1959) and Hoffstetter & Gasc (1969); \*31(1), the superior alveolar nerve canal in the maxilla is open dorsally; \*32(1), frontals at least twice as long as broad; \*33(1), supratemporal absent.

The phylogenetic analysis of the interrelationships among Uropeltinae corroborates the hypothesized basal position of the genus *Melanophidium*, the latter possibly paraphyletic. The clade comprising *Teretrurus* and the Indian species of *Uropeltis* that is consistently obtained on the basis of allozyme data (Cadle *et al.*

1990) is not supported here. By contrast, the possible paraphyly of the genus *Rhinophis* indicated by molecular data (Cadle *et al.* 1990) is also found here, although far less species were included in the morphological analysis.

*Pseudotyphlops* is larger than all other uropeltines included in the analysis, and it shows characters of cranial anatomy that appear in outgroup taxa such as *Anilius* and *Cylindrophis*, but not in other uropeltines. In the adult skull of *Anilius* and *Cylindrophis*, the part of the para-basisphenoid located behind the optic foramen has a concave ventral surface, which results in the formation of distinct lateral ventral ridges (Tchernov *et al.* 2000). This character is also observed in the relatively large skull of adult *Pseudotyphlops*. In the much smaller skull of other uropeltines, the ventral surface of the para-basisphenoid is at best very weakly concave, flat, or even slightly convex, and ventral lateral ridges are very faintly indicated (*Melanophidium*, *Platyplecturus*, *Plecturus*, *Uropeltis*, *Rhinophis*), or absent (*Teretrurus*; also in *Anomochilus*: Cundall & Rossman 1993). The same observation relates to the presence of a sagittal ridge on the parietal, well expressed in adult *Anilius*, *Cylindrophis*, and in *Pseudotyphlops* among uropeltines, much reduced and restricted to the posterior part of the parietal or absent in *Anomochilus* and smaller uropeltines. Given its relative size, and the presence of relatively plesiomorphic features in the skull, a basal position of *Pseudotyphlops* relative to other uropeltines might have been expected, but was not corroborated by cladistic analysis, although the genus is still outside the (*Plecturus* (*Rhinophis*, *Uropeltis*)) clade.

The morphological transformation that is implied in the description of the Vidian canal in uropeltines (and in its coding; the character was used unordered) is also contradicted by the cladistic analysis discussed above. The description suggests that the individualization of the prootic canal (which receives the palatine branch of the facial nerve and into which enters the internal carotid) follows its formation in association with the recess of the mandibular branch foramen, the cladistic analysis suggests otherwise. The incorporation of the opening of the prootic canal into the recess of the mandibular branch foramen is a secondary development that occurred convergently in *Pseudotyphlops* and *Rhinophis sanguineus*.

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## Appendix I List of Characters used in the phylogenetic analysis

- Anterior tip of maxilla turned medially, closely approaching or touching transverse process of premaxilla (0); anterior tip of maxilla straight, contact with premaxilla shizarthrotic (1).
- Nasals relatively broad anteriorly, notched (0); nasals gradually tapering to pointed tip anteriorly (1).
- Teeth on palatine present (0), absent (1).
- A distinct and well defined buttressing contact between the processus medialis anterior of the maxilla and an anterior lateral process of the vomer is absent (0), or present (1).
- Parietal enters optic foramen (0), optic foramen fully enclosed entirely within frontal (1).
- Crista trabecularis ends behind the (lateral) fronto-parietal suture (0), at the (lateral) fronto-parietal suture (1), in front of the (lateral) fronto-parietal suture (2).
- Supraorbital process of parietal does not (0), or does (1) participate in suspension of prefrontal (contacts prefrontal above the orbit).
- Supraoccipital separate (0), or fused (1).
- Prootic and opisthotic-exoccipital separate (0), or fused (1).
- Basisphenoid – basioccipital separate (0), or fused (1).
- Laterosphenoid narrow (0), broad (1).
- Facial nerve branches open into a recess behind the mandibular branch foramen which connects with the posterior opening of the Vidian canal (0); facial nerve branches open into a prootic canal which opens within the recession of the mandibular branch foramen and connects with the posterior opening of the Vidian canal (1); facial nerve branches open into a prootic canal which opens behind the mandibular branch foramen and connects with the posterior opening of the Vidian canal (2).
- Juxtastapedial recess wide open laterally (0; fenestra pseudorotunda may be exposed in lateral view), distinctly restricted by approximation of dorsal and ventral margin (1; fenestra pseudorotunda never exposed in lateral view).
- Jugular foramen behind juxtastapedial recess (0), recessed within juxtastapedial recess (1).
- Jugular foramen internally subdivided (0), single (1).
- More than one hypoglossal foramina (0), single but enlarged hypoglossal foramen (1).
- Stalk of occipital condyle short, depression in basioccipital for brainstem not visible in dorsal view (0), stalk of occipital condyle elongate, depression in basioccipital for brainstem visible in dorsal view (1).
- Posteroventral process of dentary distinct (0), reduced (1), absent (2).
- Exoccipitals not in contact dorsal to basioccipital in occipital condyle (0); exoccipitals in contact dorsal to basioccipital in occipital condyle (1); exoccipitals and basioccipital fused in occipital condyle (2).
- Anterior dentigerous process of palatine slender and straight (0), broadened anteriorly (1), modified into expanded lamina (2).
- Pterygoid teeth present (0), absent (1) (Tchernov *et al.* 2000).
- Suprastapedial process of stapes is not (0), or is (1) distinctly longer than shaft of stapes (Tchernov *et al.* 2000).
- Quadrangle suspension close to dorsal margin of otic capsule (0), shifted anteroventrally on otic capsule (1) (Tchernov *et al.* 2000).
- Retroarticular process unmodified (0), wrapping around posterior aspect of mandibular condyle of quadrangle (1) (Cundall *et al.* 1993).
- Premaxillary teeth present (0), absent (1).
- Contact between premaxilla and vomer overlapping (0), or in well defined recess (1).
- Preorbital ridge on frontal (Frazzetta 1966) does not (0), does (1) project beyond anterior margin of dorsally exposed surface of frontal.
- Interchoanal process of parasphenoid absent (0), present (1).
- Posteroventral part of crista circumfenestralis does not (0), or does (1) form a distinctly enlarged gliding surface for the quadrangle ramus of the pterygoid, or this gliding surface is present but “rounded off” (2).
- Occipital condyle is not (0), or is (1) modified as described by Williams (1959) and Hoffstetter & Gasc (1969).
- The superior alveolar nerve canal in the maxilla is closed (0), or open (1) dorsally.
- Frontals are not (0), are (1) at least twice as long as broad.
- Supratemporal present (0), absent (1).

# The Cretaceous marine squamate *Mesoleptos* and the origin of snakes

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**SYNOPSIS.** The poorly known marine squamate *Mesoleptos* is reassessed based on two previously known specimens and a newly referred specimen. The three specimens of *Mesoleptos zendrinii* share unique characters such as long, posteriorly tapering centra and distally straight but non-pachyostotic ribs. *Mesoleptos* had a narrow neck (and presumably small head), long laterally compressed body, and small fore- and hindlimbs. Phylogenetic analysis suggests that *Mesoleptos* is the nearest relative of snakes; this phylogenetic position is consistent with its morphology being intermediate between typical marine squamates (e.g. mosasauroids) and primitive marine snakes (pachyophiids). However, this interpretation remains tentative because *Mesoleptos* is very poorly known, and many of the characters uniting it with mosasauroids and primitive snakes are correlates of marine habits and/or limb reduction.

## INTRODUCTION

Whereas sea snakes (Laticaudinae and Hydrophiinae) and marine iguanas (*Amblyrhynchus*) are the only truly marine squamates living today, there was a more diverse and very different radiation of such forms during the Cretaceous. These extinct marine squamates included the large monitor-like aigialosaurs and mosasaurs, the small, long-necked dolichosaurs, and the medium-sized limbed snakes *Pachyrhachis*, *Pachyophis*, and *Haasiophis*. These forms were suggested by workers in the late nineteenth and early twentieth centuries to be closely related to each other and to modern snakes (e.g. Cope, 1869; Boulenger, 1891; Gorjanovic-Kramberger, 1892; Nopcsa, 1908, 1923), a view which has been supported by some recent phylogenetic analyses (e.g. Scanlon, 1996; Caldwell 1999; Lee and Scanlon 2002; but see Tchernov *et al.* 2000; Rieppel and Zaher 2000).

One poorly known form that has been associated with this radiation is *Mesoleptos zendrinii* (Cornalia and Chiozza, 1852; Gorjanovic-Kramberger, 1892; Calligaris, 1988). *M. zendrinii* was a marine squamate with a rather elongated body, long ribs, and well-developed but rather small hindlimbs. It has been repeatedly associated with other contemporary marine squamates, largely on the basis of common habitat rather than any detailed analysis of morphology. Cornalia and Chiozza (1852) suggested affinities with '*Raphiosaurus*', based on a specimen (BMNH R32268) figured under this name by Owen (1842) but later referred to *Dolichosaurus* (Owen 1850a, 1851). Subsequent workers have commented on errors in the original description, though a full redescription of the type specimen has not appeared. Gorjanovic-Kramberger (1892) referred an additional specimen to *Mesoleptos cf. zendrinii*, discussed below, and referred this genus to the Varanidae, although acknowledging that it differed from other varanids in being highly aquatic. Nopcsa (1903) referred it tentatively to Aigialosauridae, and suggested that the moderate elongation of the trunk region relative to other known aigialosaurs was analogous to the independent elongation of the body in some mosasaurs such as *Clidastes*. Later, Nopcsa (1923) compared *M. zendrinii* with *Eidolosaurus trauthi*, including both in a subfamily Mesoleptinae within his broadly conceived Dolichosauridae (Mesoleptinae, Aigialosaurinae, Dolichosaurinae). He regarded the Mesoleptinae as intermediate

between two main lineages, one consisting of the Aigialosaurinae plus their probable descendants the Mosasauridae, and the other consisting of the Dolichosaurinae plus their probable nearest relatives – though not direct descendants – the snakes. Nopcsa's (1903, 1923) classifications still represent the most complete discussion of these forms to date, and are summarised by Calligaris (1988). However, no unambiguous derived characters have been proposed linking *Mesoleptos* with any of the other marine groups or with snakes, and these interpretations need to be critically examined.

Here, we identify a new specimen of *Mesoleptos*, compare it to previously known specimens, and use the combined material to infer the phylogenetic relationships and palaeoecology of *Mesoleptos*. *Mesoleptos* emerges as on the stem lineage leading to snakes, lying phylogenetically between marine lizards (mosasauroids, dolichosaurs, *Adriosaurus*) and primitive limbed snakes (*Pachyrhachis*, *Pachyophis*, *Haasiophis*). Garth Underwood's earliest research interests included the origin and evolution of snakes, and he has contributed to possibly the two most influential papers on this topic (Bellairs and Underwood 1951; Underwood 1967). The current paper is thus a small contribution to a field of inquiry that Garth Underwood helped establish.

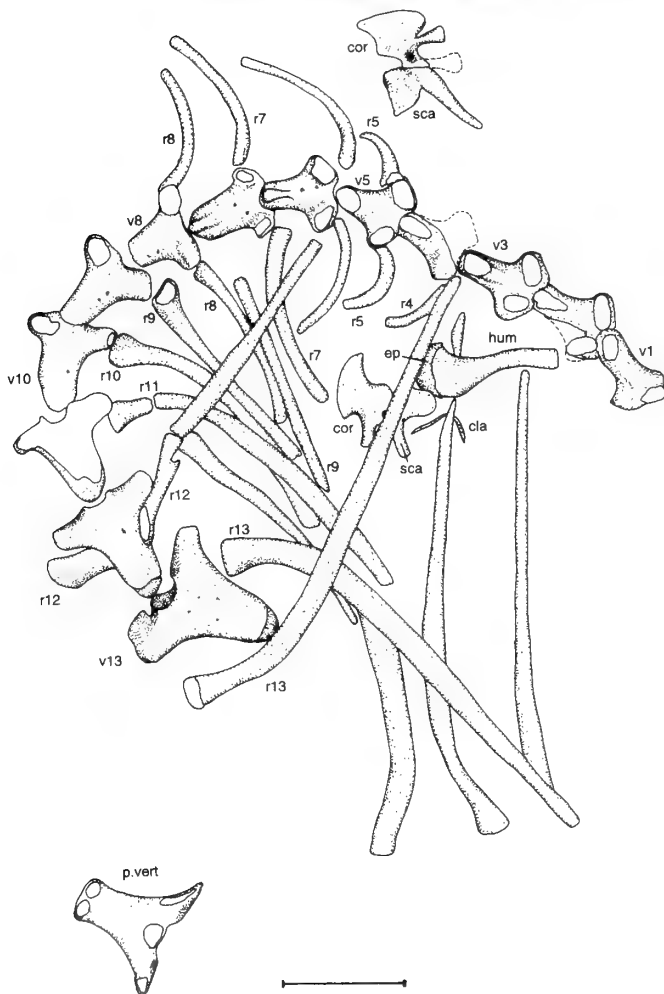
## Institutional abbreviations

HUJ PAL, Hebrew University of Jerusalem Palaeontological Collection; MCSNT, Museo Civico di Storia Naturale di Trieste; MNHN, Musée Nationale d'Histoire Naturelle, Paris; SAM, South Australian Museum.

## DESCRIPTION OF NEW SPECIMEN

### Material and horizon

The specimen consists of part and counterpart, but all morphological information is preserved on the part (Fig. 1A). Anterior vertebral column, ribs, shoulder girdle, and partial forelimbs. Locality: 'Ein Jabrud (Ain Yabrud), 7 km north-east of Ramallah (West Bank, Palestine) and 20 km north of Jerusalem. Stratigraphic horizon: Bet-Meir Formation (Lower Cenomanian; earliest Upper Cretaceous). Catalogued as HUJ-PAL EJ699.



## Vertebrae

An articulated series of thirteen vertebrae (here referred to as vertebrae 1–13) is preserved, along with an isolated element on the lower left (vertebra 14). All vertebrae are exposed ventrally only; the surfaces of vertebrae 1–7 are weathered, while that of vertebra 11 is broken. The series 1–13 represents the anterior presacral part of the column. Vertebra 1, the anteriormost, is the smallest; size then increases gradually along the series such that the last is approximately twice the dimension of the first. The cervical-dorsal boundary cannot be precisely determined because the cartilaginous sternal contacts are not preserved. However, in typical lizards (anonymous referee, pers. comm.), the cervical-dorsal boundary lies slightly behind an abrupt increase in rib length. There is an abrupt change in the size and shape of the ribs between preserved vertebrae 5 and 6 (see below), suggesting the cervical-dorsal boundary was slightly behind this region, perhaps between vertebrae 7 and 8. Both shoulder girdles, however, are preserved around the level of vertebra 5, suggesting a slightly more anterior cervical-dorsal boundary.

The centra are all elongate, the length being approximately three times the width across the middle of each vertebra. They narrow sharply behind the transverse processes, and then more gradually posteriorly. All centra are procoelous; the anterior cotyle is deeply concave and the posterior condyle strongly convex. The articular surfaces of the condyles face posteriorly; part of the surface is sometimes exposed in ventral view, so they were at most only slightly inclined dorsally.

Subcentral foramina are visible on the ventral surface of most vertebrae: two are present on vertebrae 6 to 9, and one is present on vertebrae 10 and 12. They were presumably present on the other vertebrae but are not visible due to weathering and/or damage. Where two foramina are present on a single vertebrae, they are never bilaterally symmetrical and are often both on the same side of the midline.

A sagittal keel, extending along the posterior half of the centrum, is present on vertebrae 1 to 7. The keel terminates posteriorly in a prominent knob-shaped hypapophysis, which is, however, partly weathered away on all except vertebrae 6 and 7. The keels and (where preserved) the hypapophyses are more prominent on the anteriormost vertebrae and gradually decrease in size posteriorly. On vertebra 8, there is no keel. A weak hypapophysis may have been present, but this cannot be confirmed due to breakage. Both the keel and hypapophysis are absent from vertebrae 9 to 13, and the ventral surface is completely smooth.

A pair of transverse processes extend laterally from the anterior end of each centrum. These processes extend proportionally further laterally in the more posterior vertebrae: the diameter across the transverse processes is slightly less than the length of the centrum in the anteriormost vertebra, but slightly more in the posteriormost vertebra (Table 1). Most of the transverse processes on the anterior vertebrae are weathered ventrally, but at least one is complete on most of the posterior vertebrae. The articular surfaces of the processes are not fully exposed, but appear to have been single based on the morphology of the proximal ends of the ribs.

The isolated vertebra '14' does not fit onto either end of the

**Fig. 1** (A) Photograph of the third known individual of *Mesoleptos* (HUPAL 699). (B) Specimen drawing. The anterior end of the specimen is to the top right. Unstippled areas represent areas of broken bone. Scale bar = 2 cm. Abbreviations: **cor**, coracoid; **sca**, scapula; **cla**, clavicle; **hum**, humerus; **ep**, epiphyseal ossification; **v1** first (anteriormost) preserved vertebra; **p.vert**, isolated posterior vertebra; **r5**, rib of fifth preserved vertebra; **hyp**, hypapophysis.

**Table 1.** Measurements of HUI-PAL EJ699: midline length between rims of cotyle and condyle; width across transverse processes; straight-line length of rib. The vertebrae are numbered from the first preserved centrum.

Vertebra no.	Centrum length	Greatest width	Rib length
1	22	16	—
2	20.5	19	—
3	22	20	—
4	—	—	19.5
5	19	20	20
6	20	20.5	41
7	21	20	49
8	(16+)	23	49
9	22	23	59
10	23.5	24	73
11	(23+)	(24+)	89
12	25	31	(92+)
13	26	39	121
—	—	—	132
—	—	—	139
14	23	34.5	—

articulated series. It is too large to fit next to vertebra 1, and furthermore could not be a cervical as it lacks the mid-ventral keel and hypapophysis. However, it is too small to fit next to vertebra 13. As in most squamates, after reaching maximum size (at or past vertebra 13), the centra must have again gradually decreased in size towards the posterior end of the dorsal region. The isolated vertebra appears to belong to this region. Its surface is worn in a manner that suggests there were laterally paired ventral mounds or processes defining a median longitudinal trough on the posterior part of the centrum.

## Ribs

Ribs are preserved in association with vertebrae 4 to 13. Only the left rib (right in ventral view) of vertebra 4 is preserved. Both ribs are preserved in association with vertebrae 5 to 8. Only the left ribs are associated with vertebrae 9 to 11. Both ribs are associated with vertebrae 12 and 13, but the right ribs are displaced so that they overlie the left ribs and point anteriorly. Three additional ribs belonging to the next three (missing) dorsal vertebrae are also preserved; these are presumably right ribs based on their similar orientation to the right ribs of the last two preserved vertebrae.

The anteriormost preserved rib is associated with the 4th vertebra. It is short (only as long as the centrum) and smoothly curved. The shaft is oval in cross-section and uniformly thick throughout its length. Slightly longer ribs, of similar shape, are associated with the 5th vertebra. The next pair of ribs, associated with the 6th vertebra, are much longer and quite different in shape. The distal end of the left rib (right in ventral view) is weathered away; the right rib is complete and its proximal half is smoothly curved, but the distal half is nearly straight. The more posterior ribs are similar in shape, except that the curved proximal portion occupies progressively less and less of the shaft. By vertebra 13, the curved portion only occupies the proximal one-fifth of the shaft.

The articular surfaces are visible on the left ribs associated with vertebrae 7, 8, 10 and 13, and on the second of the three isolated ribs. The ribs are all single-headed. The anterior ribs are flared at the proximal end and then nearly uniformly thick throughout their length, while more posterior ones have a distinct neck proximally before becoming thickened in the region of greatest curvature, then gradually tapering distally in the straight part of the shaft. The distal ends are truncated squarely where they joined the costal cartilages,

which are not preserved.

Approximate measurements of the vertebrae and ribs (Table 1) show a more or less steady increase in dimensions from vertebra 1 to 13, continued in the ribs belonging to the next two missing vertebrae (both ends of the last known rib are incomplete or obscured and its length is therefore not measurable). As noted above, the posteriormost preserved ribs cannot belong to vertebra 14, which is from the posterior trunk (abdominal) region.

## Shoulder girdle and forelimb

Both scapulocoracoids are preserved in medial view. The right is complete except for the dorsal scapular blade, while the left is partly covered by a rib and is missing the distal (anterior) end of the procoracoid process. A curved strip of bone adjacent to the left scapulocoracoid is probably the left clavicle. The left humerus is preserved in proximal dorsal view. All appendicular elements are very small in proportion to the axial elements.

The scapula is a simple, rectangular plate; the scapular blade is short. Its anterior margin is weakly concave; a scapulocoracoid emargination was thus present. The coracoid is single and bears two processes, and two emarginations. The more dorsal process is much longer and extends anterodorsally, forming the ventral margin of the scapulocoracoid foramen and the dorsal margin of the coracoid emargination that represents the anterior coracoid foramen. The ventral process is shorter and expanded distally. It forms the ventral border of the anterior coracoid foramen and the dorsal border of the emargination representing the posterior coracoid foramen. The ventral margin of the coracoid is smoothly convex, and the posterior margin is drawn out into a posteroventral spur. The probable clavicle is a tiny curved rod, tapered at each end. There is no ventromedial expansion or foramen. The humerus is relatively large compared to the shoulder elements, though still small compared to the axial elements. The proximal end is expanded and flattened. The entire articular surface is occupied by a large, semilunar epiphysis which caps the humerus. The distal end of the humerus is weathered.

## COMPARISONS WITH SIMILAR TAXA

The specimen is clearly a squamate, as it possesses all the synapomorphies of squamates (Estes *et al.*, 1988) for which it can be coded: single-headed ribs, cervical vertebrae with hypapophyses, procoelous vertebrae, presence of anterior coracoid emargination. Admittedly, these are relatively few because the specimen is very incomplete, but still sufficient to make a firm identification. Among squamates, it is clearly different from most groups in possessing distally straight ribs. The only taxa that possess such ribs are *Mesoleptos*, *Adriosaurus*, *Acteosaurus*, and various groups of aquatic snakes. The specimen here is compared to these forms, and to some other superficially similar taxa to which it might be related.

### *Mesoleptos zendrinii*

HUI-PAL EJ699 is extremely similar to *Mesoleptos*, which is known from two specimens. The type of *Mesoleptos zendrinii*, from the Upper Cretaceous of Comen, Slovenia, is an articulated series of dorsal, sacral and anterior caudal vertebrae with ribs and a partial hindlimb. The specimen has been illustrated as a lithographic plate (Cornalia and Chiozza, 1852: pl. 3) and an interpretive line drawing (Calligaris, 1988: fig. 2). Cornalia (in Cornalia and Chiozza, 1852) considered the specimen to be exposed in dorsal view, while Gorjanovic-Kramberger (1892) maintained it was exposed ventrally,

**Table 2.** Measurements of *Mesoleptos zendrinii* holotype (based on Cornalia and Chiozza, 1852: pl. 3), for comparison with data in Table 1. The vertebrae are numbered from the first preserved rib.

Vertebra no.	Centrum length	Greatest width	Rib length
1	—	—	45
2	—	—	—
2	—	—	75
4	12	—	90
5	13	—	116
6	12	—	120
7	12	18	125
8	12	20	119+
9	20*	23	124+
10	15	24	120+
11	15	25	120+
12	15	22	114

\* there may be inaccuracies with the outlines of some vertebrae in the original figure, or this anomalous high value could reflect longitudinal separation of two adjacent vertebrae during partial disarticulation of the skeleton before fossilisation.

but in any case most of the vertebrae are bisected by the broken surface of the slab and are thus seen as cross-sections at various levels. The intervertebral articulations are not clearly exposed, and Cornalia found no indication that the vertebrae were procoelous, though Gorjanovic-Kramberger (1892) and later authors assumed that they must have been similar to the specimen in the Novak collection (discussed below). The type specimen could not be located in recent times: Calligaris (1988) was unable to confirm it was still in the Museo Civico di Storia Naturale de Milano (Milan).

The most anterior parts preserved of the type are strongly curved ribs which probably contacted the sternum, and the first vertebral fragments are associated with the fourth visible rib. Some small elements and fragments visible between the anterior ribs may include parts of the shoulder girdle and/or forelimb. Apart from the first few, the ribs are weakly curved proximally and nearly straight for the distal two-thirds of their length. The ribs are widest at the proximal articulation and are otherwise slender, with no trace of thickening (pachyostosis) more distally. Ribs in the posterior half of the trunk are displaced to point anteriorly, corresponding to bloating and maceration of the carcass proceeding most rapidly in the area of the viscera, and the most posterior ribs are either lost or not exposed. The outlines of the first 12 preserved vertebrae are nearly triangular, indicating that they are split horizontally through the middle or lower part of the centrum. From about the 13th preserved vertebra the outlines of the trunk vertebrae are expanded posteriorly as well as anteriorly and the neural canal is exposed, indicating a more dorsal position of the break; after the 22nd there is not much visible of the vertebral centra themselves. Prominent transverse processes are visible on vertebrae 24–27, and transverse grooves on the 24th and 26th vertebrae resemble lymph channels seen on the ventral surface of the sacral and anterior caudal vertebrae in *Varanus*, suggesting that the skeleton is exposed ventrally, and that the 24th and 25th preserved vertebrae are the sacrals. After the first two caudals (26–27), represented by broad transverse processes of one side, there are indeterminate fragments of two more vertebrae, then indications of four vertebrae in lateral view showing elongate, near-vertical chevrons and a tall but antero-posteriorly narrow, slightly back-sloping neural spine. Traces of longitudinal elements under the transverse processes of the 25th–26th probably represent the ilium, slightly displaced posteriorly, medially and (if the orientation is correct) dorsally from its natural position. The femur is level with the probable sacrals; the tibia and fibula are articulated, but incomplete distally.

The two referred specimens consist of HUI-PAL EJ699 and another specimen in the Museo Civico di Storia Naturale, Trieste (MCSNT 9962: locality and other collection details undetermined). The latter consists of a shorter but similar section of the skeleton to that in the type, exposed dorsally (Calligaris, 1988). Comparisons of the vertebrae are difficult due to the different parts and orientations of the skeleton in the different specimens, but all three specimens might share the derived character of unusually long, and posteriorly tapering, trunk centra. The shape of the centrum in the type can be inferred from the cross-sectional views of the vertebrae, which in some parts of the trunk show a similar outline to the ventral views in HUI-PAL EJ699, being wide across the transverse processes and narrowing steeply behind them to be almost parallel-sided posteriorly. In MCSNT 9962, where only the upper part of the neural arch and postzygapophyses are visible, the vertebrae are about 3/4 as long (between successive neural arches) as wide (across postzygapophyses), which is similar to proportions in the more posterior part of HUI-PAL EJ699.

All three specimens share a distinctive feature of the ribs in that the distal portion, representing most of their length, is nearly straight. This is interpreted as a derived condition corresponding to lateral compression of the trunk region, as in the pachyophiids and some other groups of thoroughly aquatic snakes. All three specimens also exhibit, as far as can be seen, complete but small girdles and limbs. The development of the forelimb and shoulder girdle in the current specimen matches the development of the pelvis and hindlimb in the type and MCSNT specimens of *Mesoleptos*. The shoulder girdle and forelimb in HUI-PAL EJ699 are relatively small, but complete in that all major elements are present. All ossified shoulder girdle elements except the interclavicle are preserved, while (based on the size and ossification of the humerus) most of the distal forelimb bones were present. This is consistent with the small but well developed (though incompletely preserved) sacrum, pelvis and hindlimb in the two previously known specimens of *Mesoleptos*. The observation that the shoulder girdle and forelimb in HUI-PAL EJ699 are both reduced in size but complete, as is the pelvis and hindlimb in *Mesoleptos*, further suggests they are the same or closely related species.

Thus, HUI-PAL EJ699 can be associated with the two known specimens of *Mesoleptos* because (1) they exhibit no significant differences from each other, though they all differ from all other squamates, (2) they have derived similarities in the ribs (otherwise found only in very different forms) and, less certainly, in the vertebrae and limbs.

### '*Mesoleptos*' cf. *zendrinii*

Gorjanovic-Kramberger (1892: pl. III, fig. 4) reported a specimen in I. Novak's collection showing several articulated vertebrae with ribs, and fragments of some other elements, which he referred to *Mesoleptos*, close to *M. zendrinii*. The collection consisted of material from Cretaceous deposits of Isola di Lesina (Italian name for Hvar Island), Croatia (Gorjanovic-Kramberger, 1892). This was held after his death by his widow Antonia Novak (Kornhuber, 1901: 19) but the present location of this material is unknown (Calligaris, 1988). Gorjanovic-Kramberger interpreted the specimen as exposed ventrally, but the shape of contacts between condyles and cotyles visible in his figure suggest that the vertebra may actually be exposed in dorsal view but sectioned horizontally at the base of the neural canal; this would invalidate comparisons based on the supposed ventral surface, though not the overall outline, of the centrum. The shape of the centrum in the most complete vertebra is very similar to vertebrae 9–13 of HUI-PAL EJ699. The elongate and



posteriorly narrow centra have been regarded as diagnostic of *Mesoleptos*, and are not found in any other limbed squamates, though a similarly shaped centrum is present in some primitive snakes (e.g. *Lapparentophis*, Hoffstetter, 1960; *Patagoniophis*, Scanlon, 1993; *Coniophis*, Gardner and Cifelli, 1999).

Girdle and limb elements are also present in the Novak specimen; Gorjanovic-Kramberger (1892: 99) describes 'indistinct impressions' of the humerus, radius, ulna and two metacarpals, altogether measuring 93.3 mm in length. This must be less than the total length of the forelimb, because the elements are incompletely represented (the ends of the long bones are obscured and the humerus can not be compared in detail with HUI-PAL EJ699), but it can be concluded that a forelimb was present and equivalent in length to between three and four thoracic vertebrae, just as in the HUI specimen. Plate-like structures are also shown just anterior to the supposed humerus in Gorjanovic-Kramberger's figure, suggesting the posterior margins of a scapula and coracoid like those of the HUI specimen, although no useful details can be compared.

On the other hand the ribs, although long, are curved throughout their length. While the centrum length of the one well-preserved vertebra is about 31.5 mm, the length of the most complete rib (belonging to the preceding vertebra) is over 90 mm (Gorjanovic-Kramberger, 1892). These proportions seem to indicate a position deep within the dorsal region. In HUI-PAL EJ699, curved ribs only occur up to the anterior dorsal region while more posterior ribs are straight. Thus the Novak specimen apparently lacks this apomorphy shared by the type of *Mesoleptos zendrinii* with the MCSNT and HUI specimens (neither Gorjanovic-Kramberger nor subsequent writers have commented on this difference). It should therefore not be referred to *Mesoleptos*, but might possibly represent a species closely related to either *Mesoleptos* or the *Mesoleptos*-snake clade (see below).

### ***Adriosaurus, Acteosaurus***

*Adriosaurus suessi* Seeley, 1881 (Lee and Caldwell, 2000) and *Acteosaurus tommasinii* von Meyer, 1860 (considered identical by Nopcsa, 1923) are small marine lizards with distally straight ribs and thus, laterally compressed bodies. *Adriosaurus* is known from two specimens, from Upper Cretaceous deposits of Comen, Slovenia and Lesina (=Hvar), Croatia, while *Acteosaurus* is known from a single specimen from Comen. However, they both differ from *Mesoleptos* in lacking the distinctly small cervicals (relative to dorsals), in possessing proportionally larger limbs, proportionally shorter and wider dorsal vertebrae, and in exhibiting heavy pachyostosis of both dorsal vertebrae and ribs. They are also much smaller than *Mesoleptos*.

### ***Eidolosaurus trauthii***

Nopcsa (1923) described *Eidolosaurus trauthii* from a near-complete skeletal impression found during the demolition of a house in the Istrian region, i.e. in the same general region as Comen, but possibly within the present borders of either Slovenia, Croatia, or Italy (more precise locality details were not provided). This specimen is currently housed in the Geologische Staatsanstalt, Vienna but has yet to be completely prepared. Fragments of the skull are present in articulation with the vertebral column, so that the total number of presacral vertebrae can be determined as 34. Short, slender ribs were present on at least three posterior cervicals, but on the basis of a sharp increase in length and thickness between adjacent ribs (as there is no trace of the sternum), Nopcsa counted 11 cervical and 23 dorsal vertebrae. Two sacral and 48 or more postsacral vertebrae were also present. Nopcsa interpreted the type of *Mesoleptos zendrinii*

as also having 23 dorsal vertebrae. The numbers of cervical and trunk vertebrae in *Mesoleptos* and *Eidolosaurus* are therefore comparable. The relative femur length is similar in both, corresponding to the length of three middle dorsal vertebrae. However, there are also considerable differences: in *Eidolosaurus* the centra of trunk vertebrae are as wide as long, with no indication of a posterior taper; there is a median groove between paired ridges on the ventral surface throughout the trunk (the groove further divided by a median ridge in posterior vertebrae); all trunk ribs are strongly and uniformly curved and greatly thickened; and both the vertebrae and ribs are pachyostotic.

Nopcsa (1923: 107, footnote) also mentions 'An undescribed fossil discovered by Professor Jäkel, which came to my attention while this work was in press, shows 18 posteriorly tapering vertebral centra, which bear long, slightly curved, proximally club-shaped ribs. The specimen is 28 cm long. The vertebral centra show a shallow but well developed median longitudinal groove. The anterior centra are almost triangular and wider than long. The general habitus is *Mesoleptos*-like, but the ribs are somewhat pachyostotic. Probably this form is related to *Eidolosaurus*.' This may have been the specimen collected by Prof. O. Jäkel at Lesina which Kornhuber (1901: 3) mentioned and referred to *Carsosaurus*. It would be particularly interesting to compare this specimen with HUI-PAL EJ699, which also resembles *Mesoleptos* but has somewhat thickened ribs, but no illustration was provided and again the present location of the specimen is unknown (Calligaris, 1988: 117).

### **Dolichosaurs: *Dolichosaurus, Coniosaurus, Pontosaurus***

*Dolichosaurus longicollis* Owen, 1850a from the English Chalk (Owen, 1842, 1851; Caldwell, 2000) and *Pontosaurus lesinensis* (Kornhuber, 1873) from Hvar, Croatia, are elongate, Cenomanian marine squamates known from two or more articulated partial skeletons, and are thus important for comparison with *Mesoleptos*. They both clearly differ from HUI-PAL EJ699 and the other *Mesoleptos* specimens in the shape of the ribs (distally curved rather than straight), the more gradual changes in rib length and vertebral dimensions along the trunk, and greater number of dorsal vertebrae, all of which correspond to a more slender and cylindrical body form. Individual mid-trunk vertebrae of *Dolichosaurus* differ from those of *Mesoleptos* in being less massive, and having proportionally larger condyles and cotyles. Otherwise, they are similar in possessing broad transverse processes, a posteriorly cylindrical centrum, well-developed zygosphenes, a long neural spine, and absence of pachyostosis. Vertebral morphology of *Pontosaurus* can not yet be adequately compared because the specimens remain incompletely prepared (Calligaris, 1988). *Coniosaurus crassidens* Owen, 1850a (*Coniasaurus* Caldwell and Cooper, 1999, invalid emendation or sustained lapse) and *Coniosaurus gracilodens* Caldwell, 1999, occur in the same deposits as *D. longicollis* but comparisons are more problematic. Only very incomplete postcranial remains of *Coniosaurus* are known; the vertebrae are very similar to those of *Dolichosaurus*, and the two species are diagnosed by features of the jaws and teeth unknown in *Dolichosaurus*. Thus, one of the species of *Coniosaurus* might be synonymous with *Dolichosaurus* (Caldwell, 2000).

### ***Pachyvaranus crassispondylus***

*Pachyvaranus* was described from the Maastrichtian of Morocco (Arambourg and Signeux, 1952: 288–91, pl. 41) based on a small number of isolated vertebrae (MNHN PMC 1–4) and two doubtfully associated osteoderms (PMC 5–6), and originally referred to

Aigialosauridae. However, it has narrower condyles and cotyles, relatively longer centra and more prominent transverse processes than known aigialosaurs. This suggests it should be compared with HUI-PAL EJ699, which it resembles in size. The *Pachyvaranus* specimens are from marine phosphate deposits, and differ from HUI-PAL EJ699 in the thick and compact ossification of the vertebrae (pachyostosis). The vertebrae also differ in that the centrum of *Pachyvaranus* is triangular, tapering rather than nearly parallel-sided posteriorly, but this could be a result of pachyostosis; in other pachyostotic reptiles the centra are further expanded posterolaterally, and nearly rectangular. Further, the reported 'zygosphene' is only a small triangular projection comparable to that of *Varanus*, which does not bear facets for articulation with a zygantrum on the preceding vertebra. Arambourg and Signeux considered possible affinities with dolichosaurs (ruled out by the lack of true zygosphenal articulations in *Pachyvaranus*) as well as aigialosaurs (noting differences including the narrower condyles). The lack of zygosphenes in *Pachyvaranus* also rules out affinities with aigialosaurs, since recent studies (Carroll and DeBraga, 1992) have demonstrated the presence of well-developed zygosphenes in aigialosaurs. However, affinities with *Mesoleptos* were not considered. No material other than trunk vertebrae (and doubtfully associated osteoderms) has been described for *Pachyvaranus*, and conversely the vertebrae of *Mesoleptos* are not fully known 'in the round', so that it is not yet possible to make detailed comparisons.

### Pachyophiidae

Three long-bodied, limb reduced Cretaceous marine squamates have been referred to Pachyophiidae: *Pachyophis woodwardi* Nopcsa, 1923 (Lee *et al.*, 1999), *Mesophis nopcsai* Bolka, 1925, and *Pachyrhachis problematicus* Haas, 1979 (Haas, 1980; Lee and Caldwell, 1998; Zaher and Rieppel, 1999). Haas (1979) originally included *Pachyrhachis* in Simoliophiidae, as did McDowell (1987) who also added *Pachyophis*; but of the two family-group names proposed by Nopcsa (1923), Pachyophiidae has page priority. There is now agreement that pachyophiids are snakes but their exact position within snakes remains debated (Zaher and Rieppel, 1999; Tchernov *et al.* 2000; Lee and Scanlon, 2002). These three taxa are extremely similar, and possess small heads, heavily pachyostotic mid-body vertebrae and ribs, and distally straight ribs indicating lateral compression of the trunk. Radovanovic (1935: 411) postulated that *Mesophis* was a terrestrial snake in which the very slender distal parts of the ribs had been straightened by pressure during fossilization. However, this hypothesis is very unlikely because ribs of similar shape occur consistently in otherwise undistorted specimens of larger pachyophiids, namely *Pachyophis* and *Pachyrhachis*, as well as in other marine taxa (see below).

The specimen described here is clearly not a pachyophiid because in all known pachyophiids the forelimbs and shoulder girdle are completely absent, and the mid-trunk ribs are heavily swollen (pachyostotic). Also, the centra are long and taper posteriorly, unlike the pachyophiid condition of short centra that are of constant width throughout. The transverse processes also extend much further laterally than they do in pachyophiids.

### Haasiophis

A new limbed Cretaceous marine snake, *Haasiophis*, has been described and interpreted to have affinities with *Pachyrhachis* (Tchernov *et al.*, 2000) and by implication with pachyophiids as a group. However, certain cranial elements were apparently misidentified, and a reassessment of the morphology suggests that these taxa are not closely related, but are successive outgroups to

crown-clade snakes (Lee and Scanlon 2002). The postcranial elements of *Haasiophis* have yet to be properly described, making comparisons with *Mesoleptos* difficult. However, *Haasiophis* differs from HUI-PAL EJ699 in possessing heavy pachyostosis of the vertebrae, many more trunk vertebrae, and in completely lacking a shoulder girdle and forelimb.

### Palaeogene Marine Snakes

HUI-PAL EJ699 can be confidently excluded from the following groups of Tertiary snakes with distally straight ribs based on presence of forelimbs and very different vertebrae. *Archaeophis* (Archaeophiinae) has long, proximally curved but distally straight ribs (Janensch, 1906), and the ribs of *Palaeophis* share this morphology (Owen, 1850b). However, the neural arch is narrow and high, the centrum approximately cylindrical and the transverse processes relatively small (Rage, 1984). In the complete skeleton of *Archaeophis proavus* there are over 450 trunk vertebrae and no traces of limbs or girdles (Janensch, 1906), and there is no indication of their presence in other less completely known species. *Anomalophis* (Anomalophiidae) has similar ribs (Janensch, 1906; Auffenberg, 1959) and also small transverse processes. However, the centra are long and gradually tapering, and the neural arches are narrow and depressed, except for a backsloping neural spine. Vertebrae of other early aquatic snakes (Nigerophiidae and Russellophiidae; Rage, 1984, Averianov, 1997) have features resembling the palaeophiids, acrochordids and colubroids to a varying extent, but no ribs or articulated skeletons are known and their relationships remain obscure.

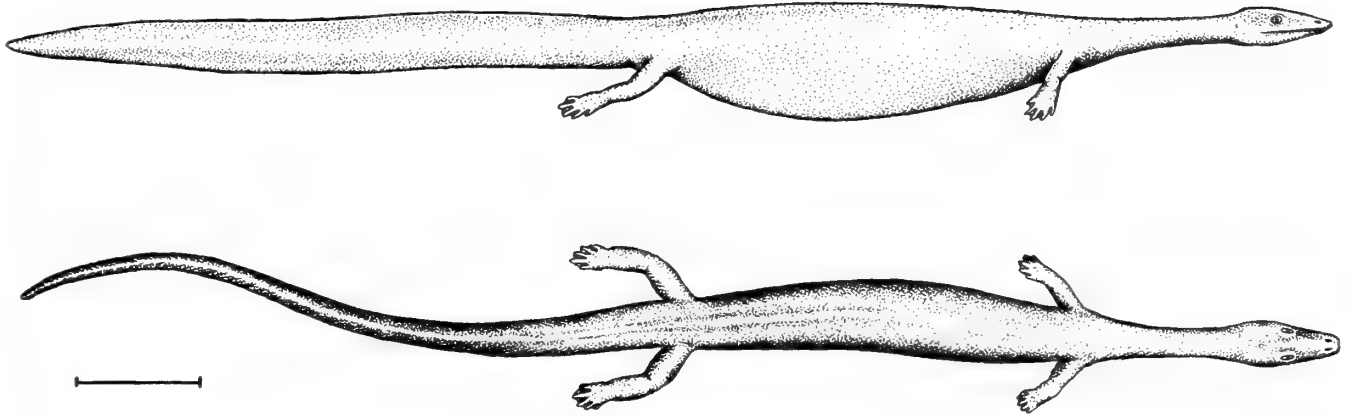
Thus, the specimen HUI-PAL EJ699 can be associated most closely with *Mesoleptos*. However, it differs from the type of *M. zendrinii* (as described by Cornalia and Chiozza, 1852; compare Tables 1 and 2) in the ribs of the anterior thoracic region being considerably shorter relative to vertebral length or width; the ribs are also thick in the curved middle portion of the shaft rather than uniformly slender. This region of the body is not preserved in the other referred (MCSNT) specimen. If confirmed, these differences would indicate a considerable variation in body shape (analogous to the differences among known specimens of aigialosaurids) which might justify erection of a new species. However, the location and condition of the type and some other important specimens are currently unknown, and the putative differences cannot be directly confirmed. There remains a possibility that the description and figure of the type are inaccurate, as they seem questionable in a number of details, and that the two specimens are identical. Thus, we have refrained from any formal taxonomic decisions pending a more comprehensive search for the type, and simply refer the current specimen to *Mesoleptos* sp. indet.

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## RECONSTRUCTION AND PALAEOECOLOGY

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Based on all three specimens, *Mesoleptos* can be reconstructed as follows (Figs. 1 and 2). Depending on where one draws the cervical-dorsal boundary, there are five to seven cervical vertebrae preserved in HUI-PAL EJ699, and as these do not include the atlas or axis there must have been at least seven to nine cervicals, and possibly several more. Seven to nine cervicals are plesiomorphic for squamates and occur in most terrestrial varanoids, aigialosaurs and some mosasaurs, while dolichosaurs, *Eidosaurus* and some mosasaurs have increased from this number (Nopcsa, 1908, 1923; Caldwell, 2000). There are 23 trunk vertebrae in the type and thus at least 30 to 32 presacrals altogether (cf. 34 in *Eidosaurus*), but not many more than this



**Fig. 2** Reconstruction of *Mesoleptos* in dorsal and lateral views. The head and tail are not known in any specimen and are thus conjectural. Note the long neck, long laterally compressed body, and short webbed limbs. Scale bar = 10cm.

unless the neck was unusually long. Short, curved ribs are present on most of the cervical vertebrae, implying a narrow cylindrical neck, which is similar to conditions in *Eidolosaurus* and some dolichosaurs, rather than aigialosaurs which have longer ribs on most of the cervicals. The cervical-thoracic boundary presumably lies around, or immediately posterior to, the sharp increase in rib length.

The anterior thoracic ribs are straight distally, implying a lateral flattening of the trunk region. Allowing for apparent variation between the three known specimens in the proportional length of the ribs, the ribs remain long throughout the mid-trunk region, where the largest vertebrae occur. Vertebral and rib dimensions increase steadily up to at least the tenth thoracic vertebra, are highest in mid-trunk and decrease, apparently more slowly, in the last ten or so presacrals. These size gradients are stronger than seen in measured skeletons of *Varanus* and *Heloderma* (Scanlon, unpublished data), and far more conspicuous than in any other marine varanoids described. Unlike some aigialosaurs and all mosasaurs, there is not a long series of shortened posterior dorsal ribs. Rather, long, distally straight ribs continue at least to within the last five presacral vertebrae (as indicated by the MCSNT specimen; the most posterior ribs have been damaged or lost in both this and the type).

The cervical vertebrae bear prominent ventral keels and hypophyses, which are reduced on the first two thoracics and then disappear. The centra of the following thoracic vertebrae are smooth ventrally, but posterior trunk vertebrae apparently have laterally paired keels defining a median trough, a feature that also occurs in dolichosaurs, *Eidolosaurus* and some aigialosaurs (but often commencing more anteriorly in the trunk). The sacral vertebrae (in the MCSNT specimen at least) are shorter than the immediately preceding trunk vertebrae, and are fused (or at least very tightly articulated) together. Parts of the first few caudal vertebrae are present in the type, indicating a laterally compressed tail with elongate but antero-posteriorly narrow neural spines and chevrons.

The trends in vertebral size (length and width) and rib length indicate an animal with a relatively small head and narrow neck in relation to its body, similar to dolichosaurs and *Eidolosaurus*. The curved cervical ribs indicate that the cervical region of the animal was approximately round in cross-section. However, the distally straight dorsal ribs indicate that the trunk region of the animal was laterally compressed and very deep. These long ribs projected only a short distance laterally from the vertebrae before curving to extend downward (and obliquely backward) for most of their length. The girdles and limbs were rather small, although most elements were probably present; compared to adjacent vertebrae, both the femur

and humerus are relatively shorter than in aigialosaurs, but the forelimb was not as reduced as in dolichosaurs or *Eidolosaurus* (Fig. 2).

In comparison with the similar-sized aigialosaurs, *Pontosaurus* and species of *Varanus*, trends in vertebral size within the column of *Mesoleptos* are somewhat different. There is a local minimum of centrum length in the posterior cervical region, but the elongation of the anterior cervicals is much less pronounced than the condition in most *Varanus* spp. (a derived condition within that genus). Gradients of vertebral length and width within the thoracic and dorsal region are stronger than in any of the other taxa. The centrum is narrower posteriorly than in aigialosaurs, *Pontosaurus* and *Varanus*, indicating a condyle-cotyle joint of smaller diameter and surface area. This in turn suggests weaker compressive forces within the column, along with a less energetic style of locomotion and/or a greater capacity for lateral flexion of the neck and trunk. On the other hand, the combination of long transverse processes and long narrow centra increases both leverage and space for muscles connecting successive transverse processes, such as the *m. interarticularis* (cf. Mosauer, 1935; Gasc, 1974). These could then be of increased importance in lateral undulation, perhaps taking over in this role from longer muscles inserting on the ribs whose effectiveness would be decreased by lateral compression of the trunk. If the above interpretation of the affinities of the Novak specimen is correct, the derived vertebral morphology evolved before the lateral compression, so that this 'takeover' could happen via an intermediate where both sets of muscles were effective. Zygosphenes, considered to be of biomechanical importance in limiting twisting between adjacent vertebrae (Gasc, 1974), are well-developed (exposed dorsally in the MCSNT specimen) and articulate with zygantra in the preceding neural arches as in other aquatic varanoids and all snakes.

Among living squamates, the only forms with distally straight ribs (and thus laterally compressed bodies) are highly aquatic caenophidian snakes, such as file snakes (acrochordids) and sea snakes (laticaudine and hydrophiine elapids). This feature has rarely been discussed in extant snakes; Hoffstetter and Gayraud (1965) do not comment on any unusual features of the ribs in *Acrochordus* or *Enhydryna* (Hydrophiinae), though it was described in '*Enhydryis*' (= *Lapemis*) *hardwickii* (Hydrophiinae) by Janensch (1906: 22). In *Acrochordus arafurae* (SAM R26956, R26966) the anterior ribs are robust and strongly curved, while those of the posterior half of the body are much more slender and only weakly curved except near the base. The pachyophiids – primitive marine snakes – also had a

similar morphology, which is functionally correlated with anguilliform swimming (Scanlon *et al.*, 1999; Lee *et al.*, 1999). It can thus be concluded that *Mesoleptos* was marine. This is also supported by the morphology of the posterior ribs. While they do not exhibit the histological features of true pachyostosis, they are nevertheless robust (in the MCSNT and HUI specimens) and might have served to reduce buoyancy, much like the pachyostotic ribs in other marine reptiles. The type of *M. zendrinii*, from the Comen locality, also comes from deposits dominated by marine fish (Gorjanovic-Kramberger, 1892) and is associated with aigialosaurs, dolichosaurs and pachyophiids. This also presumably applies to the MCSNT specimen (although its collection details have not been recorded it is probably from either Comen or Lesina). Marine habits of the present specimen are also implied by the position of the 'Ein Jabrud locality far from the palaeoshoreline (Scanlon *et al.*, 1999), and the articulated nature of the preserved elements suggesting *in situ* preservation.

The laterally compressed body and small limbs suggest that *Mesoleptos* swam primarily by lateral undulation, holding its limbs against its flanks (Carroll 1985; Lee 1999). In such forms, most of the propulsion occurs by movements of the tail, and to some extent the posterior region of the trunk. This is consistent with the observation that the posterior trunk region is most laterally compressed in *Mesoleptos* (the tail is unknown). The forelimbs and hindlimbs, however, were still large and well ossified enough to have been functional. They may have been used for slow locomotion ('walking') along the seabed, where (with the help of buoyancy) they could have supported the body. Alternatively, or additionally, they may have been used for forays on the shore.

## PHYLOGENETIC RELATIONSHIPS OF *MESOLEPTOS*

All previous interpretations of the morphology and relationships of *Mesoleptos* were based either on poorly preserved and inadequately described material (the type), or on a composite of the type with the referred Novak specimen (Gorjanovic-Kramberger, 1892) which is clearly distinct from *M. zendrinii* in rib morphology. Gorjanovic-Kramberger's inclusion of *Mesoleptos* in Varanidae was 'phenetically' based on its long ribs, as distinct from the shorter and more uniform ribs of *Aigialosaurus* (as then interpreted) and dolichosaurs. However, he recognised it as marine in habits and thus by no means a typical varanid. Nopcsa classified *Mesoleptos* doubtfully as an aigialosaur (1903), but later placed it in a separate subfamily (Mesoleptinae) with *Eidolosaurus*, close to both aigialosaurines and dolichosaurines within Dolichosauridae (1923).

McDowell and Bogert (1954) returned *Mesoleptos* and *Eidolosaurus*, again doubtfully, to Aigialosauridae, but also briefly considered that they might be related to the living earless monitor, *Lanthanotus*. Hoffstetter (1955) also retained *Mesoleptos* as a possible aigialosaurid, while recognising *Eidolosaurus* as a dolichosaur and suggesting that *Pachyvaranus* might represent a distinct family. Romer (1956) placed both *Mesoleptos* and *Eidolosaurus*, with question marks, in Dolichosauridae.

The current state of understanding of these groups is perhaps best indicated by the fact that the systematic conclusion to Calligaris' (1988) review was formed by a summary of Nopcsa's (1923) classification, without substantial additions or revisions. That these groups have been poorly studied recently is highlighted by Carroll and DeBraga's (1992) statement that only five species had been assigned to Aigialosauridae, and did not mention either *Mesoleptos* (assigned to Aigialosauridae by Nopcsa, 1903, Camp, 1923, and

McDowell and Bogert, 1954), *Eidolosaurus* (assigned by Nopcsa, 1923, and McDowell and Bogert, 1954) or *Pachyvaranus* (assigned by Arambourg and Signeux, 1952).

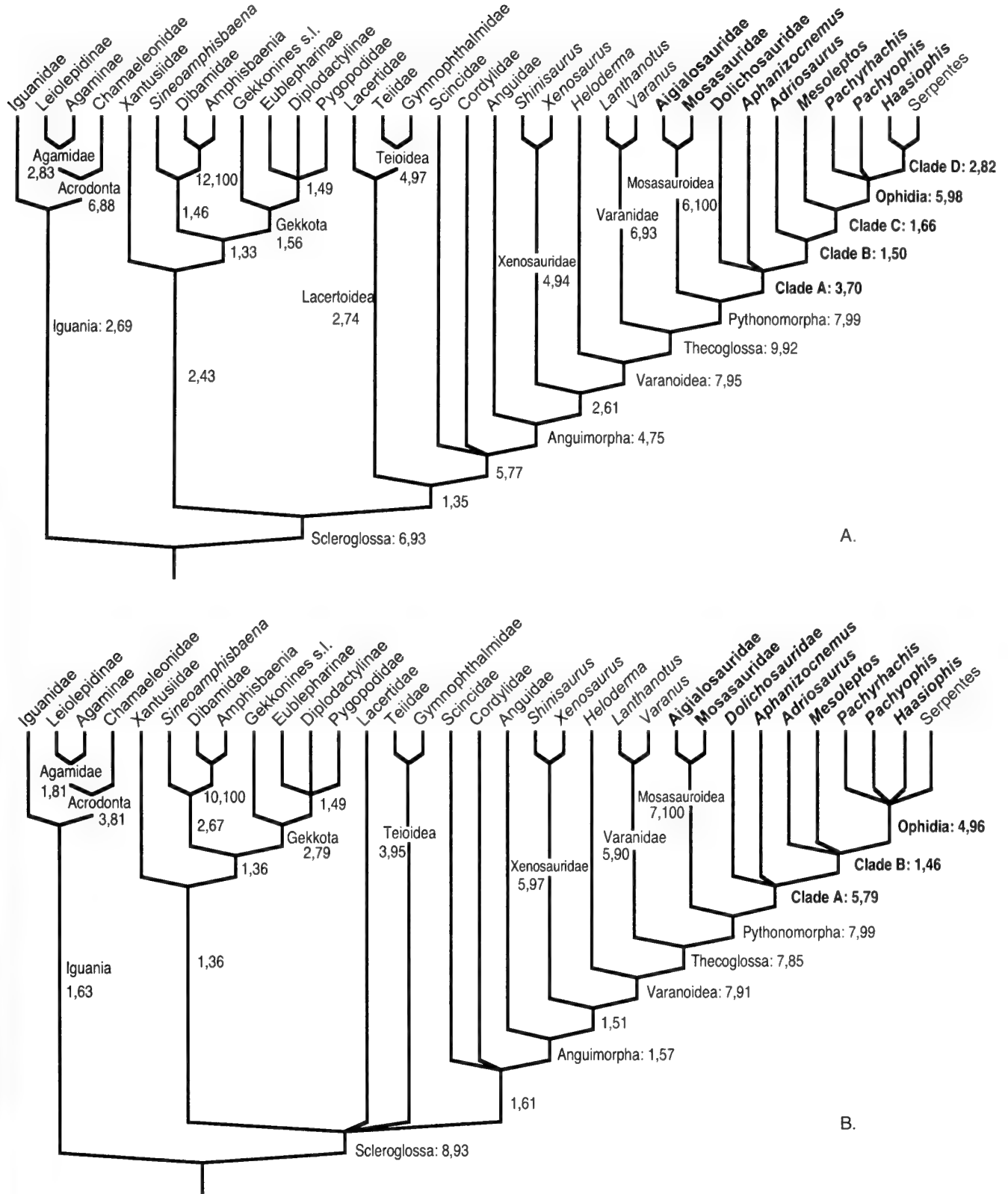
The relationships of *Mesoleptos*, therefore, remain unresolved. While a robust assessment will have to await more complete material, a preliminary analysis is undertaken here. Morphological information from the MCSNT and HUI specimens (based on examination of specimens) and the type (based on published descriptions) was used in order to evaluate its phylogenetic relationships. *Mesoleptos* was added to the data matrix used in the most recent comprehensive analysis of squamates (Lee 2002); this matrix includes 248 osteological characters, used here, and addresses recent criticisms of various characters (Rieppel and Zaher 2000). Recently described (or redescribed) elongate marine squamates were also included in this matrix: *Pachyrhachis* (Lee and Caldwell, 1998), *Pachyophis* (Lee *et al.*, 1999), *Adriosaurus* (Lee and Caldwell, 2000) and dolichosaurs (*Coniosaurus* and *Dolichosaurus*; Caldwell and Cooper, 1999; Caldwell, 1999, 2000). *Coniosaurus* and *Dolichosaurus* are here combined into a single taxon, Dolichosauridae *sensu stricto*, based on the observations that the comparable parts of the two taxa appear almost identical, they overlap stratigraphically, and as noted by Caldwell (2000) one of the *Coniosaurus* species might be synonymous with *D. longicollis*. Character codings for all taxa (except *Haasiophis*) in this matrix, including the marine fossil forms, are based on direct examination of the material. As descriptions of the remaining marine squamates discussed above are dated, and they have yet to be restudied, they have not been included in the analysis. The full matrix is presented elsewhere (Lee 2002) and only the (new) character codings for *Mesoleptos* are listed here (Appendix 1). The full matrix (including *Mesoleptos*) used in this analysis has been deposited in TreeBase (<http://www.treebase.org/treebase/>).

The enlarged data matrix with *Mesoleptos* was analysed using the heuristic algorithm of PAUP\* (Swofford, 1999) employing 100 random addition sequences. Two analyses were performed, with multistate characters ordered according to morphoclines where possible, or with all multistate characters unordered, to see if the phylogenetic analyses were contingent on assumptions of character state transitions. The degree of support for each grouping was ascertained by the support index (Bremer, 1988), calculated in PAUP using batch commands generated by TreeRot Version 2b (Sorenson, 2000). These commands were modified so that each heuristic search employed 100 rather than 20 random addition sequences. Nonparametric bootstrapping (1000 heuristic replicates each employing 100 random addition sequences) was also used to assess the robustness of each clade. As there were no fully specified a priori hypotheses for *Mesoleptos* and all other squamates, Templeton tests are inappropriate and were not performed (Goldman *et al.*, 2000).

### Phylogenetic affinities

In the ordered analysis, three most parsimonious trees were found, each of length 672, consistency index = 0.46, retention index = 0.71. The strict consensus is shown in Fig. 3A, along with nodal supports. In the unordered analysis, 4 most parsimonious trees were found when only branches with unequivocal character support were retained, each of length 639, consistency index = 0.48, retention index = 0.71. The strict consensus is shown in Fig. 3B, along with nodal supports.

The basic topologies of the ordered and unordered consensus trees are similar to each other and largely unchanged from that the previous study (Lee, 2002), so that diagnoses of all the clades within Squamata are not repeated here. The characters diagnosing additional



**Fig. 3.** The phylogenetic affinities of *Mesoleptos*, based on cladistic analyses of 248 characters across squamates. (A) Analysis with multistate characters ordered, strict consensus of 3 trees, length 672, consistency index 0.46, retention index 0.71. (B) Analysis with multistate characters unordered, strict consensus of 3 trees, length 639, consistency index 0.48, retention index 0.71. First number next to each clade refers to branch support (Bremer, 1988); second number refers to bootstrapping frequency. Clades immediately relevant to the affinities of *Mesoleptos* are in bold and are discussed in the text. The other more inclusive clades are discussed in Lee (1998). Aquatic terminal taxa are indicated in bold.

clades of immediate relevance to *Mesoleptos* are listed below. The character changes diagnosing these clades in the 'ordered' analysis under delayed transformation optimisation are listed in Appendix 2; the changes in the 'unordered' analysis are very similar, except that some clades collapse (compare Figs 3A and B). Unequivocal changes, i.e. those which occur under both delayed and accelerated optimisation, are indicated with an asterisk (\*). Note that most characters diagnosing snakes (Ophidia) are equivocal because *Mesoleptos*, the sister group of snakes, is poorly known and nearly all the characters could apply to a more inclusive clade that also contains *Mesoleptos* (clade C). As discussed below, the clades are not strongly corroborated due to missing data and possible correlation of the supporting characters, and are thus not yet named formally.

## EVOLUTIONARY IMPLICATIONS

The phylogenetic results imply that snakes arose from within a plexus of marine varanoids, an idea suggested initially by Nopcsa (1908, 1923) and later by Haas (1980). The aquatic hypothesis is often ascribed to Cope (1869), but Cope never suggested that the aquatic mosasaurs were ancestral to snakes: rather, he suggested that both had a close common ancestor, which might even have been terrestrial. However, critics subsequently misquoted Cope as suggesting that snakes evolved directly from mosasaurs and thus had marine ancestors, and then proceeded to argue that as snakes could not have evolved from mosasaurs (which possess numerous specialisations), they could not have had marine ancestors (e.g. Owen, 1877; Dollo, 1903, 1904; Janensch, 1906; McDowell and Bogert, 1954; Zaher and Rieppel, 1999). Nopcsa (1908, 1923) recognised and addressed the erroneous arguments of Owen and Janensch, and put forward a rigorous case for a marine stage in snake ancestry. More recently, by interpreting aigialosaurs as probable ancestors of snakes, McDowell and Bogert (1954) implicitly proposed a marine ancestry. In describing the second specimen of *Pachyrhachis* (= *Ophiomorpha*), Haas (1980: 191) stated that the fossil 'points to the fact that the snakelike body and loss of limbs did develop in a marine surrounding'. Despite this, the aquatic theory has in recent times been largely rejected in favour of the 'fossorial theory', i.e. that snakes evolved from small elongate burrowing lizards (e.g. Janensch, 1906; Walls, 1940; Bellairs and Underwood, 1951; Underwood, 1967; Rieppel, 1988; Greene, 1997). Thus, few modern studies rigorously surveyed marine varanoids and marine ophiomorphs for possible relationships with modern snakes.

This analysis indicates that the closest four to eight outgroups to modern (terrestrial) snakes are marine; the exact number varies depending on how the polytomies are resolved. The most parsimonious interpretation is that marine or at least semi-aquatic habits were primitive for pythonomorphs, and that snakes evolved in a marine or semi-aquatic environment and are secondarily terrestrial (Nopcsa, 1908, 1923; McDowell and Bogert, 1954; Haas, 1980). In order to maintain that the snake stem lineage was always terrestrial, between four and eight convergent invasions of marine habitats must be assumed to have occurred in mosasauroids, dolichosaur-like taxa, and basal snakes. The analysis further suggests that, of all the marine varanoids, *Mesoleptos* occupies a crucial phylogenetic position, as the nearest relative of snakes (Ophidia). If this is true, the similarities between *Mesoleptos* and primitive snakes are not convergent; these include such traits as a proportionally small head, long body, limb reduction, and lateral body compression. In these features, *Mesoleptos* appears inter-

mediate between the typical lizard-like marine varanoids (e.g. mosasaurs) and primitive marine snakes.

Two substantial caveats must be added to this interpretation. Apart from mosasaurs and aigialosaurs, all the marine varanoids are very imperfectly known. For instance, *Mesoleptos* can be scored for only 13% of characters, dolichosaurs for 35% and *Adriosaurus* for 38%. Such large amounts of missing information suggest that their positions cannot be very robust, a view confirmed by low bootstrap and Bremer supports. This missing information also reduces support throughout the tree, as the poorly known taxa can fit into many different places with only slight loss in parsimony. Additionally, many of the characters that unite dolichosaurs, *Adriosaurus* and *Mesoleptos* with mosasauroids and snakes, to the exclusion of other varanoids, are correlates of marine adaptation. Within this group (Pythonomorpha), many of the characters uniting dolichosaurs, *Aphanizocnemus*, *Adriosaurus* and *Mesoleptos* with snakes to the exclusion of mosasauroids are correlates of body elongation and limb reduction. Thus, the position of these poorly known taxa close to snakes might reflect a false signal caused by marine adaptation and body elongation, both features found in basal snakes. More complete fossil finds, and thus, information on characters not obviously correlated with habitat and body form, are required before their phylogenetic relationships can be conclusively ascertained and the early evolution of snakes clearly understood. The fundamental questions investigated by Bellairs and Underwood (1951) and Underwood (1967) regarding the affinities and ecological origins of snakes still await convincing answers.

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## Appendix 1

Additions to the osteological data matrix of Lee (2002) used in this cladistic analysis. *Mesoleptos* was added to the taxon list and could be coded for the following characters.

### Axial Skeleton

171. **Centra**. Not constricted anterior to condyle, i.e. condyle not wider than posterior end of centrum (0); slightly constricted anterior to condyle, i.e. condyle slightly wider than posterior end of centrum (1); greatly constricted anterior to condyle, i.e. condyle much wider than posterior end centrum (2). *Mesoleptos* 0.
172. **Vertebral articular surfaces**. Vertical, condyles (if present) facing posteriorly, much of the articular surface is visible in ventral view (0); slightly anterodorsal, condyles facing slightly dorsally, only the ventral edge of the articular surface is visible

- in ventral view (1); anterodorsal, condyles facing very dorsally, none of the articular surface is visible in ventral view (2). *Mesoleptos* 0.
174. **Centra.** Notochordal, i.e. perforated by persistent notochord in adults (0); not notochordal, i.e. not perforated by persistent notochord in adults (1). *Mesoleptos* 1.
175. **Centra.** Amphicoelous (0); procoelous (1). *Mesoleptos* 1.
176. **Neural spines.** Tall processes (0); low ridges (1). *Mesoleptos* 0.
177. **Zygosphenes and zygantra.** Present (0); absent (1). *Mesoleptos* 0 (Visible on the MCSNT specimen).
179. **Intercentra on dorsal (thoracolumbar) vertebrae.** Present (0); absent (1). *Mesoleptos* 1.
180. **Number of presacral vertebrae.** 23 to 25 (0); 22 or fewer (1); 26 (2); 27 to 50 (3); 50 to 119 (4); 120 to 150 (5), 150 or more (6). *Mesoleptos* 3.
182. **Transverse processes of cervicals.** On anterior end of centrum (0); on middle of centrum (1). *Mesoleptos* 0.
183. **Hypapophyses on anterior presacrals.** Only extending to the posterior end of the sixth presacral at most (0); extending to the seventh presacral or beyond (1). *Mesoleptos* 1.
185. **Anterior presacral vertebrae** (excluding atlas and axis intercentra). Not sutured or fused to preceding centrum (0); sutured to preceding centrum (1); fused to preceding centrum (2). *Mesoleptos* 2.
186. **Anterior presacral vertebrae** Not sutured or fused to following centrum (0); sutured to following centrum (1); fused to following centrum (2). *Mesoleptos* 0.
187. **Pachyostosis of mid-dorsal vertebrae and ribs.** Absent (0); present (1). *Mesoleptos* 0.
196. **Body shape.** Round, dorsal ribs smoothly curved (0); laterally compressed, middle and distal regions of dorsal ribs totally straight (1). *Mesoleptos* 1.
198. **Ribs.** Proximal end without anteroventral pseudotuberculum (0); proximal end with anteroventral pseudotuberculum (1). *Mesoleptos* 0.
199. **Ribs.** Proximal end without posterodorsal pseudotuberculum (0); proximal end with posterodorsal pseudotuberculum (1). *Mesoleptos* 0.
200. **Distally forked cloacal ribs** ('lymphapophyses'). Absent (0); present (1). *Mesoleptos* 0.
201. **Tail.** Cylindrical or only slightly lateral compressed, transverse processes well-developed, chevrons and neural spines not elongated (0); very laterally compressed, transverse processes reduced anteriorly and absent posteriorly, chevrons and neural spines elongated (1). *Mesoleptos* 1.
203. **Scapulocoracoid.** Present and large (0); present but reduced (1); absent (2). *Mesoleptos* 1.
204. **Emargination on anterodorsal edge of scapula.** Absent (0); present (1). *Mesoleptos* 0.
205. **Anterior (primary) coracoid emargination.** Absent (0); present (1). *Mesoleptos* 1.
206. **Posterior (secondary) coracoid emargination.** Absent (0); present (1). *Mesoleptos* 1.
207. **Clavicle.** Present (0); absent (1). *Mesoleptos* 0 (see text for discussion of identity of this element).
209. **Clavicles.** Rod-like, at most only slightly expanded proximally and with no notch or fenestra (0); greatly expanded proximally, usually with notch or fenestra (1). *Mesoleptos* 0 (see text for discussion of identity of this element).
218. **Forelimbs.** Large (0); small (1), absent (2). *Mesoleptos* 1.
222. **Pelvis.** Present and large (0); present and small (1); absent (2). *Mesoleptos* 1.
228. **Hindlimbs.** Well-developed (0); reduced (1); absent (2).

### *Mesoleptos* 1.

234. **Body proportions.** Head moderately large with respect to wide trunk region (0); head extremely small with respect to wide trunk region (1). *Mesoleptos* 1.
235. **Dorsal body osteoderms.** Absent (0); present (1). *Mesoleptos* 0.
236. **Ventral body osteoderms.** Absent (0); present (1). *Mesoleptos* 0.
246. **Epiphyses.** Present on appendicular and axial skeleton (0); present on appendicular, but absent on axial skeleton (1); absent from both appendicular and axial skeleton. *Mesoleptos* 1. Note *Haasiophis* was incorrectly coded with state 1 in Lee (2002); it has state 2.

## Appendix 2 Synapomorphies for Clades A–D in Fig. 3A

Character number, consistency index and direction of change (if not 0 → 1) listed in parentheses.

### Clade A: dolichosaurs, *Adriosaurus*, *Mesoleptos*, and *Ophidia*

\*More than ten cervical vertebrae (181, 0.6, 2→3), \*Scapulocoracoid reduced (203, 0.67), \*interclavicle absent (210, 0.33), \*forelimbs small (218, 0.5), \*pelvis reduced (222, 0.5), \*hindlimbs small (228, 0.67).

### Clade B: *Adriosaurus*, *Mesoleptos*, and *Ophidia*

\*Premaxilla-maxilla contact mobile (5, 1.0), frontals paired (26, 0.14), postorbitofrontal ventral process large (36, 0.5, 1→0), supratemporal superficial (52, 0.67, 1→0), \*body laterally compressed (196, 0.5), pubis not expanded distally (227, 1.0).

### Clade C: *Mesoleptos* and *Ophidia* (snakes)

\*Vertebral condyles facing posteriorly (172, 1.0, 1→0), \*head small with respect to trunk (234, 1.0).

### Clade D: *Ophidia* (snakes)

Dorsal process of maxilla on middle or anterior of maxilla (8, 0.5, 1→0), posterior process of maxilla long (10, 0.33, 1→0), lacrimal absent (11, 0.5), frontoparietal suture with sinuous contact (30, 0.2, 1→0), pineal foramen absent (40, 0.17), parietal table reduced to sagittal crest (42, 0.22, 1→0), suspensorial ramus of parietal reduced (44, 0.5), upper temporal arch incomplete (45, 0.25), tympanic crest absent (57, 0.29, 0→2), parietal downgrowths contacting parabasisphenoid (67, 1.0), optic foramina enclosed in bone (68, 1.0), anterior brain cavity floored by frontals and cultriform process (69, 0.67, 0→2), trigeminal foramina bordered at least partly by parietal (70, 1.0), supraoccipital on skull roof behind parietal (86, 0.5), posttemporal fenestra closed (89, 0.5), opening of Jacobson's organ enclosed by vomer and septomaxilla only (94, 0.4, 1→2), vomer medial to palatine (99, 1.0), palatine-vomer contact mobile (102, 1.0), palatine long (103, 0.33, 1→0), palatine with distinct rectangular process (105, 1.0), two or fewer mental foramina on lateral surface of dentary (117, 1.0), posterior margin of lateral surface of dentary deeply notched (123, 0.4, 1→2), dentary overlapped by surangular (124, 1.0, 0→2), surangular extends far over lateral surface of dentary (134, 1.0, 2→3), articular fused with prearticular and surangular (144, 0.25, 1→0), retroarticular process short (145, 1, 0→1), marginal teeth with medial and lateral carinae (153, 0.67, 1→2), palatine teeth present (166, 0.33, 1→0), palatine teeth long fangs (167, 1.0), \*at least 120 presacral vertebrae (180, 0.6, 3→5), \*lymphapophyses present (200, 0.67), \*shoulder girdle absent (203, 0.67, 1→2), \*clavicle absent (207, 0.33), ossified sternum absent (213, 1.0), \*forelimbs absent (218, 0.5, 1→2), scleral ossicles absent (241, 0.5), \*appendicular epiphyses absent (246, 0.67, 1→2).



# Phallus morphology in caecilians (Amphibia, Gymnophiona) and its systematic utility

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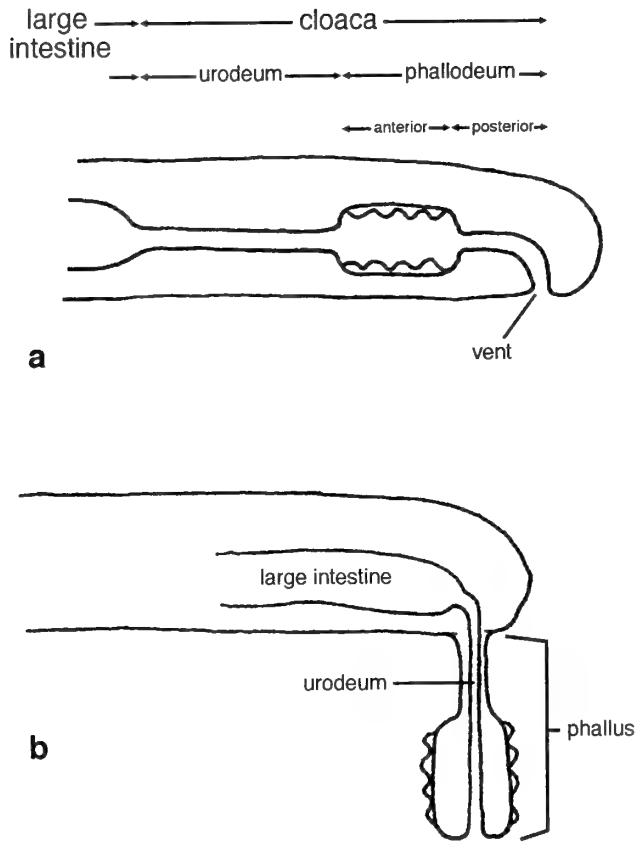
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**SYNOPSIS.** The cloaca of male caecilian amphibians (Gymnophiona) is a tube that comprises an anterior urodeum and a posterior phalloseum. The phalloseum everts (with the urodeum lying inside it) to form a phallus used for direct sperm transfer in copulation. Phalloseal morphology is rich in detail and variation, and has therefore been considered a potentially useful and much needed tool for caecilian phylogenetics and species-level taxonomy. Despite this, it has been almost entirely ignored in caecilian systematics, there is confusion regarding some aspects of morphology, and variation within and among species is poorly understood. A short review and reconsideration of phallus morphology is presented, and the systematic potential assessed. The anterior part of the phalloseum appears to offer the most obvious systematic potential, and the morphology of longitudinal ridges and their ornamentation here seem to have diagnostic and/or phylogenetic value for some taxa. Although there is evidence of intraspecific variation, at least some of which is associated with ontogeny and reproductive condition, individuals of the same species generally have a common pattern of phalloseal ridges and ornamentation, and congeners often share a similar pattern. However, these patterns are not universally species specific, at least among urodeophylids. Although variation needs to be better understood, the male cloaca offers great potential for caecilian systematics.

## INTRODUCTION

As in other amphibians, caecilians (Gymnophiona) possess a cloaca, a chamber that opens to the exterior via the vent and into which open the large intestine, the urogenital (Wolffian and Müllerian) ducts, and the bladder. In contrast to other amphibians, the cloaca of male caecilians can be everted through the vent (Fig. 1) to serve as an intromittant organ, or phallus, used in copulation to effect direct sperm transfer (e.g. Himstedt, 1996). It has long been recognised that the external surface of the caecilian phallus and the corresponding internal surface of the unverted cloaca may bear distinctive ridges and grooves, tuberosities and even spines (e.g. Duvernoy, 1849; Günther, 1864; Spengel, 1876; Noble, 1931). There is considerable interspecific variation in the complex patterns of these features, but there have been few comparative studies.

Spengel (1876) compared cloacal features in males of six species in what are now recognised as six genera from three families, and aspects of cloacal morphology were compared further in some of these species by Wiedersheim (1879). Tonutti (1931) provided a very detailed documentation of the unverted and everted cloaca of the caeciliid *Hypogeophis rostratus* (Cuvier, 1829) and compared it with the unverted cloaca of the ichthyophiid *Ichthyophis glutinosus* (Linnaeus, 1758) and of the caeciliid *Spionops annulatus* (Mikan, 1820). Tonutti (1933) expanded the comparative aspect of his study of the caecilian phallus by incorporating detailed data on a further six species, including representatives of Scolecomorphidae and Typhlonectidae. Tonutti's work remains the most detailed to date. Taylor (1968 and references therein) figured (though without labels or orientation) everted phallosea and *in situ* dissections of 12 species in eight genera and four families. The broadest comparative study of the male cloaca was presented by Wake (1972), who examined



**Fig. 1** Schematic sagittal section through the posterior of a male caecilian showing (a) main divisions of the unverted cloaca, and (b) the everted phallus with the internal, luminal surface of the phalloseum on its exterior surface, and the urodeum forming its core.

34 caecilian species, including representatives of 20 currently recognised genera and all six of the currently recognised families. Exbrayat (1991) compared cloacae of single species from four genera in three families. Wake (1998) provided comparative data on the cloacal spines and spicules of the three nominate species of *Scolecormorphus* Boulenger, 1883.

Species limits in caecilians are poorly understood and the taxonomy within many genera is best viewed as uncertain and potentially unstable (Nussbaum and Wilkinson, 1989). The inadequate state of current knowledge has been attributed to the group's tropical distribution, largely fossorial and secretive lifestyle, under-representation in museum collections, lack of detailed study, and a relative paucity of obvious external morphological features in association with their limbless bodies, reduced or absent tails, and reduced head features (e.g. Nussbaum & Wilkinson, 1989). Some 34 years after the publication of Taylor's (1968) taxonomic monograph, species level caecilian systematics is still dominated by counts of annuli, vertebrae, and teeth. Of the phallus, Taylor (1968: 31) was 'certain that most genera and many species could be identified by the characters of this organ alone' and Wake (1972: 353) stated that 'the arrangement of musculature and cloacal accessory structures is species-specific in males.' If correct, male cloacal morphology, with its complex structure and many variations, should provide a much needed tool for investigating species limits in and phylogenetic relationships among caecilians. However, not much has changed since Largen *et al.* (1972: 187) pointed out that 'The value of penis structure as a taxonomic character has yet to be fully investigated'.

We have made observations of the cloacal morphology of a broad range of caecilian species. Without assembling a thorough synthesis of these observations, we draw upon them here to provide a description of the male cloaca that emphasises some features that can be homologised across taxa, and that indicates the kind of variation that occurs. It is hoped that this contribution will clarify some points of confusion in the literature and be a stimulus to future research. Our focus here is on the male cloaca only.

## Abbreviations

### Text

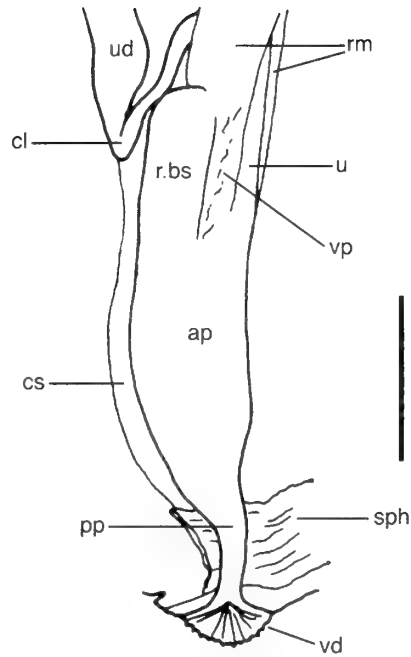
UMMZ: University of Michigan, Museum of Zoology.

### Figures

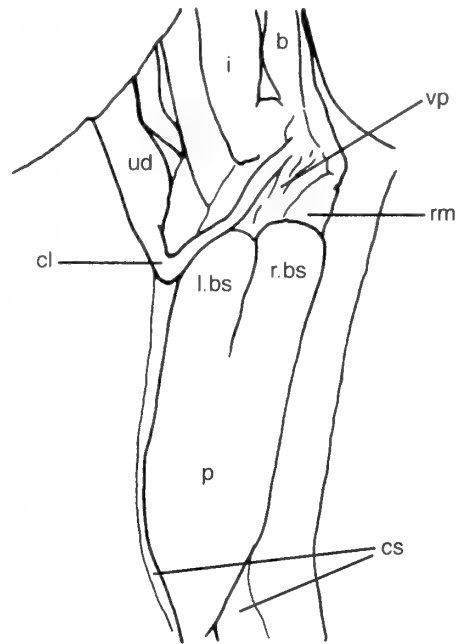
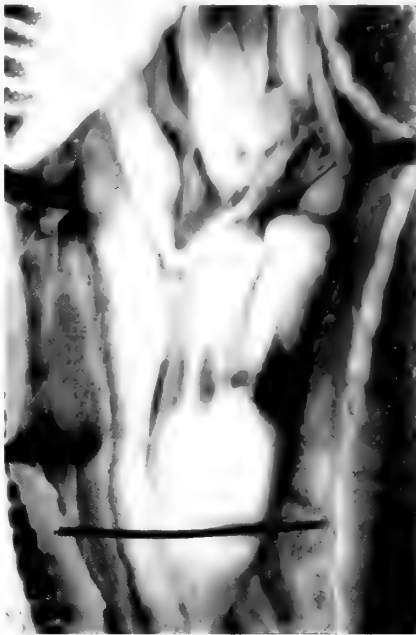
a.ll	anterior tuberosity of l.l
a.md	anterior tuberosity of md
ap	anterior part of phalloseum
a.rdl	anterior tuberosity of r.dl
a.rvl	anterior tuberosity of r.vl
b	bladder
bp	blind pit
bs	blind sac
c	colliculus
cl	copulator loop
c.md	central tuberosity of md
cs	cloacal sheath
ebs	entrance to blind sac
eu	entrance to urodeum
i	intestine
l.bs	left blind sac
l.dl	left dorsolateral longitudinal ridge
l.l	left lateral longitudinal ridge
l.vl	left ventrolateral longitudinal ridge
md	mid-dorsal longitudinal ridge
p	phalloseum
p.lvl	posterior tuberosity of l.vl
p.md	posterior tuberosity of md
pp	posterior part of phalloseum
p.rdl	posterior tuberosity of r.dl
p.rl	posterior tuberosity of r.l
p.rvl	posterior tuberosity of r.vl
r.bs	right blind sac
r.dl	right dorsolateral longitudinal ridge
r.l	right lateral longitudinal ridge
rm	retractor muscle
r.vl	right ventrolateral longitudinal ridge
s	sulcus
sph	sphincter
u	urodeum
ud	urogenital duct
umd	mid-dorsal ridge of urodeum
v	small additional ventral tuberosity
vd	vent denticulations
vp	vascular plexus

## MORPHOLOGY

**DISPOSITION OF THE CLOACA.** The cloaca of male caecilians is essentially a tube that extends between the posterior end of the intestines and the vent, and that may or may not have paired dorsal diverticula or blind sacs. The intestines, the paired urogenital ducts



**Fig. 2** *Uraeotyphlus* cf. *narayani* (field tag MW 249). Phallosome portion of undissected, unverted cloaca exposed in the coelom by a mid-ventral incision through the body wall. The phallosome has been rotated about its long axis through 90° to show its right lateral aspect. Scale on drawing = 5 mm.



**Fig. 3** *Uraeotyphlus* cf. *narayani* (field tag MW 249). Anterior phallosome portion of undissected, unverted cloaca exposed in the coelom by a mid-ventral incision through the body wall. The phallosome has been rotated about its long axis through 180° to show its dorsal aspect. See Fig. 2 for scale.

and bladder open, in close proximity, into the cloaca at its anterior end. The openings of the ducts and bladder are in the dorsolateral and ventral wall of the cloaca respectively. The Müllerian and Wolffian ducts and the intestine may extend posterior to their points of entry into the urodeum before turning back on themselves in U-bends or copulator loops that facilitate the eversion of the phallus

(Duvernoy, 1849; Günther, 1864; Spengel, 1876; Sawaya, 1942; Wilkinson, 1990; this paper: Figs. 2, 3). As documented by, for example, Rathke (1852), Günther (1864), Spengel (1876), Wiedersheim (1879: 89, Fig. 89) and Tonutti (1931, 1933: e.g. Fig. 32), the mature male cloaca sits within a membranous cloacal sheath, to which it is unattached other than at its anterior and

posterior ends (e.g. Rathke, 1852; Tonutti, 1931; Exbrayat, 1996). This loose association presumably also facilitates cloacal eversion (e.g. Spengel, 1876; Wilkinson, 1990). The sheath is continuous with the mesorchium and with the parietal peritoneum via a ventral mesentery (e.g. Tonutti, 1933: Fig. 3a).

A *musculus retractor cloacae* that is unique to caecilians originates on the mid-ventral body wall and inserts posterior to its origin on the lateral and ventral surface of the cloaca. In those taxa possessing blind sacs, the insertion is bifid and is largely or perhaps entirely on the sacs themselves (e.g. *Ichthyophis* Fitzinger, 1826; Tonutti, 1931: Fig. 30e; pers. obs.; *Uraeotyphlus* Peters, 1879, this paper: Figs. 2, 3). This muscle is thought to retract the everted phalloseum when contracted (e.g. Günther, 1864; Spengel, 1876).

**DIVISIONS OF THE CLOACA.** The cloaca can be divided along its long axis into two main regions (e.g. Duvernoy, 1849; Tonutti, 1931) – an anterior cloacal chamber, or urodeum, and a posterior cloacal chamber, or phalloseum (Fig. 1). The phalloseum of mature individuals is also broadly divisible into two regions, an anterior part with pronounced ornamentation that forms the more distal part of the everted phallus, and a structurally more simple posterior section that forms the proximal stalk of the everted phallus. Günther (1864) and Wiedersheim (1879) discussed three regions in the male cloaca. Their anterior region corresponds to the urodeum, and their middle and posterior parts correspond to the anterior and posterior sections of the phalloseum, respectively. Exbrayat (1991) also distinguished three regions of the cloaca, but these do not correspond directly to the partitions recognised by other authors. His middle section includes the posterior part of the urodeum and the anterior phalloseum.

The most obvious variations in cloacal morphology occur on the internal, luminal surface of the phalloseum, which corresponds to the external surface of the phallus. The morphology of this surface can be examined directly in caecilians preserved with the phallus fully everted, or by dissection, serial sectioning or endoscopy (Himstedt, 1996). Comparison of dissected cloacae is best effected by maintaining an approximately standard approach. Figures of dissected cloacae in the literature (e.g. Duvernoy, 1849; Günther, 1864; Spengel, 1876; Taylor, 1968; Wake, 1972; this paper) are mostly of cloacae opened with a longitudinal mid-ventral incision. This procedure gives a clear view of the dorsal surface of the phalloseum. Features of the urodeum must be determined by dissection, sectioning, or endoscopy. The caecilian phallus is sometimes referred to as the phalloseum (e.g. Duellman & Trueb, 1986), but the latter term is more properly reserved for the posterior cloacal chamber. The urodeum, at least in part, also contributes to the phallus by forming its core as it lies inside the everted phalloseum (e.g. Tonutti, 1931: Fig. 22b; this paper: Fig. 1).

In the majority of caecilians, the distinction internally between the urodeum and phalloseum is obvious in dissected specimens. The relatively simple and narrow urodeum gives way posteriorly to the broader phalloseum, which has pronounced longitudinal (and/or oblique) ridges and deep sulci extending to the phalloseal-urodeal border (e.g. see figures of *Uraeotyphlus* below). In most taxa, a mid-dorsal protuberance marks the posterior end of the urodeum. This protuberance is here termed *colliculus* (= little hill). The colliculus is perhaps equivalent, at least in part, to the 'bourrelet' mentioned by Duvernoy (1849; also Exbrayat, 1991). Typically the colliculus projects into the phalloseal chamber to a varying degree, being particularly large in some species (e.g. pers. obs. of *Gegeneophis ramswamii* Taylor, 1942, *Herpele squalostoma* (Stutchbury, 1834), and *Microcaecilia unicolor* (Duméril, 1864)). In species with blind sacs, these open into the phalloseum adjacent to its border with the

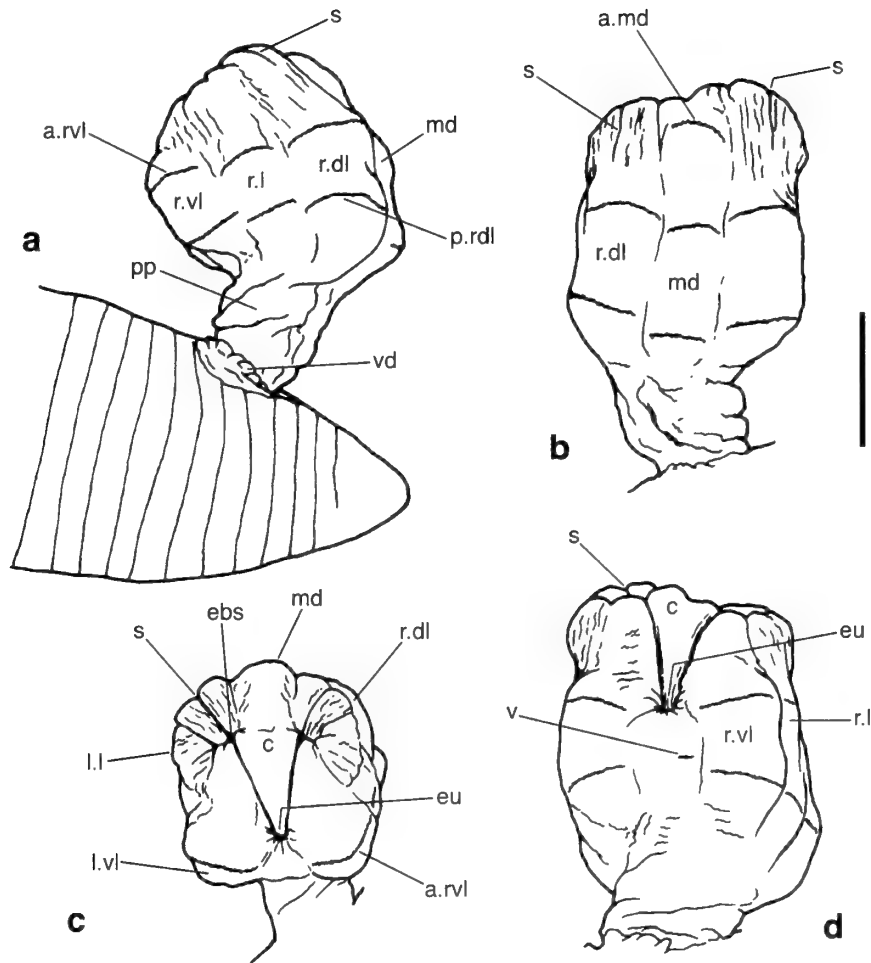
urodeum. A major exception to this general pattern is apparently restricted to the caeciliid genera *Dermophis* Peters, 1879 and *Gymnopsis* Peters, 1874 (MW, pers. obs.). In these caecilians, which lack blind sacs, there is no definite colliculus and no clear differentiation between urodeum and phalloseum. Given the apparently universal presence of distinct phalloseal and urodeal chambers in all other caecilians, including all non-caeciliids (outgroups), we interpret its absence as a putative synapomorphy of *Dermophis* and *Gymnopsis*.

Wake (1972) made no use of a clear urodeum-phalloseum division in her descriptions. She documented several features close to the openings of the urogenital ducts, which are in the anterior urodeum rather than the phalloseum. In our experience, this is a far more irregular region in which gross morphological regularities are less apparent and variation is harder to characterise than in the phalloseum. Wake (1972) mostly examined partially opened cloacae in which only the anterior part of the phalloseum could be observed.

The absolute and relative sizes of the urodeum and phalloseum may vary taxonomically but substantial variation within species might be expected given that the cloaca must serve both reproductive and alimentary functions. Exbrayat (1991) has presented evidence of seasonal variation correlated with the breeding cycle in *Typhlonectes compressicauda* (Duméril and Bibron, 1841), and short term changes might even occur with the passage of faeces. In a sample of 11 preserved *Hypogeophis rostratus*, the phalloseum ranged from 1.6 to 5.3 times the length of the urodeum (MW, pers. obs.), demonstrating considerable intraspecific variation in size in this species.

**URODEUM.** The urodeum is a relatively simple and typically narrow chamber. Its dorsal surface is characterised by a pronounced mid-dorsal longitudinal ridge (see figures of *Uraeotyphlus* below) and seemingly irregular arrangements of other, less pronounced ridges. The appearance of the lesser ridges can vary substantially with state of preservation and possibly also in life. The colliculus is an expansion of the posteriormost part of the mid-dorsal urodeal ridge, and it shows variations in form that may be of systematic value, as may differences in the overall shape of the urodeum (long and narrow or short and somewhat broader). Additional lateral or ventral more pronounced longitudinal ridges may also be present in the urodeum (Wake, 1972). Wake (1972) described considerable variation in the form of the urodeum at the points of entry of the urogenital ducts, which are often depressed and may vary in their relations to the mid-dorsal longitudinal ridge. She reported that papillae associated with the openings of the urogenital ducts were present only the typhlonectids (*Typhlonectes compressicauda*, *Chthonerpeton indistinctum* (Reinhardt and Lütken, 1861) and *C. viviparum* Parker and Wettstein, 1929) that she examined. However, one of us (MW) has observed urogenital papillae in other species, including taxa that Wake reported as lacking them (e.g. *Grandisonia sechellensis* (Boulenger, 1909) and *Geotrypetes seraphini* (Duméril, 1859)). Systematically useful variation may occur in the urodeum but we have not yet discerned clear patterns of variation.

**BLIND SACS.** Blind sacs (caecal appendage of Günther, 1864; Penisblindsack of Spengel, 1876; Blindsack of Wiedersheim, 1879; Penisack of Tonutti, 1931) are paired anterior extensions of the phalloseum that run parallel to the urodeum (Figs. 2, 3). Blind sacs vary in size and they may be free or partially fused to the adjacent urodeum (e.g. Wake, 1972). In species with blind sacs, these are a feature of the mature cloaca and may be absent or less well developed in immature males (see discussion of *Uraeotyphlus* below). In most cases, species within the same genus, or that are otherwise

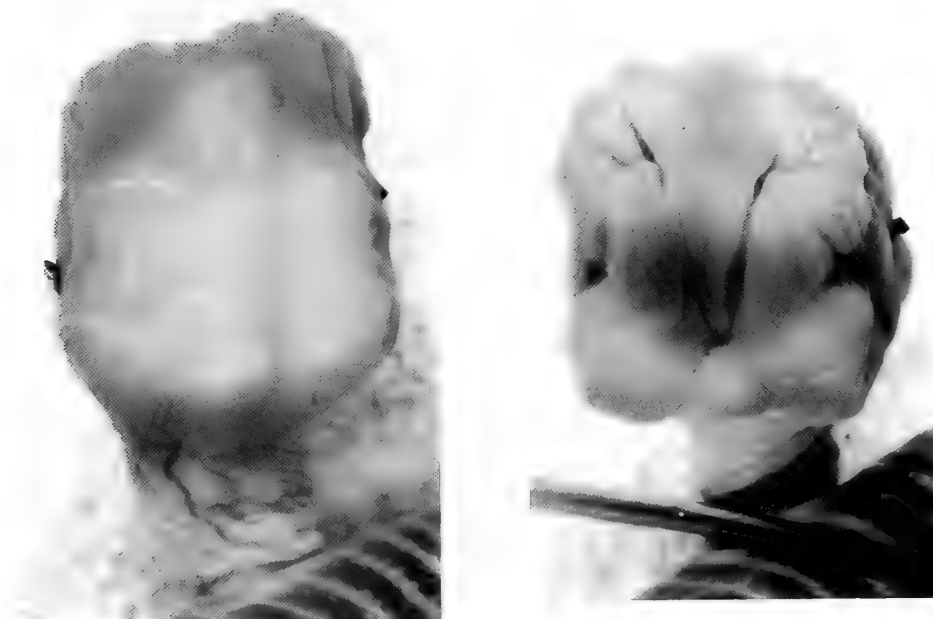


**Fig. 4** *Uraeotyphlus cf. narayani* (field tag MW 207). Views of (a) right lateral, (b) dorsal, (c) distal and slightly ventral, and (d) ventral surfaces of phallus (everted cloaca). Scale bar for Fig. 4b = 3 mm.

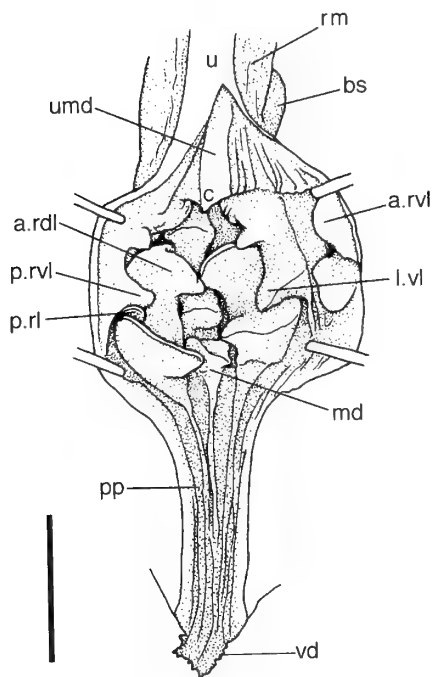
considered to be closely related, have blind sacs in a similar condition, suggesting relatively stable and systematically informative interspecific variation. Blind sacs are well developed in ichthyophiids and uraeotyphlids, caecilians that Wake (1972) considered 'primitive' in other reproductive characters, leading her to suggest that well developed blind sacs are a general caecilian feature, with reduction and loss being derived. In contrast, Tonutti (1931, 1933) considered well developed blind sacs derived. Rhinatrematids are believed to be the sister group of other extant caecilians on the basis of a wide variety of evidence (e.g. Nussbaum, 1977; Hedges *et al.*, 1993; Wilkinson, 1996). Spengel (1876) and Wake (1972) documented blind sacs in the rhinatrematids *Rhinatrema bivittatum* (Cuvier, 1829) and *Epicrionops petersi* Taylor, 1968 respectively, but we note their absence (or minimal development) in mature *Epicrionops marmoratus* Taylor, 1968 (MW, pers. obs.). This suggests homoplasy and may complicate the interpretation of polarity.

**ANTERIOR PHALLODEUM.** The luminal surface of the anterior phalloseum bears the distinctive structures seen on the external surface of the more distal part of the fully everted phallus (Figs. 1, 4 to 9). Much variation occurs here, but we discern a presumably homologous pattern anteriorly that is common to almost all caecilians. In this region there is a pair of deep dorsolateral grooves, one on either side. Each of these sulci (Figs. 4 to 9) are bordered by a pair

of well developed, parallel dorsolateral longitudinal or oblique ridges. A median mid-dorsal longitudinal ridge may or may not also be present, a variation that appears to be species specific. In species with blind sacs, the sulci and their bordering ridges run into the blind sacs, extending to their distal tips. In species lacking blind sacs, the ridges fade out and the sulci open out at the anterior of the phalloseum, either side of the colliculus. In *Hypogeophis rostratus*, the sulci run posteriorly and terminate blindly with the fusion of their associated ridges (Tonutti, 1931: Fig. 20; pers. obs.), a pattern that is consistent in the 11 specimens of this species examined by one of us (MW). Similar 'fusion' of the dorsolateral longitudinal ridges occurs in many caecilians (e.g. *Uraeotyphlus*, Figs. 6 to 9). Less commonly, the posterior end of each sulcus is open, with the more medial bordering ridge fading out or fusing with its antimeric along the dorsal midline (e.g. *Grandisonia alternans* (Stejneger, 1893), *Gegeneophis ramaswamii*, *Boulengerula boulengeri* Tornier, 1896, MW, pers. obs.). Additional major longitudinal ridges may or may not be present lateral and/or ventral to those forming the sulci. In uraeotyphlids (Figs. 4 to 9) and ichthyophiids, major longitudinal ridges are broadly distributed, whereas in some caeciliids (pers. obs. of e.g. *Grandisonia* Taylor, 1968 and *Schistometopum* Parker, 1941; this paper: Fig. 10) the ridges are more restricted to the dorsal surface of the phalloseum. Although we have discussed a single main pair of sulci, there may be other, smaller, more or less



**Fig. 5** *Uraeotyphlus* cf. *narayani* (field tag MW 207). Views of (a) dorsal, and (b) distal and slightly ventral surfaces of phallus (everted cloaca). For scale see Fig. 4.



**Fig. 6** *Uraeotyphlus* cf. *narayani* (field tag MW 254). Dissected cloaca of mature male. The cloaca has been opened mid-ventrally and pinned to reveal the luminal surface of the phallogenous papillae and posterior part of the urodeum. The incision has longitudinally bisected the right ventrolateral longitudinal ridge so that parts of it lie on each side of the open cloaca. Scale = 3 mm.

longitudinal grooves at the anterior end of the phallogenous papillae, at least some of which may enter the blind sacs, where present (e.g. *Geotrypetes* Peters, 1879, pers. obs.).

**POSTERIOR PHALLODEUM.** The distinction between the anterior and posterior phallogenous papillae is sometimes less clear cut than that between the phallogenous papillae and urodeum. Wake (1972) reported that the longitudinal ridges of the anterior phallogenous papillae continue posteriorly to the vent. We find that the major longitudinal ridges reduce greatly posteriorly, either abruptly or gradually, that they may or may not extend as far as the vent, and that the pattern of ridges within the posterior phallogenous papillae is irregular or less obviously regular than those of the anterior phallogenous papillae. The phallogenous papillae narrows dramatically posteriorly, shows considerable variation in length, and has its terminal portion surrounded by a sphincter of variable size.

**PHALLODEAL ORNAMENTATION.** The major longitudinal ridges of the anterior phallogenous papillae may be more or less invested with, or elaborated into, tuberosities, transverse ridges and grooves, longitudinal crests, or spines that are often in distinctive patterns (e.g. Figs. 6, 9). Isolated thickenings or other ornaments may also occur in the spaces between the major longitudinal ridges. The ridges associated with the dorsolateral sulci bear such features only posterior to the sulci (e.g. Figs. 4, 7, 9). Both the shape and arrangement of this ornamentation may be expected to provide systematic characters, although there is also evidence of intraspecific variation (e.g. *Scolecormorphus*, Wake, 1998). Species appear to differ in whether the ridges within the posterior phallogenous papillae bear any ornamentation or not. Where present, as in *Typhlonectes compressicauda* (Exbrayat 1996), they are not as pronounced or distinctive as the structures of the anterior phallogenous papillae (distal phallus).

**COMPOSITION OF PHALLODEAL STRUCTURES.** The composition of the main longitudinal ridges and their ornamentation is unclear from

the literature and warrants further histological examination. Tonutti (1931, 1933) viewed the longitudinal ridges as encompassing longitudinal 'propulsor' muscles but we are unable to verify this from his figured sections. Wake (1972: 354) described the ridges as 'longitudinal muscles overlain by fibrous connective tissue', but also warned (p. 363) that 'Caution must be exercised in interpreting the various folds in the cloacal wall. They may often not be muscle but may be ridges of connective tissue'. Wake (1998) referred to connective tissue ridges in *Scolecormorphus* and made no mention of previous reports that ridges are muscular (Tonutti, 1933; Wake, 1972). Wake (1972) also referred to at least some phalloseal ornamentation as transverse muscle ridges, whereas Wiedersheim (1879) stated that the prominences are hardened parts of longitudinal folds of cloacal mucosa. In at least one case it is clear that the prominences are not muscular: large recurved calcified or cartilaginous spines are present in *Scolecormorphus uluguruensis* Barbour and Loveridge, 1925 (Noble, 1931; Taylor, 1968; Nussbaum, 1985; Wake, 1998). Exbrayat (1991) showed that tuberosities in the phalloseum of *Typhlonectes compressicauda* are keratinous, and that their thickness varies with the reproductive cycle. Exbrayat (1996) described smooth transverse and striated longitudinal muscles in the wall of the cloaca of *T. compressicauda*, with the latter forming the major longitudinal ridges. Muscle therefore appears to be present in the longitudinal phalloseal ridges of at least some species, but we find no clear evidence that any of the tuberosities, crests etc found in the phalloseum are muscular.

#### RELATIONSHIP BETWEEN THE UNEVERTED CLOACA AND THE PHALLUS.

There is some confusion in the literature regarding the positional relationship between structures as seen on the internal surface of the uneverted phalloseum, and the same structures when observed on the external surface of the phallus. Wake (1972: 359, Fig. 13, 15) described and figured the blind sacs as being positioned at the proximal base of the everted phalloseum in a thickened 'blind sac sheath'. In the uneverted phalloseum, blind sacs, where present, are pockets extending from the dorsal wall of the phalloseum, very

close to the border between the phalloseum and urodeum. The sacs extend anteriorly from the anterior end of the phalloseum so that, within the coelom, they can be seen running parallel to the posterior end of the urodeum (e.g. Wiedersheim, 1879: Fig. 88; this paper: Figs. 2, 3). Thus, the blind sacs must be positioned at, or inside, the distal end of the everted phallus (Tonutti, 1931: e.g. Fig. 22b of *Hypogeophis rostratus*) rather than at its base. This can be clearly seen by comparing the figures shown here of the uneverted and everted phalloseum of *Uraeotyphlus* (Figs. 2 to 9), where the entrance to the blind sacs are seen right at the distal termination of the everted phallus (Figs. 4, 5). Preserved specimens may show various degrees of phalloseal eversion, and it is clear that Wake's figures are of partially everted organs, which may have misled her. In our experience, the major dorsolateral sulci, their associated ridges, and the colliculus are clearly visible at the distal end of a well everted phallus, although the extent of phalloseal eversion during copulation is unknown.

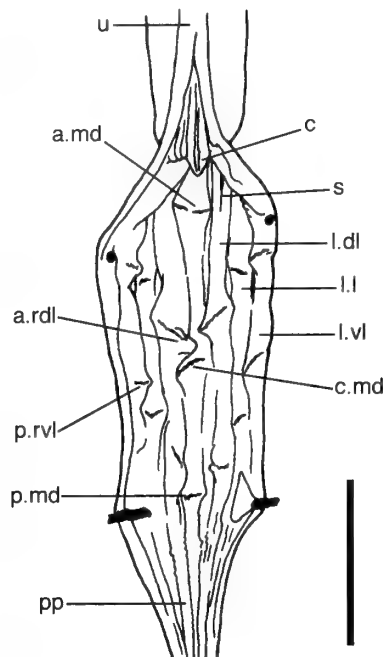
Bons (1986) and Exbrayat (1991) also figured what we consider to be partially everted phallosea of *Typhlonectes compressicauda*. *Typhlonectes* have a distinctive 'cloacal disc' surrounding the vent (Taylor, 1968) and Exbrayat's figure 3 appears to show the cloacal disk at the distal tip of the protruding phallus, and seemingly detached from the adjacent skin. However, the disc is continuous with the surrounding skin and must remain at the base of the phallus because it is everted rather than telescopically extended.

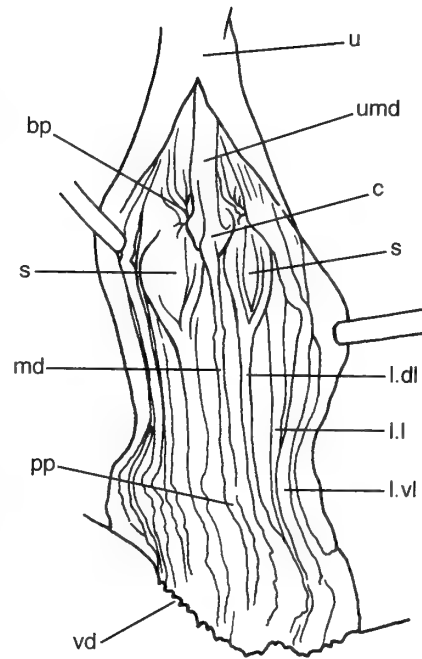
## SYSTEMATICS

IS PHALLUS MORPHOLOGY SPECIES SPECIFIC? The family Uraeotyphlidae is monotypic, comprising five currently recognised species of *Uraeotyphlus* endemic to peninsular India (Pillai & Ravichandran, 1999). Uraeotyphlidae is the extant sister taxon of the south and southeast Asian Ichthyophiidae (Wilkinson & Nussbaum, 1996; Gower *et al.*, 2002; Wilkinson *et al.*, 2002). As



Fig. 7 *Uraeotyphlus* cf. *narayani* (field tag MW 172). Anterior phalloseum of mature male, prepared as specimen shown in Fig. 6. Scale = 2 mm.



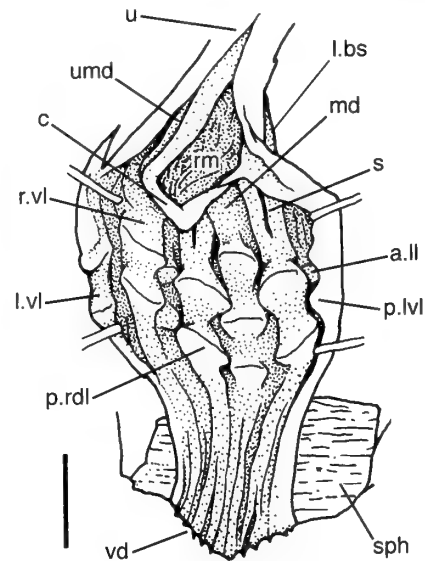


**Fig. 8** *Uraeotyphlus cf. narayani* (UMMZ 139810). Cloaca of immature male, prepared as specimen shown in Fig. 6. Scale = 2 mm.

with many groups of caecilians, the taxonomy of *Uraeotyphlus* has an inadequate basis, with some species known from only few specimens, many with poor locality data. Few diagnostic characters have been identified and current keys are not satisfactory, so that caution needs to be exercised in applying names to individuals, and in assuming species identity of groups of individuals. The following discussion draws on the examination of the cloaca in more than 30 male *Uraeotyphlus* representing at least three distinct species. The focus here is on features of the luminal surface of the anterior portion of the phallodeum, chiefly the longitudinal ridges and their ornamentation.

Figures 4 to 8 show the morphology of the phallus and dissected cloacae of four specimens. These are identified as *Uraeotyphlus cf. narayani* Seshachar, 1939, but unpublished morphological and molecular data have revealed previously unsuspected diversity in the populations that these individuals are drawn from. It is not yet apparent whether this diversity is indicative of previously unrecognised specific or subspecific taxa. Whatever their true specific identity, these four specimens share a common pattern in the major features of the anterior phallodeum. There are seven major longitudinal phallosomal ridges – a single mid-dorsal ridge, and pairs of dorsolateral, lateral, and ventrolateral ridges. As in most other caecilians, the anterior end of each dorsolateral ridge holds a major longitudinal sulcus that extends into the corresponding blind sac (Figs. 4, 5, 9). In mature individuals, each of the major longitudinal ridges bear hardened transverse thickenings. When relatively small, these thickenings bear an approximately transverse narrow line of dense, opaque tissue that stands out against the more translucent main body of longitudinal ridge. Where relatively large, the thickenings are developed into tuberosities that can be irregular, and that interlock in the unverted cloaca. The mid-dorsal ridge bears three such tuberosities and the other, paired longitudinal ridges two each. The transverse thickenings of each major longitudinal ridge are offset relative to each adjacent ridge, and they generally bear the same spatial relationship to each other in each individual (Figs. 4 to 7). Of the paired ridges, the lateral ones are the least well developed,

and sometimes they are best located by their transverse thickenings. Within this common pattern are some minor variations. In immature males (Fig. 8), the main longitudinal ridges are less well developed and bear no transverse thickenings or indications of hardened tissue, but they can still be readily identified and homologised with those in mature males. In addition, the blind sacs of immature males are not developed. Instead, there is a pair of shallow pits in their place. The relative size of the transverse thickenings or tuberosities also varies



**Fig. 9** *Uraeotyphlus cf. oxyurus* (field tag MW 469). Cloaca of mature male prepared as specimen shown in Fig. 6. The incision has longitudinally bisected the left ventrolateral longitudinal ridge so that parts of it lie on each side of the opened cloaca. The left side of the posterior end of the urodeum has been torn away from the anterior end of the phallodeum so that retractor muscle is visible through the resulting hole. Scale = 3 mm.



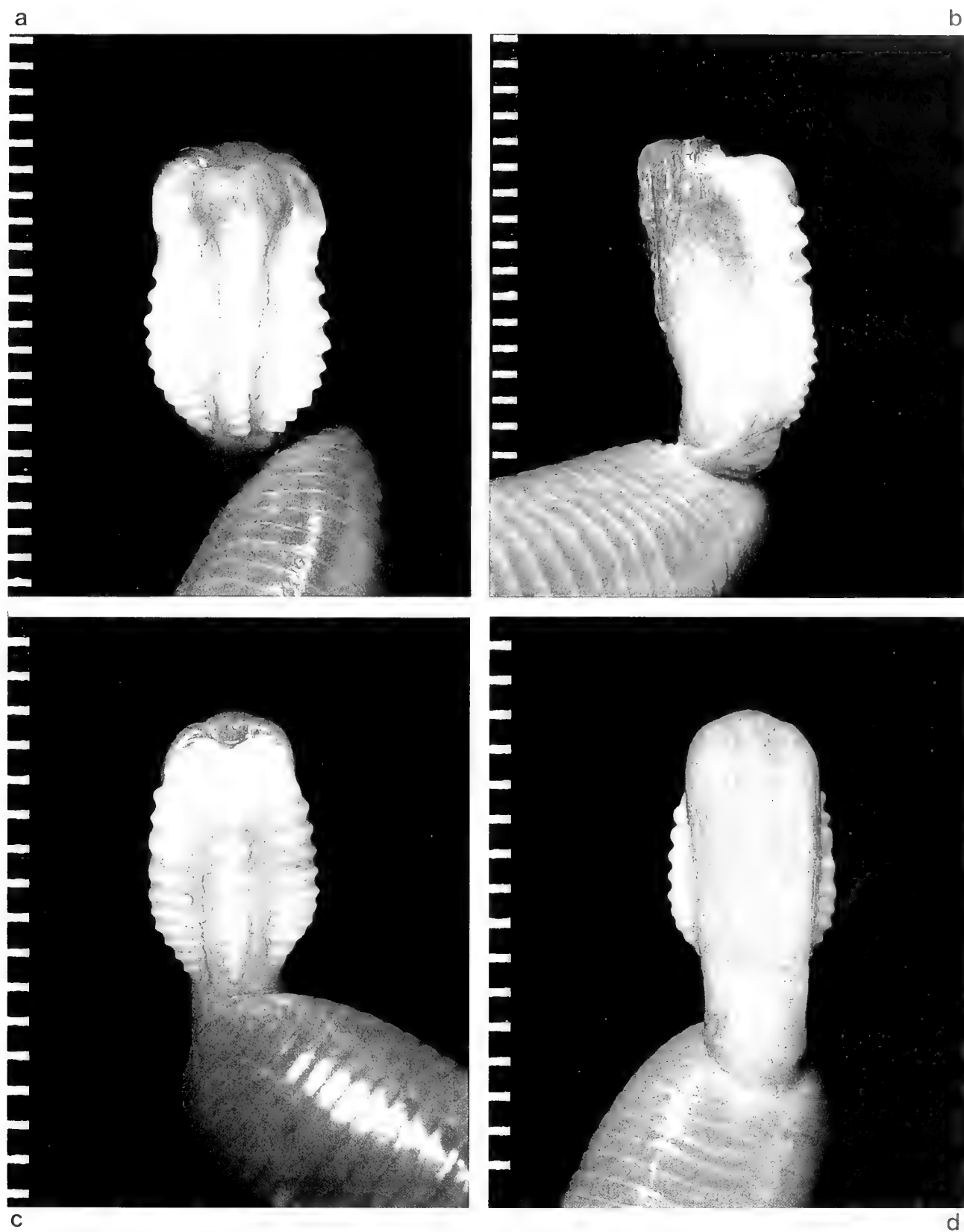


Fig. 10 *Schistometopum gregorii* from Tanzania. Views of (a) dorsal, and (b) right lateral surface of phallus of field specimen MW 3257, and (c) dorsal, and (d) ventral surface of phallus of field specimen MW 3251. Scale bars in mm.

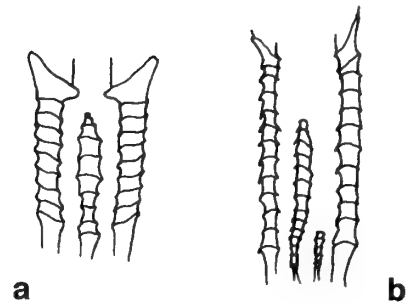
among individuals, but whether this variation is correlated with taxonomy, ontogeny, and/or temporally within any possible reproductive cycles is as yet unknown. Occasionally, minor variations in the ornamentation are seen. For example, the individual shown in Fig. 4 also has a single, poorly formed, transverse thickening ventrally. In the individual shown in Fig. 6, the posteriormost transverse thickening on the right dorsolateral longitudinal ridge extends posterior to the posteriormost transverse thickening on the mid-dorsal longitudinal ridge, whereas the reverse of this pattern (as seen on the left of this individual) is more commonly encountered. Finally, the transverse thickenings or tuberosities are sometimes multipartite.

Figure 9 depicts the phalloseum of an individual identified as *U. cf. oxyurus* (Duméril and Bibron, 1841). Although the precise specific identity of this individual also is not entirely clear, we are confident that it is referable to a species distinct from that (or those) represented in Figs. 4 to 8. For example, the *U. cf. oxyurus* individual comes from a population with substantially more vertebrae (112–115,  $n = 18$ ) than the populations represented by the other figured specimens (93–110,  $n > 100$ ). Despite their apparent specific distinctness, the phallosea of *U. cf. narayani* (Figs. 4 to 8) and *U. cf. oxyurus* (Fig. 9) share the same number and pattern of longitudinal ridges and transverse ornamentation. Thus Wake's (1972: 353) claim that the phalloseal ridges and 'cloacal accessory structures is species-specific' does not appear to hold – at least not at the level of the presence, number, or topographical relations of major features. It might yet hold for morphometric variations of phalloseal features and/or for fine morphological details of the longitudinal ridges and their ornamentation, but this needs further assessment.

That not all species of *Uraeotyphlus* share the same basic phalloseal morphology is revealed by observation of *U. cf. malabaricus* (Beddome, 1870), in which the number and arrangement of longitudinal ridges and their ornamentation is markedly different. Interestingly, analysis of mitochondrial DNA sequence data strongly indicates that *U. narayani* and *U. cf. oxyurus* share a more recent common ancestor with each other than either does with *U. cf. malabaricus* (Gower *et al.*, 2002).

**SPECIES' DIFFERENTIATION AND GENERIC IDENTITY.** Nussbaum & Pfrender's (1998) recent revision of the caeciliid genus *Schistometopum* recognised two species occurring on opposite sides of the African continent. *S. thomense* (Barboza du Bocage, 1873) is known from São Tomé island in the Gulf of Guinea, and *S. gregorii* (Boulenger, 1894) from lowland coastal regions of Kenya and Tanzania. The validity of the genus has not been seriously questioned, but it is currently diagnosed on a combination of characters, with no known unique synapomorphies.

Wake (1972: 358) described the male cloaca of *S. thomense* as having 'four regularly spaced muscle bands on each side of the cloaca', presumably features of the urodeum, and that 'the posterior part of the cloaca [more the central region, as can be seen when the cloaca is fully dissected] is arranged in three sets of transverse, crescent-shaped muscles, one mid-dorsal, the other two ventrolateral.' Tonutti (1933) described longitudinal phalloseal ridges as dorsal rather than ventrolateral in *S. thomense* and we concur with his assessment (see Fig. 10). Wake found the cloaca of *S. gregorii* to have a similar morphology to that of *S. thomense*. Although we are not convinced that the transverse ridges comprise muscle, we agree that the two species share a similar morphology, and consider the presence of three (though see discussion of *S. gregorii* below) narrow and long longitudinal ridges with a characteristic ornamentation of regularly spaced, scalloped transverse ridges and grooves to be restricted to these two species among material we have



**Fig. 11** Sketches showing disposition of major longitudinal ridges and their ornamentation in the dorsal luminal wall of the anterior part of the phalloseum of (a) *Schistometopum thomense* (UMMZ 188027), and (b) *S. gregorii* (UMMZ 147011) from Kenya. Compare with Tanzanian *S. gregorii* shown in Fig. 10. Not drawn to scale.

observed. Thus, this phalloseal structure is potentially a unique diagnostic character of *Schistometopum*.

Wake (1972) considered the phalloseal ridges of *Schistometopum* to resemble the condition in *Geotrypetes*. However, the part of the mid-dorsal longitudinal ridge that bears ornamentation in both *S. thomense* (Fig. 11a) and *S. gregorii* (Figs. 10, 11b) is relatively much longer than the comparable ornamented area in *Geotrypetes seraphini*, which is instead restricted to a small nubbin that lies at, or slightly beyond, the level of the posterior end of the ornamented part of the longitudinal ridges lateral to it (pers. obs. of e.g. UMMZ 172648). In addition, the ornamentation appears to be somewhat different in the two genera, which otherwise also have quite differently organised cloaca (for example, *Schistometopum* lacks blind sacs).

The phalloseum of a single specimen (UMMZ 147011) of *S. gregorii* from Northern Kenya has been examined and a sketch of the ornamented part of the longitudinal ridges is shown in Fig. 11b. The figured morphology is largely similar to that seen in several specimens of *S. thomense* (e.g. Fig. 11a), except that, in UMMZ 147011, there is not a single mid-dorsal ridge, but instead two paramedian longitudinal ridges, one longer than the other. Both of these ridges bear transverse crests, but they are shorter relative to the dorsolateral longitudinal ridges than in the observed specimens of *S. thomense*. The morphology of the mid-dorsal region of the phalloseum in two Tanzanian specimens of *S. gregorii* observed for this study (Fig. 10) both bear a greater resemblance to the condition in *S. thomense* (Fig. 11a) than to the single Kenyan *S. gregorii* (Fig. 11b) examined. The sample size is small, but the observed morphological variation is intriguing in light of Taylor's (1968: 677) suggestion that, based on differences in annulation, the Tanzanian and Kenyan populations of *S. gregorii* might be specifically distinct.

## DISCUSSION

The complex structure of the caecilian phallus offers great potential for caecilian systematics, both as a source of diagnostic features for species, and of characters for phylogenetics. However, to fully exploit this potential requires a better understanding of the extent of intraspecific variation that occurs within features that appear to vary interspecifically. Of course, in this regard there is no difference between the caecilian phallus and any other structure employed in systematics, and we suggest that incomplete understanding of variation should temper but not discourage the use of cloacal characters

in caecilian systematics. There is evidence of considerable ontogenetic variation in the development of blind sacs and phalloseal ornamentation, emphasising the need for systematic comparisons to be of co-ordinate developmental stages or of developmental trajectories. There is also evidence of variation in adults in the sizes of the urodeum and phalloseum, and the exact form of ridges, their ornamentation, and other phalloseal structures, at least some of which is seemingly correlated with breeding cycles. Despite Wake's (1998: 183) statement that the morphology of the phalloseum of *Scolecophorus* 'is indeed consistent within the species', the same paper clearly documents intraspecific variation in the number of phalloseal spines in *Scolecophorus uluguruensis* and *S. vittatus* (Boulenger, 1895). Functional considerations lead us to speculate that additional intraspecific variation in phalloseal ornamentation occurs because the phalloseum serves both reproductive and excretory roles. In individuals with well-developed tuberosities, these can interdigitate *in situ* to seemingly obstruct the cloacal lumen. We hypothesise that in these species, at least, cloacal ornamentation would be elaborated at times of courtship but reduced at other times. If correct, differences in reproductive condition would need to be taken into account in any systematic comparisons.

Our observations suggest that the pattern of major longitudinal ridges and often also the number and position of phalloseal tuberosities or other ornamentation is mostly constant within species. The same general pattern occurs in 11 specimens of *Hypogeophis rostratus*, the largest sample of a single species that we have examined in detail. However, detailed study of ontogenetic and population variation is needed to test this constancy and to determine whether variations in the form of phalloseal ornamentation are of systematic utility. Thus, future studies should attempt to increase sample sizes for at least some species. Of the 33 species examined by Wake (1972), her largest sample was 29 specimens of *Gymnopsis proxima* (Cope, 1877) whereas sample sizes for the remaining species were low (mean = 1.7), providing little basis for assessing variation. Wake (1972) did not discuss intraspecific variation in any species.

Closely related species (e.g. congeners) tend to have similar cloacal morphologies, providing a strong indication that the cloaca will be a source of stable phylogenetic characters. For example, the absence of a definitive colliculus or any other obvious division of the cloaca into urodeal and phalloseal chambers is a very striking putative synapomorphy of *Dermophis* and *Gymnopsis*. These genera have been considered closely related (e.g. Nussbaum & Wilkinson, 1989) but there are no previously reported uniquely derived characters. Similarly, the general form of the longitudinal phalloseal ridges and their ornamentation in *Schistometopum thomense* and *S. gregorii* appears to offer the first known unique diagnostic character for *Schistometopum*. On the other hand, congeners can sometimes be readily distinguished by clear-cut, discrete differences in the patterns of phalloseal ridges and topological relations in their ornamentation.

Contrary to Wake (1972), our investigations of *Uraeotyphlus* suggest that, in at least some cases, cloacal morphology may not be species specific. Instead, it appears that some species that can be clearly differentiated based on traditional morphological characters have a common pattern of phalloseal ridges and ornamentation. Species specific differences in these examples may yet be found in the details of the form of phalloseal morphology, but additional work is needed to test this.

In this survey we have concentrated upon the gross structural features of the caecilian cloaca. The luminal surface of the cloaca appears to be also covered in many minor ridges and grooves (striae). This micro-ornamentation may also yield useful systematic

data but, as with more macroscopic features, studies of this must take into account potential intraspecific variation. In some cases, where we have described major structures as terminating, it might be more accurate to describe them as giving rise to, or being supplanted by, striae. For example, in *Hypogeophis rostratus*, where the main dorsolateral longitudinal ridges and their sulci 'terminate' anteriorly, close to the colliculus, they more accurately continue into inconspicuous striae (MW, pers. obs.). These bend around the lateral margins of the colliculus and open into channels running alongside the main mid-dorsal urodeal ridge. We suspect this arrangement constitutes the passage through which sperm travel from the urodeum to the phalloseum, to be delivered to the female via the dorsolateral sulci that are such a prominent feature of the phallus.

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# *Holaspis*, a lizard that glided by accident: mosaics of cooption and adaptation in a tropical forest lacertid (Reptilia, Lacertidae)

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**SYNOPSIS.** *Holaspis* is the most morphologically apomorphic lacertid taxon with 42 or more derived morphological features arising on its exclusive lineage. Nearly all of these confer advantages in three specialised activities, or ameliorate problems resulting from them. The activities are: climbing on the often vertical open surfaces on tree boles and branches, utilising very narrow crevices in wood and beneath bark, and the ability, unique among lacertids, to glide from tree to tree. Although many of the features related to these activities are likely to result from direct adaptation to the situations concerned, exaptation has been critical in the development of gliding. Two behaviours present in the earliest lacertids have been coopted to this activity: rib spreading associated with basking contributes to an effective aerofoil, and balance control associated with running helps maintain appropriate posture in the air. Features originally developed in the context of crevice use also contribute to the aerofoil and a high surface: weight ratio. So, while natural selection has moulded *Holaspis* for its present activities, multiple accidents of history have also been important, as they also have in the evolution of bird flight.

## INTRODUCTION

Sometimes there has been a flurry of adaptation on a lineage after a long period of little or no obvious change. A plethora of apomorphies may have been produced, often in association with shift into a new and demanding niche or a succession of these. For instance, this occurred in the lacertid lizard genus *Meroles* where apomorphies accumulated in a series of increasingly extreme soft-sand environments (Arnold 1990, 1991). In other cases, not all the features that confer performance advantage in such a selective regime necessarily arose by natural selection in its context. In some instances, features developed by natural selection in a different situation or by some other means, and were only later coopted to a new function. Darwin (1872) was aware of this process which was named exaptation by Gould & Vrba (1982). Cases of exaptation are very widespread (Arnold, 1994; Gould, 2002) and contribute to the ability of lineages to enter new selective regimes. Usually, optimum survival in these involves combining exaptations with new features that are built by the new selective regime. Exaptations are typically a small proportion of the necessary features, but there are examples where a number of characters really critical to invading the new regime are exaptations. A case in point is the aberrant lacertid genus, *Holaspis*, the only member of the approximately 1700 species of Scincomorpha known to glide regularly and effectively.

## TAXONOMY AND RELATIONSHIPS

Until recently *Holaspis* was regarded as a single species with two well-defined subspecies, but these are now each given species status (Broadley, 2000) as *Holaspis guentheri* and *H. laevis*. *H. guentheri* occurs in Sierra Leone, Ghana, Nigeria, Cameroon, Congo, Uganda, Gabon and Angola, and *H. laevis* in Tanzania, southeast Congo, Malawi and Mozambique. *H. laevis* has six dark longitudinal stripes on the body instead of eight and has on average fewer, larger scales comprising the semitransparent window

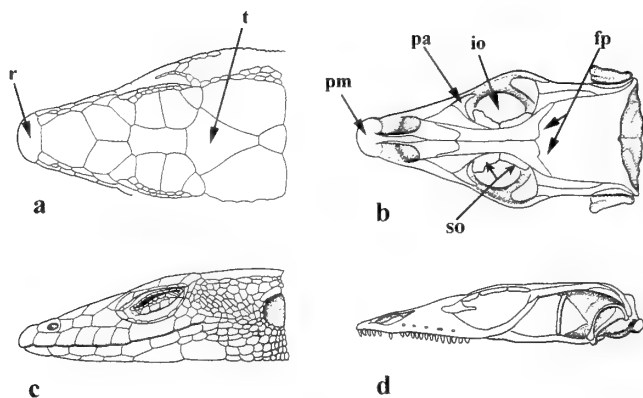
present in the lower eyelid which is generally rather better developed than in *H. guentheri*.

Within the Lacertidae, morphology indicates that *Holaspis* is a member of the subfamily Eremiainae (Harris, Arnold & Thomas, 1998) and within this of the Equatorial African clade (Arnold, 1989a, b.), which is relatively basal and has a generally primitive morphology, most of its members not differing much from members of the generally primitive subfamilies, Lacertinae and Gallotiinae. The Equatorial African clade is characterised by the following combination of derived features: pineal foramen lacking; medial area of the clavicle not markedly expanded; only one postnasal scale; parietal scale extending laterally to the edge of parietal table of the skull, and the tympanic scale small. All except *Holaspis* also have the postorbital and postfrontal bones fused, the absence of this condition in *Holaspis* being secondary (Arnold, 1989a). Among the Equatorial clade, morphology suggests *Holaspis* is the sister group of two species of *Adolfus*, *A. africanus* and *A. vaureselli* (Arnold 1989a). Studies of mitochondrial DNA sequence (Harris & Arnold, pers. obs) corroborate this relationship, although with only low bootstrap support.

## MORPHOLOGY OF *HOLASPIS*

The following account concentrates on those characters that are peculiar to *Holaspis* and derived within the Equatorial African group, and usually within the Lacertidae as a whole. These autapomorphies and are listed in Appendix 1. For illustrations of living *Holaspis* see Schmidt, 1919 (reproduced in Arnold 1989a), Schiötz (1960) and Branch (1998).

*Holaspis* are small lizards growing to a maximum of only about 53mm from snout to vent and a total length of 130mm. The whole animal is extremely depressed, and more so than any other lacertid. The index, head depth/ head width, measured on alcohol-preserved specimens somewhat exceeds that found in most other flattened lacertids (see for instance Arnold 1998a, p. 344), averaging about 0.54 when measured in adults (n = 10). This however does not give



**Fig. 1** Head and skull of *Holaspis*. a. Head from above; b. Head from side; c. Skull from above; d. Skull from side. fn frontonasal scale, fp frontoparietal suture, pa palpebral bone, pm premaxilla, r rostral scale, io inferior orbital foramen, so supraocular osteoderms, t triangular scale covering area occupied by paired frontoparietal scales in most other lacertid lizards.

a full impression of the extent of the dorsoventral flattening, largely because in fixed material shrinkage of the jaw muscles pulls the kinetic skull into its most retracted position in which the vertical extent is greatest (Arnold 1998a). Also, unlike other lacertids, the whole of the limbs and tail are depressed in *Holaspis*.

**HEAD.** The parietal area of the head (Fig. 1a, b) is flat and unarched and the snout is flattened above, being wedge-shaped in lateral view. The rostral shield is large, extending far on to the top of the snout and contacting the frontonasal scale very broadly. The nostrils are placed on the sides of the snout and are set well back from its tip. The area of the top of the head usually occupied by the interparietal and paired frontoparietal scales in other lacertids is covered in *Holaspis* by a single large triangular scale. The lower eyelid has a 'window' composed of enlarged semi-transparent scales. In *H. guentheri* these number 1–5 (mean 3.5,  $n = 15$ ) while in *H. laevis* there are usually 2–4 (mean 2.3,  $n = 8$ ) that are sometimes black-edged. The scales on the temporal area vary in size: dorsally and posteriorly they are typically large and polygonal, whereas anteriorly they are much smaller and diagonally elongated, running backwards and downwards from behind the eye in irregular lines that are separated by somewhat expansible hinge regions.

The low skull (Fig. 1c, d) is more delicately constructed and thin-boned than in any other lacertid lizard and the roof of the parietal region is so flexible in alcohol-preserved material that it can easily be deflected downwards. As in other lacertids, comparatively immobile sutures in the skull, such as that between the frontal and nasal bones, show a considerable overlap between the elements involved, giving a measure of rigidity in spite of the thinness of the components. In contrast, the frontoparietal suture, one of the main sites of

cranial kinesis, is a relatively simple abutment without the complex interdigitation found at this site in other lacertid lizards.

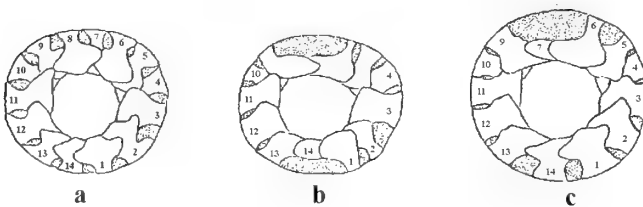
The body of the premaxilla is peculiar in forming a broad semicircular boss that is convex above and supports the extensive rostral scale. The nasal openings of the skull are situated posterior to this boss and are extremely large. They extend backwards so that the primary nasal cavities are broadly exposed dorsally. Of the bony elements normally roofing the orbits of lacertid lizards, only the palpebral bone is present in its entirety. The usual array of four supraocular osteoderms is greatly reduced; the first being absent and the others only present in adults, where they are limited to a narrow medial fringe. The inferior orbital foramen is very large. Pterygoid teeth are absent. The mandibles are slender and shallow and their retroarticular processes are directed somewhat ventrally.

**SCLERAL OSSICLES.** In the eye, the scleral ossicles are reduced, from the usual lizard number of fourteen that is present in all other lacertids, to twelve. This is by the loss of two out of the sequence made up of ossicles 5 to 9 (Fig. 2b). The twelve ossicles present are so shaped and arranged that the scleral ring is incomplete peripherally. Instead of extending from the area of the pupil to the vertical equator of the eye, the ring is strongly emarginated above and below. Dorsally this emargination is produced by the loss of the two ossicles, their neighbours extending across the gap so formed and overlapping only in the pupillar region. The ventral gap in the outer part of the ring is largely a result of the peripheral, radially directed part of ossicle 14 being missing but the peripheral sections of ossicles 1 and 13 are also skewed away from the gap thus increasing its extent.

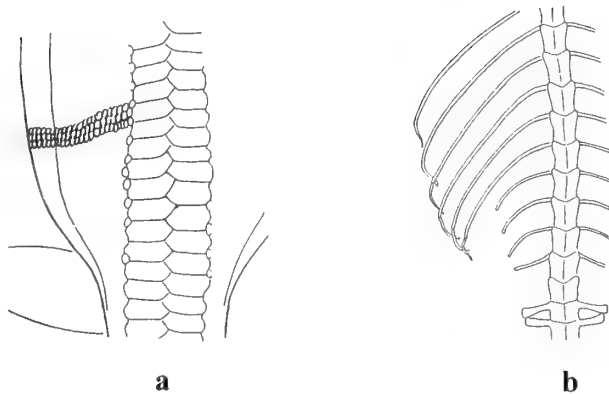
**BODY.** The neck of *Holaspis* is dorsoventrally flattened, with the skin at the sides forming a prominent sharp-edged flap in many preserved specimens that is also visible in live animals (Fig. 2, Schiøtz, 1960). The flap apparently gains some support from the first branchial and hyoid horns of the hyoid apparatus and its edge is sometimes marked by a longitudinally oval area of somewhat enlarged scales. In other preserved material, in which the pharyngeal cavity is expanded dorsoventrally, the flaps are barely apparent, suggesting that they are homologous with the slight skin folds which occur in this region in many lacertid lizards and which are necessary for pharyngeal enlargement.

The body is strongly depressed and arched in transverse section, being convex above and flat beneath. Posterior to the sternally connected ribs, the trunk has an elongated oval outline when viewed from above and the lateral edges of the body form distinct ridges. The dorsal integument consists of two very different types of scaling (Fig. 3a). Running along the vertebral region from nape to tail is a band of enlarged, broad plates. These are arranged in two longitudinal series, which are slightly staggered relative to each other. Each plate slightly overlaps the one immediately behind it and also, medially, the plate diagonally posterior to it in the other row. The hinge regions between the plates allow flexibility in the vertical plane but do not permit the plates to move much relative to each other in the plane of the integument.

The lateral areas of the dorsal integument are made up of small granular scales. At the broadest part of the dorsum, there are 30 to 41 of these on each side, between the vertebral and ventral plates. These small scales often show a differentiation in arrangement between the anterior and posterior regions of the back. On the neck and shoulders, they are non-imbricate and firmly bonded together so that they can only move slightly relative to one and other. Further back they may gradually alter, so that beyond the sternally connected ribs the scales are completely different in character. Here, they are lined up in two directions: they are arranged in rows running steeply

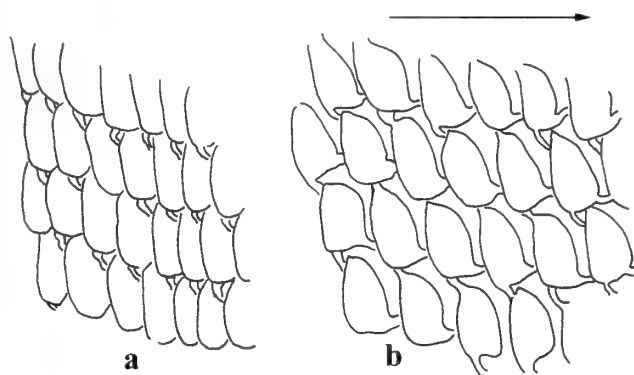


**Fig. 2** Scleral ossicles of left eye of lizards. a. Typical lacertid lizard; b. *Holaspis*; c. *Platysaurus* (Cordylidae). Ossicles are numbered according to the system of Gugg (1939); see Underwood (1970).



**Fig. 3** Dorsal views of the left posterior trunk of *Holaspis*. a. Skin, showing double vertebral band of enlarged scales and small lateral scales (only three rows shown). b. Skeleton showing elongated anterior free ribs with long cartilaginous tips; the tips usually overlap each other to form a continuous edge to the ribs, but in this cleared and stained specimen they have become partly separated.

posteriorly, and to a much lesser extent outwards from the vertebral plates, and they also form transverse rows of which there are two or three to each vertebral plate. These rows run slightly posteriorly from their origin, but further out, they curve a little so that they run more or less directly laterally and may turn slightly forwards before they reach the perimeter of the dorsum (Fig. 3a). Each scale in a transverse row strongly overlaps its neighbour on its medial flank, but if the skin is pulled laterally, it stretches easily and extensively, so that each scale is separated from its fellows (Fig. 4). It is then sometimes apparent that the scales are interconnected by 'bridges'. These are often pigmented and not very elastic and apparently contain alpha-keratin, as do the scales. They lie slightly below the level of the scales themselves and fall into two groups. One series runs approximately laterally from the posterior outer border of each scale to insert beneath the inner border of its neighbour. The other runs from the anterior inner border of every scale and joins it to the posterior inner border of the scale which lies in front of it when the skin is unstretched. These longitudinal bridges are the only ones immediately visible in preserved material, the lateral ones being hidden under the imbricating scales. When the skin is not stretched, the bridges are slack and slightly folded. The regions between the scales and their bridges are made up of soft, extensible skin,



**Fig. 4** Scales from right lateral skin of posterior trunk. a. Skin unstretched, scales overlapping medially and longitudinal bridges showing. b. Skin stretched showing lateral and longitudinal bridges and expanded areas between the scales. The bridge system is not always fully apparent. The arrow shows direction of stretching.

presumably consisting largely of beta-keratin. The development of this system of bridges shows very considerable variation among specimens.

When the skin is stretched laterally, each scale moves in a transverse direction, the excursion made by the outer scales being much greater than that made by the inner ones. This results in the originally curved transverse rows approximating more closely to a straight line. These movements can produce at least 50% increase in the area of skin. This ability of the skin to expand is not so highly developed as in many snakes, but it is certainly unique among the Lacertidae and probably among other lizard groups.

The dorsolateral skin, when unexpanded, has one or more longitudinal folds on either side. The whole of the dorsal integument is rather loosely attached to the underlying musculature by connective tissue, as in other lacertids. The area of granular scales passes round the sharp-edged lateral border of the body to contact the ventral plates. These are large and arranged in six longitudinal rows, as in many other lacertids, and are rectangular showing little imbrication. The collar is straight-edged and again not strongly overlapping.

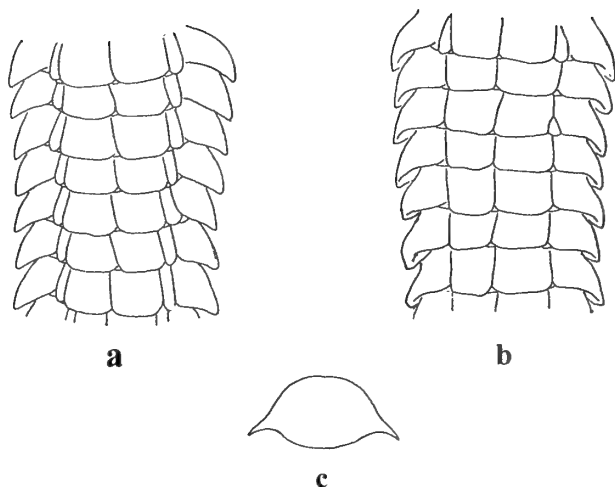
*Holaspis* has 25–26 presacral vertebrae in males and 25–27 in females. These numbers are unexceptional for lacertids in which the majority of species have 25–29 presacrals with extremes of 23 and 33 and show sexual difference in average number of dorsal vertebrae. The vertebrae of *Holaspis* differ from those of other lacertids in being distinctly depressed with virtually no neural crest or spine.

In most lacertid lizards the dorsal ribs can be divided into three groups: 1. the thoracic ribs attached to the sternum and xiphisternum; 2. the anterior free dorsal ribs which are unattached distally and have prominent cartilaginous extensions at their tips; and 3. the posterior free dorsal ribs which are usually about two-thirds the length of the more anterior ribs and have no cartilaginous extensions. In *Holaspis*, there are 7–8 anterior free ribs in males and 8–9 in females. They are markedly elongate compared with those of other lacertids, being considerably longer than the thoracic ribs and about twice as long as the posterior free dorsal ones. Their cartilaginous extensions are also exceptionally long and are turned backwards, each extending beneath the next posterior rib and running parallel with its own cartilaginous process (Fig. 3b). These overlapping processes are bound together by loose connective tissue and form a smooth border to the series of elongated ribs. It is this border which forms the prominent edge of the body that runs slightly ventrally and backwards to terminate just in front of the anterior border of the hind leg. The termination is enclosed in a fold of loose skin that connects it to the underside of the thigh.

The sternum of *Holaspis* has an extremely large central fontanelle that occupies most of its area, and the scapulocoracoid plate has two foramina compared with one in other lacertid lizards.

*Holaspis* is peculiar among lacertid lizards in having prominent slips of the *intercostalis scalaris* muscle (Maurer 1896) running from the tips of the anterior free ribs forwards and somewhat inwards to insert on the upper surface of the *rectus abdominis* muscle above the outer edge of the second row of ventral scales. The muscle fibres to the more anterior free ribs form a single block but those to the more posterior ones comprise separate slips.

**TAIL.** In nearly all lacertid lizards, the tail is cylindrical and at most slightly flattened dorsoventrally at its base. It is covered by whorls of numerous subequal scales there being two whorls to each caudal vertebra. Deviations from this pattern are usually slight but *Holaspis* differs radically. Its tail (Fig. 5) is somewhat dorsoventrally compressed and above has a double row of broad plates, which is a direct continuation of the series on the body. These enlarged scales differ from those on the back in being arranged in simple



**Fig. 5** Tail of *Holaspis*. a. Proximal segment from above; b. Proximal segment from below; c. Transverse section.

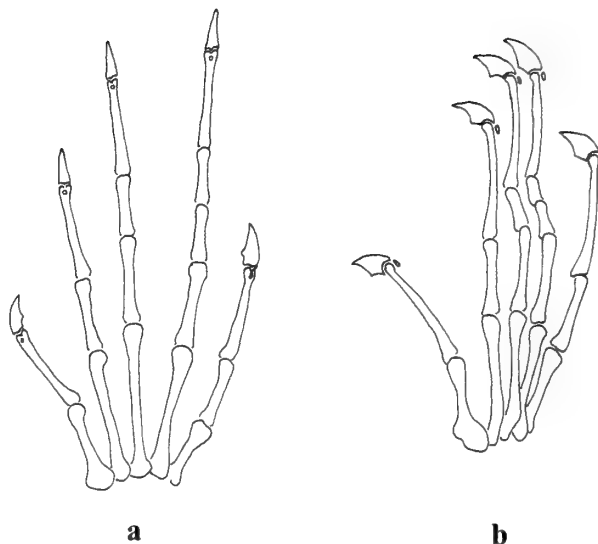
lateral pairs instead of being staggered. The plates each have several sense organs on their posterior border and, as the usual number of sense organs per dorsal caudal scale in other lacertid lizards is one, it is likely that the plates have replaced a number of smaller scales. The wide double band is flanked by one or two (rarely three) longitudinal rows of narrower scales, one row being frequent in *H. laevis* and one or two in *H. guentheri*. The number of rows sometimes increases anteriorly and these scales are replaced by granules on the tail base. The median part of the ventral surface of the tail is formed by another row of wide, paired plates, again replacing multiple small scales in other lacertid lizards.

The lateral edges of the tail are serrated and consist of a single row of strongly modified scales. In transverse section, each of these scales is more or less triangular, the broad base joining the tail, the apex pointing outwards; in this plane, the lateral scales curve downwards. Viewed from above, these scales are again approximately triangular, the point being directed obliquely backwards. Proximally, the longitudinal axis of these scales is parallel with that of the whole tail; distally, their anterior edges tend to be twisted downwards so that their longitudinal section here runs backwards and slightly upwards. Each lateral scale is capable of some movement since it is connected with contiguous scales in its whorl by flexible hinge regions. However, the motion is limited by the scale interlocking with its anterior and posterior neighbours. On the underside of each of these scales, parallel with and close to the trailing edge, is a slit-shaped cavity. The anterior portion of the following scale projects into this, giving the lateral fringes considerable stiffness.

**LIMBS.** The spans of the fore and hind limbs approach equality more closely than in any other lacertid lizard, the index, forelimb span/hindlimb span, being 0.85 in males ( $n = 3$ ), and 0.85 in females, ( $n = 4$ ) while the total range for the Lacertidae is 0.53–0.85 (Arnold 1998b).

The forelimbs are rather flattened and the single band of enlarged scales, present on the anterior surface of the upper limb of most lacertids, occurs in *Holaspis* too. However, instead of being continued as a single band on the lower limb, it is replaced by two parallel ones, one dorsal, the other ventral with their zig-zag line of contact forming a forwardly directed edge that may sometimes be quite acute.

The hind leg is similarly markedly depressed and the proximal, femoral segment has large plates above and below the leading edge;



**Fig. 6** Right manus of lacertid lizards. a. A form frequently climbing on steep open surfaces (*Lacerta oxycephala*); b. *Holaspis guentheri*.

only the lower series reaches the front of the crus. The greater part of the trailing area of the hind leg is formed by a web of loose elastic skin, which becomes taut when the leg is partly extended. This 'patagium' is continuous with a series of about four large sharp-edged, sometimes interlocking, scales which make up the trailing edge of the crus. These scales are generally similar in construction and arrangement to those on the lateral edges of the tail

The manus and pes of *Holaspis* show strong development of a syndrome of features characteristic of lacertid lizards that climb on continuous open surfaces (Fig. 6; Arnold, 1998b) and many features are better developed than in other forms. The longest digit is number 4 and all digits are strongly latero-mesially compressed; some digits are flexed downwards at the articulation of phalanges 1 and 2 and in most there is upward flexure at the penultimate articulation. Phalanges are very slender, the penultimate ones being very long and markedly curved downwards. In the manus intermediate phalanges of digits 3 and 4 are shorter than the ones bordering them and the same is true of intermediate phalanges of digits 3 and 4 of the pes. The final phalanx of each digit and the claw that covers it is short, deep and recurved. The large ventral digital tendons are offset from the articulations in the regions where digits can be abruptly flexed downwards. The articulations within the digits, except the most distal, are simple involving single cup and ball arrangement and the digits are abruptly flexed in the horizontal plane, both mesially and laterally, especially in the area of the penultimate articulation.

The manus of *Holaspis* has the following additional derived features. Digits 2–5 are subequal in length, and numbers 3 and 4 are conjoined for the length of their first phalanx. The shortening and downward flexure of phalanx 2 digit 3 and phalanges 2 and 3 of digit 4 is much more marked than in other lacertid lizards.

Digits 3, 4 and 5 of the pes each have a lateral fringe of interlocking triangular scales, which extends distally to the base of the penultimate phalanx. That on the fifth toe is continuous with the similar scales on the trailing edge of the crus. Digits 4 and 5 also have a similar mesial fringe.

**COLOUR IN LIFE.** In life, *Holaspis* is blue-black with several longitudinal pale stripes on the dorsum, the two on the vertebral plates being tinged blue posteriorly. The tail has a series of large, light, intensely blue spots on its upper surface and its lateral fringes are yellow, while the belly is red.



## BEHAVIOUR

*Holaspis guentheri* occurs especially in rain-forest situations while *H. laevis* also extends into savannah. These lizards are nearly always observed at some height on the trunks and branches of standing trees, occurring at least up to 30m, and do not usually come down to the ground (*H. guentheri*: H. Lang in Schmidt, 1919; Perret & Mertens, 1957; Schiøtz & Volsøe, 1959; Laurent, 1964; Dunger, 1967; P. Agland, pers. comm. A. P. Mead, pers. comm. *H. laevis*: Barbour & Loveridge, 1928; Loveridge, 1951, 1953; De Witte, 1953; Branch, 1998; D. G. Broadley pers. comm.), although they can occur on fallen timber (H. Lang in Schmidt, 1919). *Holaspis* spp. are active hunters, constantly moving and searching and often investigating crevices (P. Agland, pers. comm.) in which they also frequently hide when disturbed and at night (H. Lang in Schmidt, 1919; Loveridge, 1951; Laurent, 1964; pers. obs. on captive animals). They are extremely agile, moving with ease on vertical and overhanging surfaces (H. Lang in Schmidt, 1919). *Holaspis* appear to thermoregulate and at times basks in patches of sunlight for at least up to ten minutes (Dunger, pers. comm.; P. Agland, pers. comm.). As in many other basking lacertid lizards, the body is spread and flattened by the dorsal ribs being rotated forwards and in *Holaspis* the body becomes as flat and round as a coin (Dunger pers. comm., P. Agland pers. comm.).

*Holaspis* is unique among lacertid lizards in being able to glide between trees. This behaviour was first formally reported in *H. guentheri* in Ghana by Schiøtz & Volsøe (1959) and subsequently confirmed by P. Agland in Cameroun and A. P. Mead in Nigeria (pers. comms). Earlier reports also provide some collaboration. C. J. P. Ionides (quoted by Loveridge, 1955) noted that in Tanzania *H. laevis* covers long distances in leaps between trees and Laurent (1964) reported that local people in northern Angola said that *H. guentheri* can fly. According to Schiøtz & Volsøe (1959), this lizard starts from a head-downwards position, high on a tree trunk from which it leaps outwards and glides steeply downwards. The trajectory later becomes shallower, and just before the lizard alights, it turns slightly upwards. For most of the glide, the lizard is orientated with its sagittal axis along the direction of motion, but towards the end this becomes perpendicular to it, the lizard stalling and reducing speed by this means. In one measured leap a lizard travelled 10.5m horizontally while dropping 9m, an overall angle of about 42° from the horizontal. *Holaspis* appears capable of selecting a target before launching itself, and of changing direction in mid-flight.

Among the *H. guentheri* observed by P. Agland (pers. comm.) one glided 30m at an angle of 10–20°, another travelled 25m and a third 6m. Motion was fast and straight and again appeared to be directed. In some cases there was an initial drop before the trajectory levelled out but in one instance a lizard running horizontally on a branch launched itself into the air without much fall before stabilising its flight path. At the end of a dive animals again alighted head upwards, landing very fast and sometimes immediately running upwards. *Holaspis* clearly has the ability to maintain its belly-downwards posture in the air with limbs spread and to change orientation as appropriate.

## FUNCTIONAL ANATOMY

In this section an assessment is made as to whether particular morphological apomorphies of *Holaspis* could have evolved through direct adaptation by natural selection in connection with one or more of its special behaviours: frequent locomotion on very steep often

vertical open surfaces, use of very narrow crevices, and gliding. Assessment is made on two criteria: 1. perceived functional benefit of the apomorphies in the activities concerned; and 2. whether similar apomorphies have appeared independently in other lizards that have evolved similar behaviours. The second criterion is most convincing if there are multiple independent origins of the apomorphy and if these origins are correlated with appearance of the relevant behaviour on the lineages of the taxa concerned. Even if there is a *prima facie* case for functional advantage of an apomorphy in connection with a particular behaviour, its absence in forms that have evolved the behaviour independently raises the possibility that it is not connected with the activity concerned. Alternatively, it may represent one of several strategies with other taxa gaining similar advantages in different ways.

**LOCOMOTION IN TREE BOLES.** The functional advantages of near-equality in fore and hind limb spans, and of characteristic foot architecture, in climbing on steep open surfaces has been discussed elsewhere (Arnold 1998b). These features are particularly well developed in *Holaspis* and presumably related to the abundance of such surfaces in its environment. The unique manus features of *Holaspis* suggest the forelimbs are sometimes used in parasagittal planes (Arnold, 1998b). This may be when the lizard launches itself from a head-downwards position on a steep surface. Extending the forelimbs at this time would push the foreparts of the body out into a more horizontal position, putting it closer to its orientation when gliding and making an outward leap easier.

**USE OF CREVICES.** Features that confer advantages in crevice use and the functional basis for this has already been surveyed (Arnold 1998a). Many derived features of *Holaspis* occur in other lacertids that use rock crevices, having developed independently at least once in archaelocertas (*Lacerta* spp.), and in *Omanosaura cyanura* and some populations of *Podarcis hispanica*. These forms show many apomorphies similar to those of *Holaspis* although the features are less developed than in this form, especially the degree of flattening of the head, body and limbs. These low vertical dimensions enable lizards to enter narrow crevices and a variety of cranial features (Appendix 1, numbers 4, 6, 7, 8, 10 and 12) results in a deformable skull that can be inserted into irregular spaces. Increased kinesis enables the skull to be flattened further by protraction on entering a crevice and locked into place by subsequent retraction. As a result of flattening of the skull, the eyes, which are large, project well above it during normal activities and this potentially impedes entry into crevices. However, in lacertids including *Holaspis* each eye is pushed downwards as the lizard enters a crevice by contact with the crevice roof so that its lower surface deflects the flexible membrane crossing the greatly enlarged inferior orbital foramen. This enables the lower part of the eye to project into the buccal cavity, so that it can be housed within the depth of the head. Reduction of the supraocular osteoderms increases the flexibility of the skin over the eyes so that its geometry can alter during their depression. Reduced overlap of collar and belly scales increase smoothness enabling lizards to move easily both forwards and backwards in crevices. Some or all these features are paralleled in many non-lacertid crevice users including skinks (such as *Mabuya laevis* and *M. sulcata*), xantusiids (*Xantusia henshawi*), geckos (*Afroedura*) and iguanids (*Sauromalus*, *Oplurus*).

*Holaspis* has other features not found in other crevice-using lacertids but present in the most extremely flattened exploiters of rock crevices in other families, such as *Platysaurus* (Cordylidae) and *Tropidurus semitaeniatus* (Iguanidae, Tropidurinae) and probably functionally associated with such strong depression. Among these is modification of the scleral ossicles, so that there is one or

more windows in the scleral ring (Fig. 2). These enable the eyeballs to distort and flatten, so they can be housed in the narrow space available within the head. Other shared features, which also contribute to low vertical dimensions, are depression of the body vertebrae and reduction of the crests on their neural arches.

Shortening and consequent decrease in mass of the adductor muscles associated with reduction in head height probably plays a critical role in facilitating the evolution of this cranial morphology. Curtailed mass reduces the power of the muscles, so a particularly strong, thick arched parietal area of the skull is no longer necessary to resist their action, and this also permits the posterior skull roof to become thin and flat. Similarly the mandibles are subjected to reduced forces in biting and can consequently be more slender with smaller vertical dimensions. However, such shortening of the muscles carries penalties in terms of reduced efficiency in biting and prey handling (Arnold, 1998a). Change in geometry of the skull during the retraction phase of cranial kinesis ameliorates this effect by improving their angle of action on the jaw and the length of their excursion. This phenomenon is prominent in *Platysaurus*, which has an expansion area in the skin on the anterior cheek that accommodates the changes involved in the substantial kinetic movement. The similarly orientated hinge regions of *Holaspis*, between the small scales found in this region, indicates that its skull is similarly highly mobile, as does the simplified fronto-parietal suture.

The downward flexion of the retroarticular process of the mandible may permit a longer and more efficient *depressor mandibulae*, in spite of the flattened head, although this feature is not paralleled in other very flattened crevice users. Other characteristics of *Holaspis* could also plausibly be considered as adaptations to crevice use, but are not repeated in functional analogues. Thus, the large plates along the back which might possibly increase smoothness and so ease mobility within crevices; although neither *Platysurus* or *T. semitaeniatus* have this feature. The enlarged sternal fontanelle could similarly be thought to increase flexibility in this region, but *Platysaurus* has no fontanelle at all.

Another complex of *Holaspis* features may also be related to use of crevices, specifically those beneath bark. This involves the snout which is wedge shaped in lateral view (unlike that of rock crevice dwellers), with the bizarre flattened boss formed from the premaxilla, and nostrils set back from the snout tip and low on its sides. Such features are not found even in extremely flattened lizards using rock crevices, but they do occur in the flattened lygosomine skink *Aulacoplax*, which habitually conceals itself in the narrow interstices between the bases of the fronds of screw pines (*Pandanus* spp.) (Brown and Fehlmann, 1958). This arrangement may enable the skink to enlarge interstices so they are broad enough to take the rest of the animal as it moves forwards. *Holaspis* may possibly do the same when pushing beneath flexible pieces of loose bark. The frequent presence of longitudinal scratches on the dorsum of the head suggests this may be the case. Fusion of the frontoparietal and interparietal scales may increase strength and smoothness of the head surface but has no parallels elsewhere.

**GLIDING.** Since *Holaspis* descends through the air in a controlled way at relatively shallow angles it glides rather than parachutes. Gliders depend on the possession of an aerofoil which extracts a lift component as the animal moves through the air, the lift counteracting the force of gravity. For gliding at shallow angles to be possible, the ratio of surface: body weight needs to be high. Some other gliding lizards have a specialised lift surface that provides this. In the agamid *Draco*, this is formed from a membrane supported by the

elongated abdominal ribs while in the gecko *Ptychozoon* there are flaps attached to the sides of the belly that fold out, increasing surface area. In *Holaspis*, it is the whole body that acts as an aerofoil and some features that also confer performance advantage in using crevices contribute to its formation. This is particularly true of dorsoventral compression, but low ossification of the skull must help increase the surface: weight ratio. Other features appear to be specifically associated with gliding and are not found in crevice dwellers, although they may occur in other gliders. Included here is low ossification of the pectoral girdle and perhaps that of the sternum and depression of the legs and tail. This last feature, together with development of distinct trailing edges on the limbs, also occurs in *Draco* and *Ptychozoon*, which do not enter very narrow crevices. Surface area is further increased by the lateral flaps on the neck and the webs of skin that form the trailing edge of the proximal hind legs, both features again found in *Draco* and *Ptychozoon*. The modified scales on the sides of the tail, on the trailing edge of the crus and on the hind digits also increase surface very efficiently, forming stiff lateral fringe-like extensions with little increase in weight. They are exactly paralleled in structure and function by scales on the hind side of the thigh and tail base in *Draco*, while *Ptychozoon* has analogous cutaneous extensions along the length of the tail.

*Holaspis* is able to produce further temporary increase in surface area by lateral expansion of the abdominal region so that this becomes almost disc-like. The increase in surface area is brought about by the long free dorsal ribs being rotated forward around their articulations with the body vertebrae, so that instead of being directed diagonally backwards they project more laterally. In *Holaspis*, the gain in surface area this produces is large because the ribs are long. The overlapping flexible rib tips form a continuous lateral edge to the area supported by the ribs and this maintains its continuity and longitudinal orientation in spite of the movements of the ribs themselves. The rotation of the ribs is presumably partly brought about by the intercostal muscles, as seems to be the case in *Draco* (Colbert, 1967). But it is likely that the well-developed slips of the *m. intercostalis scalaris* also play a part. As they run somewhat diagonally outwards and backwards from the *m. rectus abdominis* to the rib tips, their contraction would also help swing the ribs forwards; at the same time the ribs would tend to bow laterally and bend distally downwards. The contraction would also raise the *m. rectus abdominis* and with it the ventral integument which is closely attached. These movements would produce a more aerodynamically efficient transverse section in which the dorsal surface was more strongly convex and the belly flat or slightly concave.

The skin must stretch to allow for the increase in lateral area that the rib movements produce. Its distinctive structure permits this, for expansion occurs not only at the longitudinal lateral skin folds but also at the extensible areas between the scales. The bridges that often join the scales limit the direction and extent of expansion; they also help distribute it evenly throughout the skin, discouraging wrinkling and so contributing to a smooth surface. The looseness of the connection between the skin and underlying structures usual in lizards is also important in allowing skin tension to be evenly distributed.

It is probable that the band of large broad plates in the vertebral region also has a function in producing as good an aerofoil as possible. As the hinge regions between the plates are virtually inelastic, the whole area can be regarded as a single lamina which is firmly fixed at the occiput and at the tail base. When such an elongate lamina is stretched over a flat or convex surface, and placed under tension, it becomes very resistant to lateral deformation. This

effect is increased when the tension is both along and across the lamina. It can be demonstrated by placing a strip of paper on plane surface and putting it under longitudinal tension, after which displacing the intermediate area laterally, even to a small extent, becomes very difficult.

Such rigidity appears to be developed in the vertebral area of *Holaspis*, which extends over the convex dorsum of the body. Tension is generated by the lateral skin being pulled outwards during rib spreading. This movement distorts the large plates and their hinge regions slightly, so that there is a small widening and longitudinal contraction of the vertebral band. As this is firmly attached at the occiput and the tail, tension within it is thereby increased. The slight movements of the plates exhaust the very limited internal mobility of the band, increasing its lateral rigidity further. These processes can be discerned in the detached dorsal skin of an alcohol-preserved *Holaspis*. Lateral tension alone, produces a longitudinal contraction of the vertebral band whereas, if it is applied when the ends of the band are fixed to the substrate, the band becomes laterally rigid.

The rigid vertebral band ensures that the extended lateral skin is spread evenly on both sides of the body, again helping to avoid the tendency of the tense skin to wrinkle. It may also act to keep the body straight during gliding by restricting lateral bending. This effect can be simulated by attaching a strip of adhesive paper tape along the side of an elongate rubber balloon. When this is inflated, the stretched wall of the balloon exerts tension on the paper strip, which represents the vertebral band of *Holaspis* and the air pressure provides support for this in an analogous manner to the body of the lizard. A balloon modified in this way is substantially harder to bend sideways than an unmodified one.

When the lateral skin of *Holaspis* is unstretched, the vertebral band is slack and capable of rucking upwards at its hinges. This permits the lizard a normal amount of lateral movement, when for instance walking rather than gliding, since the band now lacks lateral rigidity.

The surface: weight ratio ('wing'-loading) of *Holaspis* was roughly assessed on the assumption the whole animal acts as an aerofoil. Area was found by placing straightened preserved lizards belly downwards on squared paper and tracing their outline; maximum lateral extent of the body was then estimated by comparison with photographs of animals basking with their bodies fully expanded, and by stretching the lateral skin. Weight was calculated on the assumption that live lizards weigh 10% more than alcohol preserved ones (Colbert, 1967). The loadings for four individual adult *Holaspis* varied between 0.26 and 0.37 gm/cm<sup>2</sup>. These are relatively small figures when compared with those for *Draco* (Colbert, 1967). Such low loading is probably necessary to compensate for the relatively poor general aerodynamic shape of *Holaspis*.

**FUNCTIONAL SIGNIFICANCE OF OTHER CHARACTERS.** A minority of derived features of *Holaspis* are not functionally associated with its main distinctive behaviours. The presence of a window in the lower eyelid has developed in a wide range of small lizards that bask directly in the sun in relatively dry microclimates (Arnold, 1973; Greer, 1983). This means that such lizards can reduce the extensive water loss associated with these situations by closing their eyes but still retain vision to detect predators, passing food items etc. In agreement with this explanation, the window is better developed in *H. laevis* which extends into relatively dry savannah, than in *H. guentheri* which appears to be confined to forest. Loss of pterygoid teeth in lacertids tends to correlate with the general reduction in ossification found in *Holaspis* and may be a concomitant of this.

## EVOLUTION OF *HOLASPIS*

The order in which new features develop and the situations in which they do so can often be reconstructed by examining states on side branches on the lineage of the taxon concerned. This cannot be done with many features of *Holaspis* as they have evolved within its exclusive lineage, which by definition lacks side branches, so other cues have to be used for these autapomorphies. However examination of the relatives of *Holaspis* does give some information. Thus, a degree of climbing is widespread in lacertids as is a modest amount of crevice use. This makes it most parsimonious to assume these behaviours precede gliding, which is unique to *Holaspis*. These activities and the morphological adaptations associated with them are better developed in *Holaspis* itself. Improvement in climbing modifications may possibly have begun first, as climbing steep tree boles and branches must precede exploiting crevices in them.

Animal gliders and fliers can be stable or unstable. In stable ones, there is a long lift surface behind the centre of gravity. This means that, as an animal glides, any tendency to pitch in the sagittal plane around the centre of gravity is self-correcting. In pitching, the long posterior lift surface will rise or fall, but the air pressure produced by forward locomotion will return it and the animal as a whole to its original orientation. Unstable fliers with short lift surfaces behind the centre of gravity gain in manoeuvrability but do not self-correct and so require sophisticated neurological mechanisms to maintain appropriate posture in the air, something that is unnecessary in stable forms (Smith, 1952). Unsurprisingly, stable forms evolved before unstable ones in most of the main groups of flying animals, namely insects, pterosaurs and birds, and possibly bats too (Smith, 1952).

As might be expected from this, *Holaspis* is a stable glider. The centre of gravity of preserved *Holaspis* appears to be just behind the midpoint between the two pairs of legs. There is therefore a considerable area of lift surface posterior to the centre of gravity, made up of the hind body, hind limbs and tail. Experiments were conducted with models made out of laminated cardboard and weighted to give a wing loading and weight distribution similar to that of *Holaspis*. When gently launched in the appropriate position, these glided well, confirming that a glider of the dimensions and shape of *Holaspis* is stable.

Given inherent stability, gliding ability seems to require only an aerofoil and ability to reach and maintain an appropriate belly-down posture with limbs slightly raised, as well as some ability to trim, at least initially. In tree frogs Cott, (1926) found adoption of initial posture very critical: *Phrynohyas venulosa* spread its limbs and glided when dropped whereas *Hyla arborea*, which is morphologically similar, dropped vertically with legs flailing. It might be expected that the ability to adopt the appropriate posture would be confined to *Holaspis* among lacertids as it is the only known glider, but when tests were carried out on a number of lacertids this propensity was found to be widespread, being present in completely terrestrial lizards such as *Lacerta agilis* and *Acanthodactylus erythrurus*, as well as climbing ones (Arnold, 1989a). The wide distribution of this ability suggests it confers advantage in another more general context and may have arisen there. This context may be terrestrial locomotion. Certainly running lacertids seem to have to continuously adjust their body positions and, at some points in the stride cycle, they may be balanced on only a single toe (Arnold 1998b), so good neurological control of posture seems to be essential in this activity.

The production of an aerofoil is likely to largely result from direct adaptation, as many of the features of *Holaspis* appear to confer advantage only in gliding. However rib spreading, like balance, is

coopted from an earlier activity. All lacertids, including *Holaspis*, appear to spread their ribs when basking in relatively cool conditions, increasing surface area and rate of heat intake.

Permanent depression of the head, body and limbs of course also contributes to the aerofoil and we can ask whether this is a special feature of gliding or whether it is coopted from crevice use. As already noted there is some phylogenetic evidence of its earlier origin for crevice use, something that has occurred in many independent lineages.

Modifications for gliding in *Holaspis* are quite extensive, several organ systems being involved. It is therefore rather surprising that *Holaspis* has not developed a more efficient aerofoil such as occurs in *Draco*. However to do this would probably involve the development of a delicate patagium or extensive lateral skin flaps. It is likely that such structures would interfere with the lizard's ability to enter and move in the narrow crevices it regularly utilises. Consequently *Holaspis* is restricted to using means of broadening the body that do not project exteriorly.

As a stable glider, *Holaspis* is very dependent on its long tail, but this can break easily, even close to its base where loss might make it unstable in the air and reduce its ability to control its glide path. Nonetheless the tail is lost and often regenerated in many individuals (Arnold, 1984). This emphasises the importance of tail loss as an antipredator device and suggests the cost: benefit ratio still favours frequent tail loss in *Holaspis* even though locomotory costs may well be high.

It might be thought that cases like *Holaspis*, where entrance into a new life mode has been dependent on multiple exaptations, are rare. But this phenomenon occurs in another instance where aerial locomotion has been attained, that of birds where feathers and the complex mechanism of wing folding arose long before gliding or active flight (Gauthier & Gall, 2001).

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## Appendix 1

Derived features of *Holaspis* not found in immediate relatives in the paraphyletic genus *Adolfus*. Most features are unique in the Lacertidae as a whole and these are denoted by \*. Separate postorbital and postfrontal bones are primitive in the Lacertidae but fusion is the usual condition in the African Equatorial group and separation in *Holaspis* is a reversal (Arnold, 1989a). Most features appear to confer a performance advantage in one or more of the characteristic behaviours of *Holaspis* or ameliorate a problem associated with them. The behaviours concerned are designated as follows: L – locomotion on steep surfaces, C – use of crevices, G – gliding. Brackets indicate a relatively minor role.

### Proportions

- |   |    |
|---|----|
| 1. Head, body, limbs and tail extremely depressed*  | CG |
| 2. Snout sharply wedge-shaped in lateral view*      | C  |
| 3. Fore and hind limbs approach equality in length* | L  |

### Skeleton and musculature

- |   |      |
|---|------|
| 4. Skull light and very thin-boned with some deformability*   | CG   |
| 5. Premaxilla forming a large semicircular boss*  | C    |
| 6. Nasal openings of skull very large and widely expose primary nasal chambers  | C(G) |
| 7. Fronto-parietal suture a simple abutment, not strongly interdigitated*   | C    |
| 8. Postorbital and postfrontal bones separate   | C    |
| 9. Supraocular osteoderms very reduced*   | C(G) |
| 10. Inferior orbital foramen extremely large  | C    |
| 11. Pterygoid teeth absent  |      |
| 12. Increased cranial kinesis   | C    |
| 13. Ring of scleral ossicles reduced to twelve and emarginated above and below*   | C    |
| 14. Retroarticular process of mandible directed somewhat ventrally*   | C    |
| 15. Dorsal vertebrae depressed with very reduced neural spines*   | C    |
| 16. Anterior free ribs elongated with long cartilagenous extensions at their tips*  | G    |
| 17. Coracoid plate with an extra fontanelle*  | G    |
| 18. Sternal fontanelle very large*  | CG   |
| 19. <i>M. intercostalis scalaris</i> well developed, consisting of slips originating on tips of anterior free dorsal ribs | CG   |

- |   |   |
|---|---|
| and running forwards and medially to insert on upper surface of <i>m. rectus abdominis</i> , above outer margins of second row of ventral scales* |   |
| 20. Manus and pes have syndrome of features associated with climbing on continuous open surfaces very pronounced*                                 | L |
| 21. Length and downward curvature of penultimate phalanges of digits better developed than in other lacertids*                                    | L |
| 22. Digits 2–5 of manus subequal in length*   | L |
| 23. In manus, shortening and downward flexure of phalanx 2 of toe, 3 and phalanges 2 and 3 of toe 4, very pronounced*                             | L |

### External features

- |   |      |
|---|------|
| 24. Rostral scale very large, extending on to top of snout with broad frontonasal contact*                            | C    |
| 25. Nostrils set back, on sides of snout*   | C    |
| 26. Interparietal and paired frontoparietal scales all replaced by a single triangular scale*                         | C    |
| 27. A window in the lower eyelid made up of 1–5 enlarged semitransparent scales                                       |      |
| 28. Temporal scales differentiated with anterior ones arranged in diagonal lines*                                     | C    |
| 29. Neck with sharp-edged flap on each side when pharynx not expanded*  | G    |
| 30. Cross section of body convex above and flat below   | G    |
| 31. A double series of very large flat scales along vertebral region of body*   | (C)G |
| 32. Dorsal scales on sides of posterior trunk laterally expandable*   | G    |
| 33. Lateral dorsal scales on posterior trunk sometimes joined by a system of bridges*                                 | G    |
| 34. Collar and belly scales with very reduced imbrication   | C    |
| 35. Tail with two longitudinal rows of broad enlarged scales above and below, the former with multiple sensory pores* | G    |
| 36. Tail with lateral fringes of interconnected pointed scales*   | G    |
| 37. Two rows of large scales on front of forelimbs*   | CG   |
| 38. A patagium behind the knee*   | G    |
| 39. A row of flat triangular scales on trailing edge of crus*   | G    |
| 40. Second and third fingers of manus conjoined at base*  | L    |
| 41. Digits 3–5 of pes with a fringe of interlocking pointed scales*   | G    |
| 42. Distinctive colouring*  |      |



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Whenever possible a copy of the text, once the paper has been accepted, should also be provided on floppy disc (see below). Discs should only be sent after final acceptance, as papers generally need revision after refereeing. If it is impossible to provide an appropriate disc please ensure that the final typescript is clearly printed.

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sub-headings should be followed. All should be ranged left and be in upper and lower case. Supra-generic systematic headings only should be in capitals; generic and specific names are to be in italics, underlined. Authorities for species names should be cited only in the first instance. Footnotes should be avoided if at all possible.

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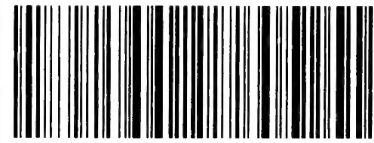
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