ON THE RICTAL GLANDS OF SOME ATRACTASPID SNAKES

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Structures around the corner of the mouth of atractaspid snakes are examined in serial sections. In addition one Madagascan and two African species of *Geodipsas* are reported. For *Atractaspis corpulenta* presence of a serous superior rictal gland is confirmed and the discovery of a hitherto unnoticed serous *inferior* rictal gland is reported. Inferior rictal glands are also reported for species of *Aparallactus, Chlorhinophis, Geodipsas, Poecilopholis* and *Polemon*. Neither superior nor inferior rictal glands are found in *Amblyodipsas, Hypoptophis, Macrelaps* or *Xenocalamus*. African species of "*Geodipsas*", now placed in the genus *Buhoma*, agree with aparallactines and differ from the Madagascan type species, *G. infralineata*, in the configuration of the rictal glands.

INTRODUCTION

Bourgeois (1961) was the first to propose a relationship between the burrowing asps, *Atractaspis*, and the aparallactine snakes, under the name Aparallactinae. Under the senior family group name Atractaspididae this has been followed by Heymans (1975), McDowell (1968) and Underwood & Kochva (1993). There has been agreement concerning most of the genera assigned to the group, but *Aparallactus* and *Macrelaps* were not included by McDowell (1968), and Underwood & Kochva (1993) included *Micrelaps* and *Brachyophis* with some doubts. Cadle (1994), however, finds no support for the association of *Atractaspis* with the aparallactines on the basis of albumin immunological distances.

Apart from the venom gland of *Atractaspis* and the mucous supralabial glands present in all snakes, Underwood & Kochva (1993) considered a gland associated with the posterior maxillary teeth. This was termed "glande parotide" by Phisalix & Caius (1918). Taub (1966), seeking to avoid confusion with the mammalian parotid gland, introduced the term "Duvernoy's" gland in reference to an early description by Duvernoy (1832). Phisalix & Caius (1918), however, point out that Duvernoy did not distinguish between the parotid and the supralabial glands. Leydig (1873) in a study of the head glands of some German snakes distinguishes between a yellow gland in the upper lip and the rest of the supralabial gland in *Natrix natrix, N. tessellata* and *Coronella austriaca*. He shows a difference in the staining reaction of the two glands. In plate 22, figure 1 he labels the yellow gland and adds, in parenthesis, "Homologon der Giftdrüse der

Vipern". This homology has not been questioned since then. The term "Duvernoy's gland", associated with modified and often grooved posterior maxillary teeth, sets it apart from a "venom gland", associated with canaliculate fangs. In that many "Duvernoy's" glands have been shown to produce a toxin which, in some cases, functions as a venom, we regard this distinction as unfortunate. We therefore prefer Saint Girons' term "glande dentale" (1987), applicable to all glands associated with teeth.

Underwood & Kochva (1993) also paid attention to a gland of the upper lip opening into the corner of the mouth. This was originally called "glande temporale antérieure" by Phisalix & Caius (1918) but Underwood & Kochva (1993) preferred McDowell's (1968) term "rictal gland" on the grounds that although the position of the gland may vary it always opens into the corner of the mouth. Some of their observations were based on serial sections of the glands of the upper lip, some on dissections. They found that, as seen in dissection, the posterior end of the supralabial gland was sometimes slightly differentiated, but not sufficiently for presence of a rictal gland to be recorded with confidence. In sections a rictal gland can be distinguished from a supralabial gland by the presence of serous, as well as mucous cells, and by the duct which passes back to open into the corner of the mouth, as distinct from the margin of the lip.

Underwood & Kochva (1993) noted that in all but one previous report the rictal gland had been found to be mesial to the quadrato-maxillary ligament. In a survey by dissection of some lower snakes they found that with the exception of *Anilius*, a rictal structure, whether a gland or a pocket, lay mesial to the ligament.

Underwood (1996) has since verified in sections that *Anilius* has a large superior rictal gland, lateral to the quadrato-maxillary ligament, and also a large inferior rictal gland; they both open into the corner of the mouth.

Haas (1930, fig. 14) reported an anterior temporal gland in *Atractaspis corpulenta*; he interpreted its position lateral to the quadrato-maxillary ligament as a derived condition. Underwood & Kochva (1993) confirmed, by dissection, Haas's observation of a lateral rictal gland in *A. corpulenta* and found one in some other species of *Atractaspis* and other forms assigned to the Atractaspididae. For some, presence or absence was confirmed in serial sections. They further found, and confirmed in sections, that in *Polemon* and some other forms, the bulk of the supralabial gland is followed in sequence by compact dental and rictal glands overlapped only by a narrow strip of the supralabial gland (their figs 9 B & C). This compact condition was regarded as derived.

Kochva (1978, fig. 31) found a "posterior" gland, which we now interpret as rictal, lateral to the caudal end of the supralabial gland, in *Vipera palaestinae*. Ineich & Tellier (1992) and Saint Girons & Ineich (1993) report a gland in *Echis* which opens to the exterior within the margins of the posterior supralabial scale. It lies above the posterior end of the supralabial gland and shows evidence of a "séro-muqueux" secretion, here taken to be serous PAS positive. We interpret this as a rictal gland. Evidently *lateral* rictal glands are not confined to atractaspid snakes and *Anilius*.

MATERIALS AND METHODS

The present investigation was motivated by the wish to check in serial sections observations made by dissection. We started by making serial sections of the head of an *Atractaspis corpulenta*, half sagittal and half transverse. We confirmed the presence of a superior rictal gland but were surprised also to find an *inferior* rictal gland. This appears to be what Haas (1930) called "Mundwinkeldrüse"; apart from this, such a structure has not to our knowledge been previously reported. This observation turned our attention to the glands of the lower lip as well as the upper lip.

This investigation is largely based on specimens in the Natural History Museum, London. The specimens were of unspecified, and in some cases poor, fixation. Although histological detail could not be recognized in some, presence or absence of a rictal gland could be ascertained in nearly all specimens. Glands from the posterior half of the upper and lower lips were dissected out and serially sectioned. The choice of species was based on gaps in the histological survey already made. We noticed that the glands of the upper lip of *Geodipsas procterae*, as figured in dissection by Underwood (1967, fig. 6), bear a close resemblance to the glands of *Polemon bocourti* (Underwood & Kochva, 1993, fig. 9). Some African species then placed in *Geodipsas,* as well as the Madagascan type

species *G. infralineata*, were therefore included in our survey.

We already had available serial sections of the heads of *Atractaspis engaddensis, Chilorhinophis gerardi* and *Micrelaps muelleri*. The further species examined are: *Amblyodipsas polylepis, Aparallactus capensis, A.modestus, "Geodipsas" depressiceps, "G". vauerocegae, G. infralineata, Hypoptophis wilsoni, Macrelaps microlepidotus, Poecilopholis cameronensis, Polemon gabonensis* and *Xenocalamus mechowi*.

Following the evidence of a lateral superior rictal gland in *Vipera* and *Echis*, a survey was made by dissection of the glands of the upper and lower lips of the following viperid and elapid snakes:

Viperidae – *Azemiops feae, Bothrops asper, Calloselasma rhodostoma, Hypnale hypnale, Trimeresurus monticola, Causus defilippi, C. lichtensteini, C. resimus, C. rhombeatus, Atheris nitschei, Bitis gabonica, Cerastes cerastes, C. vipera, Eristicophis mcmahoni, Vipera russeli* and *V. ursinii.*

Elapidae – *Aspidelaps lubricus, A. scutatus, Bungarus flaviceps, Elapsoidea guentheri, E.sundevalli, Naja mossambica, Ophiophagus hannah, Paranaja multifasciata* and *Walterinnesia aegyptia.*
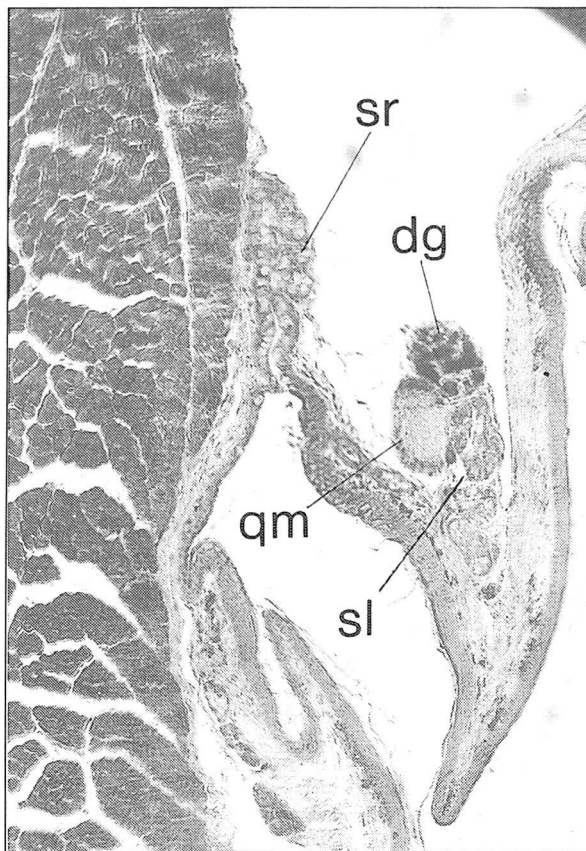

FIG. 1. Transverse section of corner of mouth of *Telescopus fallax,* to show relationships of superior rictal gland and duct opening into rictal groove, dental gland, quadrato-maxillary ligament and supralabial gland. dg, dental gland; hg, Harder's gland; il, infralabial gland; ir, inferior rictal gland; qm, quadrato-maxillary ligament; sl, supralabial gland; vg, venom gland.
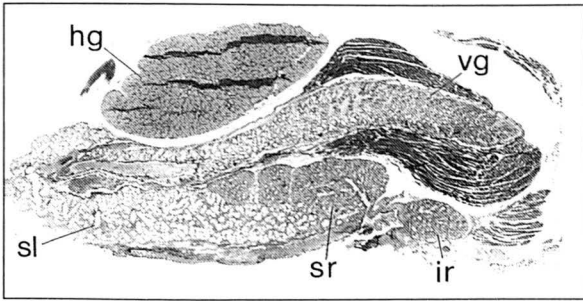
FIG. 2. Parasagittal section of head of *Atractaspis corpulenta* (BMNH 1916.5.29.3, Bitye, S.Cameroons) showing superior rictal gland, with duct opening backwards into corner of mouth, and inferior rictal gland. Abbreviations as Fig. 1.

RESULTS

We illustrate what is the most widespread condition in a transverse section of *Telescopus fallax* at the level of the opening of the superior rictal gland (Fig. 1). The superior rictal gland is mesial to the quadrato-maxillary ligament, and the duct opens into the groove between the upper and lower lips at the corner of the mouth. The dental and supralabial glands are lateral to the ligament. There is no evidence of an inferior rictal gland.
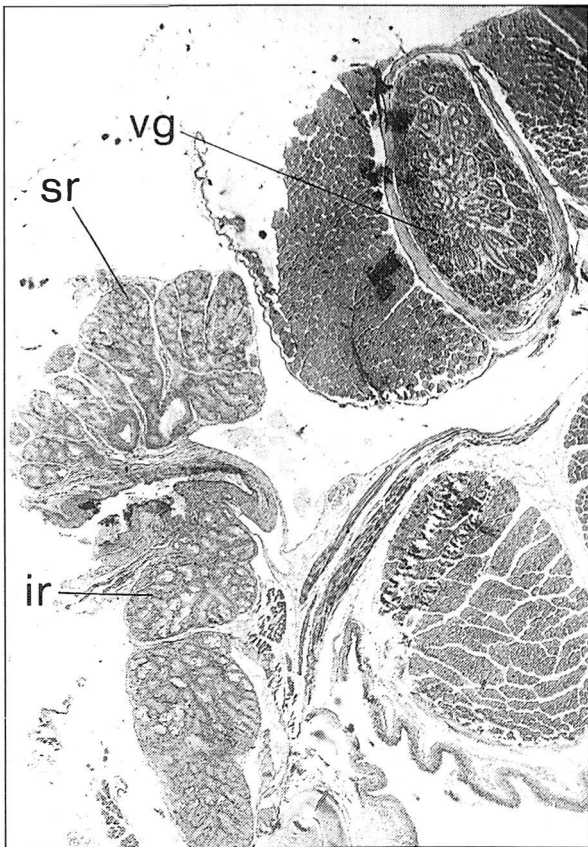

FIG. 3. Transverse section of head of *Atractaspis corpulenta* (same specimen), showing superior rictal gland with two ducts and inferior rictal gland, respectively above and below the rictal groove. Abbreviations as Fig. 1.
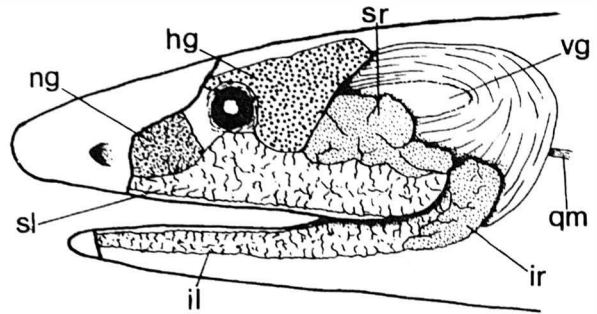

FIG. .4. Superficial dissection of *Atractaspis corpulenta* (BMNH 1909.12.3.15 & 1913.10.29.17, Bitye, S.Cameroon) to show relationships of superior and inferior rictal glands. Abbreviations as Fig. 1.

In *Atractaspis corpulenta* the superior rictal gland is more extensive than the inferior gland (Fig. 4). Both glands lie immediately beneath the skin (which has been peeled off, Fig. 3, transverse). The superior gland is lateral to the quadrato-maxillary ligament, as reported by Haas (1930). The superior gland is, vertically, much deeper than the supralabial gland, rising lateral to the venom gland. Staining with Masson's trichrome method shows that it is serous, except for the ducts which contain mucuous cells. A major duct runs through the gland and opens into the rictal fold. Two small additional ducts drain the posterior part of the gland and open somewhat caudal of the main duct. The inferior rictal gland is similar in structure (Fig. 2). No trace of rictal glands is found in *A. engaddensis*.

Aparallactus capensis has a lateral superior rictal gland with some mucous cells, mainly around the ducts. The compact dental and superior rictal glands, not overlapping one another but overlapped by a strip of the supralabial gland, are much as in *Polemon* (Underwood & Kochva, 1993, Fig. 9). *A. modestus* has a small gland at the posterior end of the supralabial gland which shows no goblet cells but nevertheless stains green, suggesting mucins. In this taxonomic con-
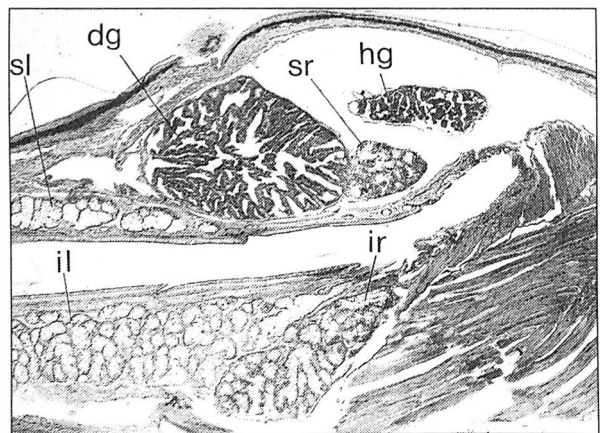

FIG. 5. Parasagittal section of corner of mouth of *Chilorhinophis gerardi*, showing superior and inferior rictal glands. Abbreviations as Fig. 1.
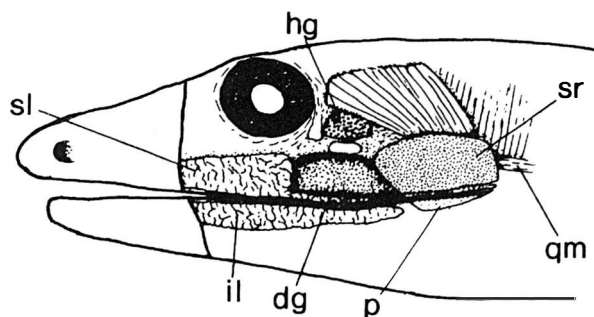
FIG. 6. Dissection of *Buhoma vauerocegae* (BMNH 1909.10.19.7, Usumbara, Tanzania) to show compact dental gland between anterior supralabial gland and large compact superior rictal gland. p, shallow pocket of buccal epithelium in lower corner of mouth. Between Harder's gland and the dental gland the anterior end of the ectopterygoid bone is visible. Abbreviations as Fig. 1.
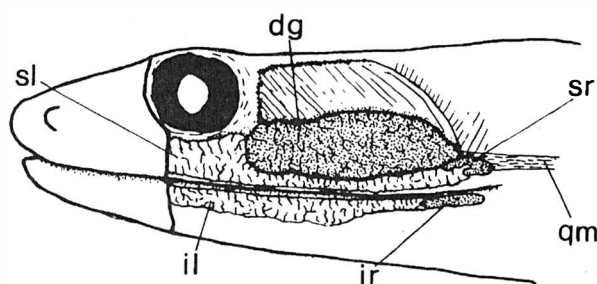

FIG. 7. Dissection of *Geodipsas infralineata* (BMNH 1930.2.2.14, Anamalagasta Forest, E. Madagascar) to show large dental gland followed by small, partly overlapping,rictal gland and inferred inferior rictal gland (subject to confirmation in sections). Abbreviations as Fig. 1.

text it seems likely that it is an atypical rictal gland but it could be a modified supralabial gland. *A. modestus* also differs from other members of the genus in the absence of grooves on the posterior maxillary teeth. An inferior rictal gland is also found.

Polemon gabonensis has a large superior rictal gland, as already reported. It also has a large inferior rictal gland. *Chilorhinophis* shows well developed superior and inferior rictal glands (Fig. 5). *Poecilopholis* has a very small serous gland in the superior rictal region and a more prominent inferior rictal gland.

The glands of the upper lip of *Buhoma vauerocegae* and *B. depressiceps*, which include a superior rictal gland, are similar to those of *Polemon* (Fig. 6). The infralabial gland of *B.vauerocegae* stops well short of the rictus; it is succeeded by a shallow pocket, the walls of which are not obviously glandular as seen by dissection. *B. depressiceps* has what we provisionally interpret as an inferior rictal gland. The condition of the *G. infralineata* is too poor for a histological report. However, in dissection it clearly has a large dental gland which extends nearly to the level of the rictus. There is also what appears to be a small discrete lateral

superior rictal gland overlapping the posterior end of the dental gland and extending back to the level of the rictus. A narrow strip of supralabial gland overlaps both of these back to the rictus. The infralabial gland, just behind the level of the rictus, appears to separate naturally into two parts, suggesting that there is an inferior rictal gland (Fig. 7).

In *Macrelaps*, despite what looked in dissection like the orifice of a gland, we found no evidence of a superior rictal gland (two specimens); there was also no evidence of an inferior gland. In *Amblyodipsas, Hypoptophis, Micrelaps* and *Xenocalamus* we found no evidence of rictal glands, superior or inferior. In *Brachyophis* we could find no evidence, by dissection, of an inferior rictal gland, but this part was damaged; Underwood & Kochva (1993) have already reported absence of a superior gland.

In *Elapomorphus nasutus* we find a complex dental gland, in two parts, one mucous the other serous, on which insert some fibres of the adductor superficialis muscle. There is a lateral superior rictal gland which has some mucous cells, mainly around the ducts. The glands of the elapomorphine snakes are being investigated by Salomão & Ferrarezzi (1993). By dissection we find evidence of an inferior rictal gland in *E. nasutus* and *E. bilineatus*, but not in *E. quinquelineatus*.

Our reports on viperid and elapid snakes are based on dissection only, unless otherwise stated. They should therefore be read with the qualification "subject to confirmation in sections". The most convincing rictal glands are discrete bodies, which may differ in colour and texture, from the labial glands.

In *Cerastes cerastes* we find a lateral rictal gland and a small inferior rictal gland. In the African vipers *Atheris nitschei* and *Bitis gabonica* we find evidence of a lateral superior rictal gland but not of an inferior.

In *Vipera russeli* and *Eristicophis mcmahoni* we find no evidence of either superior or inferior rictal glands. In *Causus lichtensteini*, which has a short venom gland, we find a swollen body at the posterior end of the supralabial gland, with pigment on the mesial face. The infralabial gland passes back to the level of the rictus without evidence of an inferior rictal gland. In *C. defilippi*, also with a short venom gland, we find no evidence of a superior rictal gland but the infralabial gland extends beyond the rictus where it turns inwards but is not otherwise differentiated. In *C. rhombeatus*, with a long venom gland, we found evidence of a superior rictal gland but not of an inferior gland. In *C. resimus*, also with a long venom gland, we found no evidence of either superior or inferior rictal glands. In *Azemiops feae* and the pit-vipers *Bothrops atrox, Calloselasma rhodostoma, Hypnale hypnale* and *Trimeresurus monticola* we find no evidence of rictal glands.

Amongst the elapids we find the clearest evidence of rictal glands in *Paranaja multifasciata*. Mesial to the

last two supralabial scales is a discrete body, rising higher than the supralabial gland and lying immediately beneath the skin. Beyond the posterior end of the infralabial gland is a small oval body, presumably an inferior rictal gland.

In *Aspidelaps lubricus* and *A. scutatus* we find evidence of a lateral superior rictal gland, and in *A. lubricus* it turns downwards around the corner of the mouth. In *Elapsoidea guentheri* and *E. sundevalli* we find a lateral superior rictal gland but no indication of an inferior gland. In *Bungarus flaviceps, Naja mossambica, Ophiophagus hannah* and *Walterinnesia aegyptia* we found no evidence of rictal glands.

DISCUSSION

Within the Atractaspididae, Underwood & Kochva (1993) had already interpreted the sequence of compact, non-overlapping, dental and superior rictal glands of *Aparallactus, Polemon* and *Chilorhinophis* as a derived feature linking these three genera. The similar condition of "*Geodipsas*" *procterae*, "*G.*" *vauerocegae* and "*G.*" *depressiceps*, in contrast to the type species *G. infralineata*, suggests that they were not properly assigned to the genus. Cadle (1996) and Ziegler *et al.* (1997) have, on the the basis of other evidence, arrived at a similar conclusion and the latter authors have erected the new genus *Buhoma* for the African species formerly assigned to *Geodipsas*.

Of the remaining atractaspids, only *Atractaspis corpulenta* is known to have well-developed lateral superior *and* inferior rictal glands, but it is clear by dissection that several other species have at least a superior rictal gland. *Poecilopholis* has small superior and inferior rictal glands. On the other hand *Hypoptophis, Brachyophis, Micrelaps, Amblyodipsas, Xenocalamus, Macrelaps* and some *Atractaspis* show no evidence of rictal glands. This distribution suggests that rictal glands are retained by some *Atractaspis, Aparallactus, Chilorhinophis* and *Polemon*, are reduced in *Poecilopholis* and are lost in the others.

Amongst henophidian grade snakes only *Anilius* has a lateral superior rictal gland; it also has an inferior rictal gland (Underwood, 1996). All of the others which have differentiated rictal structures have mesial superior glands; in many these open into a rictal pocket (Cundall & Rossman 1993, Underwood in preparation) but an inferior rictal gland has been found only in *Cylindrophis* (*Anomochilus* not examined).

Some Caenophidia have a lateral superior rictal gland and an inferior gland. These include some atractaspids, probably elapomorphines, some viperids and some elapids. *Pareas* has a lateral superior gland but no inferior gland (correction to Underwood, 1996). A larger number of Caenophidia, including xenodermatines, have a mesial rictal gland; none of these is known to have an inferior gland. Many caenophidians appear to be without differentiated rictal structures. No caenophidian is known to have a struc-

ture comparable to the rictal pocket of many henophidians (McDowell, 1986; Underwood, 1996).

We notice that all of the caenophidians with a lateral superior gland appear to be members of low grade lineages of the radiation (Underwood & Kochva, 1993; Knight & Mindell, 1994). We note also a particular resemblance between *Anilius scytale* and *Atractaspis corpulenta* in respect of the rictal glands. On the other hand "higher" caenophidians have a mesial superior gland (albeit without a rictal pocket) and, as far as we know, no inferior gland; in this they resemble "boids". Kluge (1991, preliminary) and Cundall *et al.* (1993) have published analyses of henophidian grade snakes based on a variety of characters. Kluge has bolyerines, which are without differentiated rictal structures (Underwood, in preparation), as sister to Caenophidia; Cundall *et al.* (1993) have tropidophids, which have superior rictal glands, opening into a rictal pocket, as sister group. On either of these views, the Caenophidia derive from one of the higher branches of the henophidian radiation without an inferior rictal gland. Both analyses agree that *Anilius* is on one of the lower henophidian branches.

We see two alternative interpretations. The higher Caenophidia inherit from henophidian ancestors a primitive mesial condition of the superior rictal gland, with loss of rictal pocket, and the lower Caenophidia share a derived lateral condition in parallel with *Anilius*. On this view, tropidophines would fit better than bolyerines as sister group. Alternatively, the lateral condition is primitive for *Anilius* and for the Caenophidia, and the higher caenophidians share a derived mesial condition in parallel with most henophidians. This view would suggest that *Anilius* is sister to the Caenophidia. The Scolecophidia are so highly modified that they do not help this judgement. Underwood & Kochva (1993) included the South American *Elapomorphus* and *Apostolepis* in their investigation of the relationships of *Atractaspis*. They concluded that they are at about the same grade level but did not find clear evidence of affinity. The *lateral* condition of the superior rictal gland and the presence of an inferior rictal gland in *Elapomorphus* add to the grade resemblance.

We note a complex dental gland in one species of *Elapomorphus*. From the survey of the glands of elapomorphines by Salomão & Ferrarezzi (1993) it is evident that there is a considerable range of variation of the dental glands within the group. The interest of elapomophines is further enhanced by Lema's report (1978) that *Elapomorphus bilineatus* is dangerously venomous. Within South America, all of the other forms so far examined have a superior rictal gland mesial to the quadrato-maxillary ligament. These include representatives of *Alsophis, Clelia, Liophis, Lystrophis, Phimophis, Philodryas, Siphlophis, Pseudoboa, Thamnodynastes, Waglerophis* and *Xenodon* (Underwood, personal observations).

Cadle (1984) finds immunological evidence linking *Apostolepis* with South American xenodontines. This implies that a switch from lateral to mesial took place within the xenodontine lineage.

Radovanovic (1935) comments on a special gland of *Coluber najadum* and *C. gemonensis,* mesial to the ligament, which he regarded as undoubtedly homologous with the "anterior temporal gland". By dissection Smith & Bellairs (1947) found a rictal gland in some colubrine snakes of the genera *Coluber, Elaphe, Lytorhynchus* and *Ptyas.* They note that it is "partly overlapped by the posterior end of the supralabial gland and the ligamentum zygomaticum" (quadrato-maxillary ligament), i.e. it is mesial. Gabe & Saint Girons (1969) find a mesial rictal gland in the genera *Coronella* and *Oligodon.*

On the basis of dissection, McDowell (1986) reports a rictal gland, mesial to the quadrato-maxillary ligament, in species of many genera, including: *Alsophis, Calamaria, Carphophis, Coniophanes, Diadophis, Duberria, Heterodon, Hydrops, Manolepis, Nerodia, Oxyrhopus, Pseudoxenodon, Rhadinaea* and *Tantalophis.* He comments on the large size of the gland in *Rhadinaea multilineata.*

Cadle (1994) made an extensive immunological survey of African "colubrid" snakes. Relevant to the present investigation are *Amblyodipsas polylepis, A. unicolor, Aparallactus capensis, A. lunulatus, Atractaspis bibroni* and *Macrelaps microlepidotus.* Two analytical procedures found distant links between *Atractaspis, Amblyodipsas* and Madagascan *Leioheterodon,* (Cadle, 1994: Fig. 1). His overall conclusion is however that *Atractaspis, Amblyodipsas* and *Leioheterodon* represent separate lineages deriving from the "basal radiation" with no more than the "marginal association" noted above. Cadle (1994) considers the bearing of his data on the group which we treat as atractaspids. He finds "no significant association" of *Atractaspis* with "aparallactines" and at best a very distant relationship of *Aparallactus* with either *Atractaspis* or *Amblyodipsas.* On the other hand, affinity of *Macrelaps* with *Amblyodipsas* is clear. If presence of a lateral superior rictal gland plus an inferior gland are derived features within the Caenophidia then our new data would give further support to a link between *Atractaspis* and *Aparallactus*; otherwise they suggest a shared low grade level. If, as we suspect, the absence of rictal glands is derived then this would add weak support to the link between *Macrelaps* and *Amblyodipsas.*

It is already clear that rictal glands occur in many snake lineages and that their distribution is far from completely surveyed. That they persist in many lineages suggests that they have some functional significance notwithstanding their usual small size. That they have been lost from some lineages suggests that they are not important to all lifestyles. Study of the secretion was begun by Phisalix and Caius in 1918, but does not appear to have been taken further in the following 80 years!

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