

HEMIPENIAL MORPHOLOGY OF THE
SOUTH AMERICAN XENODONTINE
SNAKES, WITH A PROPOSAL FOR A
MONOPHYLETIC XENODONTINAE
AND A REAPPRAISAL OF
COLUBROID HEMIPENES

HUSSAM ZAHER

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ABSTRACT

The New World xenodontine "colubrids" represent two immunologically distinct assemblages—the Central and South American lineages, neither of which has been well diagnosed to date. I follow this nomenclature and recognize the Central American lineage as containing 22 genera. This clade is supported by the synapomorphy of a sulcus spermaticus bifurcating within or at the base of the capitulum (Cadle, 1984; Myers and Cadle, 1994). The remaining xenodontines constitute a total of 68 presently recognized genera, of which 41 are placed in the subfamily Xenodontinae sensu stricto. The other 27 genera are considered incertae sedis, pending further research. The Xenodontinae sensu stricto are hypothesized as being monophyletic on the basis of the following hemipenial synapomorphies: (1) presence of enlarged lateral spines on the hemipenial body, and (2) two distinctly ornamented regions on the lobes, the asulcate surface bearing enlarged spinulate or papillate calyces (= body calyces). Some taxa recognized as Xenodontinae sensu stricto lack body calyces but have a nude area in the same topographical position (e.g., *Psomophis*, *Tropidodryas*). This pattern is viewed as the result of secondary loss. The rationale for this conclusion is based on the hypothesis that body

calyces are merely enlarged capitular calyces of the asulcate/medial surfaces of the lobes. In the Xenodontinae, the body calyces are almost always separated from the calyces of the capitulum by a more or less developed overhang (except in a few genera). This overhang is generally retained on the hemipenes where the asulcate/medial surfaces of the lobes are nude (e.g., *Psomophis*), which supports the view that the body calyces were secondarily lost. Body calyces are also found on the surface of the hemipenial body in its asulcate side (e.g., *Philodryas*, *Pseudablades*, *Xenoxybelis*). Because body calyces are interpreted as modified "capitular calyces," which are restricted to the lobular region and crotch, the presence of these structures far on the hemipenial body is here viewed as a more derived state where the body calyces extend from the lobes to the body.

Various presumably monophyletic units are defined within the Xenodontinae sensu stricto. *Conophis*, *Heterodon*, and *Farancia* are clearly assigned to the Xenodontinae sensu stricto.

The hemipenial morphology of various suprageneric "colubrid" taxa are described and compared. The variation of some hemipenial features within the colubroid radiation, as well as their bearing on the higher level phylogeny of colubroids, is investigated.

INTRODUCTION

No unambiguous synapomorphy is known to diagnose the family "Colubridae." Additionally, phylogenetic relationships within the "Colubridae" remain largely unknown (Cadle, 1994). Although some monophyletic subgroups within the family have been diagnosed successfully using morphological features (e.g., the *Thamnophiini* [Rossman and Eberle, 1977] and the *Psammophiinae* [Bogert, 1940; Bourgeois, 1968]), the vast majority of "colubrid" genera are assembled on the basis of overall similarity, unpolarized character states, and/or immunological distances. The South American xenodontines represent an example of immunologically cohesive assemblages (Cadle, 1984a, 1984b, 1984c, 1988) with no described synapomorphies (Myers and Cadle, 1994).

For the sake of clarity, the following names will be used in the text to refer to three distinct "assemblages": (1) the subfamily *Xenodontinae* sensu stricto or *xeno-*

dontines will refer solely to a South American clade as redefined in the present study (containing 41 genera; table 1); (2) the subfamily *Dipsadinae* or *dipsadines*, which corresponds roughly to Cadle's (1984b) and Myers and Cadle's (1994) Central American assemblage (containing 22 genera; table 1); and (3) the **New World xenodontines** or "**xenodontines**" sensu lato, which are composed of the *Xenodontinae*, *Dipsadinae*, and 27 genera of uncertain assignment (Cadle, 1984a, 1984b, 1984c, 1988, 1994; table 1). The terms **South American xenodontines** and **Central American xenodontines** will be also used herein as interchangeable with *Xenodontinae* and *Dipsadinae*, respectively. The "xenodontines" are here viewed as likely paraphyletic. Genera referred to the "xenodontines" are listed in table 1; all are New World snakes.

The present study reviews the hemipenial variation found in the Colubroidea, providing

TABLE 1
List of Genera Placed Within the Xenodontinae and Dipsadinae^a

Xenodontinae		Dipsadinae
<i>Alsophis</i>	<i>Manolepis</i>	<i>Adelphicos</i>
<i>Antillophis</i>	<i>Oxyrhopus</i>	<i>Amastridium</i>
<i>Apostolepis</i>	<i>Phalotris</i>	<i>Atractus</i>
<i>Arrhyton</i>	<i>Philodryas</i>	<i>Chersodromus</i>
<i>Boiruna</i>	<i>Phimophis</i>	<i>Coniophanes</i>
<i>Clelia</i>	<i>Pseudablables</i>	<i>Cryophis</i>
<i>Conophis</i>	<i>Pseudoboa</i>	<i>Dipsas</i>
<i>Darlingtonia</i>	<i>Pseudoeryx</i>	<i>Eridiphas</i>
<i>Ditaxodon</i>	<i>Psomophis</i>	<i>Geophis</i>
<i>Drepanoides</i>	<i>Rhachidelus</i>	<i>Hypsiglena</i>
<i>Elapomorphus</i>	<i>Saphenophis</i>	<i>Imantodes</i>
<i>Erythrolamprus</i>	<i>Siphlophis</i>	<i>Leptodeira</i>
<i>Farancia</i>	<i>Tripanurgos</i>	<i>Ninia</i>
<i>Helicops</i>	<i>Tropidodryas</i>	<i>Pliocercus</i>
<i>Heterodon</i>	<i>Umbrivaga</i>	<i>Pseudoleptodeira</i>
<i>Hydrodynastes</i>	<i>Uromacer</i>	<i>Rhadinaea</i>
<i>Hydrops</i>	<i>Uromacerina</i>	<i>Sibon</i>
<i>Hypsirhynchus</i>	<i>Waglerophis</i>	<i>Sibynomorphus</i>
<i>Ialtris</i>	<i>Xenodon</i>	<i>Tretanorhinus</i>
<i>Liophis</i>	<i>Xenoxybelis</i>	<i>Trimetopon</i>
<i>Lystrophis</i>		<i>Tropidodipsas</i>
		<i>Urotheca</i>
Xenodontinae and Dipsadinae Incertae Sedis		
<i>Calamodontophis</i>	<i>Echinanthera</i>	<i>Nothopsis</i>
<i>Carphophis</i>	<i>Emmochliophis</i>	<i>Opisthoplus</i>
<i>Cercophis</i>	<i>Enuliophis</i>	<i>Pseudotomodon</i>
<i>Contia</i>	<i>Enulius</i>	<i>Ptychophis</i>
<i>Crisantophis</i>	<i>Gomesophis</i>	<i>Rhadinophanes</i>
<i>Diadophis</i>	<i>Hydromorphus</i>	<i>Sordellina</i>
<i>Diaphorolepis</i>	<i>Lioheterophis</i>	<i>Synopsis</i>
		<i>Tachymenis</i>
		<i>Taeniophallus</i>
		<i>Tantalophis</i>
		<i>Thamnodynastes</i>
		<i>Tomodon</i>
		<i>Xenopholis</i>

^a I have taken as a starting point the list of Dowling and Duellman (1978). However, Dowling and Duellman's (1978) and Jenner's (1981) tribal arrangements are not recognized here. Various additions and corrections to this list have been made in order to include genera omitted by these authors as well as taxonomic changes proposed recently. The corrections regarding invalid names or junior synonyms have been largely based on Williams and Wallach (1989). The additions of new taxa as well as the taxonomic rearrangements are as follows: *Cercophis* (Hoogmoed, 1982), *Crisantophis* (Villa, 1971), *Echinanthera* (sensu Myers and Cadle, 1994), *Elapomorphus* (sensu Ferrarezzi, 1993), *Emmochliophis* (Fritts and Smith, 1969; see Hillis, 1990), *Enuliophis* (McCranie and Villa, 1993), *Hydromorphus* (sensu Crother, 1989a), *Phalotris* (sensu Ferrarezzi, 1993), *Philodryas* (sensu Thomas and Fernandes, 1996, including *Platyinon*), *Pseudoleptodeira* (Dowling and Jenner, 1987), *Psomophis* (Myers and Cadle, 1994), *Rhadinaea* (sensu Myers, 1974; Myers and Cadle, 1994; see also Di-Bernardo, 1992), *Rhadinophanes* (Myers and Campbell, 1981), *Sibon* (sensu Kofron, 1985a,b), *Synopsis* (sensu Hillis, 1990), *Tantalophis* (Duellman, 1958b; see also Myers and Campbell, 1981), *Tropidodipsas* (Wallach, 1995), *Tropidodryas* (Thomas and Dixon, 1977), *Urotheca* (sensu Myers and Cadle, 1994; but see Savage and Crother, 1989). Genera of uncertain phylogenetic position within the xenodontines demarcated as incertae sedis.

diagnoses for the major groups of colubroid snakes, with emphasis on their hemipenial morphology. Hemipenial evidence for the monophyly of these groups, including the two groups of "xenodontines," is evaluated, and a monophyletic clade of South American

xenodontines is proposed and discussed. A detailed discussion of the newly defined Xenodontinae is then provided, with a summary of diagnosable groups within that group as well as of taxa of problematical placement. This study also provides a refined hemipenial

terminology for the South American xenodontines and detailed descriptions of the hemipenial morphology of each genus placed in the Xenodontinae, as well as the ones retained incertae sedis.

HEMIPENIAL MORPHOLOGY IN SNAKE SYSTEMATICS, WITH EMPHASIS ON THE XENODONTINES

Hemipenial morphology has been used extensively in snake systematics, providing a large array of phylogenetically informative data. After Cope's (1893, 1894, 1895, 1900) innovative works on the hemipenial morphology of snakes, Dunn (1928) and Bogert (1940) attempted classifications of the New World and African "colubrid" faunas, respectively, relying on various hemipenial characters.

Subsequently, various authors attempted suprageneric classifications of the "colubrids" in which the hemipenis was accorded great importance but with mixed success (e.g., Dowling, 1975; Dowling and Duellman, 1978; Jenner, 1981; Jenner and Dowling, 1985). A number of important works dealt exclusively with the hemipenial morphology of particular groups of snakes (Vellard, 1928, 1946; Domergue, 1955, 1962; Branch, 1981, 1986).

Dunn (1928) was the first to recognize the "xenodontines" (his Ophiinae) as a distinct New World "colubrid" group, characterized by the presence of a bifurcated sulcus spermaticus in the hemipenis. However, this condition is likely an ancestral state because, apart from being present in almost all colubroid lineages (Cadle, 1984c, 1987), it is unambiguously present in the two successive outgroups to the colubroids, Acrochordoidea and Tropidophioidea (see below).

A recent attempt to synthesize our knowledge on this group was that of Cadle (1984c: 646), who suggested that the Central and South American xenodontine assemblages, previously recognized by him on the basis of albumin immunology, correspond to two different hemipenial types: "Members of the Central American lineage can generally be characterized as having a capitate, calyculate hemipenis with the sulcus spermaticus bifurcating (if at all) within the capitulum. The

hemipenis may be bilobed or single, and the sulcus spermaticus is single in some. Members of the South American lineage usually have a noncapitate or semicapitate hemipenis, with the sulcus bifurcating often near the base of the hemipenis and usually on the basal half of the organ." The author stressed that both definitions fail to provide any synapomorphy for these groups. Indeed, the definition for the South American assemblage can be applied to various viperid, elapid, and African "colubrid" snakes. However, the condition of a sulcus spermaticus bifurcating within the capitulum is unique to the Dipsadinae and may represent a synapomorphy of this subfamily (see below). Myers and Cadle (1994: 27) already suggested that this character, along with reduction or loss of bilobation and unicapitation, are derived features characterizing the Dipsadinae. Such a definition, however, also encompasses *Diadophis* and *Carphophis* for example (except for their noncapitate condition), two genera considered by Cadle (1984a, 1984b, 1984c) as only remotely related to the Central and South American assemblages. This problem will be treated in more detail in the following section.

Dowling (1975) and Dowling and Duellman (1978) assigned almost all "xenodontine" genera to various tribes, relying heavily on a few generalized hemipenial and osteological features. Subsequently, Jenner, in an unpublished dissertation (1981), proposed for the first time to divide the xenodontine assemblage of Dunn and Dowling in two distinct groups which she called the "Northern and Southern groups." This partition is very similar to Cadle's (1984a, 1984b, 1984c) subsequent proposals. However, most of the tribes recognized by Jenner (1981) on the basis of exclusively hemipenial characters represent paraphyletic groups (Cadle, 1984a, 1984b, 1984c). Dowling et al. (1983) recognized two subfamilies corresponding to Jenner's (1981) Northern and Southern groups, the Xenodontinae (including the tribes Diaphorolepidini, Philodryadini, Pseudoboini, and Xenodontini) and the Dipsadinae (including the Alsophiini, Dipsadini, and Leptodeirini). Subsequently, Jenner and Dowling (1985) transferred the Alsophiini to the Xenodontinae, without any discussion.

However, this new arrangement is supported by the similar hemipenial morphology shown by the Alsophiini and the Xenodontinae (Maglio, 1970; Thomas, 1976; Dowling and Duellman, 1978). Jenner and Dowling (1985) also formalized the tribe Pseudoboini, previously recognized by Bailey (1939a, 1967). However, their inclusion of *Tropidodryas* and *Saphenophis* in the Pseudoboini rendered the redefined tribe polyphyletic (Dessauer et al., 1987; Zaher and Caramaschi, 1992; Zaher, 1994a). Such disagreements concerning the systematics of the New World xenodontines is not, as one may think, due to the practical limitations inherent in the use of only one source of character data in a phylogenetic analysis, but rather results from oversimplified interpretations of structures, leading frequently to erroneous assumptions of homology (see also Myers and Cadle, 1994: 26).

Although Dowling made important contributions to the knowledge of snake hemipenial morphology and phylogeny, the taxonomic arrangements proposed by him (Dowling, 1975, Dowling and Duellman, 1978) have been criticized by Cadle (1984c) and Whistler and Wright (1989). The classificatory scheme proposed later by Dowling et al. (1983) was also rejected by Cadle (1984c) (however, see Blackburn [1985] and Smith and Smith [1993], who recognized the tribes proposed by Dowling and Duellman [1978] and Jenner [1981], respectively).

McDowell (1987: 40) also proposed a definition for the "xenodontines:" "with sulcus spermaticus forked (except in some genera with a capitate hemipenis) and centrolineal, or centripetal near the crotch but becoming centrolineal distally, or (the majority) centrifugal (i.e., its branches taking the position farthest from the midline of the organ); most genera with well defined calyces; some (e.g., *Nothopsis*, *Amastridium*) with natricine posterior hypapophyses but most with posterior hypapophyses reduced to keels." This definition, however, neither corresponds to the two subfamilies proposed by Dowling et al. (1983), nor does it follow Cadle's (1984a, 1984b, 1984c) suggestions.

It emerges from these comments that two fundamental problems have contributed to the destabilization of xenodontine systemat-

ics. First, apart from some osteological features (mostly on vertebrae), the hypotheses of relationships between the taxa belonging to the xenodontines are mostly based on a restricted set of hemipenial structures and on general molecular similarity. Second, various influential nomenclatural decisions have been made and subsequently changed without discussions of evidence (compare Dowling, 1975; Dowling and Duellman, 1978; Jenner, 1981; Dowling et al., 1983). Another important, but unrelated, nomenclatural issue is Smith's (1964) choice, as first reviser, of the family-group name Heterodontidae Gray, 1845 (a nomen oblitum) over the name Xenodontina Bonaparte, 1845. However, he used the subfamily Heterodontinae to accommodate the genera *Heterodon*, *Lystrophis*, *Xenodon*, and *Leioheterodon*, thus creating a highly heterogeneous group. Rossman and Wilson (1964) rejected Smith's (1964) nomenclatural proposition for this reason and also because the name Heterodontidae Gray, 1851, is widely used for a family of sharks (type genus *Heterodontus*). Smith agreed and withdrew his formal application to the International Commission of Zoological Nomenclature for validation of the snake name Heterodontinae (fide Rossman and Wilson, 1964). Smith et al. (1977) retained the Xenodontinae Bonaparte, 1845, and elevated Dowling's (1975) tribes to familial rank.

Herein, I present evidence that supports the monophyly of the Xenodontinae sensu stricto that includes *Heterodon* and *Xenodon*, among others. However, for the sake of stability, only the name Xenodontinae will be used, even though Heterodontinae has priority (Smith, 1964).

The tribes proposed by Dowling (1975), Dowling and Duellman (1978), Jenner (1981), Dowling et al. (1983), and Jenner and Dowling (1985) are not recognized in the present study, except for the Xenodontini (see Dowling, 1975; Dowling and Duellman, 1978; Dixon, 1980; Myers, 1986), and the Pseudoboini sensu stricto (see Dessauer et al., 1987; Zaher and Caramaschi, 1992; Myers and Cadle, 1994; Zaher, 1994a), which are satisfactorily characterized.

I do not intend to propose a comprehensive phylogenetic hypothesis for the Xenodontinae. Rather, I aim to reevaluate the

hemipenial variation present in the colubroids and define, based on two uniquely derived hemipenial features, a monophyletic clade—the *Xenodontinae* sensu stricto. Hemipenial evidence is also evaluated that supports monophyletic subgroups as well as rejects previously recognized taxa within the *Xenodontinae*.

SOURCES OF INFORMATION ON HEMIPENIAL MORPHOLOGY OF COLUBROID SNAKES

Hemipenial materials available for each species placed in the *Xenodontinae* and in *incertae sedis* are listed under the genus to which the species belongs, in the section titled "Generic Synopsis of Hemipenial Features."

Published descriptions and illustrations represented an important source of information for determining the hemipenial pattern of the remaining colubroid taxa. The two synapomorphies of the *Xenodontinae* proposed herein were absent (or inapplicable) in all available descriptions and figures of nonxenodontine colubroids. The following works were used as sources of information for such comparisons:

- General:** Cope (1895), Cei (1993), Clark (1944), Dowling (1975), Dowling and Duellman (1978), Dowling and Savage (1960), Dunn (1928), McDowell (1975, 1979, 1987), Sabnis and Indurkar (1977), Schätti and McCarthy (1987), Smith (1943), Underwood (1967, 1979), Vellard (1928, 1946)
- Elapidae:** De Silva (1987), Mao (1993), Mao and Chen (1974, 1980), Mao et al. (1984), Marx (1953), McDowell (1967, 1969, 1970), Rasmussen (1992), Vellard (1928, 1946), Williams and Parker (1964).
- Viperidae:** Branch and Wade (1976), Campbell (1985), De Silva (1983, 1988), Domergue (1955, 1962), Gasc (1968, 1969), Hoge (1947, 1959), Hoge et al. (1959), Koba and Kikukawa (1971), Mao (1993), McCranie (1988), Murphy and Barker (1980), Mao et al. (1984), Malnate (1990), Pesantes (1994), Vellard (1928, 1946).
- Dipsadines and "xenodontines" incertae sedis:** Bailey (1939b), Bogert (1964), Cadle (1989), Clark Jr. (1970), Crother (1989a), Di-Bernardo (1992, 1996), Duellman (1958a, 1958b), Dunn and Dowling (1957), Fernandes (1995), Grant (1943), Hoge (1952), Jenner (1981), Kofron (1982, 1985a, 1985b), Lema and Deiques (1995), McCranie and Villa (1993), Mendelson

and Kizirian (1995), Myers (1974, 1982), Myers and Cadle (1994), Myers and Campbell (1981), Myers and Donnelly (1996), Pinou and Dowling (1994), Porto and Fernandes (1996), Villa (1970, 1971), Walker (1945).

Other "colubrids": Amaral (1929a, 1929b, 1929c, 1929d), Blaney (1977), Bogert (1939, 1940, 1947), Branch (1976), Branch and Wade (1976), Broadley (1971), Brongersma and Wehlburg (1933), Cadle (1996a, 1996b), Clark Jr. (1964), Cliburn (1975), Cole and Hardy (1981), Darevsky and Orlov (1992), Dixon et al. (1993), Domergue (1955, 1962, 1963, 1972, 1983, 1986, 1987, 1991, 1994), Dowling (1957, 1958, 1959, 1960, 1969a, 1975, 1990), Dowling and Fries (1987), Dowling and Maxson (1990), Dowling and Price (1988), Lambiris (1997), Lanza (1964), Lopez et al. (1993), Mao (1965a, 1965b), Malnate (1953), McDowell (1972, 1984), Oliver (1948), Ortenburger (1923), Ota and Ross (1994), Rasmussen (1985, 1986, 1989, 1993a, 1993b, 1997), Rossman and Blaney (1968), Rossman and Eberle (1977), Schätti (1987, 1988), Schätti and Lanza (1989), Schätti and McCarthy (1987), Schätti and Vanni (1986), Stull (1940), Underwood and Kochva (1993), Van Devender and Cole (1977), Vellard (1928, 1946), Wilson (1967, 1970), Ziegler et al. (1997).

METHOD OF HEMIPENIAL PREPARATION

The present study is based on observations of variation in everted hemipenes of representatives of the majority of the New World "xenodontine" genera and of various suprageneric colubroid groups. Almost all hemipenes were prepared from previously fixed and preserved specimens, using the method described by Pesantes (1994). Either the left or the right organ was removed from any one specimen and submerged in a solution of 3% KOH either for 1 to 6 hours or overnight (depending on the size of the organ). When the tissues became translucent and flexible, a small incision was made at the base of the organ, on the asulcate side, in order to evert manually the whole structure. This was done by using a pair of forceps with rounded tips which served to force the inverted organ toward its base. The everted organ was then filled with a liquid solution of agar-agar (Manzani and Abe, 1988) or with colored petroleum jelly (Myers and Cadle, 1994). If the organ, particularly the lobes that are made of

very delicate tissue, was torn during eversion, the hole was patched with cyanocrylate glue before the injection of agar-agar or petroleum jelly (excess alcohol must be removed before using the glue). This method of preparation worked well, even with the hemipenial material extracted from specimens that were fixed and stored at the end of the 19th century.

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HEMIPENIAL TERMINOLOGY

Although hemipenial morphology has been used extensively for taxonomic and phylogenetic purposes, only one work (Dowling and Savage, 1960) has comprehensively treated snake hemipenial terminology. However, various other papers have contributed to the clarification of available terms or named new structures (Myers and Trueb, 1967; Myers, 1974, 1986; Rossman and Eberle, 1977; Myers and Campbell, 1981; Branch, 1986; Donnelly and Myers, 1991; Myers and Cadle, 1994). I Herein use most of the previously proposed and largely followed terms (Dowling and Savage, 1960;

Myers, 1974; Myers and Trueb, 1967; Myers and Campbell, 1981; Myers and Cadle, 1994). Some new terms will be proposed for structures unique to the Xenodontinae (fig. 1). Also, various other names regarding distinct regions of the hemipenis are suggested in order to account for the different ornamentations found on these regions. Some of these ornaments are found only on the asulcate side of the organ. Curiously enough, most of the works using hemipenial features have given little or no attention to the asulcate surface of the organ and its proper ornamentation, with the notable exceptions of Duellman's (1958a) and Myers' (1974) monographs on the genera *Leptodeira* and *Rhadinaea*, respectively, where most of the photographs and drawings of everted organs show their asulcate side.

The names used in the present study, with a brief description of each structure, are as follow (fig. 1): (1) *hemipenial body* (all the hemipenis, excluding the lobes and the surface ornamented with the capitular calyces and/or flounces on the hemipenial body); (2) *basal or proximal region of the lobes* (the proximal area of both lobes, including the lobular crotch and the distal end of the asulcate side of the hemipenial body); (3) *enlarged lateral spines* (those spines that are clearly larger than the other spines on the hemipenial body, and are mostly distributed on both lateral surfaces of the body; however, the basalmost lateral spines usually invade the sulcate surface on the proximal region of the body, and the distalmost spines usually invade the asulcate surface on the distal region of the body); (4) *body calyces* (these are enlarged calyces present on the medial and/or asulcate surfaces of the lobes and, often, on the asulcate surface of the hemipenial body; the body calyces are spinulate or papillate and always larger than the calyces forming the capitulum); (5) *lobular crest or ridge* (a structure mostly confined to the asulcate and/or medial surfaces of the lobes; generally resulting from the confluence or fusion of the vertical walls of the body calyces; in some cases the lobular crest is inflated and bears enlarged lateral spines; in other cases, it is simply a papillate or spinulate ridge of tissue; both "ridge" and "crest" are used herein as general terms that

apply to similar but not necessarily homologous structures); (6) *calycular pockets* (typical of the Pseudoboini, these structures are derived from the body calyces and ornament the lobular crotch); (7) *capitular groove* (defined by Myers [1974] as an "overhanging edge of the capitulum," it is the more-or-less deep groove that delineates the capitulum); (8) *asulcate and/or medial surface of the lobes* (these two distinct terms correspond to the two topographically recognizable areas that are always on the *opposite side* of the capitulum; the distinction is made between medial and asulcate surfaces because, depending on the degree of rotation or extension of the capitulum, the opposite noncalyculate region will be either in an asulcate or a medial position, or on both; generally, when the capitulum is directed laterally, the noncalyculate region of the lobe is medially situated and the sulcus spermaticus is usually centrifugal; when the capitulum tends to be facing the sulcate surface, most of the noncalyculate surface is in an asulcate position and the sulcus spermaticus is centrolateral; the acalyculate side of the lobes often encompasses both medial and asulcate surfaces; these surfaces may form a uniformly ornamented or nude region or may be divided by a crest or bear differentiated ornaments); (9) *capitular calyces* (these are the calyces that form the capitulum; they are spinulate or papillate like the body calyces but are smaller; this new name is proposed to differentiate these calyces from the body calyces); (10) *intrasulcar region* (the region on the sulcate surface of the organ delineated by the divergent branches of the sulcus spermaticus laterally and the capitula distally; generally, the region encompasses the distal surface of the hemipenial body and the proximal surface of the lobes); (11) *enlarged intrasulcar spines* (enlarged spines may often be present in the intrasulcar region of the hemipenial body; when present, they preclude the presence of calyces or flounces on the intrasulcar region).

Recently, Myers and Cadle (1994: 13) proposed a new name—pseudocalyculate—for the "false calyces" ornamenting the hemipenial lobes of *Psomophis* species. These structures are viewed by the authors as not being homologous to the calyces of other xenodontines. However, I interpret the false ca-

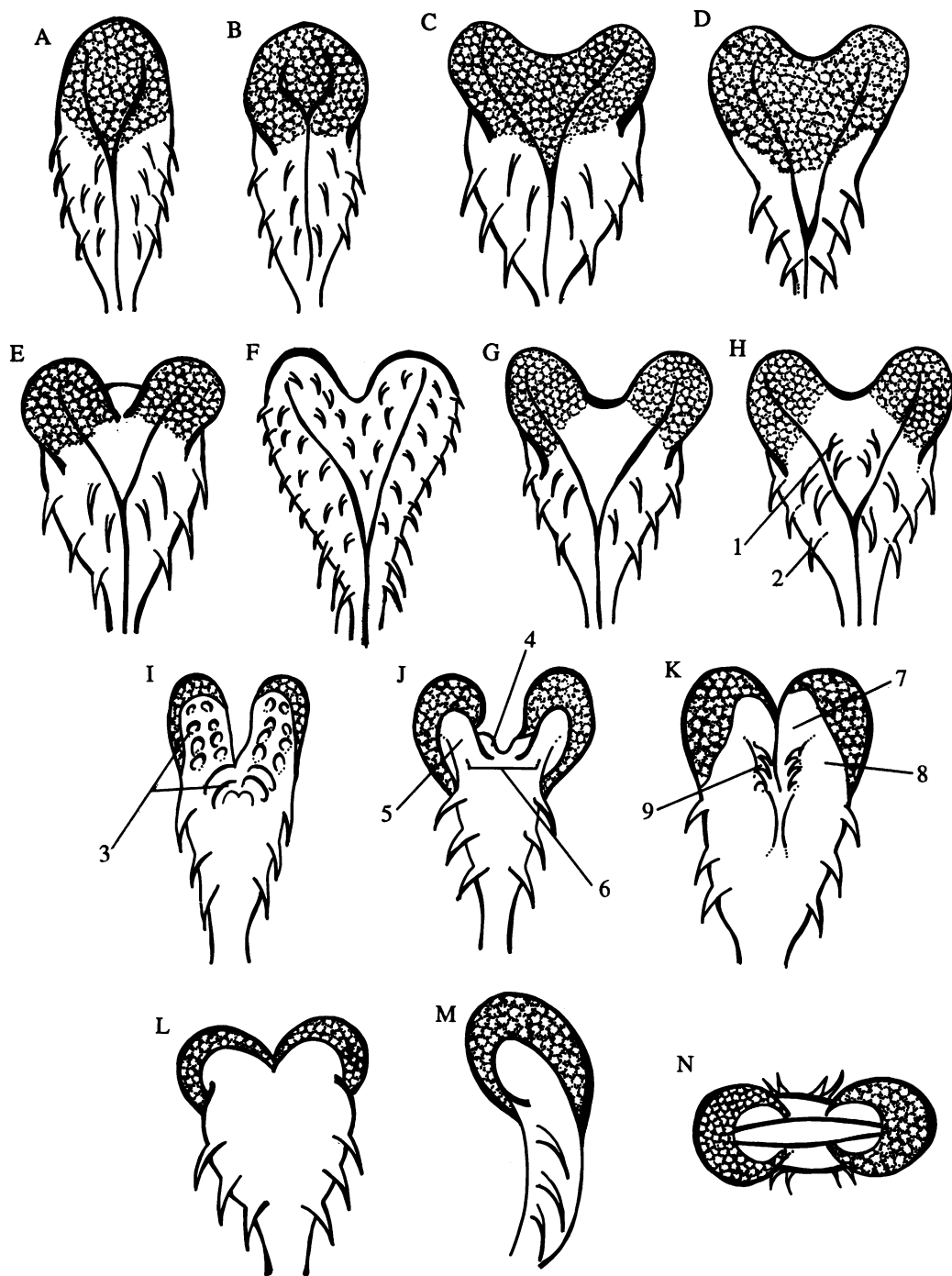


Fig. 1. Schematic representations illustrating the hemipenial terminology used in this study. **A**, unicalyculate, noncapitate; **B**, unicapitate; **C**, semicalyculate, semicapitate; **D**, semicalyculate, noncapitate; **E**, bicalyculate, bicapitate; **F**, noncalyculate, noncapitate; **G**, bicalyculate, semicapitate; **H**, a bicalyculate, semicapitate hemipenis with (1) enlarged intrasulcar spines and (2) enlarged lateral spines; **I**, the asulcate surface of a hemipenis with (3) rows of body calyces; **J**, the asulcate surface of a

lyces of *Psomophis* as being reduced calyces, and the "large spinulate papillae" as being true papillae, homologous of the ones ornamenting the calyces in most xenodontines. The papillae are highly developed in *Psomophis*, whereas the calyces bearing them have almost disappeared. Indeed, all the area comprised in each capitulum (except for the distal region and its large overhanging wall of tissue that bear very large unconnected papillae) show folds of tissue (= calycular walls) connecting the bases of the papillae. Although the calycular walls have almost disappeared on the sulcate surface of the capitulum, they are clearly present proximally, near the medial edge of the capitulum. Myers and Cadle (1994: 13) described the pseudocalyces as being "formed from expansible, interconnected folds of tissue connecting the base of the spinulate papillae," and suggested that the expansible nature of the folds of tissue represented a new structure not homologous to the calycular walls of the true calyces. However, the same expansible nature is present in the calycular walls of the calyces ornamenting the expanded distal region of the lobes of a number of species belonging to genera with clearly calyculate lobes (e.g., *Ptyas mucosus*, *Spilotes pullatus* and *Leptophis ahaetulla*).

Myers and Cadle (1994: 13) noted the confusion of investigators about capitation. Indeed, two distinct structures are generally involved: the presence of *capitular grooves* (Myers' [1994: fig. 1] "overhanging edge of capitulum"; or Myers and Cadle's [1994: 13] "overhang") and the degree of invasion of the *capitular calyces* (or capitulum) through the intrasulcar region of the hemipenial body. Generally, these two conditions are intimately associated. Most Pseudoboini have an unambiguous bicapitate condition where a capitular groove is present on both sides of each capitulum. Indeed, a bicapitate condition represents a restriction of each capitulum

to its own lobular surface, without any extension of the capitular calyces onto the intrasulcar area, thus allowing the appearance of capitular grooves on the intrasulcar region. However, these two structures can be dissociated in some taxa, as in *Tropidodryas* where the hemipenis clearly shows capitular calyces in a typical "bicapitate" condition (i.e., distinctly restricted to their lobular surface) but lacks capitular grooves (Zaher and Caramaschi, 1992). All the examined species of *Philodryas* have a semicapitate condition, but only part of *Philodryas* (the "*chamissonis*" group; see discussion) has well-developed capitular grooves on the lateral sides of the organ. Similarly, in *Hydrodynastes*, the hemipenis is clearly semicapitate, with well-developed capitular grooves present only along the lateral edge of each capitulum, but lacking on the intrasulcar surface. The invasion of most of the intrasulcar region by the capitular calyces prevents the formation of a capitular groove in this region.

Myers (1974: 31) already defined both structures clearly: "most *Rhadinaea* have a *capitate* hemipenis, which is to say that the capitulum has a free overhanging edge except where crossed by the sulcus spermaticus. The capitulum is *calyculate*, or surfaced with a reticulum of *calyces*" (italics as in original). As shown in his definition, the term *capitate* is unambiguously associated with the presence of an overhanging edge, whereas the term *calyculate* corresponds to the presence of capitular calyces. Thus, *Tropidodryas*, one of the examples used above, actually has a bicalyculate and noncapitate hemipenis.

Very few works have attempted to distinguish adequately these two features. For this reason, I propose to restrict the use of the terms *noncapitate*, *bicapitate*, and *semicapitate* to describe the absence or presence of the capitular grooves on the intrasulcar and/or lateral surfaces of the organ. The term *un-*

←

hemipenis with (4) calycular pockets, (5) lobular crests, and an enlarged (6) lobular crotch; **K**, the asulcate surface of a hemipenis showing nude medial (7) and asulcate (8) surfaces of the lobes (both medial and asulcate surfaces form the noncapitulate region of the lobe), as well as a row of vertically directed large papillae (9) on each lobe; **L**, an asulcate view; **M**, a lateral view; **N**, a distal view. Figures A–H are in a sulcate view.

icapitate (or *capitate*) is restricted to unilobed or barely bilobed organs. Similarly, the terms *semicalyculate* and *bicalyculate* may be used to describe the degree of invasion into the intrasulcar region by the capitular calyces or, in other words, the degree of restriction of the capitulum on the lobe. The term *noncalyculate* may refer to an organ with nude lobes, whereas *unicalyculate* (or *calyculate*) may be used to describe organs with a continuous reticulum of calyces or derived structures (e.g., flounces) all around the lobe(s)

(i.e., on the lateral, sulcate, and asulcate surfaces of the lobes, including the intrasulcar region). Unicapitate and unicalyculate organs are present in some Dipsadinae (e.g., *Tretanorhinus*), whereas noncapitate and noncalyculate organs are found in the Xenodontini and in the genus *Enuliophis*.

Although the words capitulation and capitulation may be viewed as synonyms, the terms *noncapitulate* and *capitulate* are used in the text specifically to refer to the areas of the lobe without and with a capitulum, respectively.

HEMIPENIAL MORPHOLOGY OF COLUBROIDEA AND ITS BEARING ON MONOPHYLY OF ITS CONSTITUENTS

The relatively few hemipenial characters of potential phylogenetic value pointed out herein are insufficient for a broad cladistic analysis of "colubrid" interrelationships. Therefore, a cladistic study using the hemipenial data alone is not attempted here. Nevertheless, variation found in the hemipenial morphology of colubroids provides some interesting characters that are highly conservative among large suprageneric groups. The discussion below is devoted to the hemipenial evidence supporting the monophyly of various groups of colubroids, including the Xenodontinae, and the possible phylogenetic signal of some hemipenial characters for the higher-level phylogeny of "colubrids."

Unfortunately, the great diversity present in "colubrids" and the rarity of some taxa precluded an extensive analysis of all known representatives, forcing some a priori decisions on the choice of terminal taxa (= terminals) to be used in this section. To avoid nonmonophyletic terminals, I opted to retain taxa based on the presence of one or more synapomorphies. However, some of the present arrangements may still represent nonmonophyletic assemblages because of our scarce knowledge of the morphological variation of most of the characters studied here and the lack of any phylogenetic analysis of the "colubrids" to guide the choice of historically natural terminals. For these reasons, the following proposals of "colubrid" assemblages and their definitions are better understood as working hypotheses. The provi-

sional suprageneric arrangement followed herein and all presently recognized genera of "colubrids" are shown in appendix 1 (genera for which representatives were available for study are signaled by an asterisk and are listed in appendix 2).

Because colubroid interrelationships are still under debate (see Cadle [1987] for a review), two subsequently more inclusive taxa to the colubroids—namely the Acrochordoidea and Tropidophioidea (sensu Zaher, 1994b, 1994c)—have been added to the discussion. The latter taxon is here considered to include only *Tropidophis* and *Trachyboa*, with *Exiliboa* and *Ungaliophis* being part of the "booids" sensu stricto (Zaher, 1994b, 1994c; see below).

The Acrochordoidea and the Colubroidea are considered to form a monophyletic clade, Caenophidia, supported by the following synapomorphies (Groombridge, 1979a, 1979b; Rieppel, 1988; Cundall et al., 1993): (1) septomaxilla contacting the frontal bone; (2) vomer globular in shape and pierced by many foramina for the passage of the vomeronasal nerve; (3) pars anterior of the muscle intermandibularis anterior inserting on the intermandibularis ligament; (4) hemipenis bearing small to medium-sized spines (also found in some uropeltines; see Dowling and Duellman, 1978). The complete loss of pelvic vestiges may also represent a synapomorphy of Caenophidia; however, this derived feature cannot be placed with confidence at that level of universality because it

is also absent in uropeltines, *Xenopeltis*, and bolyeriids, and occurs irregularly in typhlopids and anomalepidids.

Morphological evidence supporting a sister-group relationship between the Caenophidia and the Tropicophioidea is as follows (Rieppel, 1978; Groombridge, 1984; Cundall et al., 1993; Zaher, 1994b): (1) presence of a parallel hyoid complex; (2) facial carotid artery passing dorsally to the mandibular branch of the trigeminal nerve; (3) loss of the pars anterior of the muscle adductor mandibulae externus medialis; (4) loss of the coronoid bone (also in the Ungaliophiidae); (5) lateral and mesial frontal flanges fused.

An additional derived feature from the vertebrae may support a Tropicophioidea + Caenophidia clade; that is, the presence of strongly projecting hypapophyses on all cervical and trunk vertebrae. However, this condition is also present in the bolyeriids (Underwood, 1967), and may be a synapomorphy of a more inclusive group including the tropidophioids, caenophidians, and bolyeriids. The phylogenetic position of the last taxon is presently not resolved. In all other alethinophidian snakes, the middle and posterior trunk vertebrae lack hypapophyses. This character is variable within the colubroids, the derived condition being present in the "boodontines," "xenodermatines," "pseudoxyrhophiines," homalopsines, natri-cines, elapids, and viperids (Auffenberg, 1963; Underwood, 1967; Malnate, 1972; personal obs.), and is very reduced or absent in the atractaspidids, colubrines (except for the Sibynophiini; Underwood, 1967), xenodontines, dipsadines, pareatines, and calamariines, (Underwood, 1967; Malnate, 1972; Dowling et al., 1983; McDowell, 1987). Within the elapids, some taxa may have short hypapophyses posteriorly; however, these are present on all the trunk vertebrae of the elapids examined. The acrochordoids clearly have the derived condition (Hoffstetter and Gayrard, 1965). In the tropidophioids, the hypapophyses are present on all trunk vertebrae, and show a peculiar bladelike condition (Bogert, 1968).

OUTGROUPS

TROPIDOPHIOIDEA

The monophyly of the Tropicophioidea sensu stricto is supported by (1) presence of

keel-shaped hypapophysis on the trunk vertebrae (Bogert, 1968), and (2) facial vein passing laterally to the muscle adductor mandibulae externus profundus (Zaher, 1994b). *Exiliboa* and *Ungaliophis*, which lack both of these features, share with the "booids" (sensu Zaher, 1994b) a differentiated pars anterior of the muscle adductor mandibulae externus medialis. This feature may be a synapomorphy of a Booidea sensu stricto—including the bolyeriids, boids, and ungaliophiids—or may represent a synapomorphy of the macrostomatans (excluding *Xenopeltis* and *Loxocemus*), secondarily lost in the Tropicophioidea and Caenophidia. The hemipenial morphology of the tropidophioids can be summarized as follows (Stull, 1928; Gibson, 1970; McDowell, 1987): hemipenis deeply bilobed, or quadrifurcated in some *Tropicophis* (Gibson, 1970), with a sulcus spermaticus bifurcating in the crotch and running centripetally or slightly centrolineally on the surface of the lobes; hemipenial body almost entirely nude, but with large papillae on its distal region (these enlarged papillae may extend to the proximal region of the lobes); lobes mostly covered with papillate or unornamented flounces.

ACROCHORDOIDEA

Depending on the author, this taxon includes one or two genera of highly modified aquatic snakes. It is supported by a suite of uniquely derived features, which include (1) the position of the optic foramen within the parietal, (2) reduced prefrontals, and (3) discoidal supratemporals (see Hoffstetter and Gayrard [1965], McDowell [1975], and Rieppel [1988] for more details). Except for *Acrochordus arafurae*, which has a slightly bilobed and nude hemipenis, this genus is characterized by having a deeply bilobed hemipenis, lobes covered with numerous small spines (except for the tip and near base of the lobes, which are smooth), a nude hemipenial body, and a slightly centrolineal sulcus spermaticus dividing in the crotch (McDowell, 1979: fig. 26).

COLUBROIDEA

As already summarized by Rieppel (1988: 82), the Colubroidea are a well-supported

group with at least seven known synapomorphies: (1) loss of the right carotid artery, (2) intercostal arteries arising throughout the length of the trunk from the dorsal aorta at intervals of several body segments, (3) specialized costal cartilages, (4) presence of a muscle protractor laryngeus, (5) presence of a separate muscle protractor quadrati, (6) vomers with a more globular enclosure as compared to the Acrochordoidea, and (7) separate spinalis and semispinalis portions in the epaxial trunk. Another synapomorphy is the presence of spinules or spines covering the hemipenial body. Spinules/spines are absent in the Tropidophioidea, whereas they are present but restricted to the lobes in the Acrochordoidea. Spines covering the body are present in all the colubroid groups recognized here (except for the pareatines examined in which spines or spinules are completely lacking). Some taxa within the "colubrids" have apparently completely lost any kind of ornamentation, including their spines and spinules (e.g., the Psammophiinae). The presence of a distinct venom (serous) gland associated with a fang also possibly represents a synapomorphy of the Colubroidea if one accepts the absence of such a venomous complex in "colubrids" as a result of secondary loss, as argued by various authors (Underwood, 1967; McDowell, 1975, 1987; Cadle, 1982; Underwood and Kochva, 1993; Zaher, 1994b).

ELAPIDAE

McDowell (1968) suggested that *Homoroselaps* is not an elapid but an aparallactine "colubrid." This hypothesis was rejected by McCarthy (1985), who diagnosed the family. Underwood and Kochva (1993), Zaher (1994b), and Cadle (1994) also rejected McDowell's suggestion based on different lines of evidence. *Homoroselaps* is herein considered to belong to the Elapidae. However, the question remains controversial because the evidence supporting the monophyly of this family (including *Homoroselaps*) is restricted to two derived features: (1) presence of an anterior enlarged fang on the maxillae by loss of the anterior maxillary teeth (Jackson and Fritts, 1995), and (2) presence of a mucous accessory gland on the course of the

duct of the venom gland (Kochva and Wollberg, 1970; McCarthy, 1985; Underwood and Kochva, 1993). A third possible synapomorphy is the presence of a muscle adductor mandibulae externus superficialis acting as a compressor glandulae. However, this feature is not unique to the elapids, being also present in *Apostolepis* and *Atractaspis* (see Zaher, 1994b). Additionally, Kochva and Wollberg (1970) and Underwood and Kochva (1993) reported the presence of a superficialis acting as a compressor glandulae in *Dispholidus*, *Mehelya*, and *Brachyophis*. The elapid hemipenial morphology can be summarized as follows (see fig. 2): organ generally slightly or weakly bilobed, but sometimes unilobed (e.g., *Calliophis gracilis*); sulcus spermaticus always divided when the organ is not clearly unilobed, and centripetal or slightly centrolineal, bifurcating in the crotch; organ generally ornamented with spinules or medium-sized spines; calyces and flounces, when present, restricted to the lobular region; ornamentation uniformly distributed on the organ (i.e., ornamentation does not vary on sulcate and asulcate sides).

VIPERIDAE

The monophyly of this taxon seems hardly questionable at first glance (Groombridge, 1986). However, when examined critically, the evidence is not extensive and, as for the elapids, rests mostly on characteristics of the venom delivery system (Cadle, 1992). The following synapomorphies support this group (Kochva, 1978; Underwood and Kochva, 1993): (1) highly reduced and movable maxillary bone, (2) venom gland with a wide lumen, and (3) globular accessory gland situated anteriorly on the duct of the venom gland. One of the most striking derived features of vipers—the profundus origin of their muscle compressor glandulae with the muscle adductor superficialis passing through the loop of the latter (Kochva, 1962, 1963)—was reported to be present in *Atractaspis* (Zaher, 1994b). One additional derived feature from the vertebral complex may support viperid monophyly: the presence of well-developed, strongly anteroventrally directed, parapophyseal processes. However, this condition is also found in the natricines, (Auffenberg,

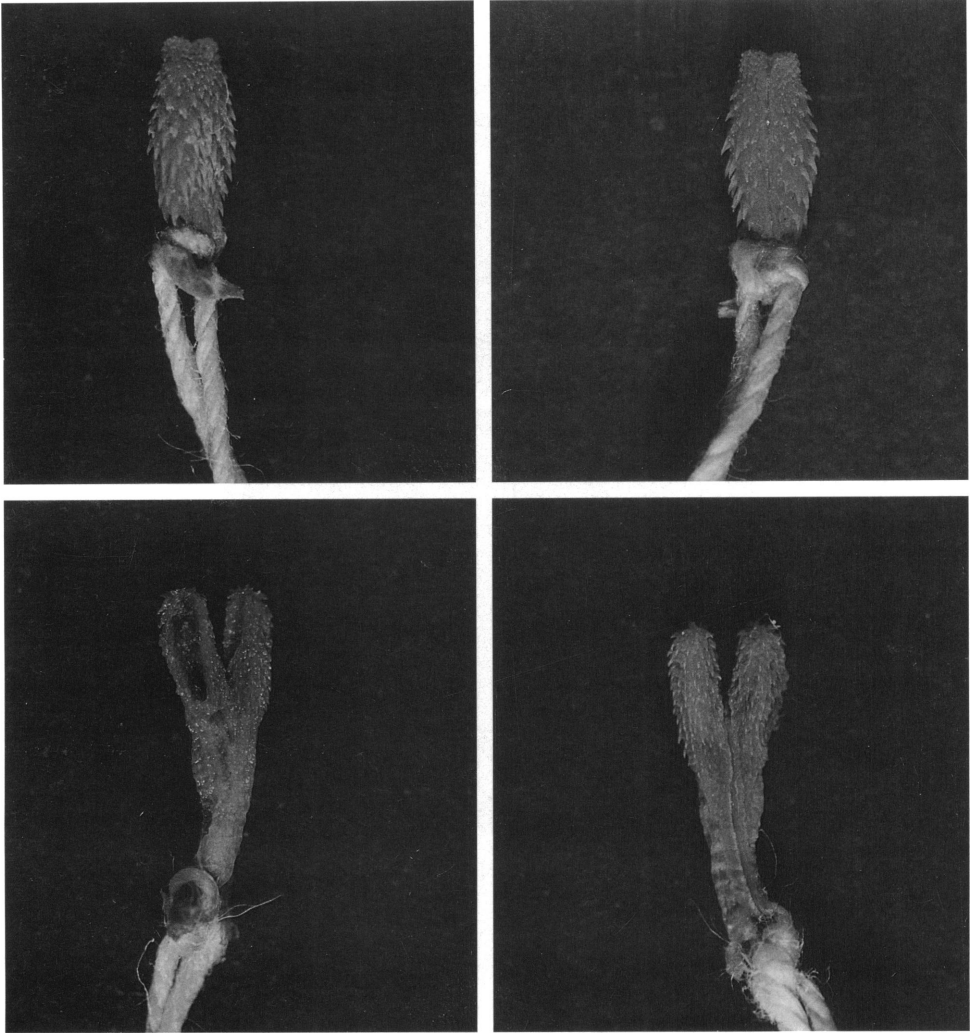


Fig. 2. Hemipenes of *Homoroselaps dorsalis* (upper; AMNH 94690) and *Calliophis japonicus* (lower; AMNH 67190; left lobe with a huge hole on the asulcate side). Asulcate (left) and sulcate (right) views.

1963; personal obs.), although to a less developed degree.

The hemipenial morphology of vipers can be summarized as follows: organ deeply bilobed, usually with lobes two or more times longer than the hemipenial body (rarely the opposite as in *Trimeresurus s. stejnegeri*; see Mao, 1993: fig. 20); lobes generally ornamented with calyces distally and spines proximally, with the degree of extension of each ornament on the lobes varying significantly; sulcus spermaticus bifurcating in the crotch or just below it and running in a centripetal

or slightly centrifugal position along the lobes (except in *Trimeresurus s. stejnegeri*); hemipenial body generally ornamented with spinules and medium to large spines or (rarely) nude. There is no clear differentiation between ornaments on the asulcate and sulcate sides.

ATRACTASPIDIDAE

McDowell (1968, 1987) and Underwood and Kochva (1993) placed *Atractaspis* and the "aparallactine" genera together in the

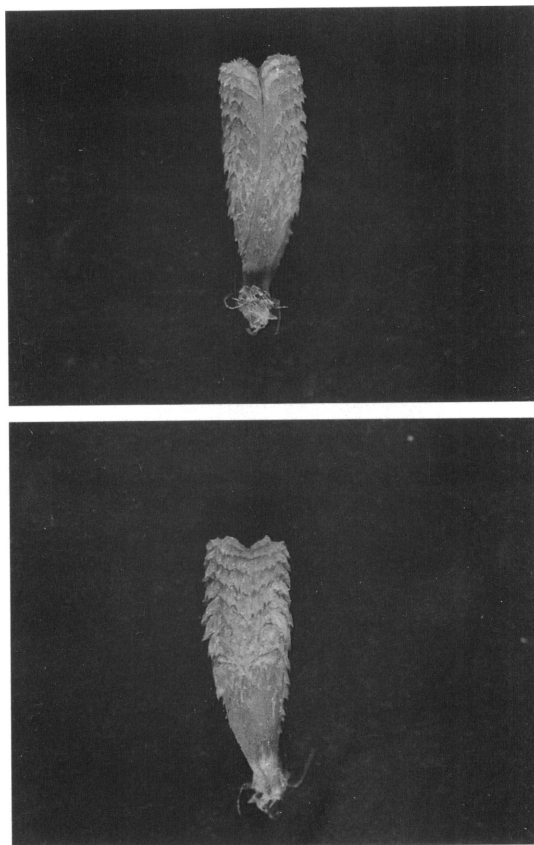


Fig. 3. Hemipenis of *Aparallactus capensis* (AMNH 18214). Sulcate (left) and asulcate (right) views.

family Atractaspididae, reviving Bourgeois's (1968) hypothesis of an aparallactine affinity for the mole viper. Cadle (1988, 1994) disputed this hypothesis, based on discordant evidence obtained in his immunological studies of colubroid snakes. According to Underwood and Kochva (1993), the monophyly of the Atractaspididae is supported by two synapomorphies: (1) presence of a wedge-shaped dorsal process of the premaxillae intruding between the nasals, and (2) the position of the rectal gland lateral to the quadrato-maxillary ligament. The last character was scored for only a few taxa (Underwood and Kochva, 1993), pending further research.

All atractaspidids have a similar hemipenial morphology. Representatives of *Aparallactus* (fig. 3), *Amblyodipsas* (fig. 4), *Atractaspis* (fig. 4), *Macrelaps* (fig. 5), and *Polemon* (fig. 5) were examined for their hemi-

penial morphology. All have very short lobes, with *Amblyodipsas*, *Aparallactus*, *Macrelaps*, and *Polemon acanthias* presenting a unilobed condition. *Atractaspis* and *Polemon christyi* have slightly bilobed organs. The sulcus spermaticus is always in a clearly centripetal position and divides distally in the lobular crotch or just below the tip of the organ in the unilobed forms. Even in the unilobed organs, the sulcus spermaticus is divided and positioned in a typical centripetal position, although the branches are very short. In *Macrelaps microlepidota*, the sulcus tends to be single, but is enlarged distally. All taxa examined show hemipenes covered with a series of horizontally arranged parallel rows of medium-sized spines. In *Atractaspis*, *Aparallactus*, *Polemon*, and *Macrelaps* almost all the organ is covered with spines, except for the base, which is nude, whereas in *Amblyodipsas* it is the whole basal half of

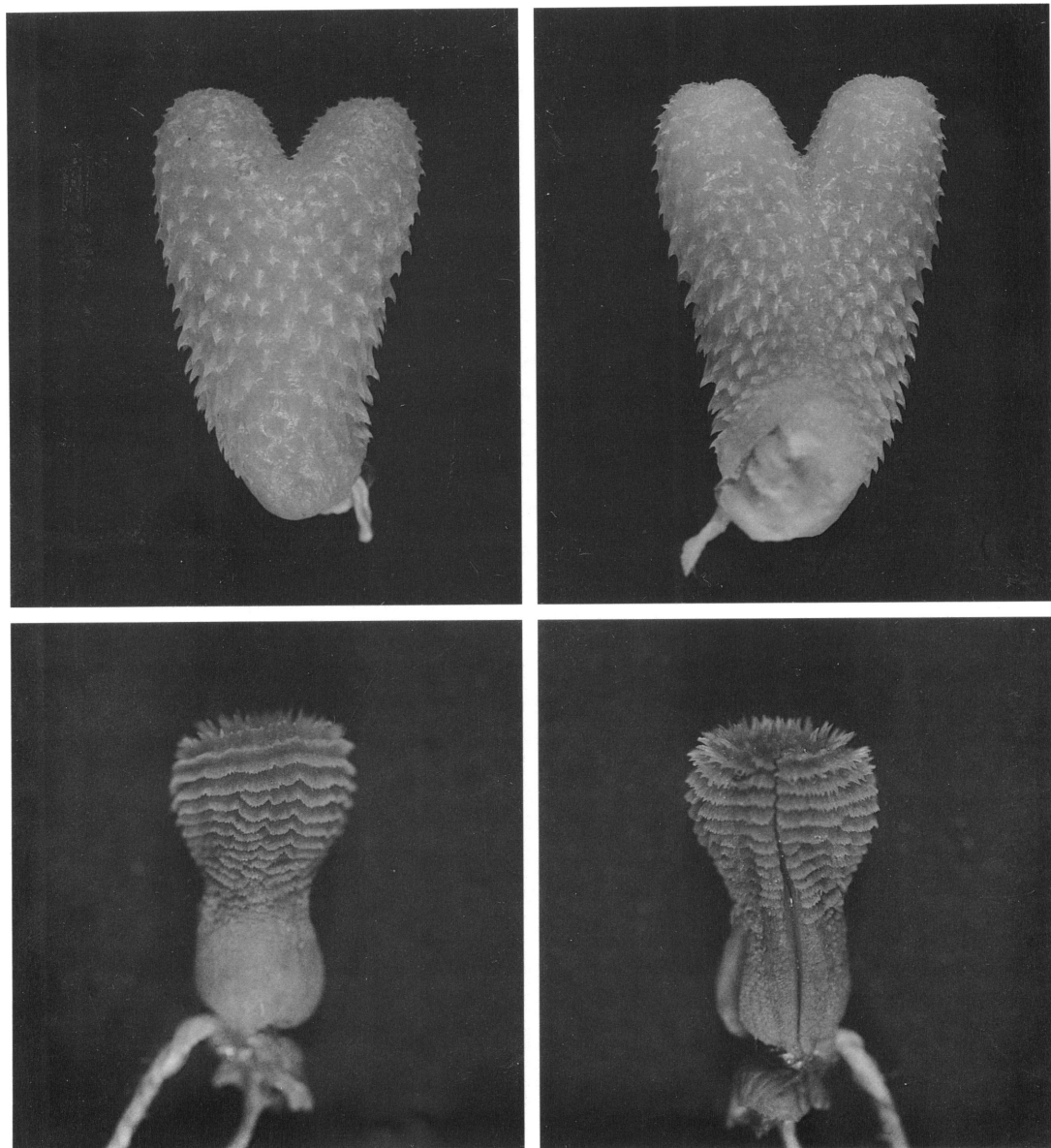


Fig. 4. Hemipenes of *Atractaspis fallax* (upper; AMNH 102298) and *Amblyodipsas polylepis* (lower; AMNH 82408). Asulcate (left) and sulcate (right) views.

the organ that is nude (Dowling and Duellman, 1978). In *Macrelaps*, *Aparallactus*, *Polemon*, and *Amblyodipsas* the spines forming the more distal rows are interconnected by a ridge of tissue forming spinulate flounces. Only *Atractaspis* lacks ridges of tissues between spines. All taxa can be characterized as having a centripetal sulcus spermaticus. Broadley's (1971) descriptions of the hemi-

penes of several species of *Amblyodipsas* and *Xenocalamus* and figures of the sulcate side of the organs of *X. bicolor* and *A. polylepis* agree perfectly with the present description of atractaspidid hemipenial morphology.

"XENODERMATINAE"

Among the "Xenodermatinae," only the hemipenes of *Oxyrhabdium modestum* (fig.

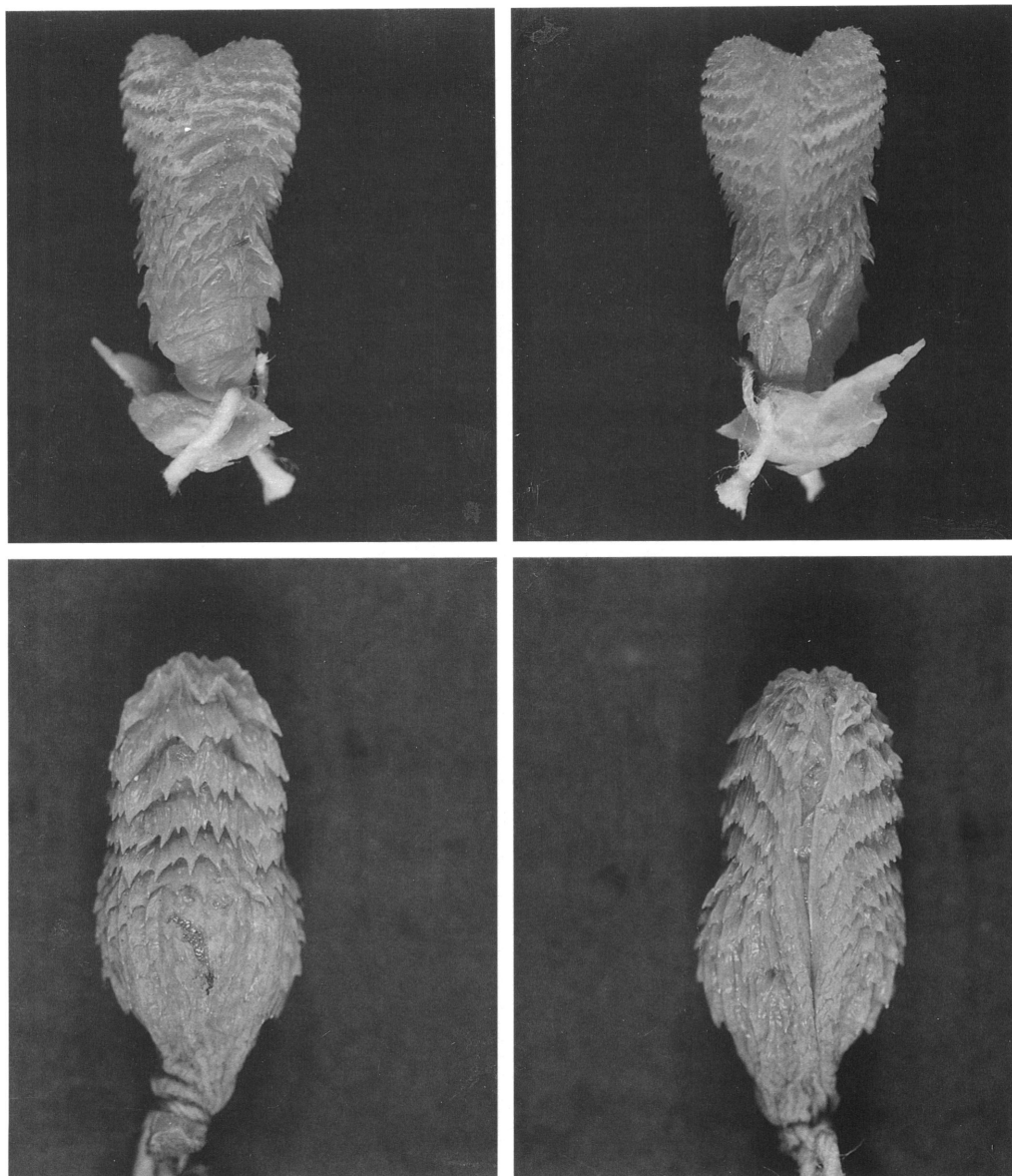


Fig. 5. Hemipenes of *Polemon acanthias* (upper; AMNH 142421) and *Macrelaps microlepidotus* (lower; AMNH 57636). Asulcate (left) and sulcate (right) views.

6) and *Xenodermus javanicus* were investigated. Both organs are similar. The lobes are very long, being almost twice the length of the body. The sulcus spermaticus is centripetal to slightly centrolineal, bifurcating at the distal end of the hemipenial body (almost inside the lobular crotch) and ending at the tip of each lobe. Both lobes and distal half of the body are covered with small to medium-

sized spines, the basal half of the body being nude. The whole hemipenial pattern is thus very simple and the only ornamentation found are the spines. McDowell (1987) reported flounces on the hemipenial lobes of *Xylophis* and *Achalinus*.

McDowell's (1987) revised definition of the "Xenodermatinae" is followed herein, although no unambiguous synapomorphy is

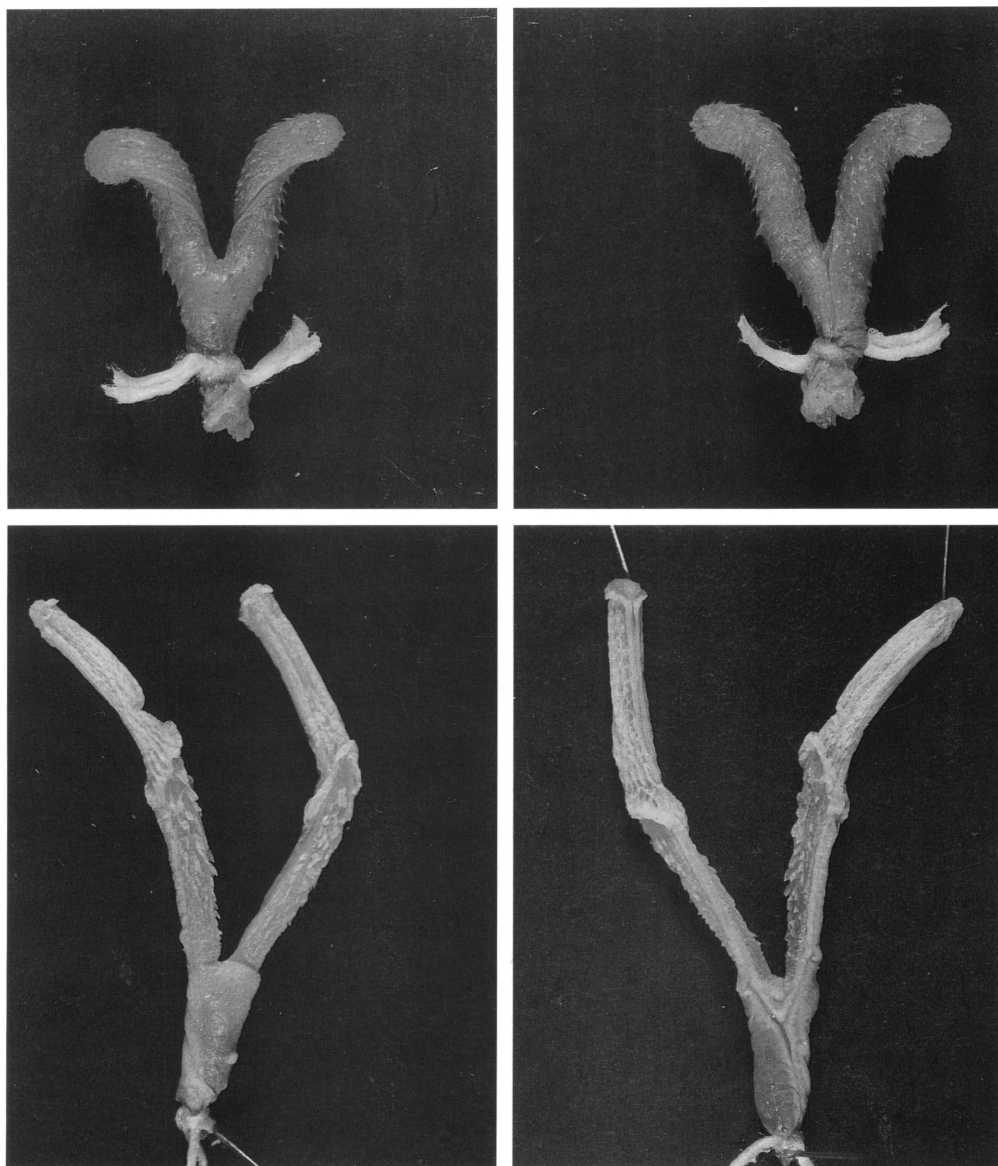


Fig. 6. Hemipenes of *Oxyrhabdion modestum* (upper; CNHM 68907) and *Pareas margaritophora* (lower; AMNH 27770). Asulcate (left) and sulcate (right) views.

known to support this subfamily. The presence of an expanded, concave nasal shield that accommodates the nostril may represent a synapomorphy of *Achalinus*, *Stoliczkaia*, *Xenodermus*, *Oxyrhabium* (weakly developed), and *Fimbrios*, but excludes *Xylophis*. *Achalinus* and *Fimbrios* share the derived condition of anterior labials with feebly raised, everted margins.

PAREATINAE

The Pareatinae, for which only *Pareas margaritophora* (fig. 6) and *P. stanleyi* were available, also have a simplified hemipenial morphology that is only superficially similar to the "Xenodermatinae." The hemipenis is deeply bilobed with long, slender lobes (at least twice the length of the body); the sulcus spermaticus

is clearly centrolineal and bifurcates in the distal region of the body; the basal half of the lobes is covered with medium-sized spinelike papillae whereas the very base of the lobes and the body are ornamented with spinules (contra McDowell, 1987: 36). There is a gradual transition between the papillae and spinules, with the former reducing in size and becoming thicker. The distal half of the lobes is covered with shallow calyces with fleshy, unadorned ridges ("tripelike calyces" of McDowell, 1987: 26). These calyces are structurally similar to the ones present in various booids and scolecophidians (see Branch, 1986; Kluge, 1993a, 1993b). However, a homology between the pareatine calyces and the "calyces" found in booids and scolecophidians is not implied here. The two distinctly ornamented regions are separated by an enlarged, horizontally directed fold of tissue that surrounds each lobe, forming a complete ring of tissue on the mid-region of the lobes. According to McDowell (1987), *Aplopeltura* has the same basic hemipenial pattern as *Pareas*, except that it shows many flounces.

Brongersma (1956, 1958) long ago suggested that the snail-eating pareatines may form a monophyletic group not closely related to the Neotropical snail-eating genera. Aside from the characters discussed by this author, a number of other nonhomologous anatomical features are found to respond, in both groups, to the same functions related to the malacophagous behavior, thus suggesting a homoplastic origin of the snail-eating behavior. For example, in the pareatines, the muscle levator anguli oris always inserts directly on the infralabial gland and acts as a compressor glandulae (Haas, 1938; Savitzky, personal commun.; personal obs.). In the Dipsadini, the muscle levator anguli oris also extends downward and forward, around the corner of the mouth, but always inserts on the lateral surface of the dentary (*Tropidodipsas* and *Sibon*) or on the tip of the dentary (*Dipsas* and *Sibynomorphus*) (the more lateral fibers insert on the posterior edge of the infralabial gland in *Tropidodipsas* and *Sibon*, but never surround the gland as in pareatines; personal obs.). I found a muscular bundle acting as a real compressor glandulae only in some species of *Dipsas*, but it was always the pars posterior of the muscle intermandibularis poste-

rior that switched its position from a medial to a lateral one, surrounding the posterior region of the infralabial gland (Zaher, 1996b; in prep.). These two nonhomologous muscular patterns are clearly associated with the malacophagous habits of the pareatines and dipsadines, and they likely represent additional synapomorphies supporting these two independent monophyletic lineages. Rao and Yang (1992) recently erected the new genus *Internatus* to accommodate *Pareas laevis* and *P. malaccanus*, two taxa that were not available for the present study.

CALAMARIINAE

Among the Calamariinae (sensu McDowell, 1987), only *Calamaria linnaei* (fig. 7), *C. virgulata*, *C. septentrionalis*, and *Macrocalamus lateralis* (fig. 7) were available for study. According to McDowell (1987), all calamariine genera share the synapomorphy of both frontal and parasphenoid bones forming the border of the orbital foramen and excluding the parietal. All three species of *Calamaria* show an almost identical hemipenial morphology that is, in turn, very similar to the one found in *Macrocalamus*. In both genera the hemipenes are slightly bilobed with a centrifugal sulcus spermaticus, the lobes are covered with calyces with unadorned ridges, and the body is completely nude. The ridges of calyces are much larger on the crotch than on the lobes. In *Calamaria*, the sulcus bifurcates in the middle of the body, whereas in *Macrocalamus* the bifurcation is located on the distal half of the body. The hemipenis of *Macrocalamus* is peculiar in having a constricted area around the body on its distal region, just below the lobes, and a large vertical ridge of tissue on each side of the body running from the base of the organ to just below the constriction. *Calamaria* lacks the constricted area on the distal half of the body, but shares with *Macrocalamus* the ridges of tissue on both lateral surfaces, although they are much smaller and may be seen only in everted organs. The last characteristic is regarded here as a derived condition because it is absent in the tropidophioids and in any other caenophidian group.

"HOMALOPSINAE"

The "homalopsines" have been recently redefined by McDowell (1987), who includ-

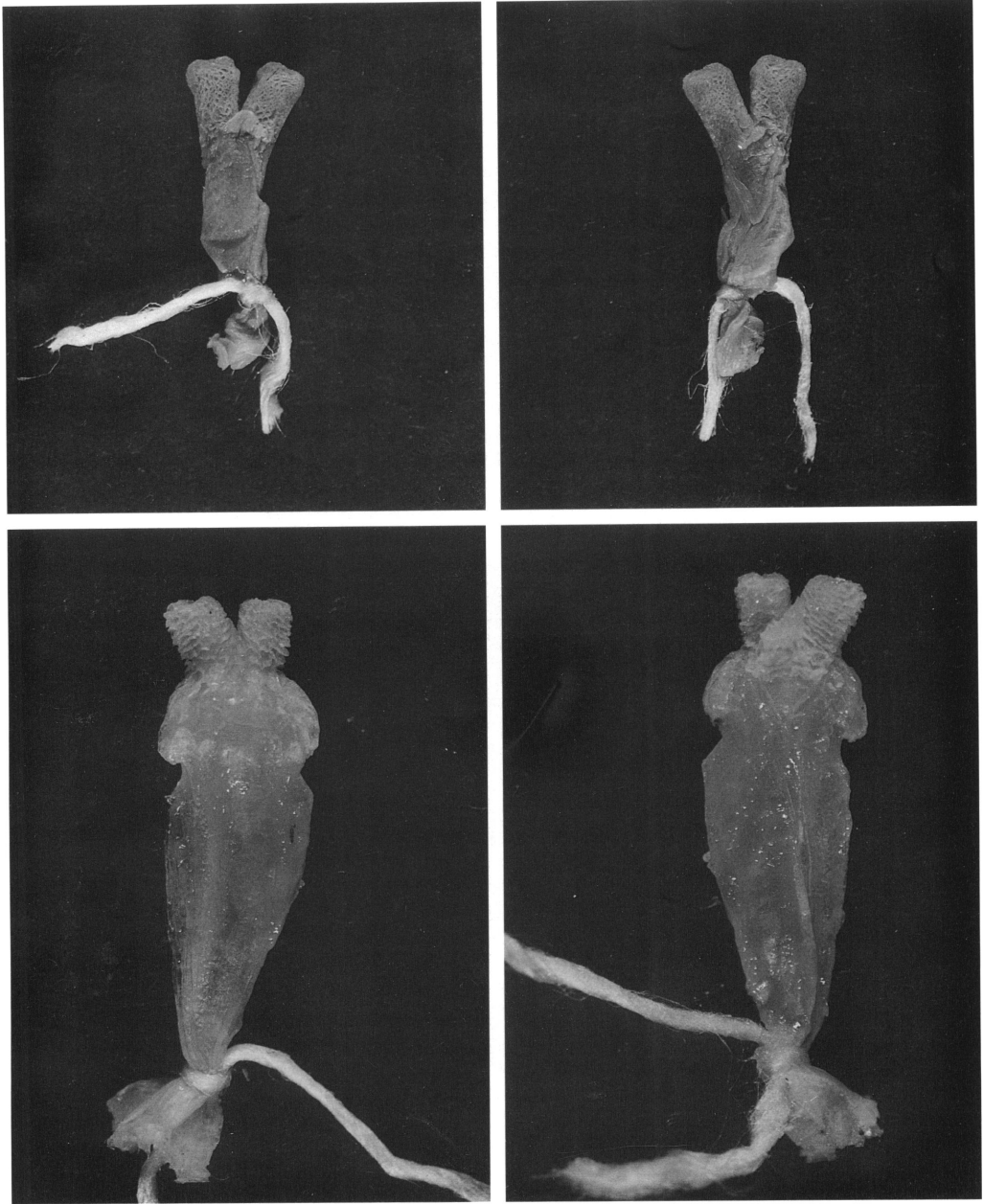


Fig. 7. Hemipenes of *Calamaria linnaei* (upper; AMNH 31943) and *Macrocalamus lateralis* (lower; CNHM 109943). Asulcate (left) and sulcate (right) views.

ed the genus *Brachyorrhos*. Although this group has long been recognized (Underwood, 1967), no unambiguous synapomorphy is known to support it except for a strictly aquatic life-style (except for *Brachyor-*

rhos) and live-bearing derived conditions. The hemipenial morphologies among the "homalopsine" taxa studied appear to be extremely similar. No derived hemipenial feature was found to be unique to them. Most

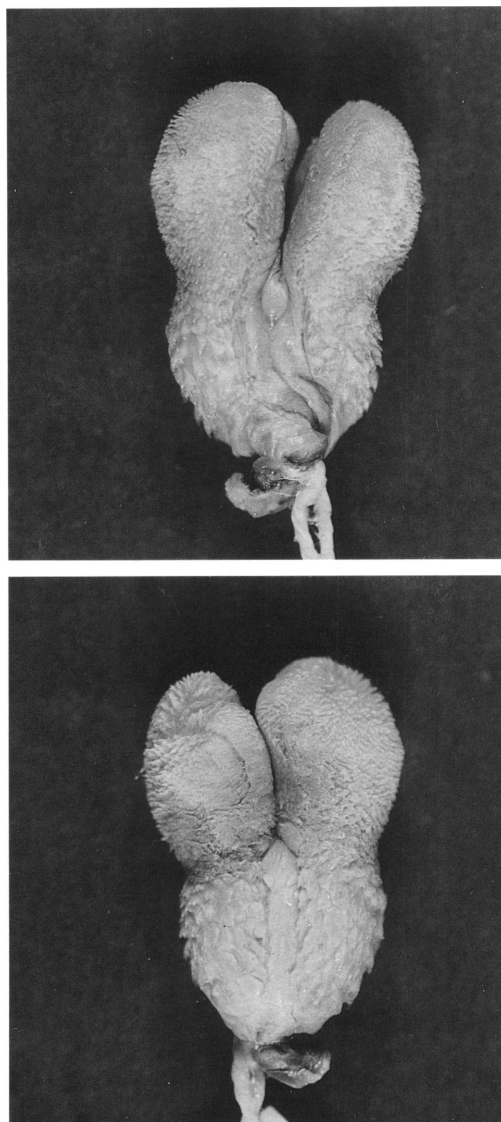


Fig. 8. Hemipenis of *Fordonia leucobalia* (AMNH 86240). Sulcate (upper) and asulcate (lower) views.

of their hemipenial features are also found in various Madagascan taxa, such as *Liophilidium*, *Leioheterodon*, *Ithycyphus*, and *Lio-pholidophis* (see below), which share a very similar hemipenial morphology with the "homalopsines." Representatives of the following genera were available for study: *Gerarda*, *Brachyorrhos*, *Cantoria*, *Bitia*, *Fordonia* (fig. 8), and *Homalopsis*. All taxa have a slightly bilobed hemipenis with a highly

centripetal sulcus spermaticus bifurcating within the lobular crotch. The lobes are covered with minute, densely arranged spinules. The hemipenial body is covered with more sparse, medium-sized spines, except in *Cantoria*, in which the body is spineless. In *Gerarda* and *Bitia*, only the distal half of the body has spines. The ornamentation is uniformly distributed throughout the surface of the organ (i.e., no differentiation occurs be-

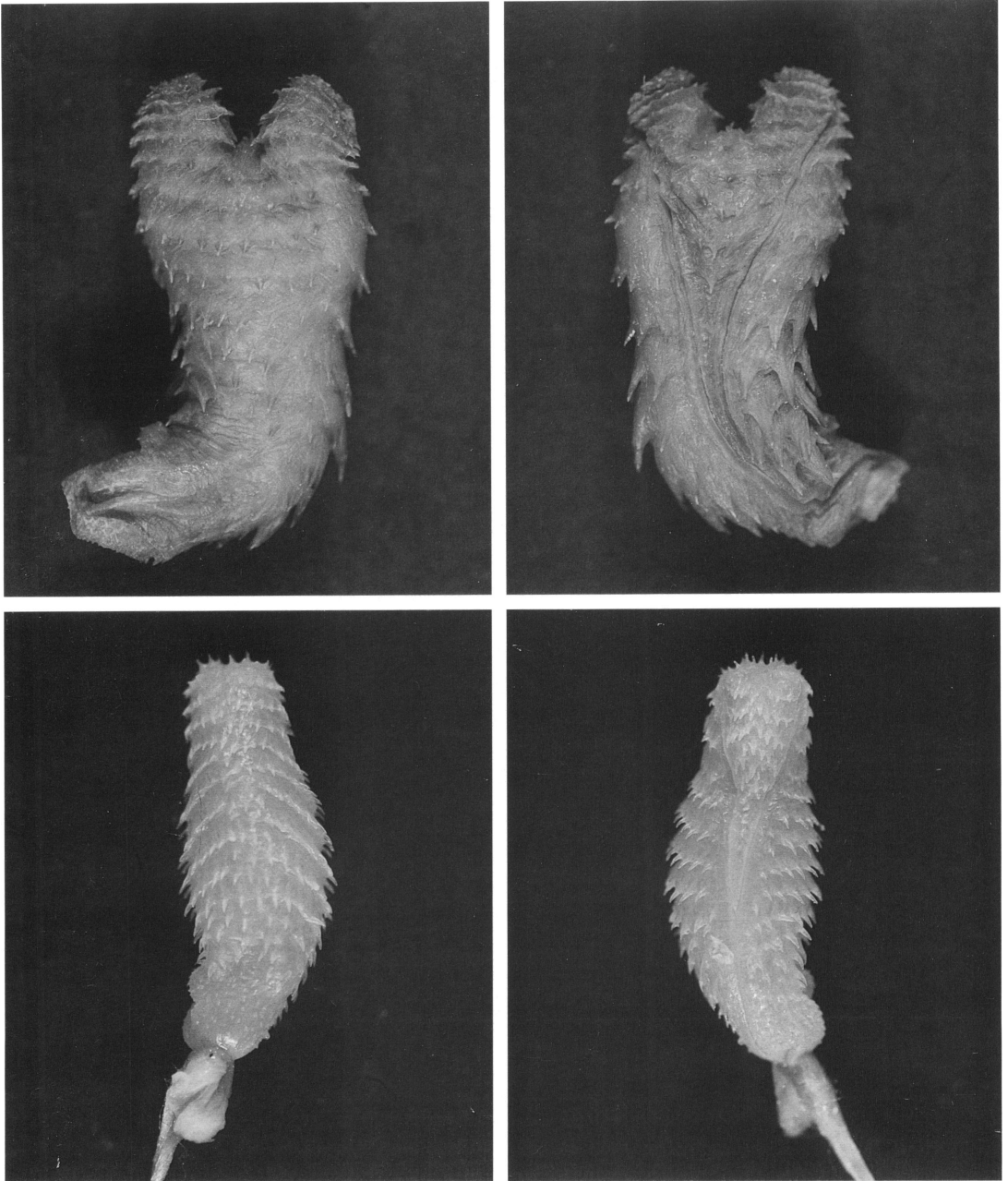


Fig. 9. Hemipenes of *Lamprophis olivaceus* (upper; AMNH 12001) and *Lycodonormorphus rufulus* (lower; AMNH 140278). Asulcate (left) and sulcate (right) views.

tween asulcate and sulcate ornaments of the same kind).

“BOODONTINAE”

Monophyly of the “Boodontinae” recognized here (representing Dowling and Duell-

man’s [1978] Boodontini and Lycophidiini) has not been demonstrated, and the group is conceivably paraphyletic. However, all taxa studied have a very similar hemipenial morphology (see figs. 9 and 10) and are retained together for the sake of convenience. The or-

gans are covered with longitudinal rows of medium-sized spines that are, in most taxa, interconnected by a ridge of tissue that forms spinulate flounces. The hemipenes are slightly bilobed (except in *Lycodonomorphus*, in which the organ is unilobed; fig. 9), and the sulcus spermaticus is clearly centrolineal (often turning to a centrifugal position distally) and bifurcates in the middle region of the hemipenial body.

Recently, Ziegler et al. (1997) erected the genus *Buhoma* to accommodate the African species of *Geodipsas* (see also Cadle [1996a] who revised the Madagascan species of *Geodipsas*). Precise descriptions and figures of the hemipenis of *Buhoma* and *Geodipsas* species are furnished by these authors. According to their descriptions, all species of *Buhoma* have a hemipenial morphology similar to the one present in the "boodontines," with a centrolineal sulcus bifurcating in the middle of the body and with longitudinal rows of medium-sized spines covering the organ and, in some species, interconnected by a ridge of tissue, thus forming spinulate flounces (also found in the "atractaspidids"). Similarly, the Madagascan and African genera *Dromicodryas* (fig. 11) and *Montaspis* (Lambiris, 1997) show the same "boodontine" hemipenial morphology. For this reason, *Buhoma*, *Dromicodryas*, and *Montaspis* are here placed in the "boodontines" as incertae sedis.

"PSEUDOXYRHOPIINAE"

The "Pseudoxyrhophiinae" recognized herein—that is, including Dowling and Duellman's (1978) Pseudoxyrhophini and Geodipsadini—also may represent a paraphyletic group. This assemblage is retained only for convenience, as it corresponds to the poorly known, geographically isolated, and diversified Madagascan colubrid fauna. Some subgroups can be defined on the basis of derived character states found on their hemipenial morphology. However, all hypothesized derived features were also found to be present in other subgroups of "colubrids," precluding their placement with confidence at that level of universality.

There are virtually no comparative data

on the anatomy of these snakes, with the exception being perhaps their hemipenial morphology (Domergue, 1963, 1972, 1983, 1986, 1987, 1991, 1994; Cadle, 1996a, 1996b; Ziegler et al., 1997). In the "pseudoxyrhophiines," the hemipenis is weakly bilobed (*Stenophis*, *Madagascarophis*, fig. 12; *Geodipsas*, fig. 12; *Alluaudina*), slightly bilobed (*Itacyphus*, *Leioheterodon*, fig. 13; *Langaha*, *Pseudoxyrhopus*, fig. 13), or deeply bilobed (*Stenophis*, *Liopholidophis*, *Liophilidium*, fig. 14). The hemipenial body is either nude (*Madagascarophis*, *Itacyphus*, *Leioheterodon*, *Langaha*, *Geodipsas*, *Alluaudina*) or ornamented with small or medium-sized spines (*Liopholidophis*, *Liophilidium*, *Pseudoxyrhopus*). In all these genera, the lobes are densely covered with spinules and the sulcus spermaticus is slightly centripetal to centrolineal and divides on the distal end of the hemipenial body, except in *Stenophis* and *Madagascarophis*, in which the sulcus bifurcates at the middle of the body but the branches retain the centripetal position on the weakly developed lobes. In *Alluaudina*, a centripetal condition of the sulcus is also present on weakly developed lobes. In *Geodipsas*, the same centripetal condition of the sulcus is present, although the organ is unilobed. As noted by Cadle (1996a: 72), evidence for the simple organ of *Geodipsas* being derived from a primitively bilobed condition is given by the presence of a divided retractor muscle in the four species studied by this author.

The hemipenis of *Micropisthodon ochraceus*, recently described and illustrated by Domergue (1991), is very similar to that found in *Itacyphus* and *Leioheterodon*. Densely spinulate lobes are also present in the "Homalopsinae" and may represent a shared derived feature with the "pseudoxyrhophiines."

Domergue (1994) recently revived the genus *Stenophis* for all Madagascan species previously assigned to *Lycodryas*, restricting the last genus to the species of the Comores and Mayotte. He further divided *Stenophis* into three subgenera—*Stenophis* Boulenger, 1896, *Phisaxella* (new), and *Parastenophis* (new)—that have distinct hemipenial morphologies. Only the subgenus *Stenophis* is represented in the present paper.

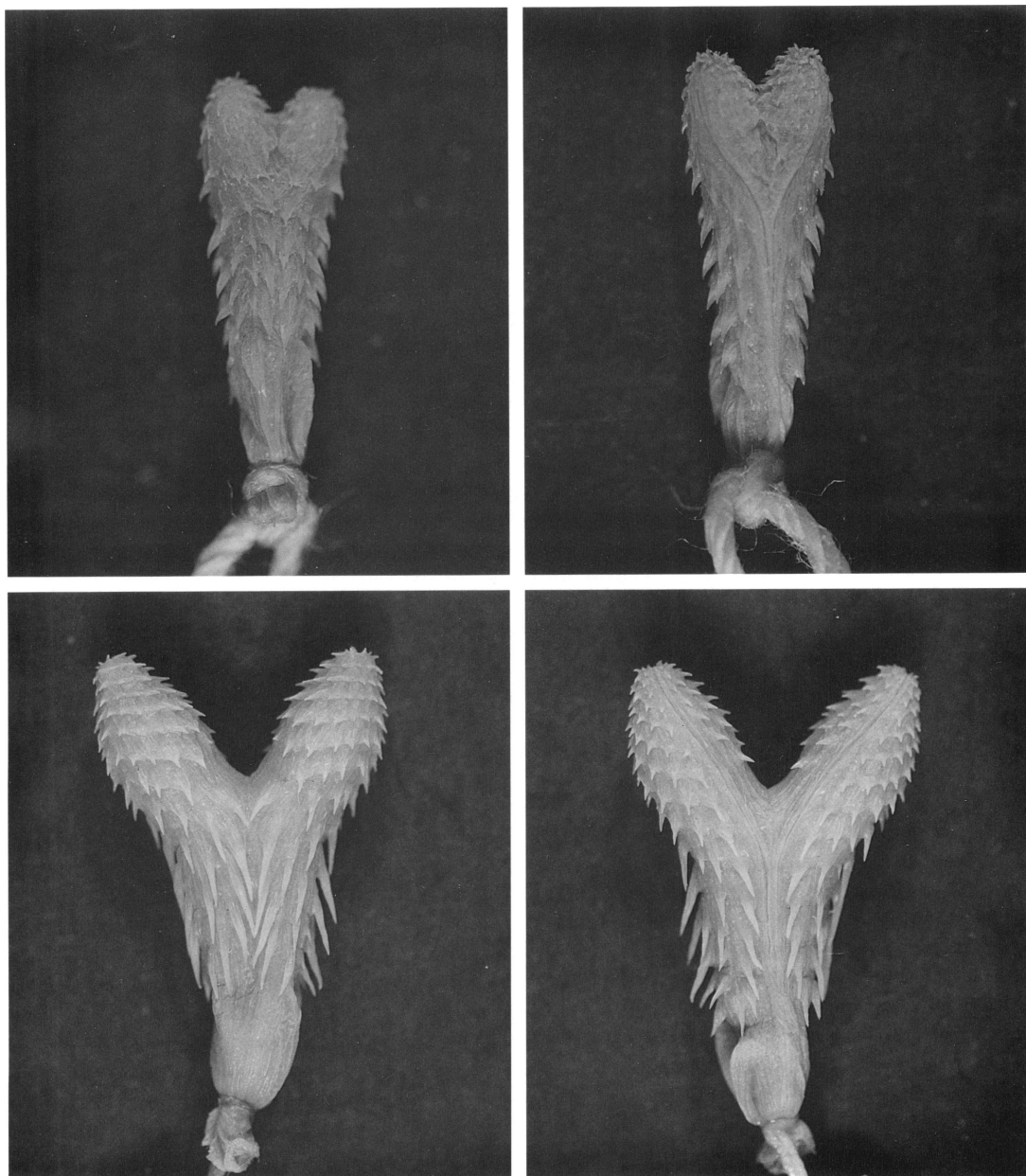


Fig. 10. Hemipenes of *Lycophidion capense* (upper; AMNH 60109) and *Bothrolycus ater* (lower; AMNH 11971). Asulcate (left) and sulcate (right) views.

COLUBRINAE

The colubrine clade is diagnosed by the loss of one branch of the sulcus spermaticus. All other colubroids (with few clear exceptions), the acrochordoids, and the tropidophioids have a divided sulcus spermaticus. A

simple sulcus is found in some unrelated genera (e.g., *Macrelaps*, *Arrhyton*) and in the Natricinae. However, natricine and colubrine conditions are not homologous, as already documented by McDowell (1961, 1987) and Rossman and Eberle (1977). Most natricines do possess a truly divided and centripetally

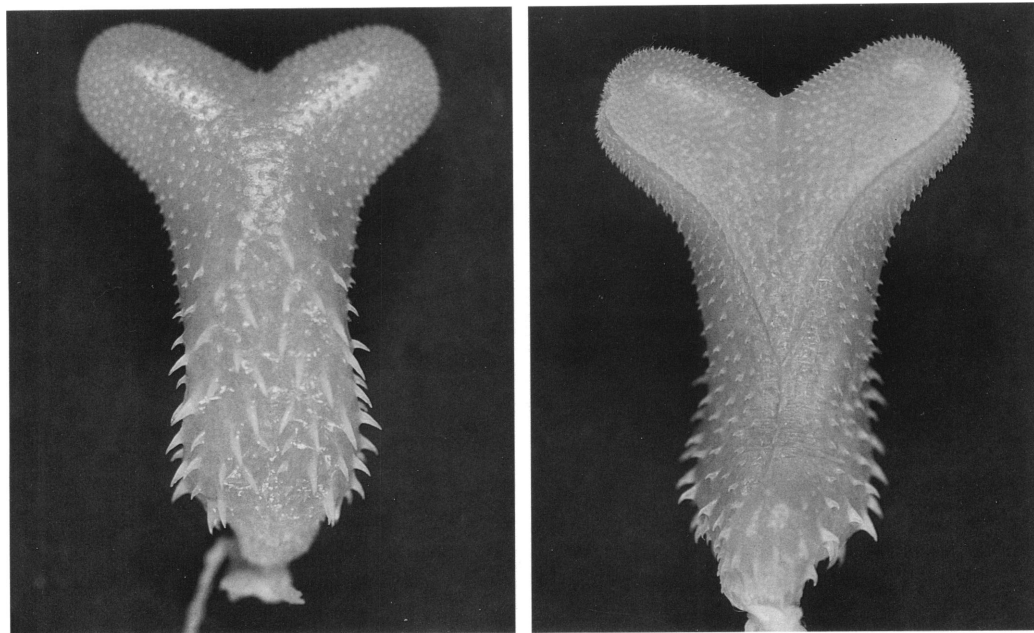


Fig. 11. Hemipenis of *Dromicodryas bernieri* (UMMZ 218166). Asulcate (left) and sulcate (right) views.

positioned sulcus spermaticus wherein the divergent branches are arranged on the lobes in a highly centripetal position (i.e., in the distal surface of the lobes). The apparent simple sulcus of most natricine genera actually corresponds to the undivided part of the sulcus, with the divergent branches being generally broadly expanded in the distal surface of the lobes and forming a nude distal end (McDowell, 1961; Rossman and Eberle, 1977). When a truly simple branch of the sulcus spermaticus is present in natricines, it is always the left one, whereas in colubrids, when this occurs, it is always the right branch (McDowell, 1961; Rossman and Eberle, 1977).

McDowell (1972) considered *Dinodon* to be a close relative of *Stegonotus*. This is corroborated by the hemipenial pattern found in *Dinodon* (fig. 14), which closely resembles the hemipenial morphology of *Stegonotus* as described by McDowell. In *Dinodon*, however, the calyces present on the tip of the lobe are weakly developed and almost imperceptible. The tip of the lobe is bulbous instead of having a terminal concavity as described by McDowell (1972: 9) in *Stegonotus*. The

last structure may be an artifact of incomplete eversion.

McDowell's (1987) proposal to include in the colubrids the genera *Blythia*, *Cyclocorus*, *Trachischium*, *Elapoidis*, and *Haplocercus* is not accepted herein because no evidence was provided supporting this view. No hemipenial material was available for these genera which are therefore viewed as "colubrids" incertae sedis. The Sri Lankan genus *Aspidura*, which was also suggested by McDowell to belong to the colubrids, is placed in the natricines since its entirely spinose hemipenis presents a clearly centripetal sulcus spermaticus in which the branches are enlarged to form a nude area in the crotch and medial region of the lobes.

Broadley's (1980) description and illustration of the hemipenis of *Prosymna* confirm the presence of calyces (Broadley's "pseudocalyces") and of an undivided sulcus, which places it in the Colubrinae (also suggested by Cadle's immunological data [1994]). *Thermophis* is here placed in "Colubridae" incertae sedis. Its divided sulcus in a single calyculate lobe (Malnate, 1953) is a

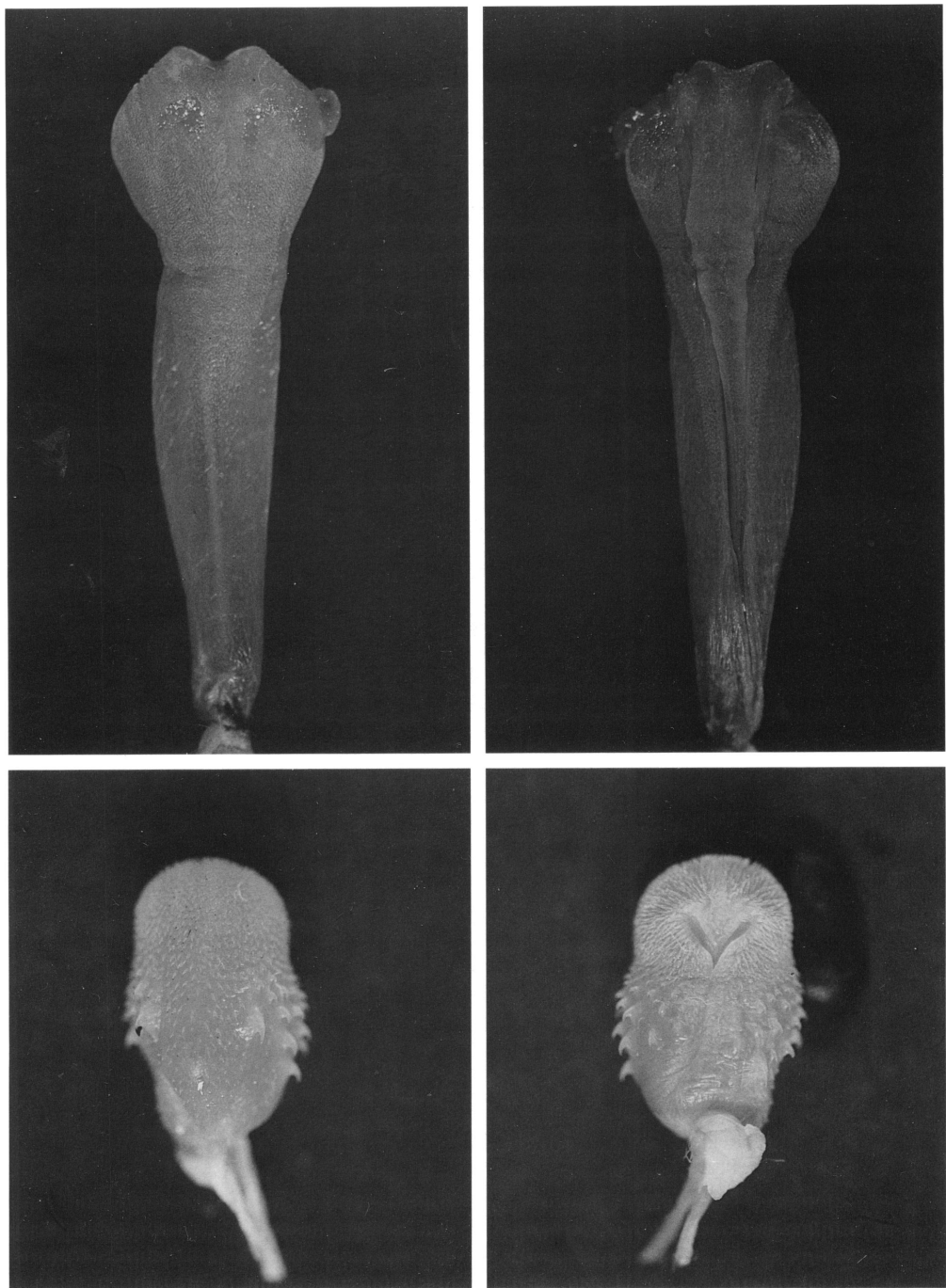


Fig. 12. Hemipenes of *Madagascarophis colubrinus* (upper; UMMZ 197210) and *Geodipsas heimi* (lower; UMMZ 197141). Asulcate (left) and sulcate (right) views.

dipsadine condition. This problem merits study in more detail.

As pointed out by McDowell (1987), the genera *Dryocalamus*, *Lycodon*, and *Oligodon* have a single sulcus spermaticus and distal calyces and/or flounces on their hemipenial lobe, which place them in the Colubrinae. I failed to see traces of calyces in the only specimen of *Phyllorhynchus* examined in this study (see appendix 2). However, Dowling and Duellman (1978: fig. 112b.9) figured poorly developed calyces on the lobe of *Phyllorhynchus* sp., suggesting that this genus belongs to the colubrinae.

The Sibynophiini, including *Scaphiodontophis* (fig. 15) and *Sibynophis* (fig. 15) but excluding *Liophidium* (fig. 14), is here regarded as a monophyletic subgroup of colubrine snakes. Unlike *Liophidium*, their hemipenes are typically colubrine: unilobed, calyculate, and with a simple sulcus spermaticus. The group shows one hemipenial synapomorphy: a sharply curved U-shaped convolution of the sulcus spermaticus in the proximal region of the hemipenial body. This feature was not found in any other snake examined. Hemipenial evidence places the Sibynophiini within the colubrine clade; however, their peculiar condition of tooth implantation shared with the Madagascan genus *Liophidium* (Savitzky, 1981) may point to a sister-group relationship between these taxa, rejecting the arrangement retained here. At the present, this question cannot be addressed adequately without additional information. The placement of the Sibynophiini within the colubrinae is therefore provisional.

PSAMMOPHIINAE

Bogert (1940) recognized the close affinities between the genera *Psammophis*, *Rhamphiophis*, *Malpolon*, *Hemirhagerris*, and *Psammophylax* based on their similar reduced hemipenes and differentiated maxillary dentition. Indeed, the Psammophiinae form a monophyletic clade supported by their highly derived hemipenial morphology—a very reduced, papilliform hemipenis with an undivided sulcus running from base to tip on the same side, and no ornamentation of any kind.

Dowling and Duellman (1978) followed

Bogert and placed the five genera and *Mimophis* (which has the same reduced hemipenial morphology) in the tribe Psammophiini, within their "Lycodontinae." According to these authors, this subfamily is supported by a characteristic hemipenis and by the presence of hypapophyses on all trunk vertebrae, and includes the "boodontines," "pseudoxyrhophiines," "xenodermatines," and pareatines, among others. However, as shown below, the first feature does not hold since each subgroup of "lycodontines" shows very different hemipenial morphologies, and the second feature is a plesiomorphy at that level of universality (see discussion above).

More recently, Dowling et al. (1983) recognized the difficulties in assessing the relationship of this group within the "colubrids," because of their highly simplified hemipenial morphology, but maintained them within their paraphyletic "Lycodontinae" "because of features of dentition" (Dowling et al., 1983: 321). Dowling et al.'s (1983) conclusion that the psammophiines share a differentiated maxillary dentition with the "Lycodontinae" (= part of the "Boodontinae") is unlikely since not all the psammophiines nor the "lycodontines" have differentiated teeth (see Bogert [1940: fig. 15] for an illustration of this character). Additionally, the enlarged teeth are in different places on the maxillae in both groups, being just below the prefrontal-maxillary articulation in the psammophiines and significantly anterior to the articulation in the "lycodontines" (see Bourgeois, 1968). This suggests that the peculiar maxillary dentitions of these groups are not homologous.

The absence of hypapophyses on the posterior vertebrae of the Psammophiinae is a marked difference from the "Boodontinae," "Pseudoxyrhophiinae," and Natricinae. The undivided sulcus spermaticus suggests that they may be related to the colubrinae. However, there is presently no known unambiguous evidence relating the psammophiines to any other "colubrid" group.

PSEUDOXENODONTINAE

As described by McDowell (1987), *Pseudoxenodon* (the only taxon available for this analysis; fig. 16) has a deeply bilobed hem-

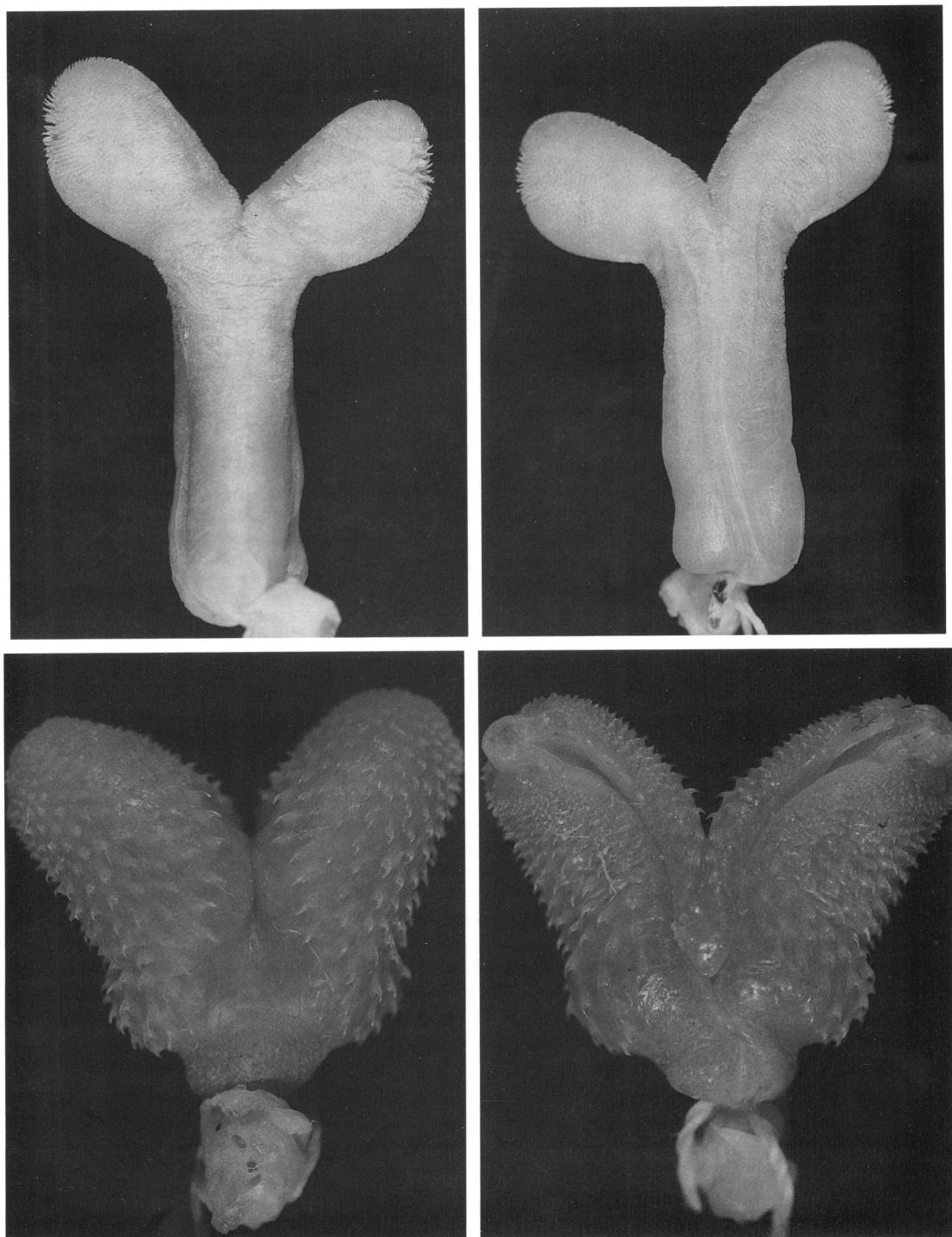


Fig. 13. Hemipenes of *Leioheterodon madagascariensis* (upper; UMMZ 201618) and *Pseudoxyrhophus tritaeniatus* (lower; UMMZ 195854). Asulcate (left) and sulcate (right) views.

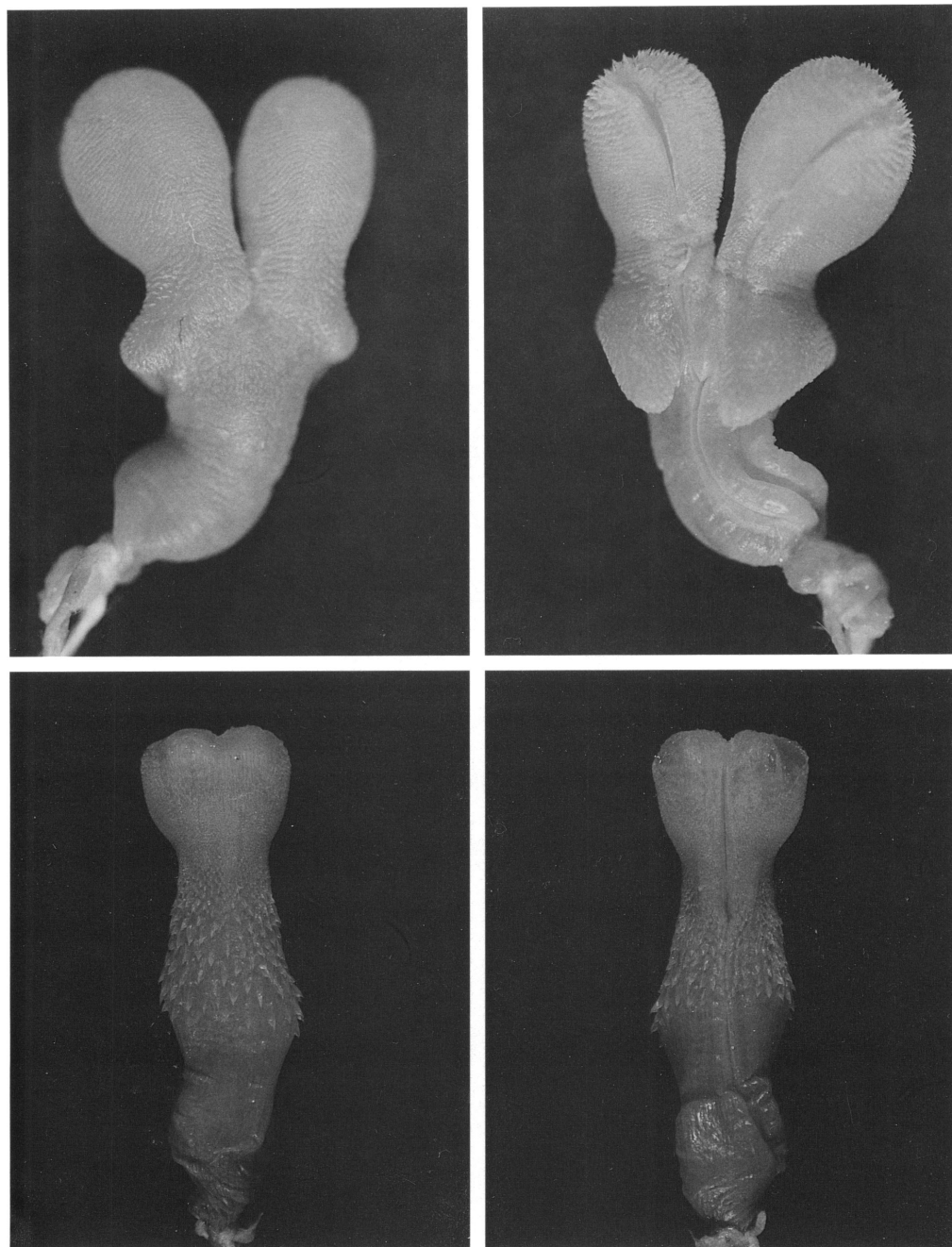


Fig. 14. Hemipenes of *Liophidium torquatus* (upper; UMMZ 209430) and *Dinodon flavozonatum* (lower; AMNH 34372). Asulcate (left) and sulcate (right) views.

ipenis, with a centrifugal sulcus spermaticus dividing on the proximal region of the hemipenial body, and lobes ornamented with diminutive spinulate calyces distally and rows

of medium-sized spines basally. The calyces are gradually replaced by spinules proximally, which gradually become medium-sized spines. The medial surface of each lobe is

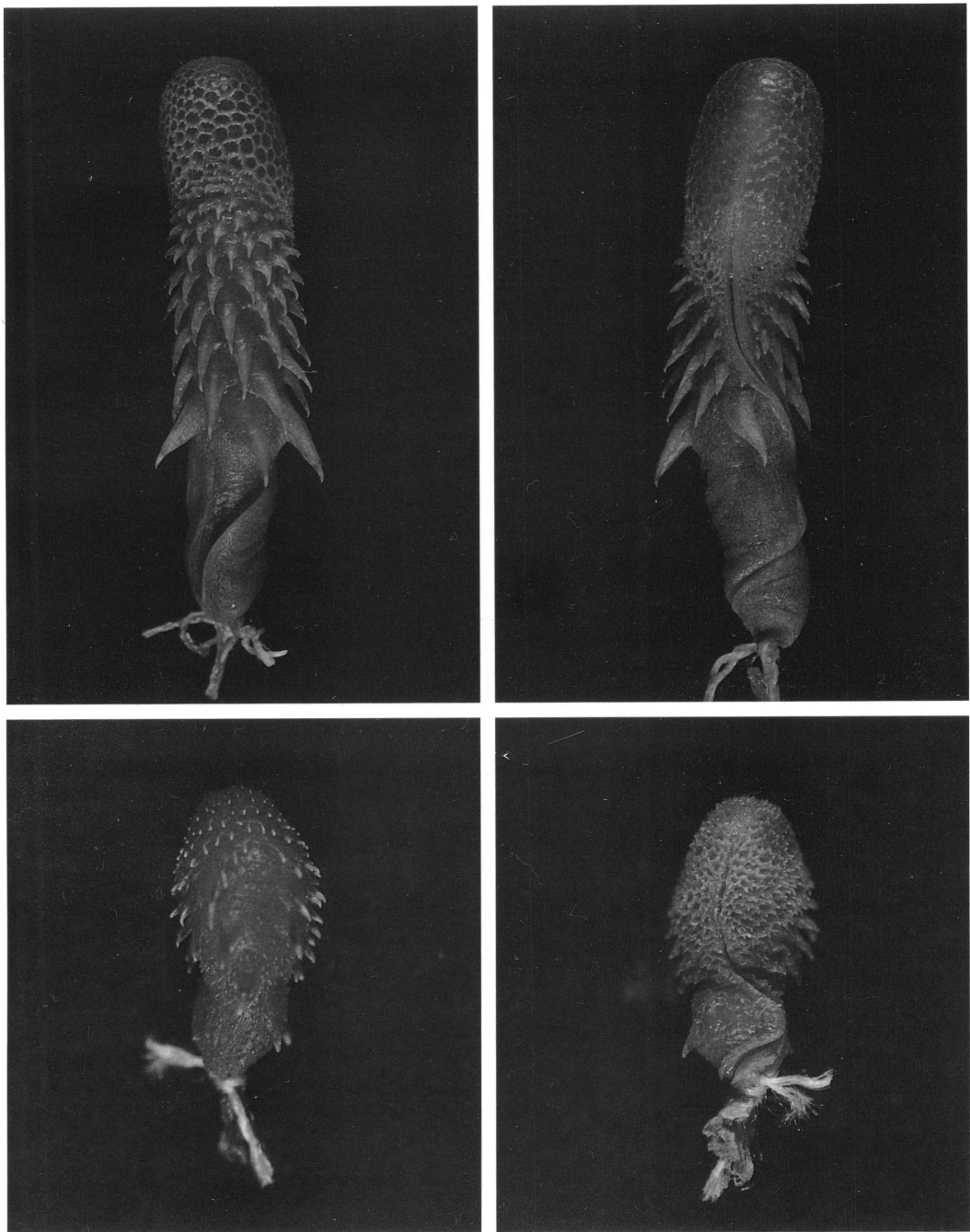


Fig. 15. Hemipenes of *Scaphiodontophis annularis* (upper; KU 191073) and *Sibynophis chinensis* (lower; AMNH 34102). Asulcate (left) and sulcate (right) views.

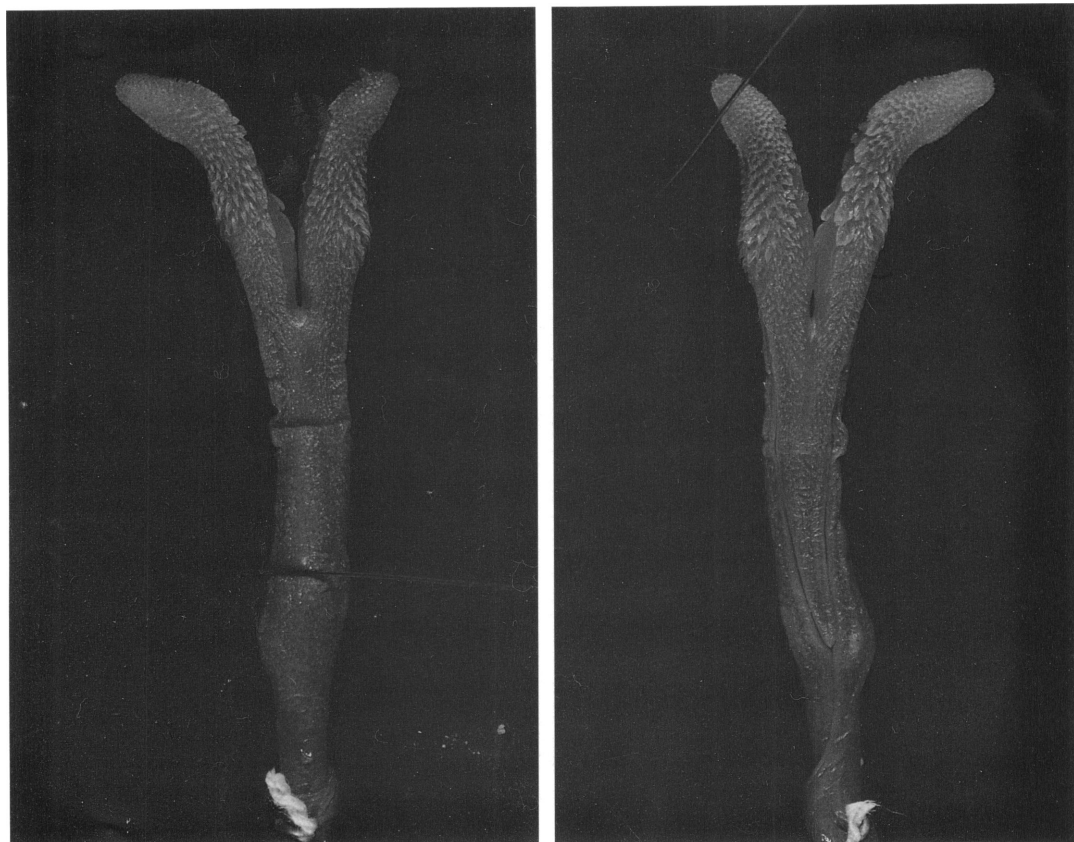


Fig. 16. Hemipenis of *Pseudoxenodon striaticaudatus* (AMNH 34675). Asulcate (left) and sulcate (right) views.

nude and the calyces are arranged in a bicalyculate condition, with each capitulum being ornamented on its edge by large papillate fringes. The nude medial surface on the lobes is not associated with the calyces, as in the xenodontines. It is rather restricted to the area below the calycular region, at the level of the spinulate lateral and sulcate surfaces. The hemipenial body is covered with small spines.

NATRICINAE

McDowell (1987: 39) stated that "it seems impossible to resolve the precise limits of the Natricinae without much more information on various Boodontinae." However, as pointed out above, all natricine genera (except *Amplorhinus*, *Xenochrophis*, and *Psammodynastes*; fig. 17) do share the derived condition of a highly centripetal sulcus with

broad divergent branches that tend to form a more or less developed nude area on the medial surface of the lobes (e.g., *Atretium* in fig. 17). A simple sulcus extending on the left side of the organ is viewed as a further derived condition within natricines. As pointed out above, this definition excludes *Amplorhinus*, *Xenochrophis*, and *Psammodynastes*, but not *Afronatrix* (fig. 18), *Hydraethiops* (fig. 18), *Sinonatrix*, *Opisthotropis*, and *Rhabdophis* (contra McDowell, 1987: 39). In the first three genera, the sulcus branches do not expand to form a distal nude area. These genera are here considered as Natricinae incertae sedis.

I follow Dowling and Duellman (1978) in recognizing *Natriciteres* (fig. 19) and *Limnophis* (fig. 19) as closely related taxa because of their derived hemipenial morphology (a unilobed organ with a highly con-

stricted distal region). These taxa show a natricine pattern in lacking calyces, having a simple sulcus spermaticus extending to the center of the distal end, and in having an organ covered with medium-sized spines. However, their highly derived hemipenial morphology does not allow a direct comparison with the above definition of the natricines; that is, the presumed synapomorphy of natricines (a highly centripetal sulcus with broad divergent branches) is inapplicable to them. For this reason, both genera are considered incertae sedis.

As previously suggested by Dowling and Duellman (1978), *Aspidura* is thought to belong to the Natricinae since it shows a typical natricine hemipenis covered with medium-sized spines, with a sulcus spermaticus extending to the center of the distal end of the organ and dividing centripetally to give rise to two enlarged branches that form a distal nude area.

DIPSADINAE

The dipsadine assemblage corresponds essentially to Cadle's Central American group. Recently, Myers and Cadle (1994) suggested three synapomorphies for this group: (1) reduction or loss of bilobation, (2) (uni)capitulation, and (3) distal division of the sulcus spermaticus (i.e., dividing within or at the base of the capitulum). Although character 1 is less reliable because it is present in various "colubrid" groups, as well as in some xenodontines, character 3 is nearly unique to the dipsadines, being otherwise present only in the Madagascan genus *Geodipsas*. Character 2 is variable within the Dipsadinae and may represent a synapomorphy supporting a less inclusive group of dipsadines. The condition in *Geodipsas* is regarded as nonhomologous to the one present in the dipsadines because, unlike the latter, the former taxon lacks calyces and shows a typically spinulate "pseudoxyrhophiine" lobe. As suggested by Cadle (1996a), the unilobed hemipenis of *Geodipsas* is derived from a bilobed condition and is more parsimoniously hypothesized as being derived from a bilobed "pseudoxyrhophiine" type instead of a bilobed "xenodontine" type because the latter scenario would have to ac-

count also for the loss of calyces and subsequent acquisition of a densely spinulate ornamentation.

Additions to Cadle's assemblage, as well as the placement of a particular genus as incertae sedis, were made following the only available synapomorphy discussed above (i.e., the sulcus spermaticus dividing distally within or at the base of the capitulum). Nevertheless, various genera regarded by previous authors as of uncertain position in the "colubrids," and retained here as incertae sedis, show the dipsadine derived state. These are *Diadophis*, *Contia*, *Carphophis*, *Hydromorphus*, *Nothopsis*, *Synopsis*, *Xenopholis*, and all "tachymenine" genera (except *Tachymenis peruviana*). The exclusion of these genera from the dipsadines may render the subfamily, as defined by Myers and Cadle (1994), paraphyletic. They are therefore included here in the Dipsadinae as incertae sedis, pending more study.

Within the dipsadines, the Dipsadini are likely to compose a monophyletic unit. The close affinity of the genera *Dipsas*, *Sibon*, *Sibynomorphus*, and *Tropidodipsas* is hardly disputable, because several uniquely derived features corroborate this group (Peters, 1960; Wallach, 1995). Similarly, *Atractus* and *Adelphicos* are here viewed as closely related since they share a highly developed muscle cervicomandibularis that extends posteriorly, far beyond the neck (personal obs.). Preliminary observations on the head anatomy of the dipsadine genera have shown that the Dipsadini, along with the genera *Geophis*, *Ninia*, *Enulius*, *Enuliophis*, *Chersodromus*, as well as the *Atractus/Adelphicos* clade, share the presence of a well-developed and completely differentiated muscle levator anguli oris. This apomorphic trait, present otherwise only in the sibynophiine *Scaphiodontophis* among the New World "colubrids," is regarded as an indication of the monophyly of this large group of highly specialized snakes. Also, *Ninia*, *Chersodromus*, *Enulius*, *Enuliophis*, and *Geophis* share the derived condition of highly developed Harderian glands that reach the anterodorsal surface of the muscle adductor mandibulae externus medialis pars posterior (sensu Zaher, 1994b). Additionally, *Enulius*, *Enuliophis*, and *Geophis* share a posterior expansion of the in-

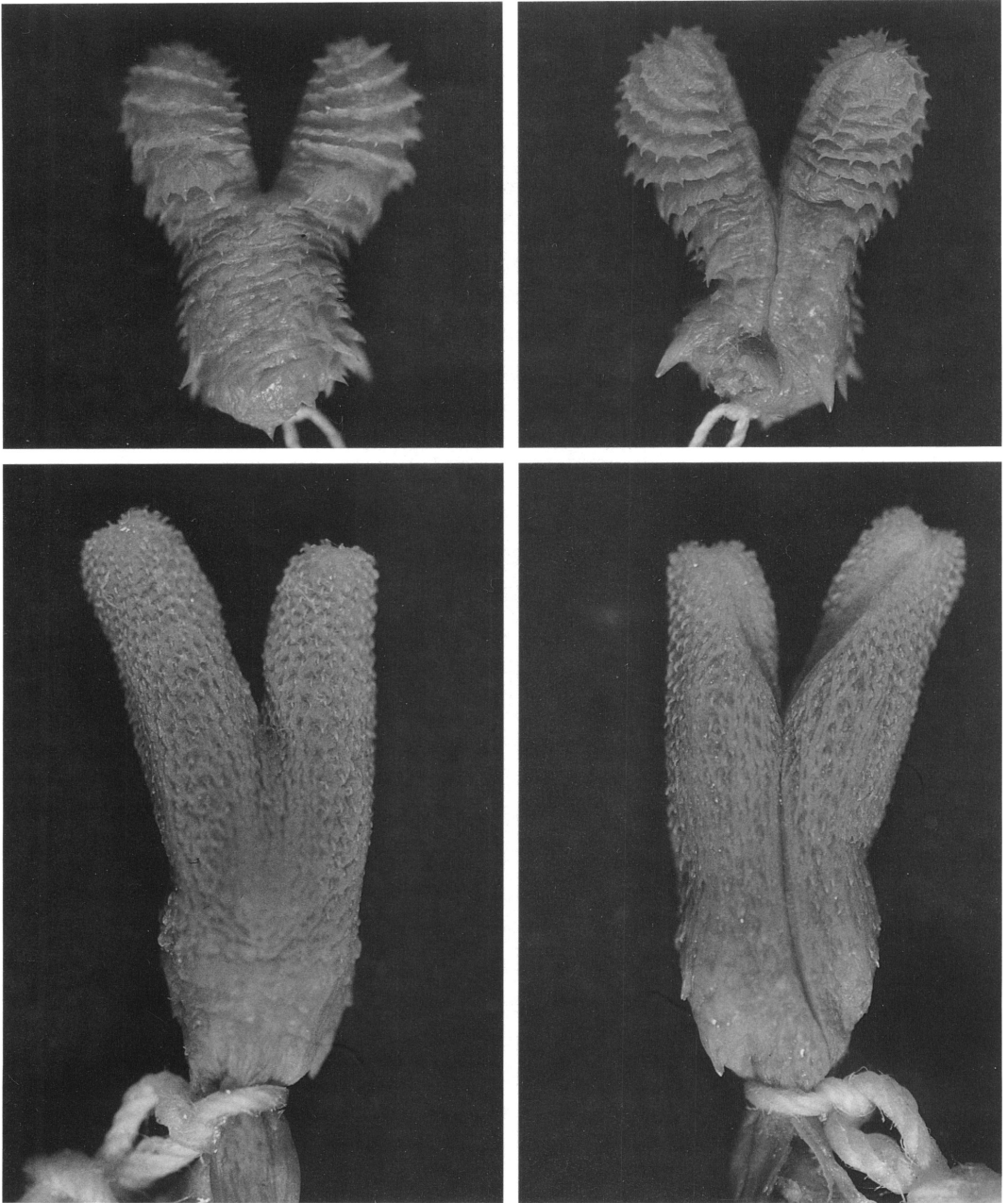


Fig. 17. Hemipenes of *Psammodynastes pulverulentus* (upper; AMNH 84547) and *Atretium schistosum* (lower; AMNH 96075). Asulcate (left) and sulcate (right) views.

fralabial glands that tends to be surrounded by the more lateral fibers of the muscle adductor mandibulae externus medialis pars posterior. These fibers most probably act as a "compressor glandulae."

The above conclusions point to a probable

paraphyletic condition of the nothopsines (sensu Savitzky, 1974) when all dipsadine genera are taken in consideration, with *Ninia* and *Chersodromus* being more closely related to *Geophis*, *Enulius*, and *Enuliophis* instead of their presumed nothopsine relatives

(Dunn, 1935; Dunn and Dowling, 1957; Bogert, 1964; Savitzky, 1974; Hillis, 1990).

A second assemblage of genera—the Lep-
todeirini—with the same generalized, unilobed, unicalyculate hemipenial condition as the Dipsadini, has been considered monophyletic (Cadle, 1984b). This assemblage, however, is apparently supported only by the close immunological distances shown by all five genera (including *Cryophis*), although *Leptodeira*, *Eridiphas*, *Hypsigena*, and *Imantodes* may represent a monophyletic unit diagnosed by the synapomorphic condition of an almost entirely undivided sulcus spermaticus (usually retaining a weak bifurcation at the distal tip) (Cadle, 1984b). On the other hand, two genera of uncertain assignment, *Tantalophis* and *Rhadinophanes*, have been mentioned as possible relatives of *Leptodeira* (Myers and Campbell, 1981), which could render the leptodeirines a paraphyletic assemblage as presently conceived.

XENODONTINAE

The present analysis of “colubrid” hemipenial morphology, with emphasis on the South American xenodontine genera, furnished the ground for the elaboration of a working hypothesis corresponding to a monophyletic Xenodontinae sensu stricto. This presumed clade is characterised by two apomorphic hemipenial traits: (1) rows of enlarged lateral spines mostly restricted to the sides of the hemipenial body (except for their distal and proximal extremities, which generally extend to the asulcate and sulcate sides, respectively), and (2) two distinctly ornamented regions on the lobes, with the sulcate surface bearing a capitulum and the asulcate surface bearing weakly developed or enlarged body calyces, or being completely nude. The body calyces may be spinulate or papillate.

All other “colubrids” investigated, including the Dipsadinae and the genera incertae sedis (see table 1 and appendix 1), lack both traits. *Diadophis*, *Carphophis*, and the “tachymenines” show an intermediate condition of slightly enlarged calyces on the asulcate side of the lobes, but no clear division of the lobular surface in calyculate and noncaly-

late regions, the enlarged calyces being clearly part of the capitulum.

Cadle’s (1984a, 1984b, 1984c, 1985, 1987, 1988) and Dessauer’s et al.’s (1987) immunological studies suggested that six North and Central American genera of xenodontine snakes are only distantly related to the two distinct xenodontine assemblages and to each other. However, I consider three of these genera—*Conophis*, *Heterodon*, and *Farancia*—to belong to the Xenodontinae because they have the two synapomorphies described above (i.e., enlarged lateral spines and body calyces). On the other hand, I follow Cadle’s view concerning the other three genera (*Contia*, *Carphophis*, and *Diadophis*) and retain them as incertae sedis, although they have a dipsadine hemipenial pattern as already stressed above. This question is not addressed herein because a more detailed review of dipsadine hemipenial morphology is needed.

A detailed explanation of the two Xenodontinae synapomorphies is given below.

1) *Two distinctly ornamented regions:* Body calyces are present in the asulcate and medial surfaces of the lobes. However, when the sulcus spermaticus is centrolineal, the body calyces are mostly restricted to an asulcate position on the lobes, and when the sulcus is centrifugal, the body calyces tend to be on a medial position on the lobes.

When the asulcate and/or medial surfaces of the lobes lack well-defined body calyces, they bear large vertically directed flounces, lobular crests, enlarged papillae, or are mostly (or entirely) nude. On the other hand, the sulcate and/or lateral surfaces of the lobes are always ornamented with a capitulum of calyces or flounces derived from calyces. Both regions are always on opposite sides on the lobes. Body calyces are always well differentiated from the capitular calyces. Indeed, when these two structures are present in the lobes, they can be easily distinguished. Generally, body calyces are present also on the distal region of the hemipenial body, in a straight line with the ones on the lobular surface. This straight line becomes interrupted or sinuous when the body calyces of the lobes are on a more medial position (= medial surface of the lobes) (e.g., *Boiruna maculata* and *Hydrodynastes*).

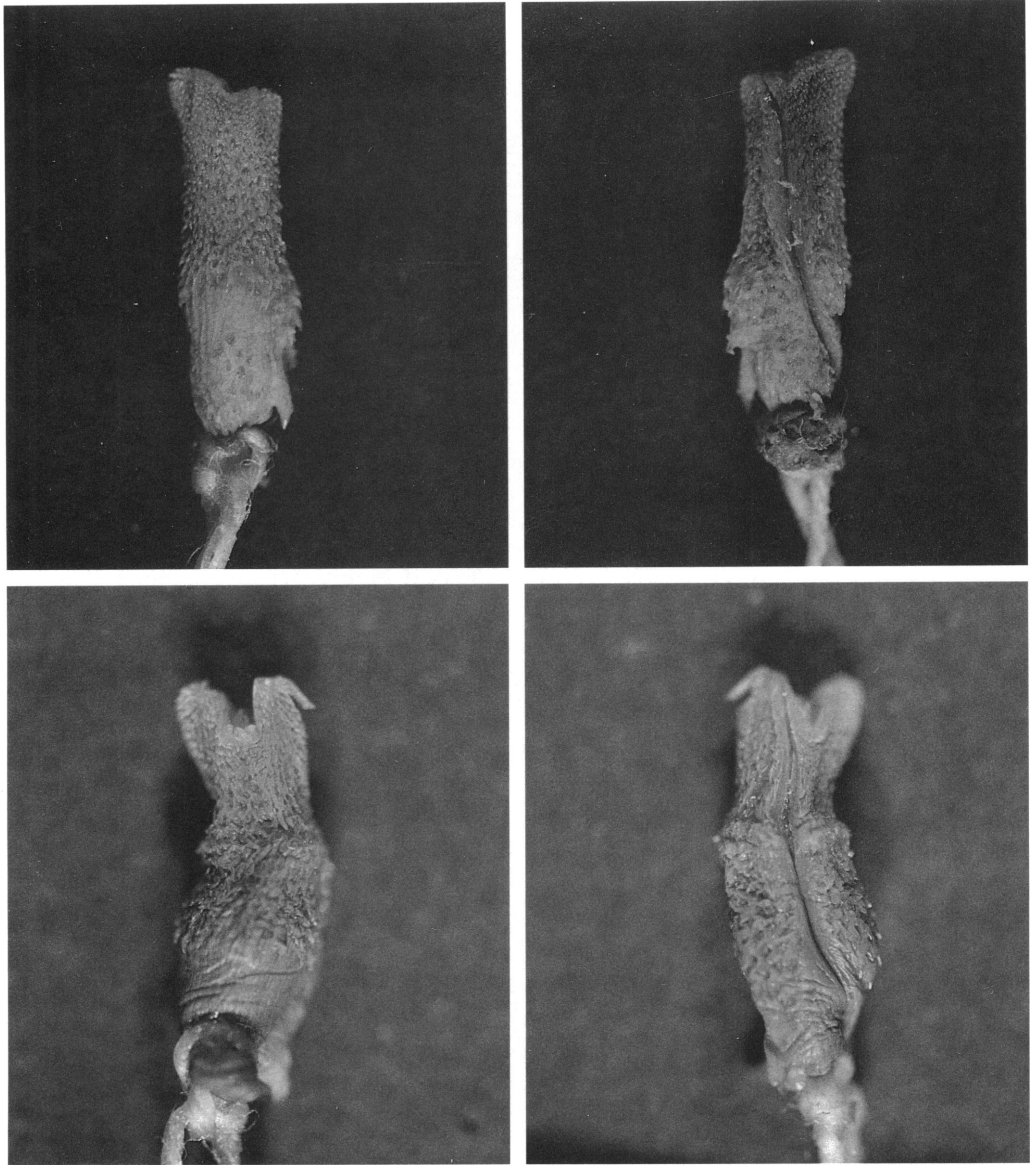


Fig. 18. Hemipenes of *Afronatrix anoscopus* (upper; AMNH 50524) and *Hydraethiops melanogaster* (lower; AMNH 11959). Asulcate (left) and sulcate (right) views.

I regard the condition of “completely nude asulcate/medial surfaces of the lobes” present in various Xenodontinae as the result of secondary loss, with the plesiomorphic condition for the Xenodontinae being represented by asulcate/medial surfaces ornamented with distinct body calyces. I base this on the assertion that body calyces are merely enlarged capitular calyces restricted to the asulcate/medial surfaces, that is, the result of re-

gional differentiation of the capitular calyces by enlargement of the latter and formation of an overhanging edge separating the enlarged body calyces from the capitular calyces. Indeed, in the Xenodontinae, the body calyces are almost always separated from the capitular calyces by a more or less developed overhang (except in a few genera). This overhang is generally present on the hemipenes where the asulcate/medial surfaces of

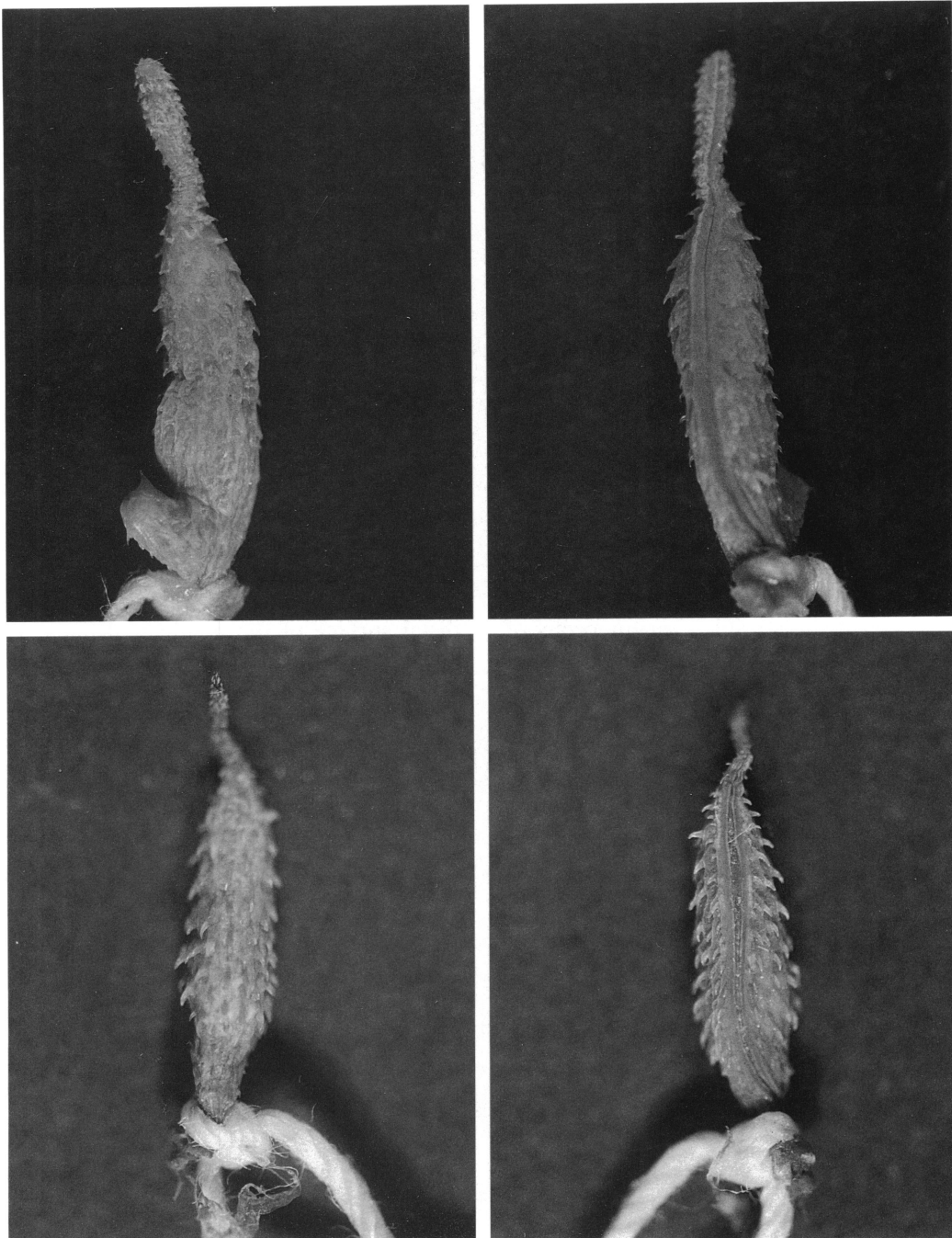


Fig. 19. Hemipenes of *Natriciteres olivacea* (upper; AMNH 11915) and *Limnophis bicolor* (lower; AMNH 50533). Asulcate (left) and sulcate (right) views.

the lobes are nude (e.g., *Psomophis*), supporting the view that the body calyces were secondarily lost. Poorly developed calyces or completely nude asulcate/medial surfaces of the lobes are thus derived from enlarged body calyces by reduction or complete loss. However, this may have happened independently in various lineages within the Xenodontinae, as suggested by their different patterns of reductions (see below).

Body calyces are present in most Xenodontinae examined. However, they have not drawn attention of investigators working on this group, with the exception of Thomas (1976) and Donnelly and Myers (1991). Thomas (1976: 57) referred to the body calyces in the following terms: "enlarged calyces extending down the asulcate surface." Donnelly and Myers (1991: 49) defined them as "very large shallow calyces extending down the distal one-third of the asulcate surface." Donnelly and Myers (1991) thought this feature was a possible synapomorphy of the genus *Philodryas*. However, body calyces are also found to extend far down the surface of the hemipenial body in *Pseudablades* and *Xenoxylbelis* (see below). Because body calyces are modified "capitular calyces" that are restricted to the lobular region and crotch, I view the presence of these structures far down on the hemipenial body as a more derived state where the body calyces extend from the lobes to the body.

Among the outgroups, all the other colubroids that have lobes ornamented with calyces have a more or less uniform distribution of the calyces on the lobular surface; in other words, the calyces forming the capitulum are similar all around the lobe(s) and lack any kind of differentiation such as enlarged and diminutive calyces on opposite surfaces (except for some colubrine species that do have enlarged calyces on the asulcate side of their lobe).

2) *Enlarged lateral spines*: These are present on two or more rows situated on the lateral sides of the hemipenial body. The rows are separated on the sulcate side by the sulcus spermaticus and by a region covered with spinules or body calyces on the asulcate side. Generally, the rows of spines meet their contralaterals at the base of the hemipenial body on its asulcate surface.

Among the South American xenodontine genera considered here, *Conophis*, *Manolepis*, *Uromacerina*, the *Hydropsini* sensu stricto (to be defined below), and the *Xenodontini* have peculiar hemipenial morphologies that are discussed in more detail below.

Maglio (1970) proposed a close affinity between *Conophis* and his "*cantherigerus* group" of *Alsophis*. However, the hemipenis of *Conophis*, very similar to that of *Manolepis*, differs greatly from that of the *cantherigerus* group in my observations. Cadle (1984a, 1984c) also questioned Maglio's proposal (1970) (see also Myers, 1974; Thomas, 1976), arguing against a close affinity between *Conophis* and any other xenodontine taxon. *Conophis* retains distinct enlarged lateral spines and large, shallow, spinulate flounces in a typical semicalyculate condition. The larger spinulate flounces, here viewed as modified body calyces, are distributed on the proximal surface of the lobes and distal surface of the hemipenial body. Both synapomorphic traits of the Xenodontinae are thus present in *Conophis*.

The genus *Manolepis* also has been considered to be of ambiguous phylogenetic position within the New World xenodontines. However, it shows well-developed enlarged lateral spines and shares with *Conophis* the presence of large and shallow spinulate flounces on the asulcate surface. The latter condition is viewed as a synapomorphy of these two genera. The hemipenial morphology of *Manolepis* also places it within the South American xenodontine radiation. Contrary to Thomas (1976: 262), I do not see any particular similarity between the hemipenes of *Manolepis* and *Philodryas*, except for a superficial resemblance that characterizes the hemipenial pattern of the Xenodontinae.

Previous attempts to resolve the affinities of the genera *Hydrops* and *Pseudoeryx* have failed (see Rossman, 1973; Cundall and Rossman, 1984). When one considers *Hydrops* and *Pseudoeryx* together, the dissimilar hemipenial morphologies suggest that they are not closely related (Rossman, 1973). Indeed, the only similarity seems to be the presence of medium-sized spines covering the body, a dipsadine characteristic. In contrast, their differences are numerous. *Pseu-*

doeryx lacks a capitular groove whereas *Hydrops* retains one. The latter shows greatly reduced lobes with only a few spinulate calyces ornamenting the distal area of the lobes, whereas the former has a slightly bilobed organ with a unicalyculate capitulum made up by numerous spinulate flounces distributed all around the lobes. As shown above, both genera have different hemipenial morphologies that do not approach the xenodontine hemipenial pattern described here. However, *Hydrops* and *Pseudoeryx* are here viewed to be part of the Xenodontinae because they share with *Helicops*, at least, one synapomorphy (see below). They also share with *Helicops* the presence of an extended trachea (extending through the ventral surface of the right lung up to its posterior end). Nevertheless, the tracheal feature is present in various other xenodontine genera and may be a synapomorphy at a higher level of universality within the Xenodontinae.

The genus *Helicops* is diagnosed by the presence of nude flounces on the lobes of the hemipenis. These structures are well developed and clearly derived from papillate or spinulate calyces, as shown by the retention of a calyculate ornamentation in the apex of the lobes of various species (e.g., *H. angulatus* and *H. carinicaudus*). All specimens examined show a "semicalyculate" (or feebly "bicalyculate") configuration with the calyces replaced by flounces (in the "feebly "bicalyculate" condition, the flounces are also present in the intrasulcar region), enlarged lateral spines, and a centrolinal sulcus spermaticus bifurcating on the proximal region of the hemipenial body. These characteristics place *Helicops* within the Xenodontinae. The body calyces seem to be absent; however, they may be vestigially present in some species (see descriptions herein and Rossman, 1973: fig. 2). It is here hypothesized that *Helicops*, *Hydrops*, and *Pseudoeryx* form the Hydropsini sensu stricto, a monophyletic unit characterized by the presence of a greatly enlarged muscle adductor mandibulae externus superficialis on its origin site (the width of the muscle, at its attachment point on the parietal and postorbital, is as long as or longer than the length of its fibers). This derived character state is otherwise present only in some "tachymenines"

and in two dipsadines (*Tretanorhinus* and *Hydromorphus*). The genus *Farancia*, which was associated phylogenetically with *Hydrops* and *Pseudoeryx* by Neill (1964; see Cundall and Rossman, 1984, for rebuttal), also lacks an enlarged adductor superficialis. The presence of a xenodontine hemipenial pattern in *Helicops* suggests that *Hydrops* and *Pseudoeryx* have secondarily lost the enlarged lateral spines and body calyces.

Dowling and Duellman (1978) and Jenner (1981) considered the genus *Uromacerina* to be a member of the Xenodontinae. Indeed, *Uromacerina* has distinct enlarged lateral spines and reduced papillate body calyces on the lobes, lobular crotch, and distal region of the hemipenial body. Each capitulum, however, is unusually enlarged and largely invades the asulcate surface of the lobes, restricting the body calyces to the proximal surface of the lobular crotch. The few well developed lateral spines are restricted to the distal half of the hemipenial body. However, both synapomorphic traits of the Xenodontinae are considered to be present in *Uromacerina*, which is therefore assigned to the subfamily.

All six genera of Xenodontini (sensu Dixon, 1980) have a Xenodontinae hemipenis with enlarged lateral spines. The lack of body calyces, capitulum, capitular groove and any microornamentation in the lobes (except the apical disks and numerous spinules) is considered as a secondary loss (Myers, 1986: 6). Apical disks are shared by all the members of this tribe, characterizing it as a monophyletic group (Dowling, 1975; Dowling and Duellman, 1978). A behavioral synapomorphy also appears to support their monophyly (Myers, 1986). A similar but not homologous "disk" (= nude distal area) is present in *Oxyrhopus* (Myers, 1986; Zaher and Caramaschi, 1992). Most of the species of *Oxyrhopus* do have completely nude "disks," but some (e.g., *O. formosus*) show an intermediate condition where weakly developed calycular walls are still present within the "disk's" surface, suggesting that these areas were formed by the loss of the walls forming the calyces. *Oxyrhopus* and the Xenodontini show the same enlarged fringe of tissue forming the edge of the disks, suggesting that both groups have gained distal

nude areas on their lobes by the same (but not homologous) process of reduction of the walls of the calyces.

Recently, V.L.F. Yuki (1993) named the new genus *Thalesius* to accommodate *Xenodon werneri*, which, according to the author, differs from the other species of *Xenodon* by the lack of apical disks in the hemipenial lobes. Furthermore, the new taxon is viewed by Yuki as of uncertain tribal and subfamilial allocation because of its aberrant hemipenial pattern. I disagree with both statements made by Yuki and consider *werneri* as belonging to the genus *Xenodon*. Yuki's latter argument is clearly refuted by the fact that *Thalesius*, *Waglerophis*, *Xenodon* and *Lystrophis* show several peculiar features of the head muscles and ligaments that are unique to them. These features were already described and discussed by Anthony and Serra (1949) and Romano and Hoge (1972), but were not mentioned by Yuki (1993). Particularly, the expansion of the insertion site of the muscle cervicomandibularis through the dorsal edge of the ligament quadrato-maxillaris, anteriorly to the quadrato-mandibular capsule, is here viewed as a derived character state shared by the genera *Thalesius*, *Xenodon*, *Lystrophis*, and *Waglerophis*, thus supporting this group as monophyletic and placing *Thalesius* unambiguously within the Xenodontini tribe. Indeed, all species examined in this monophyletic group show a tendency toward a completely independent anterior bundle of the muscle cervicomandibularis associated with an independent stripe of the quadrato-maxillaris ligament. *Waglerophis merremi* and *Xenodon guentheri* present the more derived condition as originally described by Anthony and Serra (1949; personal obs.). Additionally, *W. merremi* shares with *X. werneri* and *X. rabdocephalus* the derived condition of a pair of elongated lobes covered with medium-sized spines. The last two species show almost identical hemipenes, where the apical disks are absent (*X. werneri*) or poorly developed (the tip of the lobes in *X. rabdocephalus* are nude, a condition regarded as representing poorly developed apical disks). The vestigial presence or complete absence of apical disks in these species is here viewed as a secondary loss (probably due to the very slender

condition of their lobes) because all the Xenodontini, including the other species of *Xenodon*, have well-developed disks.

The morphological evidence presented above suggests that the presence of two distinct genera to accommodate *merremi* and *werneri*, as argued recently by Dixon (1980) and V.L.F. Yuki (1994), is likely to render the genus *Xenodon* paraphyletic.

The greatly simplified hemipenial morphology of the tribe Xenodontini precluded decisions on their affinities within the Xenodontinae.

THE WEST INDIAN GENERA OF XENODONTINAE AND ALLIED TAXA: The following text is concerned with the West Indian "alsophiines." All are considered to belong to the Xenodontinae because they have enlarged lateral spines and two distinctly ornamented regions on the lobes (most "alsophiines" present weakly developed body calyces). They are represented by the West Indian xenodontine genera *Alsophis*, *Antillophis*, *Darlingtonia*, *Hypsirhynchus*, *Ialtris*, *Uromacer*, the Cuban and extra-Cuban species of *Arrhyton*, and *Arrhyton exiguum*. The mainland and Galapagos species of the genus *Alsophis* and the genus *Saphenophis* are also treated here since they are considered to be more closely related to each other than to the other species of *Alsophis*. However, no evidence supporting the monophyly of the West Indian radiation was found on their hemipenial morphology. In addition, the genus *Saphenophis* and the mainland and Galapagos species of *Alsophis* lack any clearly derived feature that would relate them with any particular group of the West Indian radiation.

The West Indian species of the genus *Liophis*, forming Maglio's "melanotus assemblage," are not included in the West Indian Xenodontinae since this genus clearly pertains to the mainland Xenodontini. These will be treated independently below, following the account on the West Indian taxa.

The "alsophiines" tend to have a reduced number of ornamentations on the asulcate surface of the lobes. The genera *Ialtris*, *Uromacer*, the Lesser Antillean *Alsophis*, and the "callilaemum group" of *Arrhyton* show the least ornamented medial/asulcate surfaces of the lobes. In most of these taxa, the reduced ornamentation of the medial/asulcate surfac-

es has quite distinct patterns, suggesting that these may be the result of several independent ornamental reductions.

A comparison between the hemipenial morphology of the genus *Arrhyton* and the other West Indian xenodontine genera suggests that the genus, as presently conceived, is paraphyletic with respect to *Antillophis* and *Darlingtonia*. In fact, *Arrhyton* has had a controversial phylogenetic history since Maglio (1970) expanded the generic concept to include *A. exiguum*, *A. callilaemum*, *A. funereum*, and *A. polylepis*. To address this question, Schwartz and Garrido (1981) considered the extra-Cuban species as constituting a distinct group from the Cuban species assemblage, referring to the former as the "*callilaemum* group." However, hemipenial evidence leads to a distinctly different hypothesis of relationships than those proposed by Maglio and by Schwartz and Garrido. No conspicuous derived hemipenial feature was found to be shared by all species of *Arrhyton*.

On the other hand, three geographically demarcated assemblages with strikingly different hemipenial patterns were identified: (1) the Cuban species (*A. taeniatum*, *A. landoi*, and *A. vittatum*), (2) the Jamaican species (*A. funereum*, *A. polylepis*, and *A. callilaemum*), (3) the Puerto Rican species (*A. exiguum*). Each assemblage has at least one synapomorphy. Schwartz and Garrido's "*callilaemum* group" does not constitute a monophyletic unit because *A. exiguum* shows a very different hemipenial morphology, sharing with *Antillophis parvifrons* and *Darlingtonia haetiana* the synapomorphy of a row of large papillae aligned vertically on the lobular crotch and proximal region of the lobes (fig. 20) (Schwartz and Thomas [1965: fig. 4] described and figured this character). The Cuban assemblage is clearly set apart from the extra-Cuban species by their conspicuously different hemipenes. The three Cuban species examined share the synapomorphy of a medial papillate crest extending from the lobular crotch to the edge of the capitulum on each lobe, and forming a Y-shaped structure on the distal region of the body (fig. 20).

Both Cuban species and *A. exiguum* have a clearly xenodontine hemipenial pattern with conspicuous enlarged lateral spines.

Their medial papillate crests, extending from the lobular crotch to the edge of each capitulum, as well as the enlarged papillae in the lobular crotch are here hypothesized to be modified (vestigial) body calyces (fig. 20).

Within the extra-Cuban group of *Arrhyton*, from which *A. exiguum* has to be removed, only *A. callilaemum* shows a slightly but clearly bilobed organ (Myers and Campbell, 1981: fig. 12c) with still recognizable enlarged lateral spines. The hemipenis of this species shows the least derived condition from a typical xenodontine hemipenis, whereas *A. funereum* presents the more derived condition and *Arrhyton polylepis* an intermediate one. Their hemipenial morphology can be arranged in at least two ordered multistate characters reflecting (1) the progressive reduction of the enlarged lateral spines, and (2) the fusion of the lobes leading to an unilobed condition.

The three Jamaican species of *Arrhyton* share at least two synapomorphies: (1) complete loss of the capitular calyces, and (2) presence of an apical awn (secondarily lost in *A. funereum* due to the complete reduction of the distal region of the lobes). *Arrhyton funereum* and *A. polylepis* share the presence of a crest on the tip of their unique lobe, a presumably shared derived condition absent in *A. callilaemum*.

In conclusion, all species of *Arrhyton* are considered to belong to the Xenodontinae because they present at least one of the presumptive synapomorphies of the subfamily. However, I failed to find any derived feature shared by all the species of this genus. The highly divergent hemipenial morphology in each assemblage and the presence of a presumably uniquely derived feature shared by *A. exiguum*, *Darlingtonia*, and *Antillophis parvifrons* suggests that *Arrhyton* is paraphyletic. The above considerations contradict the phylogenetic hypothesis proposed by Maglio (1970: figs. 35, 36; where *A. funereum* is shown as the basal species of the genus). The present results also reject Maglio's (1970) hypothesis of a close affinity between *Arrhyton* and *Rhadinaea*. Crother (1989b; cited by Schwartz and Henderson, 1991) has recently proposed including the extra-Cuban *Arrhyton* in the genus *Darlingtonia*. No clear association based on hemipenial features was

found between *Arrhyton* and a particular mainland group.

Within the Greater Antillean taxa, *Alsophis cantherigerus*, *A. vudii*, and *Antillophis andreae* show a similar hemipenial morphology with enlarged papillate body calyces in the basal region and medial surface of the lobes (the asulcate surface being almost completely nude in the two species of *Alsophis*). All three species show flounces in the medial surface of the lobes, which extend to the asulcate surface in *A. andreae* and confer to it the "enigmatic" flounced condition already described and discussed by Grant (1943). These flounces result from the reduction of the vertically directed walls forming the body calyces, which are present but poorly developed on the lobular crotch. *Alsophis cantherigerus*, *A. vudii*, and *A. andreae* have the least modified hemipenial condition within the West Indian taxa examined, with well-developed papillate body calyces present in the lobular crotch and papillate flounces in the medial surface of the lobes (both medial and asulcate surfaces in *A. andreae*). An expanded papillate circular area is present in the lobular crotch of *A. cantherigerus* and *A. vudii*. *Antillophis andreae* shows a similar configuration in the lobular crotch. This feature is absent in all the other Xenodontinae examined and may well represent a synapomorphy uniting these species.

The Lesser Antillean *A. antillensis*, *A. rijersmai*, *A. rufiventris*, and *A. antiquae* share the derived condition of a bicalyculate, semicapitate hemipenis with the Hispaniolan *Alsophis anomalus*, *Hypsirhynchus ferox*, and the Puerto Rican *A. portoricensis*. This derived character may represent a synapomorphy of this group of snakes. The species of *Ialtris* examined lack calyces but have lobes ornamented with flounces in a typical "bicalyculate" position. I regard the flounced condition in *Ialtris* as derived from a bicalyculate condition as the one found in the Lesser Antillean, Hispaniolan, and Puerto Rican taxa cited above. *Ialtris* may be referred tentatively the latter assemblage.

Alsophis rijersmai, *A. rufiventris*, and *A. antiquae* have very similar hemipenes, with one clearly apomorphic feature: the presence of a thin fringe of tissue ornamenting the capitular edges. These three species share with

Uromacer and *Hypsirhynchus* the presence of a moderately inflated spinulate crest on the asulcate surface of the lobes. In *Uromacer*, the crest is ornamented with a row of well-developed spines instead of bearing a row of spinules. This derived condition is diagnostic of the genus. The crest is absent in *A. antillensis*, which, on the other hand, shares with *A. rufiventris*, and *A. antiquae* a groove-like depression on the lateral surface of the hemipenial body between the first and second groups of enlarged lateral spines (*A. rijersmai* may also present this condition; see description of the genus). *Alsophis anomalus*, *A. portoricensis*, and *Hypsirhynchus ferox* also show a topographically identical groove-like depression between the first and second rows of enlarged lateral spines. However, these three species lack the other rows of lateral spines, a condition that may be due to a secondary loss since all other West Indian snakes have more than two rows. The loss of these rows of enlarged lateral spines may represent a derived condition uniting these species. *Alsophis rufiventris*, *A. antiquae*, and *A. antillensis* share with *Ialtris* the presence of enlarged intrasulcar spines and a highly centrifugal condition of the lobes.

The hemipenial morphology was not sufficient to highlight the probable affinities of *Alsophis ater* within the West Indian radiation since it lacks any of the features discussed above. Also, the precise phylogenetic position of *Uromacer*, *Hypsirhynchus*, and *Ialtris* is still problematical. Maglio (1970) proposed a close affinity between *Ialtris* and *Alsophis*. This point of view was rejected by Schwartz and Rossman (1976) who concluded that, in the absence of evidence, *Ialtris* remains with uncertain affinities within the West Indian Xenodontinae.

No synapomorphy was found uniting unambiguously all the Lesser Antillean species of the genus *Alsophis* to the exclusion of the other West Indian taxa.

The genus *Saphenophis* was erected by Myers (1973) to accommodate five enigmatic "South American xenodontine" species. *Saphenophis* clearly belongs to the Xenodontinae, as shown by its hemipenial pattern. Maglio (1970) had suggested that *Lygophis* (= *Saphenophis*) *boursieri* was closely related to his new genus *Antillophis*. However,

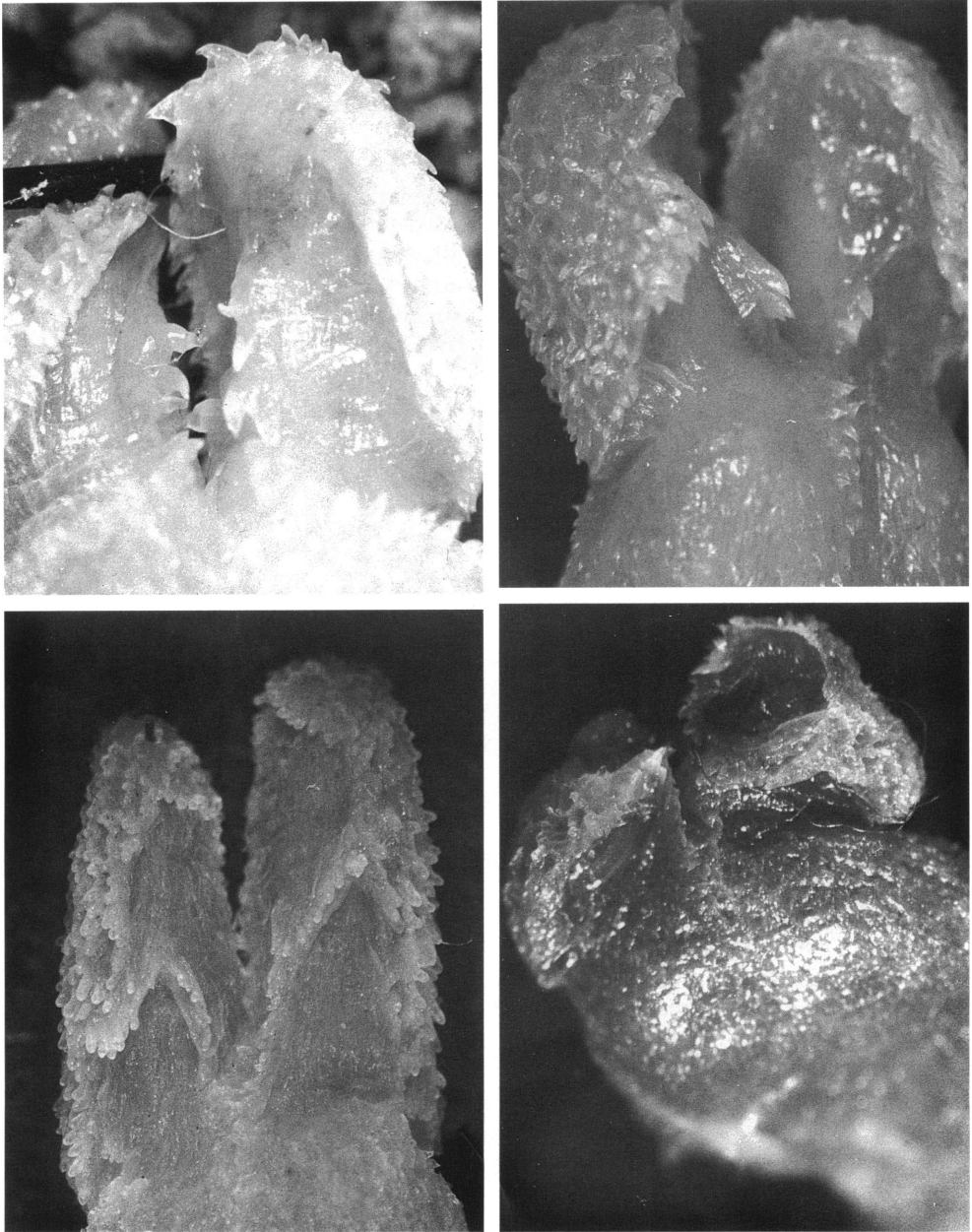


Fig. 20. Asulcate and medial surfaces of the lobes of *Arrhyton exiguum* (upper left; RT 10079), *Darlingtonia haetiana* (upper right; RT 6141), *Arrhyton taeniatum* (lower left; MNHN 695), and *Arrhyton landoi* (lower right; KU 268377).

Maglio's (1970) hypothesis could not be corroborated by Myers (1973).

As noted above, there is no evidence relating *Saphenophis* and the mainland (*A. elegans*) and Galapagos (*A. biserialis*, *A. hoodensis*, *A. occidentalis*, *A. steindachneri*) spe-

cies of *Alsophis* with any particular taxon of the West Indian radiation, except that they all show a tendency toward the reduction and loss of the ornamentation on the asulcate and medial surfaces of the lobes and lobular crotch. On the other hand, *A. steindachneri*

and the genus *Saphenophis* share a topographically similar papillate ridge on the medial surface of the lobes. Myers (1969: 16) already described this ridge: "there is a bare pocket on the lobe, in addition to the bare strip present in [*S.*] *boursieri*, but the important feature is probably the ridge of tissue that separates these two unadorned areas. The ridge possibly forms a characteristic protuberance on the nude side of the lobe, when the hemipenis of [*S.*] *tristriatus* is everted." Aside from the presence of a ridge on their hemipenes (very weakly developed in *S. boursieri*), these two species of *Saphenophis* show strikingly different hemipenial morphologies. Among the mainland and Galapagos species of the genus *Alsophis*, *A. hoodensis* shows the least conspicuous papillate ridge. The inflated papillate ridge on the medial surface of the lobes of *Saphenophis* and the Galapagos and mainland species of *Alsophis* is here considered as a synapomorphy of this group. In addition, in the Galapagos *Alsophis* and in *A. elegans*, the ridge is placed very far medially (on the medial surface of the lobes) in an almost sulcate position, a condition that is here considered to be a synapomorphy of these species.

In conclusion, Maglio (1970) proposed several assemblages, some of which are in contradiction with the present hemipenial evidence. Among these contradictions, the most important are (1) the Galapagos species of *Alsophis* are thought to be more closely related to *A. elegans* and the genus *Saphenophis* than to *Antillophis*; (2) the "*cantherigerus* assemblage" is paraphyletic, or polyphyletic if one includes *Philodryas chamissonis*, *P. tachymenoides*, and *P. simonsi* as suggested by Maglio (1970: 22); (3) the genus *Antillophis* seems to be paraphyletic, as previously hinted by Myers (1973); and (4) Maglio's "*funereus* assemblage" is paraphyletic since *A. exiguum* is more closely related to *Darlingtonia* and *Antillophis parvifrons* than to any other species of *Arrhyton*. However, as argued above, I was unable to associate with certainty the "*callilaemum* group" of *Arrhyton* (the extra-Cuban species) with any other group of Xenodontinae; the systematic position of the last group of *Arrhyton* poses a real problem that necessitates further attention.

After the conclusion of this paper, I received a manuscript from Crother (presently in review in *Cladistics*) where the author reaches similar conclusions concerning the affinities of the West Indian xenodontines. This work (Crother, MS) estimates the phylogenetic relationships of 42 mainland and West Indian species from 25 genera based on allozyme data from electrophoresis. Various nomenclatural changes, similar to the ones suggested in the present study, are proposed by Crother (MS).

THE MAINLAND GENERA OF XENODONTINAE: All the following genera show enlarged lateral spines and weakly or well-developed body calyces: *Apostolepis*, *Boiruna*, *Clelia*, *Ditaxodon*, *Drepanoides*, *Elapomorphus*, *Farancia*, *Heterodon*, *Hydrodynastes*, *Oxyrhopus*, *Phalotris*, *Philodryas*, *Phimophis*, *Pseudablakes*, *Pseudoboa*, *Rhachidelus*, *Siphophis*, *Tripanurgos*, *Uromacerina*, and *Xenoxybelis*.

The following South American genera show enlarged lateral spines but instead of body calyces, they have nude asulcate/medial surfaces on the lobes or else have lobes ornamented only by spinules or flounces: *Erythrolamprus*, *Conophis*, *Helicops*, *Liophis*, *Lystrophis*, *Manolepis*, *Psomophis*, *Tropidodryas*, *Waglerophis*, and *Xenodon*. Most species of *Helicops* have papillate flounces on their lobular crotch which are here considered to be derived from the body calyces (see hemipenial description of the genus).

Hydrops and *Pseudoeryx* are the only South American genera that are here considered as belonging to the Xenodontinae despite the lack of both hemipenial synapomorphies. This conclusion is based on one morphological feature (i.e., a greatly enlarged muscle adductor mandibulae externus superficialis on its origin site) that relates them to *Helicops*, clearly a member of the Xenodontinae (see above).

For most of these genera the hemipenial morphology is not sufficient to illuminate their phylogenetic position within the Xenodontinae. A more thorough review including a comparison of all other available morphological evidence is needed to address the question of Xenodontinae interrelationships. However, several hemipenial features of pos-

sible phylogenetic value were found and are discussed below.

The genera *Xenoxybelis*, *Philodryas*, and *Pseudablables* have very similar hemipenes. *Xenoxybelis argenteus*, as a result of its highly derived morphological specializations for arboreality, is set apart from all other taxa recognized here as Xenodontinae. The only exception is the genus *Uromacer*, which shows the same degree of specialization to arboreality; however, no affinities between these two genera can be seriously hypothesized, since they show highly different hemipenial patterns. Indeed, the genus *Uromacer* has mostly nude medial surfaces of the lobes, whereas *Xenoxybelis* has a semicalyculate hemipenis with a heart-shaped pattern retaining well-developed body calyces on all the asulcate surface of the hemipenial body and lobes, enlarged lateral spines invading the lateral surface of slightly bilobed lobes, and the capitulum of each lobe restricted to the sulcate surface of the organ. This morphology is strikingly similar to the hemipenis of *Philodryas cordata* figured by Donnelly and Myers (1991). The same heart-shaped hemipenis is present in *Philodryas viridissima* and *P. olfersii*. *Xenoxybelis* and the last three species of *Philodryas*, here called the "*olfersi* group," may form a monophyletic unit characterized by the following derived character states: (1) developed body calyces over nearly all the asulcate surface of the hemipenis, extending from the tip of the lobes to the base of the organ; and (2) a heart-shaped hemipenis with the capitulum of each lobe confined to the sulcate surface of the organ.

On the other hand, *Philodryas psammophidea*, *P. aestiva*, *P. chamissonis*, *P. patagoniensis*, *P. borellii*, and *P. livida* have a long hemipenis with body calyces confined to the asulcate surface of the lobes, the lobular crotch, and the distal surface of the hemipenial body on its asulcate side. The enlarged lateral spines do not invade the lateral surface of the lobes as in the "*olfersi* group." The sulcate and lateral surfaces of the lobes are ornamented with well-developed capitula. This group of *Philodryas* will be called the "*chamissonis* group." However, no unambiguous derived character state was found for this group, which may represent a paraphyletic assemblage. Their hemipenial pat-

tern is very similar to that shown by *Pseudablables*, with which they share a distal surface of the hemipenial body covered with body calyces as well as a very long, slender hemipenial body. However, both conditions are also found in *Hydrodynastes* (see fig. 51) and *Phalotris* (see fig. 63) and thus could not be viewed as an uniquely derived feature uniting the "*chamissonis* group" and *Pseudablables*.

The paraphyly of the genus *Philodryas* is suggested here based on the presence of two derived character states shared by part of the "*olfersi* group" and *Xenoxybelis* (i.e., body calyces extending from the tip to the base of the asulcate side of the hemipenis and a heart-shaped organ). The genus *Pseudablables* may also be part of *Philodryas* because of the similar hemipenial morphology shared with the "*chamissonis* group." However, as noted above, I failed to find any derived character state shared unambiguously by the "*chamissonis* group" and *Pseudablables*. No nomenclatural decision should be taken until a more thorough phylogenetic analysis of the genus *Philodryas* and its allies becomes available.

The Pseudoboini as here delineated includes the genera *Boinuna*, *Clelia*, *Drepainoides*, *Oxyrhophis*, *Phimophis*, *Pseudoboa*, *Rhachidelus*, *Siphophis*, and *Tripanurgos*. Zaher (1994a, 1996c) has shown that the taxonomic situation present in the Pseudoboini requires important nomenclatural changes in order to represent the evolutionary hierarchy of the tribe. Nevertheless, the monophyly of the Pseudoboini is corroborated by eight synapomorphies of which the following are hemipenial: (1) presence of a pair of calycular pockets in the lobular crotch; (2) enlarged lateral spines extending onto the lobular crests; (3) lobular crests inflated, at least in their basal region; (4) hemipenis slightly or deeply bicalyculate and bicapitate (Jenner and Dowling, 1985).

Jenner and Dowling (1985) suggested that the genera *Saphenophis* and *Tropidodryas* belong to the Pseudoboini; however, these genera do not share the eight synapomorphies of the Pseudoboini, and thus are definitively removed from this tribe (see also Des-sauer et al., 1987; Zaher and Caramaschi, 1992; Myers and Cadle, 1994). Most of the

genera in the Pseudoboini have weakly developed body calyces on the medial and asulcate surfaces of the lobes. All of them lack body calyces on the hemipenial body. However, the pair of calycular pockets lying on the lobular crotch is here viewed to be derived from the body calyces.

Ferrarezzi (1993) has shown that the monophyly of the Elapomorphini, including the genera *Elapomorphus*, *Phalotris*, and *Apostolepis*, is well corroborated. A preliminary analysis of the head muscles of representatives of these genera (Zaher, 1994a) has shown that they share the presence of a muscle adductor mandibulae externus superficialis with dorsal fibers forming a U around the Duvernoy's gland and ventral fibers attaching to the fascia of the gland (acting as a compressor glandulae, except in *E. quinquelineatus*; Savitzky, 1979), a hypertrophied muscle retractor quadrati with a greatly developed insertion zone (Zaher, 1994a), the rearward displacement of the muscle adductor mandibulae externus superficialis to reveal the Harderian gland dorsally, and the reduction or loss of the quadrato-maxillary ligament (except for *E. quinquelineatus*, where the ligament is still present and well developed). The hypothesis suggested by Underwood and Kochva (1993) of a close affinity with the "aparallactines" is here rejected based on the hemipenial pattern shown by the Elapomorphini, which clearly places them within the Xenodontinae (Zaher, 1994a). Indeed, the Elapomorphini have a semicalyculate hemipenis with enlarged lateral spines and body calyces on the asulcate surface of the lobes and hemipenial body. Species examined of *Apostolepis* have a single lobed hemipenis that is here hypothesized to be derived from the bilobed condition present in the other Elapomorphini and Xenodontinae, since they retain the other features of the Xenodontinae discussed in the present study.

COMMENTS ON SOME GENERA OF PROBLEMATIC ASSIGNMENT: The genus *Sordellina* was considered by Jenner (1981) as closely related to *Rhadinaea*, suggesting an affinity with the dipsadines. However, she placed this taxon in the Diaphorolepidini, which belongs to her "Southern group," without any discussion. Neither hypothesis is supported by the

hemipenial morphology. Because no data are presently available, the genus *Sordellina* is maintained as incertae sedis.

The genus *Echinanthera* was revived recently by Di-Bernardo (1992) to accommodate the "brevirostris-group" of *Rhadinaea*, previously identified and defined by Myers (1974), and the "*Liophis*" *undulatus* group. Myers and Cadle (1994) restricted *Echinanthera* to the *undulatus* group (including *E. amoena*, *E. cyanopleura*, *E. melanostigma*, and *E. undulata*) and resurrected *Taeniophallus* to accommodate the species of the "*Rhadinaea*" *brevirostris* group (Myers, 1974).

Myers (1974) had suggested a closer affinity between the "brevirostris-group" and the Xenodontinae instead of with any other group of *Rhadinaea* (see also Cadle, 1984b). Concerning their hemipenial morphology, the genera *Echinanthera* and *Taeniophallus* present a generalized dipsadine pattern suggested by the unilobed condition of the organ, the bifurcation of the sulcus spermaticus within a unicalyculate, a unicapitate capitulum, and the presence of numerous medium-sized spines on the hemipenial body. According to the hemipenial drawings figured by Myers (1974) and Di-Bernardo (1992), *Echinanthera* has several rows of spines mostly restricted to the lateral and sulcate sides of the organ. However, these are clearly not homologous to the enlarged lateral spines of the Xenodontinae. Indeed, a comparison made between both genera has shown that several intermediate conditions are present between a hemipenial body almost entirely covered with medium-sized spines and a body with a nude asulcate surface and rows of spines almost restricted to the lateral sides. The large, undulated nude region in the asulcate surface of most species results from the rearrangement of the rows of spines on this region that tend to migrate to the lateral sides. Such a tendency is more or less conspicuous on each species. However, most species present the generalized dipsadine pattern of medium-sized spines covering most of the surface of the hemipenial body. The nude area corresponds to an evolutionary novelty that may represent a synapomorphy of *Echinanthera* and *Taeniophallus* (see descriptive accounts of both genera). Neverthe-

less, their phylogenetic position remains ambiguous as they lack enlarged lateral spines and body calyces. For this reason, both genera are viewed as *incertae sedis*.

The hemipenis of the genus *Xenopholis* clearly has a dipsadine pattern that lacks distinct enlarged lateral spines and body calyces. *Xenopholis* is placed in *incertae sedis*, along with its probable nothopsine relatives, because it does not show a clear affinity with either the Xenodontinae or any of the subgroups of dipsadines.

The genus *Enuliophis* was recently erected by McCranie and Villa (1993) to accommodate *Enulius sclateri*, which has a hemipenis differing markedly from the other species of the genus. Both genera were considered to be closely related because of their long, thickened, fragile tail, a feature thought to have evolved independently in *Urotheca* (Savage and Crother, 1989). Their hemipenial morphologies, described by McCranie and Villa (1993), correspond to the dipsadine one due to the presence of a sulcus spermaticus bifurcating in the distal region of the organ and (scarce) enlarged spines uniformly distributed on the surface of the hemipenial body. Nevertheless, *Enuliophis* has a greatly reduced number of spinules and spines and lacks other hemipenial ornamentations such as calyces, thus preventing further phylogenetic considerations. Both *Enulius* and *Enuliophis* are placed in *incertae sedis* despite the fact that they share with *Geophis* a derived condition of the infralabial glands associated with the adductor muscles (personal obs.). This is a conservative position that reflects my belief that any new taxonomic arrangement of these genera must depend on a better understanding of the phylogenetic relations among all the dipsadines and the genera placed here in *incertae sedis*.

The hemipenial morphology of *Crisantophis*, *Rhadinophanes*, and *Tantalophis* has been described already in the literature (Villa, 1971; Myers and Campbell, 1981). The available descriptions confirm that all three genera have a generalized dipsadine pattern and lack the presumptive synapomorphies of the Xenodontinae. These genera are thus maintained in *incertae sedis*.

The genera *Tachymenis*, *Thamnodynastes*, *Tomodon*, *Ptychophis*, *Gomesophis*, *Pseudo-*

tomodon, and *Calamodontophis* represent Bailey's (1967, 1981; see also Amaral, 1935; McCoy and Richmond, 1966) Tachymenini. The genus *Opisthoplus* was considered by Bailey (1967) to be a synonym of *Tomodon*, whereas Peters and Orejas-Miranda (1970) and Vanzolini (1986) considered it a valid genus. Apart from the question of its validity, it seems justified to consider *Opisthoplus* to be a close relative of *Tomodon* (Bailey, 1967), and thus a member of the Tachymenini. McCoy and Richmond (1966) and Bailey (1967) recognized viviparity as an unifying character for these taxa. However, viviparity also occurs in two presumably unrelated genera—*Helicops* (Amaral, 1927; Rossman, 1973) and *Pseudoeuryx* (Cunha and Nascimento, 1981). Porto and Caramaschi (1988), in describing the biology of *Ptychophis*, argued for an independent appearance of viviparity in the "tachymenines" on the one hand, and in *Helicops* and *Pseudoeuryx* on the other hand, as a result of the adaptive advantages provided by this kind of reproduction to forms living in an aquatic environment (Fitch, 1970: 216; Rossman, 1973). They may also have been influenced by Fitch's (1970: 214) statement that "the attainment of viviparity seems an easy step in [squamatan] evolution." No additional evidence corroborating the monophyly of this group is presently available. The hemipenes of the "tachymenines" (*Opisthoplus*, *Pseudotomodon*, and *Calamodontophis* [not available]) have a dipsadine pattern with a sulcus spermaticus bifurcating in the capitulum (except in *Tachymenis peruviana*), a poorly defined bilobation, and a hemipenial body covered with medium-sized spines. None of them show any vestige of body calyces or enlarged lateral spines. For this reason, the "tachymenines" are placed in *incertae sedis*.

COMPARATIVE MORPHOLOGY OF HEMIPENIAL PATTERNS IN COLUBROIDS: A PRELIMINARY VIEW

As argued above, viperids and elapids are supported as monophyletic units (Underwood, 1967; McCarthy, 1985). On the other hand, there is no unequivocal evidence to support a monophyletic "Colubridae," and such a hypothesis is not retained in this discussion. Molecular data suggest that the atractaspidids and

"boodontines" represent basal "colubrid" lineages (Cadle, 1988, 1994; Heise et al., 1995; Dowling et al., 1983, 1996), but these show conflicting results for the phylogenetic position of the "xenodontines" (Cadle, 1988; Dowling et al., 1983, 1996). The hemipenial morphology of the atractaspidids, "xenodermatines," "homalopsines," natricines, and pseudoxhyrophiiines is rather plesiomorphic because they retain at least three character states found in the acrochordoids and tropidophioids: (1) a centripetal or slightly centrolineal sulcus spermaticus, (2) a sulcus that bifurcates distally within or just below the crotch, and 3) the absence of calyces. The "boodontines" lack calyces but their sulcus spermaticus shows the derived conditions of being in a clearly centrolineal or centrifugal position and in bifurcating more proximally on the hemipenial body, at least on the middle of it.

The viperids and elapids retain both plesiomorphic conditions of the sulcus spermaticus but have calyces on their lobes (except for *Homoreselaps* and part of *Calliophis*).

Among the other "colubrids," the colubrines, xenodontines, pseudoxenodontines, pareatines, and calamariines have both derived conditions for the position and bifurcation of the sulcus and also retain calyces. Whether the presence of calyces is a synapomorphy for all these taxa, the elapids, and viperids or has arisen independently in two or more lineages is a question that will have to be addressed within a broader phylogenetic analysis. The dipsadines are peculiar in having a sulcus spermaticus that is centrolineal or centrifugal but bifurcates distally on the organ. However, examination of the condition present in dipsadines shows that most of them have a rather proximal bifurcation of the sulcus, at least at the level of the middle or distal half of the organ (the exceptions are *Tretanorhinus*, *Hydromorphus*, some *Leptodeira*, *Contia*, and

various "tachymenines"), and that the branches are always in a clearly centrolineal or centrifugal position (the exceptions being *Tantalophis* and *Rhadinophanes*, which have centripetal sulci; Myers and Campbell, 1981). The dipsadine condition is here viewed to be further modified from a centrolineal or centrifugal sulcus spermaticus dividing on the middle or proximal half of the organ.

The sulcus spermaticus is considered to divide basally in the colubrines because when the hemipenis is bilobed, the asymmetrical simple sulcus is in a centrolineal position within the proximal region of the hemipenial body. An asymmetrical condition of the sulcus is considered primitive to a symmetrical one because the former is present in all other caenophidians with a divided sulcus (both branches of a sulcus run asymmetrically). In colubrines, the symmetrical sulcus is always associated with a unilobed organ. On the other hand, the asymmetrical sulcus is often present in bilobed organs but may also be present in a unilobed hemipenis (e.g., *Chionactis*; Dowling and Duellman, 1978: fig. 112c.6). Variation of the sulcus within colubrines is here viewed as an ordered multistate character transformation: (0) sulcus divided (and therefore asymmetrical) in a bilobed organ (plesiomorphic condition), (1) sulcus simple and asymmetrical in a bilobed organ, (2) sulcus simple and symmetrical in a unilobed organ. The criterion for this choice is morphological intermediacy.

Finally, the presence of spines/spinules in the hemipenis is regarded as a synapomorphy of the Caenophidia. The presence of spines on the hemipenial body is here viewed as a synapomorphy of the Colubroidea because spines/spinules are restricted to the lobes in the Acrochordoidea. However, this hypothesis will have to be tested by congruence with other characters.

GENERIC SYNOPSES OF HEMIPENIAL FEATURES IN THE XENODONTINAE

The following section presents a comparison of hemipenial variation within each genus considered to belong to the Xenodontinae as well as for those placed in incertae sedis. Genera for which hemipenes were not

available are not included below. The dipsadines (table 1) are not included since they are beyond the focus of the present review.

Genera presented below are organized in alphabetical order. Published illustrations and

relevant references are listed and discussed in the section titled "References and Remarks." This section is not intended to be exhaustive. For genera with more than one species, I opted to present synopses focusing on the differences found between them instead of providing an accurate description for each species, because most species of many genera have not been examined. Thus, these synopses are not definitive and are intended primarily to provide a useful framework for future investigations.

Table 1 lists genera that belong to the Dipsadinae (sensu Cadle, 1984c; Myers and Cadle 1994), the Xenodontinae (as defined in the present study), and those considered as incertae sedis. Among the genera placed in the Xenodontinae, hemipenes were unavailable only for *Umbrivaga*. However, this genus clearly belongs to the Xenodontini as shown by the data already available (see Roze, 1964; Dixon, 1980; Myers, 1969, 1973).

Two other genera presumed to belong in the Xenodontinae, *Lioheterophis* and *Cercophis*, are here considered as incertae sedis because little information is available concerning their affinities and morphologies. Hoogmoed (1982) resurrected the genus *Cercophis* and tentatively included it in the "xenodontines." However, the author clearly stated that additional data and material were needed to confirm such arrangement.

No hemipenial material was available for the following genera placed in incertae sedis: *Calamodontophis*, *Cercophis*, *Crisantophis*, *Diaphorolepis*, *Emmochliophis*, *Enuliophis*, *Enulius*, *Hydromorphus*, *Lioheterophis*, *Opisthoplus*, *Pseudotomodon*, *Rhadinophanes*, and *Tantalophis*. However, *Crisantophis* (Villa, 1971), *Echinanthera* (sensu Myers and Cadle, 1994), *Enulius*, *Enuliophis* (McCranie and Villa, 1993), *Hydromorphus* (Crother, 1989a), *Rhadinophanes*, and *Tantalophis* (Myers and Campbell, 1981) have had their hemipenial morphology well described and figured.

As for the remaining "xenodontine" genera retained as incertae sedis, knowledge of their hemipenial morphology has shown that all the above taxa lack the xenodontine synapomorphies described herein. However, most of these taxa have a dipsadine hemi-

penial morphology, fitting perfectly the definition given by Cadle (1984c) and by Myers and Cadle (1994), and likely belong in the Dipsadinae. This is also true for the genera *Diadophis*, *Contia*, and *Carphophis*, considered by Cadle (1984b) to be only distantly related to the xenodontines. Nevertheless, because this problem needs to be addressed in more detail, I adopt a conservative approach, following propositions made by Cadle who reviewed the phylogenetic position of the taxa in question. Additionally, taxa that do have a dipsadine hemipenis, but were considered to be of uncertain assignment by the last reviewer, are maintained as incertae sedis instead of being included in the Dipsadinae (see above discussions for more detail).

Alsophis

Figures 21–30

SPECIES EXAMINED: *A. anomalus* (AMNH 44839), *A. antiquae* (AMNH 2832), *A. antillensis* (MNHN 1991.1486, 1991.1487, 1991.1489; USNM 11214, 325085), *A. ater* (MNHN 497), *A. dorsalis* (USNM 115614), *A. cantherigerus* (AMNH 83207; MNHN 1883.384, 1883.385), *A. elegans* (MNHN 7630; one uncataloged specimen), *A. hoodensis* (MNHN 1963A99; USNM 96005), *A. occidentalis* (AMNH 91474), *A. portoricensis* (AMNH 99545, 13774, 102577, 32984), *A. rijersmai* (MNHN 1991.439), *A. rufiventris* (AMNH 2932; MNHN 3560, 3559), *A. steindachneri* (AMNH 42887), *A. vudii* (AMNH 77017; MPMH 22048).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Ocyophis ater* (= *Alsophis ater*) and *Alsophis angulifer* (= *A. cantherigerus*). Brongersma (1959) published a diagram of a dissected organ of *A. rufiventris* showing the relative position of enlarged spines. Maglio (1970) compared the hemipenial morphology of various *Alsophis* species with other West Indian taxa and provided drawings of dissected organs of *A. ater* and *A. portoricensis*. Jenner (1981) figured the sulcate side of the hemipenis of *A. slevini* (= *A. occidentalis*) (see also Jenner and Dowling, 1985: fig. 5). Maglio (1970), in his review of the West Indian xenodontine radiation, expanded the genus *Alsophis* to accommodate the Galapagos forms previously

assigned to the genus *Dromicus*, as well as the mainland *Philodryas chamissonis* and *P. tachymenoides*. *Philodryas elegans* remained of uncertain affinities. Thomas (1977) placed *Philodryas chamissonis* and *P. tachymenoides* (assigned to *Alsophis* by Maglio) back in the genus *Philodryas*, concluding that all mainland species previously assigned to *Alsophis* actually belong to the genus *Philodryas*.

The three Galapagos species of *Alsophis*, *Alsophis elegans*, and the genus *Saphenophis* are here viewed as representing a monophyletic unit since they share at least one presumed hemipenial synapomorphy. Their general hemipenial morphology is very similar and highly divergent from that present in the West Indian *Alsophis* and mainland *Philodryas*. This assemblage is currently under study and will be treated in more detail elsewhere. Recently, Thomas (1997) reviewed the Galapagos species of *Alsophis*, recognizing four distinct species: *Philodryas hoodensis*, *Antillophis slevini* and *A. steindachneri* (new combinations in his works), and *Alsophis biserialis* (with three subspecies). Although I agree with Thomas that *hoodensis* constitutes a distinct species within the Galapagos radiation, its placement in the genus *Philodryas* is not sustained by hemipenial morphological evidence. As noted above, *hoodensis* and the other Galapagos species of *Alsophis* have very similar hemipenes, strikingly distinct from any species of *Philodryas*, and share with *Saphenophis* at least one presumed synapomorphy (see below). The same is true for *steindachneri*, a species resurrected by Thomas and placed in *Antillophis* (no hemipenial material was available for *A. slevini*). The hemipenial morphologies of the West Indian species of *Antillophis* are very distinct from the one present in *A. steindachneri* (see descriptions for *Antillophis*). Therefore, the generic reallocations made by Thomas (1997) are rejected here. Additionally, the two subspecies of *Alsophis biserialis* recognized by Thomas (*A. b. dorsalis* and *A. b. occidentalis*) show distinct hemipenial morphologies and I therefore regard them as distinct species (see below).

HEMIPENIAL MORPHOLOGY: As many as six widely different hemipenial morphologies are present in the genus *Alsophis*: (1) *A.*

cantherigerus, *A. vudii*; (2) *A. ater*; (3) *A. portoricensis*, *A. anomalus*; (4) *A. rufiventris*, *A. antiquae*, *A. rijersmai*; (5) *A. antillensis*; (6) *A. elegans*, *A. dorsalis*, *A. hoodensis*, *A. occidentalis*, *A. steindachneri*. All six different hemipenial types are treated below. Although some of these groupings may represent monophyletic units (Maglio, 1970; Cadle, 1984a; Crother and Hillis, 1995), they are used here for descriptive purposes. Their widely divergent hemipenial patterns and the presence of several presumed apomorphic features shared with other West Indian genera (e.g., *Ialtris*, *Uromacer*, *Hypsirhynchus*, and *Antillophis andreae*) suggest that the genus *Alsophis* is paraphyletic.

Alsophis cantherigerus (fig. 21) and *A. vudii* (fig. 27) comprise assemblage 1 and have almost identical hemipenes. Both species bear a semicalyculate, semicapitate, deeply bilobed hemipenis with well-developed enlarged lateral spines. The sulcus spermaticus is centrolineal, with a slight tendency toward becoming centrifugal on the tip of the lobes in *A. cantherigerus*. In both species, the capitula are formed by papillate calyces that tend to lose their vertically directed walls, thus forming papillate flounces, principally in the proximal region of each capitulum. Whereas the lobular crotch and medial surface of the lobes are ornamented with well-developed horizontally directed papillate flounces, the asulcate surface of the lobes is completely nude and bears a large overhanging edge of the capitulum. I consider these flounces to be derived from body calyces. An expanded papillate circular area is present on the lobular crotch of *A. cantherigerus* and *A. vudii*.

Alsophis ater (fig. 22) alone shows the second hemipenial type, which presents a puzzling hemipenial pattern. The organ is semicalyculate, semicapitate, and deeply bilobed, with a few well-developed enlarged lateral spines arranged in two nearly parallel rows. However, the sulcus spermaticus takes a centrifugal position as soon as its branches reach the proximal region of the lobes. The calyces forming the capitula are large and papillate. The lobular crotch is ornamented with a row of large papillae that runs from the sulcate to the asulcate surfaces. The capitula are positioned very laterally. The me-

dial surface of each lobe is almost nude, except for a series of large papillae that tend to form a row from the proximal edge of the lobes, on the asulcate side, to the distal portion of the nude medial area.

Assemblage 3 is composed of *A. portoricensis* (fig. 23) and *A. anomalus* (fig. 24). Both species show a bicalyculate, semicapitate, and deeply bilobed hemipenis. Well-developed enlarged lateral spines are arranged in two parallel rows on the lateral sides of the hemipenial body. The hemipenial body wall enclosed between the two rows of lateral spines is more or less depressed, having a groovelike condition. The sulcus spermaticus is centrolineal, with a slight tendency to a centrifugal condition at the tip of the lobes in *A. portoricensis*. Both species bear capitula formed by papillate calyces. In *A. portoricensis*, the lobular crotch and medial surface of the lobes are almost completely nude, except for the presence of a few small papillae on a bulbous projection from the medial surface of the proximal region of each lobe. The distal region of the nude area extends below the overhanging edge of the distal tip of the capitulum, thus forming a depression just below the overhanging edge of the latter. A slight groove runs parallel to the rows of enlarged lateral spines on each side of the asulcate surface of the hemipenial body from its distal portion to the middle of the organ. In *A. anomalus* the distal region of the nude area extends somewhat below the overhanging edge of the capitulum. The asulcate and medial surfaces of the lobes are nude, with only weakly developed, vertically and horizontally directed papillate flounces and a few small papillae arranged on a bulbous projection present in the middle of the medial surface of each lobe. A deep groove runs parallel to the rows of enlarged lateral spines on each side of the asulcate surface of the hemipenial body from its distal portion to the middle of the organ.

Assemblage 4 is composed of *A. rufiventris* (fig. 25), *A. antiquae* (fig. 26), and *A. rijersmai* (fig. 27), which share almost identical hemipenes. All three species have a bicalyculate, semicapitate, deeply bilobed hemipenis. Both *A. rufiventris* and *A. antiquae* bear one enlarged intrasulcar spine on each side of the intrasulcar region, whereas

A. rijersmai retains three spines. Well-developed enlarged lateral spines are present in all three species. *Alsophis rufiventris* and *A. antiquae* share a groovelike depression on each lateral surface of the hemipenial body between the first and second groups of enlarged lateral spines. I did not observe this condition in *A. rijersmai* because the only specimen has a partially inflated organ. All three species show centrifugal branches of the sulcus spermaticus from the middle to the tip of the lobes. Both *A. rufiventris* and *A. antiquae* lack an asulcate surface on the lobes due to the highly centrifugal condition of their sulcus. On the other hand, *A. rijersmai* maintains an asulcate surface as a result of the slightly centrifugal condition of its sulcus. The lobular crotch, asulcate, and medial surfaces of the lobes are almost completely nude in the three species, except for the presence of a vertically directed spinulate crest running from the distal tip of the rows of enlarged lateral spines to the tip of the lobes. The spinules are diminutive in all three species, and the crest is inflated in *A. rufiventris* and *A. antiquae* but it retains a fringelike condition in *A. rijersmai*. All three species share a peculiar capitular overhanging edge composed of a thin fringe of tissue. In *A. rufiventris* and *A. antiquae*, the spinulate crests and adjacent nude area extend toward the sulcate side of each lobe on the distal region. In *A. rijersmai* there is no such invasion of the capitula.

Assemblage 5 corresponds to *A. antillensis* (fig. 28), which shows a highly modified hemipenial morphology. The hemipenial material available for *A. antillensis* represents two subspecies, *A. antillensis danforthi* and *A. antillensis sibonius*. Both subspecies show the same general pattern but differ markedly in the length of the hemipenial body and lobes. The lobes constitute one-third of the whole length of the organ (10 of 32 mm) in the former subspecies, whereas the latter has lobes that are almost as long as the hemipenial body (8 of 17 mm). Also, the well-developed awn present in the distal tip of the lobes of *A. a. danforthi* is weakly developed in *A. a. sibonius*. Such differences are sufficient evidence for their recognition as different species. Apart from the differences described above, however, both subspecies

have identical hemipenial morphologies; that is, the hemipenis is bicalyculate, bicapitate, and deeply bilobed. The sulcus spermaticus is clearly centrifugal from the base to the tip of the lobes. The lobes lack an asulcate surface since the capitula are laterally directed and the branches of the sulcus are in a highly centrifugal position. Two or three enlarged intrasulcar spines are present on each side of the intrasulcar region. However, these spines are situated on the proximal surface of the lobes instead of being on the hemipenial body surface. Well-developed enlarged lateral spines are present. There is a groovelike depression on each lateral surface of the hemipenial body between the first and second groups of enlarged lateral spines. The lobular crotch, asulcate, and medial surfaces of the lobes are completely nude except for each capitulum, which invades the distal region of the lobes. The capitular calyces are complete only on the distal tip of the capitula; they tend to turn into flounces on the rest of the capitular surface by losing their vertically directed walls. Their papillae also tend to change in spinules on the proximal surface of the capitula. The tip of each lobe may or may not bear an awn (see subspecies descriptions above).

Assemblage 6 is composed of the mainland *A. elegans* (fig. 29) and the Galapagos species *A. dorsalis* (fig. 30), *A. hoodensis* (fig. 29), *A. occidentalis* (fig. 30), and *A. steindachneri* (*A. slevini* is tentatively allocated here, although no hemipenial material was available). In all five species the hemipenis is slightly (*elegans*) or deeply bilobed, bicalyculate, and semicapitate, with a forked sulcus spermaticus dividing on the proximal half of the body. Each branch of the sulcus extends centrolineally until the base of the capitula, where it takes a centrifugal position on the lobe, ending in the distal region. The organ lacks intrasulcar spines, but the enlarged lateral spines are numerous and of moderate size. The intrasulcar region is mostly nude, except for the presence of spinules and some sparsely distributed papillae. The capitula are made by diminutive papillate calyces and are mostly restricted to the sulcate side. The asulcate and medial surfaces of the lobes are almost completely nude except for the presence of a medial papillate

and inflated crest (or ridge) that runs from the lobular crotch to the distal edge of the capitulum. This ridge is conspicuous in all species except *A. hoodensis*, where it is less developed. Both ridges can be visualized in a sulcate view, where they have a medial position between the lobes. The medial crests of *A. occidentalis* are more conspicuous than the ones found in *A. dorsalis*, terminating abruptly on their distal end instead of gradually as in the latter species. The medial crests in *A. elegans* are in a dorsal position with respect to the lobes, thus widening largely the lobular crotch. A similar condition is found in *Saphenophis tristriatus* (see descriptions of this genus below). The tissue in the distal region of the hemipenial body bearing the more distal enlarged lateral spines is slightly, or greatly (*A. elegans*), inflated. In all four species most of the asulcate surface of the body is covered with spinules.

Antillophis

Figure 31

SPECIES EXAMINED: *A. parvifrons* (MNHN 1993.1617; MPMH 18878), *A. andreae* (MNHN 7457, 1883.387, 1883.388).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Dromicus* (= *Antillophis*) *parvifrons*. Grant (1943) described and figured the lateral and asulcate sides of the hemipenis of *Dromicus* (= *Antillophis*) *andreae*. Maglio (1970) described and compared the hemipenial pattern of *Antillophis* with that of other West Indian xenodontines and with *Lygophis* (= *Saphenophis*) *boursieri*, figuring the dissected organ of *A. parvifrons*.

HEMIPENIAL MORPHOLOGY: These two species have distinctly different hemipenes (fig. 31), being similar only in their general forms. Both have a strongly bilobed organ, enlarged lateral spines, and a deeply forked sulcus spermaticus dividing at the proximal region of the hemipenial body, with each branch extending centrolineally about halfway up the middle of each lobe to take a more or less centrifugal position through the distal portion of the lobes.

Antillophis andreae has a semicalyculate, semicapitate hemipenis with long lobes ornamented with spinulate calyces in the sul-

cate surface and large transversely directed papillate flounces on the asulcate surface. The papillate flounces decrease in size proximodistally, with the lobular crotch bearing the larger one. The lobular crotch have two developed papillate ridges that tend to face one another, giving the impression of an expanded papillate circular area. The distal portion of each branch of the sulcus spermaticus is clearly in a centrifugal position along the distal region of the lobes.

Antillophis parvifrons has a semicalyculate, semicapitate organ and relatively small lobes with papillate calyces in their sulcate surface. The asulcate surface is completely nude except for a row of two to three enlarged papillae aligned vertically on the lobular crotch and proximal region of the lobes (on the middle of the asulcate and medial surfaces). The papillae ornamenting the edge of the capitulum are significantly larger than the other papillae and are calcified-like spines. The distal portion of each branch of the sulcus spermaticus takes a slight centrifugal position along the distal region of the lobes. A basal pocket is present in the proximal region of the body on its asulcate side, being also visible in a sulcate view.

The hemipenes of *Antillophis parvifrons*, *Arrhyton exiguum*, and *Darlingtonia haeti-ana* show great similarities (see descriptions of the latter two genera and compare figures 31 and 37). The papillate flounces of *A. andreae* and the unique row of papillae of *A. parvifrons* are here viewed as being derived from the body calyces, the former by loss of the vertically directed walls of each body calyx (thus leading to flounces) and the latter by loss of nearly all the body calyces except for the few papillae at the base of the crotch.

Apostolepis

Figure 32

SPECIES EXAMINED: *A. assimilis* (IB 52754, 54071), *A. dimidiata* (uncatalogued specimen).

REFERENCES AND REMARKS: None.

HEMIPENIAL MORPHOLOGY: The general pattern is of a simple to slightly bilobed hemipenis. The organ of *Apostolepis assimilis* is almost simple, whereas that of *A. dimidiata* shows two greatly reduced but still visible

lobes (fig. 32). However, the distal end of the retractor muscle is divided. Because of the simple condition, the hemipenes show an unicalyculate capitulum that is noncapitate in the former species and unicapitate in the latter. Both species have two or three well-developed rows of enlarged lateral spines that decrease in size from the lateral to the sulcate side of the body, with the sulcate surface being covered with spinules. The forked sulcus spermaticus divides approximately at the middle of the organ just below the capitulum. The branches, which extend centrolineally in both species, are terminal (i.e., reach the distal tip of the lobes) in *A. dimidiata*, whereas in *A. assimilis* the branches end at the middle of the capitulum. In both species the lobe is distinctly ornamented on its sulcate and asulcate sides. The capitulum, which is confined to the sulcate side in *A. assimilis* but invades the distal tip of the asulcate side in *A. dimidiata*, is formed by papillate capitular calyces. The distal region of the asulcate side bears papillate body calyces in *A. dimidiata* and transversely directed papillate flounces that are derived from typical body calyces in *A. assimilis*. Indeed, in *A. assimilis* the first two or three distal flounces are entire, running from one side of the asulcate surface of the lobe to the other, whereas the more basal region of the lobe, presumed to be homologous to the lobular crotch of bilobed organs, retains one or two pairs of typical body calyces.

In *A. dimidiata* the entire asulcate surface of the lobe bears two rows of large body calyces. These rows of calyces reduce in the region of the lobular crotch where only the vertical walls of each body calyx remain, forming two greatly developed lateral papillate walls that have their apical tips fused together to form an inverted V-shaped structure. I consider the inverted V-shaped structure to be the product of the fusion of the walls of the vertically directed body calyces because the vestiges of transversely directed walls are still present laterally and between the two branches of the "V". In addition, a similar condition is present in *Elapomorphus lepidus*, where the two branches of the "V" are present but, instead of being fused distally, are confined to their respective lobes inasmuch as the hemipenis is deeply bilobed.

I hypothesize that the loss of the bilobed condition in *A. assimilis* and *A. dimidiata* led to the fusion of the rows of body calyces on the lobes and, in the latter, also to the fusion of the distal tips of each vertically directed wall of the lobular crotch (see also descriptions for the genera *Phalotris* and *Elapomorphus* in this section).

Arrhyton

Figures 33–37

SPECIES EXAMINED: *A. callilaemum* (MPMH 22707), *A. exiguum* (RT 4686, 10079), *A. funereum* (MPMH 22789), *A. landoi* (AMNH 36703; KU 268377), *A. polylepis* (MPMH 22703), *A. vittatum* (AMNH 46727), *A. taeniatum* (MNHN 695).

REFERENCES AND REMARKS: Buden (1966) described and compared the hemipenes of *Dromicus* (= *Arrhyton*) *callilaemus*, *D. funereus*, and *D. polylepis* and presented drawings of the sulcate side of the latter two species. Maglio (1970) described and discussed hemipenial intrageneric variations, and figured the dissected organs of *A. funereum* and *A. vittatum*. Myers and Campbell (1981) figured the sulcate side of the organ of *A. callilaemum*.

HEMIPENIAL MORPHOLOGY: Three strikingly different hemipenial patterns are present in *Arrhyton* that correspond to three clearly demarcated geographic units: (1) the Cuban species (*A. taeniatum*, *A. landoi*, and *A. vittatum*), (2) the Jamaican species (*A. funereum*, *A. polylepis*, and *A. callilaemum*), and (3) the Puerto Rican species (*A. exiguum*). Although these assemblages show distinctly different hemipenes, they present both synapomorphies of the Xenodontinae (except assemblage 2, which lacks the distinctly ornamented areas in the lobes). Additionally, they show a deeply forked centrolineal sulcus spermaticus dividing in the proximal region of the hemipenial body.

All three species of assemblage 1 have a semicalyculate, semicapitate hemipenis and a centrolineal sulcus spermaticus. The few enlarged lateral spines are conspicuous. Very minute spinules are present on the proximal half of the hemipenial body. The sulcate side is almost identical in all three species except for the lobular calyces, which are still present

at the level of the sulcus bifurcation or just above it in *A. landoi* (fig. 33) and *A. vittatum* (fig. 33), and vanish in the distalmost region of the hemipenial body in *A. taeniatum* (fig. 34). All three species have papillate capitular calyces, with *A. taeniatum* bearing the larger ones. On the asulcate side, differences are confined to the lobular crotch and lobular surface. All three species have an almost completely nude medial region of the lobes and differently ornamented asulcate surfaces. *Arrhyton taeniatum* has the least ornamented lobes, with an asulcate surface bearing only a large papillate crest that runs from the lobular crotch to the lateral side of the lobes, where it fuses with the overhanging edge of the capitulum.

Both crests are in contact in the middle of the lobular crotch, where they converge to form a narrow row of minute papillae that extend down the midline of the asulcate surface of the hemipenial body on its distal region. Both crests are arranged in such a way to form a Y-shaped structure on the asulcate surface of the hemipenial body. *Arrhyton landoi* and *A. vittatum* also share the presence of the Y-shaped papillate crests on the lobular crotch. However, both *A. landoi* and *A. vittatum* have well-developed calyces ornamenting the the asulcate surface of the lobes. *Arrhyton landoi* differs from *A. vittatum* by having the papillate calyces of slightly larger size than the capitular calyces, with both being difficult to distinguish at their junction on the lateral sides of the lobes. However, they are conspicuously larger on the proximal asulcate region of the lobes and lobular crotch. On the other hand, *A. vittatum* shows large, conspicuously different spinulate calyces on most of the asulcate surface of the lobes. These calyces, present on the asulcate surface of the lobes and lobular crotch of the three species, are considered to be homologous with the "body calyces" described in the present study. I regard the unique crest ornamenting each lobe of the hemipenis of *A. taeniatum* as homologous with the series of large calyces ornamenting the same region in the lobes of *A. landoi* and *A. vittatum*.

Assemblage 2 shows the most divergent pattern from a typical xenodontine hemipenis, with *A. callilaemum* (fig. 34) having a

slightly bilobed hemipenis, and *A. funereum* (fig. 35) and *A. polylepis* (fig. 36) a single (unilobed) hemipenis. The latter condition is here viewed as derived from a bilobed condition, similar to the one present in *A. callilaemum*, because all the other Xenodontinae show some kind of bilobation (except some Elapomorphiini that have a completely unilobed organ). The sulcus spermaticus takes a centrifugal position in the lobes and bifurcates in the proximal region of the hemipenial body as in most Xenodontinae. The three species share the derived condition of completely unornamented lobes, covered uniquely by diminutive spinules.

Both *Arrhyton callilaemum* and *A. polylepis* have several rows of small spines that are arranged laterally on the hemipenial body and considered here as homologous to the enlarged lateral spines characteristic of the Xenodontinae. Indeed, *A. callilaemum* exhibits an intermediate condition where the more distal spines are still enlarged, decreasing in size from the distalmost position to the base of the hemipenis. *Arrhyton polylepis* has several rows of small spines lateral to the sulcus that extend from the base of the hemipenis to the base of the lobe. Each row of spines meets its contralateral on the asulcate side, thus surrounding the lobe completely. *Arrhyton funereum* also has a hemipenis with a series of small spines surrounding the base of the single lobe. This condition may be easily derived from the one present in *A. polylepis* since the rows of spines extending to the base of the hemipenial body, and easily perceived in *A. polylepis*, are also present in *A. funereum* (figured in Buden's [1966: 6] and Maglio's [1970: fig. 34A] drawings). Additionally, these species share the condition of a single lobed hemipenis. Actually, both characters (single lobation and complete rows of spines surrounding the base of the lobes) are here viewed as resulting from the same process that led to the single-lobed condition. Both hemipenial lobes of *A. callilaemum* bear a well-developed apical awn that is also present, but poorly developed, on both sides of the single-lobed hemipenis of *A. polylepis*. The distal half of the single hemipenial lobe of *A. funereum* is adpressed laterally to form a vertical expansion on which the two branches of the sulcus run laterally

(a typically centrifugal condition, as present in the other two Jamaican species). Buden's (1966: 6) figure shows only a partially everted organ of *A. funereum* in which the vertical expansion of the lobe is retracted; also, the left branch of the sulcus spermaticus is missing on the lateral wall of the expansion drawn by him, which may be due more to an omission than to the actual anatomy in this particular specimen. The distal region bears a well-developed papillate crest that extends from the sulcate to the asulcate surface of the tip of the expansion.

Arrhyton polylepis has, in the distal region of the lobe, a poorly developed crest that has the same topographical position as the one in *A. funereum*. Both crests are here viewed as homologous structures. The apical papillae are absent in *A. funereum*.

The third assemblage comprises only the Puerto Rican species *A. exiguum* (fig. 37), which differs greatly from the former two assemblages regarding its hemipenial morphology. The hemipenis is semicalyculate, semicapitate, and bears a centrolineal sulcus spermaticus. However, each branch of the sulcus has a slight tendency toward a centrifugal position at the tip of the lobes. Each capitulum is formed by papillate calyces and is restricted to the sulcate and lateral surfaces of the lobes. The papillae ornamenting the edge of the capitulum are larger than the other papillae. The lobes are almost completely nude on the asulcate and medial surfaces, except for a row of three to four large papillae aligned vertically on the lobular crotch and proximal region of the lobes, just on the middle of the asulcate and medial surfaces. The separate medial surface of each lobe extends down the lobular crotch, forming a deep groove that can be seen only when the lobes are separated. The hemipenial body shows a gradual transition from a narrow proximal region to a bulbous distal region. The rows of enlarged lateral spines are formed of large spines in the bulbous region. The spines gradually diminish in size in the proximal region of the sulcate surface. The asulcate surface bears a well-developed nude pocket on the proximal surface of the hemipenial body that can be seen laterally on a sulcate view. The distal region of the asulcate surface is covered with small papillae. The hemipenes

of *A. exiguum*, *Antillophis parvifrons*, and *Darlingtonia haetiana* are strikingly similar (see description of *Antillophis* and *Darlingtonia*).

Boiruna

SPECIES EXAMINED: *B. maculata* (IB 1642, 31061, 31658, 32156, 40884, 53526, 54348, 55415; MRSN R-119, R-1797, R-1799), *B. sertaneja* (IB 42717; MNHN 1990.4322; MNRJ 2386).

REFERENCES AND REMARKS: Zaher (1996a) erected the new genus *Boiruna* to accommodate *Clelia maculata* and the new species *B. sertaneja*, since they represent the sister-taxon of all other pseudoboines (Zaher, 1994a). Both sulcate and asulcate sides of their hemipenes are figured in Zaher (1996a).

HEMIPENIAL MORPHOLOGY: The hemipenial morphologies of both species differ in several ways, sharing only a deeply bilobed organ with two rows of well-developed papillate body calyces on the asulcate and medial surfaces of the lobes, and a centrifugal sulcus spermaticus dividing on the proximal region of the body. In *B. maculata* the hemipenis is bicalyculate and semicapitate or weakly bicapitate. The long lobes are ornamented with diminutive spinulate calyces on their sulcate and lateral surfaces. The asulcate proximal region of the lobes bears an inflated crest that is confluent basally with the rows of enlarged lateral spines. Inflated crests result from the expansion (and inflation) of the medial vertical walls of the body calyces. The hemipenial body has three to four rows of well-developed enlarged lateral spines. The basal region of the body is ornamented with diminutive spinules. The lobular crotch has a pair of weakly defined calycular pockets. The intrasulcar region is covered with sparse spinules.

In *B. sertaneja* the hemipenis is deeply bicalyculate and bicapitate. The lobes are ornamented with diminutive spinulate calyces. The capitulum is directed laterally. The medial and asulcate surfaces of the lobes are ornamented with two parallel rows of papillate body calyces. The basal region of each lobe has a weakly developed inflated crest. The hemipenial body is smooth, lacking any type of spine or other kind of ornamentation.

The lobular crotch lacks the pair of calycular pockets.

Clelia

Figures 38, 39

SPECIES EXAMINED: *C. bicolor* (MRSN R-1802), *C. clelia* (AC 1978.77; KU 187257, 96980; LSUMZ 26828, MCZ 101237, 152210; one uncatalogued specimen), *C. equatoriana* (BMNH 60.6.16.47; IB 8692; KU 140401, 95766), *C. errabunda* (MNHN 7598), *C. montana* (IB 15692, 16243, 43072), *C. plumbea* (CEPLAC 423, 576, 687, 87.161; IB 20677; MNRJ 2681, 2730), *C. quimi* (IB 1350, 53786, 54903), *C. rustica* (IB 45878; MNHN 1990.4301), *C. scytalina* (KU 67646; USNM 111266).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Oxyrrhopus plumbeus* (= *C. clelia*). Zaher (1996a) figured both sulcate and asulcate sides of the hemipenes of *C. bicolor*, *C. clelia*, *C. plumbea*, *C. rustica*, and *C. scytalina*, as well as the asulcate surface of the right hemipenial lobe of *C. equatoriana* and *C. errabunda*. Franco et al. (1997) figured both sides of the organs of *C. quimi* and *C. montana*. As presently conceived, the genus *Clelia* still remains polyphyletic since *C. bicolor*, *C. quimi*, and *C. montana*, representing a distinct monophyletic group, is more closely related to the clade formed by the genera *Oxyrrhopus*, *Siphlophis*, and *Tripanurgos* than to the remaining species of *Clelia* (Zaher, 1994a). This problem will be addressed elsewhere. I restrict the following description to the major differences found within the genus (see Zaher, 1994a, 1996a, for further details).

HEMIPENIAL MORPHOLOGY: The general pattern in all nine species is that of a strongly bilobed hemipenis with enlarged lateral spines and a deeply forked sulcus spermaticus dividing on the proximal region of the hemipenial body, with each branch extending centrolineally onto the distal region of the body and centrifugally on the lobes. Despite their similar general aspect, two clearly divergent hemipenial patterns can be distinguished for the following assemblages of species: (1) *C. bicolor* (fig. 38), *C. quimi* (fig. 38), *C. montana* (fig. 39); (2) *C. clelia*, *C.*

equatoriana, *C. errabunda*, *C. plumbea*, *C. rustica*, *C. scytalina*.

The hemipenis in group 1 is bicalyculate and bicapitate. The intrasulcar region bears one row of three spines on each side. All three species lack body calyces and calycular pockets on the asulcate/medial surfaces of the lobes and lobular crotch. However, the vertical row of large papillae running on the medial surface of each lobe (from the distal end of the rows of enlarged lateral spines to the distal tip of the capitulum) is considered to be derived from body calyces. In *C. montana*, this straight row of papillae turns into numerous densely arranged papillae on the distal region of each lobe. The enlarged lateral spines are arranged in two or three rows laterally.

The hemipenial morphology of all species belonging to group 2 has been described in detail by Zaher (1996a). All species have a bicalyculate and bicapitate organ with a centrifugal sulcus spermaticus. *Clelia plumbea* is the only species that lacks spines and spinules on the hemipenis. All other species have one or two intrasulcar spines and two or three rows of enlarged lateral spines. All species, including *C. plumbea*, have a pair of well-developed calycular pockets and weakly developed body calyces on the asulcate and medial surfaces of the lobes. Intraspecific variation in the number of enlarged lateral spines was found in *C. clelia*, as described by Zaher (1996a).

Conophis

Figures 40, 41

SPECIES EXAMINED: *C. lineatus* (AMNH 126423; MNHN 3740), *C. pulcher* (MNHN 5981), *C. vittatus* (AMNH 66337, 123917).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Conophis lineatus*. Wellman (1963) figured the sulcate side of the organ of *C. vittatus*. Amaral (1923) suggested without discussion that *Conophis* and *Platyion* are closely related.

HEMIPENIAL MORPHOLOGY: All three species have a similar hemipenial pattern, with a tendency toward unilobation comparable to that present in the *Arrhyton callilaemum* assemblage. Whereas *C. pulcher* (fig. 40) and *C. lineatus* (fig. 40) have a slightly bilobed

hemipenis, *C. vittatus* (fig. 41) has an almost unilobed hemipenis with two distinct tips on the distal extremity of the lobe, with each one bearing a laterally directed branch of the sulcus spermaticus. The latter condition is considered to be derived from a bilobed condition because the other species of *Conophis* and most Xenodontinae (except some Elapomorphiini taxa and two species of *Arrhyton*) show some degree of bilobation. The sulcus spermaticus is centrolineal, with a slight tendency to a centrifugal position in the distal region of the lobes. It bifurcates in the proximal region of the hemipenial body, as in most South American xenodontines. The lobes bear spinulate flounces, which most probably have been derived from spinulate calyces by the loss of the vertically directed walls of the latter. The flounces are distributed in a typical semicalyculate condition. However, the lobes lack any capitulation, being thus semicalyculate and noncapitate.

Conophis pulcher and *C. lineatus* show well-developed spinulate flounces in the asulcate surface of the lobes, lobular crotch, and distal surface of the hemipenial body. These flounces and spinules are distinctly larger than those ornamenting the rest of the lobes. The same distinctly larger spinulate flounces are present on the asulcate surface of the single lobe and on the distal region of the hemipenial body of *C. vittatus*. The hemipenial body of the three species is covered with moderate to large spinules that, in *C. lineatus* are difficult to distinguish from the enlarged lateral spines since they are of the same size. In *C. pulcher* and *C. vittatus* the enlarged lateral spines, although of moderate size when compared to other South American taxa, are clearly distinguishable and conspicuously larger than the spinules.

The large spinulate flounces present on the asulcate side of the hemipenis of these three species are considered to be derived from the body calyces. *Conophis* and *Manolepis* have very similar hemipenial morphologies (figs. 40, 41).

Darlingtonia

Figure 37

SPECIES EXAMINED: (monotypic) *D. haeti-ana* (KU 268441; RT 6141).

REFERENCES AND REMARKS: None.

HEMIPENIAL MORPHOLOGY: The hemipenis is strongly bilobed, semicalyculate, and semicapitate, with few enlarged lateral spines and a deeply forked sulcus spermaticus dividing in the proximal region of the hemipenial body (fig. 37). Each branch of the sulcus extends centrolineally to the tip of the lobe where there is a slight tendency to a centrifugal position. The lobes are relatively long, representing almost half the total length of the organ. Each capitulum is restricted to the sulcate and lateral surfaces of the lobes, and it is formed by papillate calyces that have slightly larger papillae ornamenting the edge of the capitulum. The lobes are completely nude on the asulcate and medial surfaces, except for a row of three large papillae aligned vertically on the lobular crotch and proximal region of the lobes, just on the middle of the asulcate and medial surfaces. One young specimen (KU 268441) lacks such papillae, showing completely nude asulcate and medial surfaces. The hemipenial body presents well-developed enlarged lateral spines on the lateral and sulcate surfaces. The asulcate surface is ornamented with spinules. The basal pocket, present in the similar hemipenes of *Arrhyton exiguum* and *Antillophis parvifrons*, is absent in *Darlingtonia*. *Arrhyton funereum*, *Darlingtonia haetiana*, and *Antillophis parvifrons* share the presence of a row of enlarged papillae aligned vertically on the lobular crotch and proximal region of the lobes (see also descriptions of *Arrhyton* and *Antillophis*).

Ditaxodon

Figure 42

SPECIES EXAMINED: (monotypic) *D. taeniatus* (IB 40751).

REFERENCES AND REMARKS: None.

HEMIPENIAL MORPHOLOGY: The hemipenis is nearly unilobed, being bilobed only in the distal tip of the organ (fig. 42). It is semicalyculate, semicapitate, and bears a completely centrolineal sulcus. The sulcus bifurcates in the basal region of the hemipenial body, and both branches run parallel until reaching the tip of the organ. The tip of the organ, corresponding to the two weakly developed lobes, is completely ornamented

with papillate calyces on the sulcate, asulcate, and lateral sides. The calyces extend proximally on the sulcate side of the body, vanishing at midbody. The papillate calyces are well developed on the intrasulcar surface. The calyces on the lateral and asulcate sides are succeeded proximally by enlarged body calyces, with the two most proximal ones on the asulcate surface forming two very large and shallow pockets. One unique row of enlarged lateral spines is present on each side of the hemipenial body in a more or less asulcate position. One row of four large, vertically directed spines is present on the midline of the distal region of the hemipenial body between the two large pockets. Below this pair of pockets, the surface of the asulcate side is almost nude.

Drepanoides

Figure 42

SPECIES EXAMINED: (monotypic) *D. anomalus* (MNHN 1895.16; MNRJ 2989).

REFERENCES AND REMARKS: Jenner and Dowling (1985) provided a figure of the sulcate side of the organ of this species.

HEMIPENIAL MORPHOLOGY: The hemipenis is strongly bilobed, bicalyculate, and bicapitate, with a deeply forked sulcus spermaticus dividing more or less in the middle of the hemipenial body (fig. 42). Each branch of the sulcus extends centrolineally until the distal region of the hemipenial body where they take a centrifugal position, ending at the base of an awn present on the tip of both lobes. The lateral sides of the body are ornamented with numerous enlarged lateral spines that invade the base of the lobes distally on their asulcate surfaces. The lobes are long (twice as long as wide). The capitula are made by spinulate calyces (although some papillae ornament the distalmost calyces) and are in a lateral position on the lobes. The latter have a nude medial surface. The intrasulcar surface of the hemipenial body bears a row of three or four enlarged intrasulcar spines on each side. The lobular crotch does not have any particular ornamentation. The rest of the hemipenial body is covered with spinules.

The simplified hemipenial pattern present in *D. anomalus* is the result of secondary losses of several structures present in the oth-

er pseudoboine genera, which are diagnostic for this radiation (character polarity and transformation series are discussed in Zaher, 1994a).

Elapomorphus

Figures 43, 44

SPECIES EXAMINED: *E. quinquelineatus* (IB 52731), *E. lepidus* (CEPLAC 748).

REFERENCES AND REMARKS: Lema (1985) illustrated an everted and a dissected organ of *E. lemniscatus*. Ferrarezzi (1993) revived the genus *Phalotris*, restricting *Elapomorphus* to the two species here analyzed and *E. wuchereri*.

HEMIPENIAL MORPHOLOGY: These two species have greatly different organs, being similar only in their deeply bilobed condition and the forked sulcus spermaticus that bifurcates in the middle of the organ (= distal region of the hemipenial body) just below the capitulum. *Elapomorphus quinquelineatus* (fig. 43) has an almost completely unornamented hemipenis where only the lobes, lobular crotch, and intrasulcar region bear structures (the rest is totally nude). These regions are ornamented uniquely by transversely directed flounces (lacking any papillae or spinules, except for some weakly developed papillae present at the tip of each lobe) that run transversely and parallel to each other around each lobe from one side of the sulcus branch to the other. In the region of the lobular crotch, the flounces run in the same position, except that they go from the lateral edge of the right sulcus branch to the lateral edge of the left sulcus branch. In the intrasulcar region, the flounces also run transversely. The two branches of the sulcus spermaticus are greatly dilated in the region of the lobes. There is no evidence of enlarged lateral spines, spinules or any ornamentation in all the hemipenial body region.

The hemipenis of *E. lepidus* (fig. 44) has a typical xenodontine pattern; that is, the organ is strongly bilobed and has two or three rows of enlarged lateral spines. The sulcus divides in the middle of the organ, with each branch extending centrolineally about halfway up the middle of each lobe to take a centrifugal position on the distal portion of the lobes. The hemipenis is semicalyculate and semicapitate laterally and in the sulcate

side, with long lobes (twice as long as wide) ornamented with a capitulum of papillate/spinulate calyces on the sulcate and lateral surfaces, and with slightly developed and scarce papillate body calyces on the asulcate and medial surfaces. The lobular crotch has two vertically oriented papillate walls on each side that are confluent with the rows of enlarged lateral spines, and a vertically oriented papillate wall medially that is confluent with the proximal tip of the medial edge of each capitulum. These three papillate walls are considered to be derived from body calyces that have lost their transversely oriented walls. The basal region of the hemipenial body is covered with spinules. The lobes are almost as long as the hemipenial body.

Erythrolamprus

Figure 45

SPECIES EXAMINED: *E. aesculapii* (MNHN 1990.4326), *E. mimus* (AMNH 12697), *E. bizona* (AMNH 35576).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Erythrolamprus venustissimus*. Dowling and Savage (1960) figured the sulcate side of the organ of *E. aesculapii*.

HEMIPENIAL MORPHOLOGY: All three species show almost identical hemipenial patterns, with ornamentation reduced to only lateral and enlarged intrasulcar spines, spinules, and apical disks (fig. 45). The hemipenes are slightly bilobed, with a deeply forked sulcus spermaticus dividing more or less in the middle of the hemipenial body. There is no evidence of calyculatation or capitation on the lobes. However, as already pointed out, the condition in *Erythrolamprus* (and in other genera of the Xenodontini) might have been derived from a bicalyculate and bicapitate condition, as is suggested by the presence of slightly enlarged intrasulcar spines and a centrifugal sulcus. Both branches of the sulcus diverge almost directly to a centrifugal position, being clearly centrifugal within the area of the apical disk. Each branch ends on the distal region of the disk. Each lobe bears on its lateral side a large nude area—the apical disk. The disks present a plicate surface. The rest of each lobe is ornamented with spinules. The hemipenial

body in each of the three species has moderately large, enlarged lateral spines arranged in several rows. One of these rows extends to the lobular crotch on the asulcate side. The asulcate surface of the hemipenial body is nearly nude except for a row of spines arranged vertically on the midline of the distal region of the body.

Farancia

Figure 46

SPECIES EXAMINED: *F. abacura* (AMNH 8131; MNHN 1903.325), *F. erytrogramma* (AMNH 126497).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Farancia abacura* and *Abastor* (= *Farancia*) *erytrogramma*. Burger (1948) published photographs of both sides of the hemipenis of *F. abacura*. Dowling and Duellman (1978) figured the organ of *F. abacura*.

HEMIPENIAL MORPHOLOGY: The organ of both species is semicalyculate, semicapitate, and slightly bilobed. The sulcus spermaticus bifurcates approximately on the middle of the hemipenial body, with each branch extending centrolineally until the distal tip of the lobes. In *F. abacura* (fig. 46) the lobes are ornamented with papillate capitular calyces (only on their distal region) that fade proximally, being replaced by longitudinal rows of large spinules. The medial and asulcate sides, as well as the lobular crotch and distal region of the hemipenial body, are ornamented with large shallow spinulate body calyces. The capitulum, which corresponds to the papillate calyces and longitudinal rows of spinules, is distributed along all the sulcate and lateral surfaces of the lobes, also invading the distal edge of the asulcate surface.

In *F. erytrogramma* (fig. 46) the lobes are greatly reduced in size compared to *F. abacura*, and they are ornamented with papillate capitular calyces on the sulcate and lateral surfaces. The asulcate surface of the lobes bears slightly larger papillate calyces, which are probably homologous to the well-developed body calyces present in *F. abacura*. Body calyces are absent from the lobular crotch and distal region of the hemipenial body of *F. erytrogramma*. Both species have

a shallow capitation of the lobes on the asulcate and lateral sides of the organ, which may be interpreted as a deep constriction of the proximal region of the lobes. The organ of both species bears two distinct rows of enlarged lateral spines on each side of the body. However, *F. abacura* has well-developed, distinct lateral spines whereas *F. erytrogramma* has poorly developed lateral spines that are only slightly larger than the spinules covering the rest of the hemipenial body. In both species there is a large gap between the first and second rows of enlarged lateral spines that tends to be depressed, giving to this region a groove like condition. Almost all spinules along the organ are well developed in both species.

I regard the peculiar shallow capitation of the lobes on the asulcate and lateral sides of the organ as a synapomorphy of the genus. The depressed region between the rows of enlarged lateral spines may well also represent an additional synapomorphy. However, this condition is ambiguous since it is also present in assemblage 4 of the genus *Alsophis*.

Helicops

Figures 47–50

SPECIES EXAMINED: *H. angulatus* (LSUMZ 26818, 26819, 26820; one uncatalogued specimen), *H. carinicaudus* (MNRJ 4299), *H. danieli* (AMNH 97461), *H. leopardinus* (LSUMZ 40470; MNRJ 4777), *H. modestus* (AMNH 5741), *H. pastazae* (AMNH 57342), *H. polylepis* (AMNH 101856; one uncatalogued specimen).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Helicops fumigatus* (= *H. angulatus*). Rossman (1973) figured both sides of the hemipenes of *H. angulatus* and *H. leopardinus* and compared the hemipenial morphology of this genus with that of *Hydrops* and *Pseudoeryx*. R. N. Yuki (1994) figured both sulcate and asulcate sides of the organ of *H. danieli*.

HEMIPENIAL MORPHOLOGY: All specimens examined have a semicalyculate or feebly bicalyculate configuration with the calyces replaced by flounces. Because several species of *Helicops* have been shown to retain vestiges of calyces on their lobes, and because

the flounces in *Helicops* retain the same configuration on the lobes as when calyces are present, I regard the flounced condition in *Helicops* as derived from a calyculate condition. For this reason, I retain the same terminology used here for describing the condition of calyculature and capitulation presented by the capitulum.

All species show very similar hemipenial morphologies, except *H. leopardinus* (fig. 47) and *H. modestus* (fig. 48), which present weakly developed lobes, conferring a peculiar shape to the organ. The hemipenes of *H. angulatus* (fig. 47), *H. danieli* (fig. 49), *H. carinicaudus* (fig. 50), *H. pastazae* (fig. 48), and *H. polylepis* (fig. 49) are strongly bilobed, semicalyculate (or feebly bicalyculate in *H. carinicaudus* and *H. danieli*), and semicapitate, with a deeply forked sulcus spermaticus dividing in the proximal region of the hemipenial body. In *H. leopardinus* and *H. modestus* the hemipenis is feebly bilobed, with the lobes being barely present or weakly developed, respectively. Both species have a semicalyculate and semicapitate condition, but the sulcus divides more or less in the middle of the hemipenial body instead of proximally. In all seven species the branches of the sulcus diverge slightly from each other (in a centrolateral position) until reaching the base of the lobes, where they change radically to a centrifugal position. Such a drastic change of direction places the branches in an almost horizontally directed position in the sulcate side of the lobes, changing again to a vertically directed position when they reach the lateral side of the lobes. The branches end on the tip of the lobes in their lateral side. The peculiar S-like condition of the branches of the sulcus spermaticus, present in all examined species, may well represent a synapomorphy of this genus.

In *H. angulatus*, *H. carinicaudus*, *H. danieli*, *H. pastazae*, and *H. polylepis* the hemipenial body is ornamented with several rows of well-developed enlarged lateral spines. In *H. leopardinus* and *H. modestus* the distal region of the hemipenial body is covered with small spines, whereas the proximal region is almost completely nude. However, in *H. modestus* several enlarged lateral spines are still recognizable in the lateral side of the

organ since they are slightly larger than the small spines surrounding them.

All species show lobes ornamented with horizontally oriented papillate flounces that completely encircle their lobe, even in *H. leopardinus* and *H. modestus*, which retain such structures on their reduced lobes. *Helicops angulatus*, *H. carinicaudus*, *H. danieli*, *H. pastazae*, and *H. polylepis* bear some well-defined papillate calyces around the tip of the sulcar branches. The vertically directed walls of the papillate calyces disappear suddenly as they get far from the tip of the branches, leading to the typical papillate flounces present in the rest of the lobular surface. All seven species show a deeply constricted (capitate) condition of the basal region of the lobes in the asulcate surface of the organ. *Helicops angulatus*, *H. danieli*, *H. leopardinus*, *H. modestus*, and *H. pastazae* have papillate flounces on the lobular crotch that are here considered to be derived from the body calyces. On the other hand, *H. polylepis* and *H. carinicaudus* show a completely nude lobular crotch. I was able to confirm the presence of a more or less developed basal pocket in all species except in *H. modestus* and *H. pastazae*, for which the proximal region of the organ is damaged. The rest of the hemipenial body is covered with spinules.

Heterodon

Figure 50

SPECIES EXAMINED: *H. platyrhinos* (LSUMZ 43216, 43218), *H. nasicus* (MNHN 127, 3636).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Heterodon nasicus* and *H. platyrhinos*. Dowling and Savage (1960) and Dowling and Duellman (1978) figured the sulcate side of *H. platyrhinos*.

HEMIPENIAL MORPHOLOGY: Both species have very similar hemipenes. The general pattern is of a clearly bilobed, semicalyculate, and semicapitate organ with three or four rows of enlarged lateral spines (fig. 50). The sulcus spermaticus bifurcates on the proximal region of the hemipenial body, with each branch extending centrolaterally until the tip of each lobe. The capitula are restrict-

ed to the sulcate side of the lobes, and are formed by large papillate calyces. The calyces forming the edge of each capitulum bear more developed papillae. The asulcate surface of the lobes and lobular crotch are ornamented with well-developed papillate body calyces that form two parallel rows on the distal region of the hemipenial body. Between the two rows of body calyces, on the middle of the lobular crotch, there is an inflated area bearing numerous papillae. The latter condition is made up by the confluence of the more medial rows of body calyces. The intrasulcar region is very narrow owing to the centrolineal position of the branches of the sulcus spermaticus, which is totally covered with capitular calyces. The hemipenial body is covered with spinules in most of the areas surrounding the body calyces and rows of enlarged lateral spines.

Hydrodynastes

Figure 51

SPECIES EXAMINED: *H. gigas* (AMNH 57956), *H. bicinctus* (AMNH 60822; MNHN 1993.1618; MNRJ 4495).

REFERENCES AND REMARKS: Dowling and Gibson (1970) figured the sulcate side of the hemipenes of *Hydrodynastes bicinctus* and *H. gigas*.

HEMIPENIAL MORPHOLOGY: Both species show a deeply bilobed, semicalyculate, semicapitate organ with several rows of enlarged lateral spines (fig. 51). The sulcus spermaticus bifurcates on the proximal region of the hemipenial body, with each branch extending centrolineally until the proximal region of the lobes, then diverging to a centrifugal position and ending on the lateral tip of the lobes. The capitula are mostly on the sulcate lateral sides of the lobes and are formed by papillate calyces. In *H. bicinctus* the calyces forming the edge of the capitulum bear more developed papillae. The medial and asulcate surfaces of the lobes, the lobular crotch, and the asulcate distal region of the hemipenial body are ornamented with well developed body calyces. In *H. gigas*, these are much more shallow and remain well developed on the lobular crotch and hemipenial body, whereas *H. bicinctus* bears only weakly developed body calyces in the same regions.

The body calyces present in the lobes are papillate whereas those of the lobular crotch and hemipenial body tend to lose their papillae. The body calyces are arranged in two distinct parallel rows on the lobes, with their confluent vertically directed medial walls forming a papillate crest just on the middle of the asulcate and medial regions. Both crests are confluent on their proximal end with the enlarged lateral spines. The conspicuous body calyces present on the lobular crotch and distal region of the body in *H. gigas* are absent in *H. bicinctus*, where they are represented by two parallel grooves running from the lobular crotch to the middle of the hemipenial body on its asulcate surface. The hemipenial body is covered with spinules in most of the areas surrounding the body calyces and the rows of enlarged lateral spines.

Hydrops

Figure 52

SPECIES EXAMINED: *H. martii* (MNHN 5349), *H. triangularis* (IB 51496; LSUMZ 42643; MNHN 1978.2500).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Hydrops martii*. Rossman (1973) figured the sulcate side of the hemipenis of *Hydrops martii* and compared it with that of *Helicops* and *Pseudoryx*. Jenner (1981) presented a drawing of the sulcate side of *H. martii*.

HEMIPENIAL MORPHOLOGY: Both species have almost the same peculiar hemipenial morphology. The sulcus spermaticus bifurcates more or less on the middle of the hemipenial body, with the branches diverging to assume a more or less centripetal position on the lobes (fig. 52). The organ is slightly bilobed and mostly noncalyculate, with only the presence of few poorly developed, unornamented calyces around the tip of each sulcar branch. Small spines are also present on the sulcate surface of the lobes. The organ is considered semicapitate since it has a deep constriction extending along the base of each lobe on the asulcate and lateral surfaces. The asulcate and medial surfaces of the lobes and the lobular crotch are nude except for the presence of several longitudinally directed flounces distributed along the nude region

and for a spinulate crest running vertically on the middle of the lobular crotch and distal region of the hemipenial body. The rest of the hemipenial body is covered with small spines identical to the ones present on the sulcate surface of the lobes. Enlarged lateral spines are lacking in both species.

Hypsirhynchus

Figure 52

SPECIES EXAMINED: (monotypic) *H. ferox* (MPMH 23385).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of this species.

HEMIPENIAL MORPHOLOGY: The hemipenis is slightly bicalyculate, semicapitate, and moderately bilobed (fig. 52). Well-developed enlarged lateral spines are arranged in several parallel rows. The sulcus spermaticus divides on the proximal region of the hemipenial body. The branches of the sulcus run in a centrolineal position, with a slight tendency to a centrifugal condition on the tip of the lobes. Each lobe bears a capitulum formed by papillate calyces that are almost completely restricted to the sulcate surface. The lobular crotch, medial and asulcate surfaces of the lobes, and asulcate distal region of the hemipenial body are almost completely nude except for the presence of a row of small papillae arranged on a bulbous projection found in the proximal region of each lobe. The row of papillae is confluent with the distalmost row of enlarged lateral spines. The surfaces surrounding the enlarged lateral spines on the proximal region of the body are completely covered with spinules.

Ialtris

Figure 53

SPECIES EXAMINED: *I. dorsalis* (AMNH 58063, 51764; KU 268620, 268621), *I. parishi* (KU 268629).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Ialtris dorsalis*. Schwartz and Rossman (1976) figured the hemipenis of *I. dorsalis* and *I. parishi*. Dowling and Duellman (1978) figured the sulcate side of *I. dorsalis*.

HEMIPENIAL MORPHOLOGY: As in *Helicops*, I regard the flounced condition in *Ialtris* derived from a calyculate condition, although

both species examined lack vestiges of calyces on their organ. However, the presence of enlarged intrasulcar spines and the bicalyculate configuration of the flounces on the lobes suggests that the morphology found in *Ialtris* may have derived from a typically bicalyculate condition. As in *Helicops*, the flounces in *Ialtris* retain a comparable configuration on the lobes as the one shown by calyces. For this reason, I retain the same terminology as used to describe calyculate and capitate conditions.

Both species have a very similar hemipenial ornamentation with a highly reduced number of ornaments as compared to other West Indian xenodontines. The organ is deeply bilobed and the lobes are noncapitate and may be considered as bicalyculate (fig. 53). Except for the horizontally directed papillate flounces ornamenting their distal half and some enlarged intrasulcar spines, the lobes lack any ornamentation, being nude on their proximal half. The sulcus spermaticus bifurcates at the base of the hemipenial body, taking almost instantaneously a centrifugal position until the tip of the lobes. Thus, the diverging branches extend along almost all the length of the sulcus, running along the lateral sides of the organ from its base to the tip of the lobes. The hemipenial body is nude except for the presence of lateral and enlarged intrasulcar spines. The enlarged lateral spines are arranged in two parallel rows on each side of the organ, running from the base of the lobes to the base of the organ. The enlarged intrasulcar spines form one exceptionally long row of well-developed spines on each side of the intrasulcar region, running almost parallel to each other from the proximal region of the hemipenial body to the base of the lobes (in *I. dorsalis*) or up on the lobes (in *I. parishi*). The size and number of spines on the organs the two species differ markedly (Schwartz and Rossman, 1976).

Liophis

Figures 53–55

SPECIES EXAMINED: *L. almadensis* (AMNH 22458; IB 53445), *L. cobella* (AMNH 81468), *L. dilepis* (MNHN 1967.147), *L. frenata* (two uncatalogued specimen), *L. juliae* (MNHN 1977.1617), *L. poecilogyrus*

(MNHN 1993.1624; one uncatalogued specimen), *L. reginae* (one uncatalogued specimen).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Aporophis anomalus* (= *L. anomalus*), *Opheomorphus alticolus* (= *L. albiventris*), *O. brachyurus* (= *L. typhlus*), *O. cobella* (= *L. cobella*), *O. typhlus* (= *L. typhlus*), *Xenodon almadensis* (= *L. almadensis*), and *X. reginae* (= *L. reginae*). Maglio (1970) compared the hemipenial morphology of the West Indian species of *Liophis* with that of the other West Indian taxa and figured the dissected organs of *L. cursor* and *L. lineatus*. Dowling and Duellman (1978) figured the sulcate side of the hemipenis of *L. cobella* and *L. lineatus*. Myers (1986) figured the dissected organ of *L. problematicus* and the sulcate side of the everted organ of *L. williamsi*. Donnelly and Myers (1991) described and figured both sides of the hemipenis of *L. torrenicola*. Cei (1993) figured the hemipenes of *L. miliaris* and *L. poecilogyrus*.

HEMIPENIAL MORPHOLOGY: All the species show a remarkably similar hemipenial pattern. As in *Erythrolamprus* (see description above), the organ bears a reduced number of ornaments. All hemipenes are slightly bilobed, with *L. dilepis* having the smallest lobes (fig. 54). The sulcus spermaticus divides at the middle of the hemipenial body except in *L. dilepis*, where it divides proximally. In all species the branches diverge to a centrifugal position and end on the distal region of the apical disks, which are in a lateral position on the distal region of the lobes. The apical disks have a plicate surface. The lobes lack any calyculuation or capitulation, and they are covered with spinules except in the proximal region of their asulcate surface, which is nude. *Liophis dilepis* has one row of three well-developed enlarged intrasulcar spines on each side of the intrasulcar surface, whereas the other species have very weakly differentiated intrasulcar spines (*L. frenata*, *L. juliae*, *L. reginae*) or no intrasulcar spines at all (*L. almadensis*, *L. cobella*, *L. poecilogyrus*). The hemipenial body in each species has enlarged lateral spines that are numerous and arranged in several rows in *L. almadensis* (fig. 54), *L. cobella*, *L. frenata* (fig. 54), *L. juliae* (fig. 55), *L. poecilogyrus*, and *L.*

reginae (fig. 53). In these species most of the lateral spines tend to be concentrated in an inflated area on each side of the asulcate and lateral surfaces of the hemipenial body, with only one or two rows extending toward the distal region of the asulcate surface of the body. The two inflated regions are located on the proximal region of the organ. *Liophis dilepis* has an elongated hemipenis, whereas the other species have a more reduced and bulbous configuration. The hemipenis of *Liophis dilepis* lacks any inflated region and has only two rows of enlarged lateral spines arranged on the lateral and asulcate surfaces of the hemipenial body. In all the species there is at least one row of enlarged lateral spines extending to the lobular crotch on the asulcate side of the organ. *Liophis cobella* and *L. frenata* have a row of larger spinules arranged vertically on the midline of the distal region of the hemipenial body on its asulcate side. The rest of the hemipenial body is covered with spinules in all species.

Lystrophis

Figure 56

SPECIES EXAMINED: *L. dorbignyi* (one uncatalogued specimen), *L. histricus* (MNRJ 4615).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Lystrophis dorbignyi*. Orejas-Miranda (1966) and Dowling and Duellman (1978) figured the sulcate side of the hemipenis of *L. dorbignyi*. Scrocchi and Cruz (1993) figured both sides of the hemipenis of *L. matogrossensis*.

HEMIPENIAL MORPHOLOGY: Both species show a similar hemipenial morphology with a few number of ornaments (i.e., enlarged lateral spines, spinules, and apical disks) (fig. 56). The hemipenes are slightly bilobed, with the sulcus spermaticus dividing more or less at the middle of the hemipenial body. Both branches diverge to a centrifugal position, ending on the distal region of the apical disks. Each lobe has an apical disk (a large spheric nude area) laterally on its distal region. The disks have a plicate surface. The lobes lack any calyces or capitulation. The lobes are covered with spinules except in their medial surface, which is nude. In both species the intrasulcar region of the hemi-

penial body and the immediately proximal surface of the lobes bear together two rows of moderately large, enlarged intrasulcar spines. Their hemipenial bodies also bear moderately large, enlarged lateral spines arranged in several rows mostly restricted to the lateral sides. The rest of the body is covered with spinules.

Manolepis

Figure 41

SPECIES EXAMINED: (monotypic) *M. putnami* (AMNH 65133; MNHN 8406; USNM 110337).

REFERENCES AND REMARKS: None.

HEMIPENIAL MORPHOLOGY: *Manolepis* hemipenial morphology is remarkably similar to that of *Conophis* (fig. 41). The organ is slightly bilobed. The sulcus spermaticus is centrolineal, bifurcating in the proximal region of the hemipenial body. The lobes bear spinulate calyces distally and spinulate flounces proximally, and they are noncapitate. The calyces are arranged in a bicalyculate condition. The spinulate flounces extend to the lobular crotch and to the distal surface of the hemipenial body. The flounces and their spinules found in the latter two regions of the organ and in the proximal region of the asulcate surface of the lobes are distinctly larger than those ornamenting the rest of the lobes. The hemipenial body shows three to four rows of well-developed enlarged lateral spines. The rest of the body is covered with spinules.

The large spinulate flounces present on the asulcate side of the hemipenis of this species are considered to be derived from the body calyces.

Oxyrhopus

Figures 57–62

SPECIES EXAMINED: *O. clathratus* (IB 12464; MNRJ 3895), *O. erdisii* (AMNH 53318; LSUMZ 26812; MCZ 178172; MBH 4393), *O. guibei* (MNHN 8750, 1990.4324; ZUEC 846; two uncatalogued specimen), *O. formosus* (AMNH 129255, 55620, 101391; MNHN 1978.2498), *O. fitzingeri* (BMNH 46.1.14.27; MCZ 160792), *O. leucomelas* (QCAZ 1495), *O. melanogenys* (IB 52863), *O. cf. melanogenys* (LSUMZ 19707; TCWC

42139), *O. petola* (MNHN 1989.3787, 1990.4323, 1990.4324), *O. rhombifer* (IB 16559; MNHN 1990.4325; MBH 2074; one uncatalogued specimen), *O. trigeminus* (IB 53968, 54428; IVB 633; MCZ 22444; MNHN 1990.4321; MNRJ 3998).

REFERENCES AND REMARKS: Cope (1895), Dowling and Duellman (1978), and Jenner and Dowling (1985) figured the hemipenis of *O. petalarius* (= *O. petola*). Cope showed a dissected organ, whereas Dowling and colleagues figured the sulcate side of an everted hemipenis. Zaher and Caramaschi (1992) compared the hemipenial pattern of various species of *Oxyrhopus* and figured both sides of the organ of *O. guibei*, *O. trigeminus*, *O. rhombifer*, and the dissected organ of *O. cf. melanogenys*. Zaher (1994a) presented evidence that this genus is polyphyletic. Thus, the description provided herein intends to present only overall hemipenial similarity within this complex of species. However, some of the characters described below correspond to synapomorphies supporting several monophyletic species groups. These will be defined formally elsewhere within an explicit cladistic framework. Also, an examination of the type specimens of *O. venezuelanus* Shreve, 1947 and of *O. doliatus* Duméril, Bibron, and Duméril, 1854 reveals that they are conspecific, with the former being a junior synonym of the latter (Zaher, in press). In the same study, *Drepanodon erdisii* Barbour, 1913 is revalidated because it differs markedly from the newly redefined *O. doliatus*. The former was previously placed in the synonymy of *O. doliatus* by Bailey (1970). These nomenclatural changes are followed in the present study.

HEMIPENIAL MORPHOLOGY: All species have a deeply bilobed, bicalyculate, bicapitate hemipenis with well-developed enlarged lateral spines arranged in three or four rows. The sulcus spermaticus divides on the proximal half of the hemipenial body, with each branch running to the lateral sides of the organ where they take a centrifugal position. The lobes are ornamented with papillate calyces that tend to be spinulate on the edges of the capitulum. All species except *O. clathratus* (fig. 57) and *O. leucomelas* (fig. 58) have a nude area in the lateral region of the tip of each lobe. In *O. trigeminus* (fig. 58),

O. rhombifer (fig. 59), *O. guibei*, *O. melanogenys* (fig. 60), *O. cf. melanogenys*, and *O. petola* (fig. 60) the nude area is very large, whereas in *O. formosus* (fig. 61) and *O. erdisii* (fig. 59) it is very poorly developed. In *O. fitzingeri* (fig. 62) the rounded edge delimiting the area is present and conspicuous. However, a series of papillate walls are present within the delimited surface of the area, forming several large papillate calyces. The round nude area present in *Oxyrhopus* resembles somewhat the apical disk of the *Xenodontini*. However, these structures are considered to have been derived independently in each group since a nude area is lacking in all other, more closely related pseudoboines (Zaher, 1994a).

The capitulum is directed externally in a lateral position, whereas the noncapitulate surface of the lobes are nearly facing one another. The sulcate surface of the proximal region of the lobes bears one or two rows of enlarged intrasulcar spines. The rest of the intrasulcar surface is covered with spinules. The medial surface of the lobes is ornamented with a conspicuous crest. Most of the surface of the crest is inflated. The distal end touches the capitulum and the proximal end is confluent with the rows of enlarged lateral spines. In all species except *O. clathratus* and *O. leucomelas* the crests are invaded by a row of enlarged lateral spines that extends along the entire length of the crest to the edge of the capitulum. In the latter two species the distal end of the crests is not inflated and is papillate. This crest is weakly developed or lacking in *O. guibei*, *O. melanogenys*, *O. cf. melanogenys*, and *O. petola*, owing to the downward extension of the capitulum over almost all the asulcate surface of the lobes. *Oxyrhopus fitzingeri* has a peculiar condition, with bulbous and feebly bicapitate lobes and with weakly developed calyces surrounding an enlarged nude area. Each nude area is ornamented with dispersed, very thin, feebly developed calycular walls.

In *O. guibei*, *O. melanogenys*, *O. cf. melanogenys*, *O. petola*, and *O. fitzingeri* the capitula are formed by large calyces, whereas in the remaining species they are formed by numerous small calyces. Most species bear a pair of nude pockets in the lobular crotch. These pockets are of different sizes and

shape, being conspicuous in *O. trigeminus*, *O. rhombifer*, and *O. formosus*, moderately developed in *O. clathratus*, *O. leucomelas*, and *O. erdisii*, weakly developed in *O. guibei*, *O. melanogenys*, *O. cf. melanogenys*, and *O. petola*, and lacking in *O. fitzingeri*. Apart from the crest and pair of pockets, the region of the lobular crotch and asulcate surface of the lobes is nude.

Oxyrhopus guibei, *O. melanogenys*, *O. cf. melanogenys*, *O. petola*, and *Oxyrhopus fitzingeri* have a short bulbous hemipenis with lobes almost as long as the hemipenial body. *Oxyrhopus trigeminus*, *O. rhombifer*, *O. formosus*, *O. leucomelas*, and *O. erdisii*, on the other hand, have an elongated hemipenis with lobes less than half as long as the hemipenial body. *Oxyrhopus clathratus* has the smallest lobes, bearing small rounded capitula in a T-shaped organ. This peculiar condition of the organ is due to the great enlargement of the distal surface of the hemipenial body and lobular crotch, forcing the lobes and their capitula to be in the same horizontal plan of the lobular crotch. Apart from several rows of enlarged lateral spines, the hemipenial body is covered with spinules.

Phalotris

Figure 63

SPECIES EXAMINED: *P. mertensi* (MNHN 1993.1621; 3 uncatalogued specimens), *P. nasutus* (IB 28950).

REFERENCES AND REMARKS: Ferrarezzi (1993) revived the genus *Phalotris*, previously viewed as a subgenus of *Elapomorphus*, defining it as the monophyletic sister-group of *Apostolepis*. According to Ferrarezzi (1993) and Puerto and Ferrarezzi (1993), the genus *Phalotris* is composed of 11 species distributed in three monophyletic species groups—*bilineatus*, *nasutus*, and *tricolor*. The present description is based on only one representative each of the *tricolor* and *nasutus* groups. Lema (1985) figured the hemipenis of *P. lemniscatus* on both everted and dissected conditions.

HEMIPENIAL MORPHOLOGY: The organ of *Phalotris mertensi* is only slightly bilobed, whereas *P. nasutus* has a more bilobed hemipenis (fig. 63). Their hemipenial patterns are

very different, resembling only one another in the position of the sulcus furcation, which is in the proximal region of the hemipenial body, and in the centrolineal condition of the branches. *Phalotris mertensi* has a unicalyculate noncapitate condition with a capitulum confined to the sulcate side of the organ, with the asulcate side of the lobe being ornamented with several rows of well-developed body calyces. These rows retain the same position as those present in bilobed organs, forming the complex V-shaped pattern shown by the simple organ of the genus *Apostolepis*. The V-shaped structure is clearly present in two of the four hemipenes of *P. mertensi* available for examination. The other two organs have a lobular crotch with four more or less distinct parallel rows of body calyces. Both capitular and body calyces are spinulate. There is no vestige of enlarged lateral spines except for the presence of two or three slightly more developed spinules on each side of the hemipenial body. The latter is covered with spinules except around the base of the organ.

Phalotris nasutus has the most plesiomorphic hemipenial pattern within the elapomorphines studied, being very similar to the "chamissonis group" of *Philodryas*. The organ is clearly but not deeply bilobed, semicalyculate, and semicapitate, and the capitulum invades the distal and lateral regions of the tip of the asulcate side of the lobes. The rest of the asulcate surface, all the medial surface of the lobes, the lobular crotch, and the distal region of the hemipenial body are ornamented with large body calyces. Two more or less hypertrophied structures, clearly formed from contiguous vertically directed walls, can be identified on each side just above the pair of large parallel rows of body calyces on the lobular crotch and body region. These structures are here viewed as representing a least modified condition of the V-shaped structure present in the genera *Elapomorphus* and *Apostolepis* (see descriptions of their hemipenial pattern in this section). Only two rows of enlarged lateral spines are present, being confined to the lateral surface of the organ. The hemipenial body is covered with spinules.

Philodryas

Figures 64–69

SPECIES EXAMINED: *P. aestiva* (IB 54407), *P. burmeisteri* (USNM 52961), *P. chamissonis* (AMNH 36077; MNHN 3553, 1991.429; one uncatalogued specimen), *P. livida* (IB 40953, 41200), *P. mattogrossensis* (AMNH 141663), *P. nattereri* (IB 48404), *P. olfersii* (CEPLAC 1016; MNHN 1993.1620), *P. patagoniensis* (MNHN 7641), *P. psammophidea* (AMNH 36203), *P. viridissima* (MNHN 3837, 1978.2569).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Monobothris chamissonis* (= *Philodryas chamissonis*), *P. nattereri*, *P. schotti*, and *P. viridissima*. Dowling (1969b) reviewed some aspects of Cope's contribution and figured an everted organ of *P. olfersi* and a dissected organ of *P. elegans*. Thomas and Dixon (1977) figured both sides of the organ of *P. nattereri*. Donnelly and Myers (1991) described and figured both sides of the hemipenis of *P. cordata*. Cei (1993) figured a partially everted organ of *P. trilineata*.

Donnelly and Myers (1991) have shown that the gender of *Philodryas* is feminine, which is followed here. Thomas and Fernandes (1996) placed the monotypic genus *Platynion* in the synonymy of *Philodryas*, arguing that *P. lividum* shows the same meristic and hemipenial features diagnostic of the genus *Philodryas* as conceived by the senior author (Thomas, 1976). However, the monotypic genus *Pseudablades* meets most of the criteria established by the diagnosis given by Thomas and Fernandes (1996: 272–273) (except for the dorsal scale rows that are constant throughout the body), including the presence of "enlarged calyces extending along the distal one-third of the asulcate surface." The newly recognized genus *Xenoxylbelis* also presents this same hemipenial feature, showing a surprisingly similar hemipenial pattern to those of *P. olfersii*, *P. viridissima*, and *P. cordata*.

These observations suggest that the genus *Philodryas*, as defined by Thomas and Fernandes (1996), still represents a paraphyletic unit, pending a broader evaluation of its delimitation within the Xenodontinae. However, their conclusions are followed herein until

new material concerning the phylogeny of the genus is proposed. In their phylogenetic analysis of the genus *Philodryas*, Lobo and Scrocchi (1994) did not address the phylogenetic position of the possibly closely related genera *Platynion*, *Pseudablades*, and *Xenoxobelis*.

HEMIPENIAL MORPHOLOGY: Two widely different hemipenial patterns are present in *Philodryas*, corresponding basically to the "very short" and "very long" hemipenial types of Thomas (1976) (Thomas's type 2 and types 1, 3, and 4, respectively).

Philodryas olfersii (fig. 64) and *P. viridissima* (fig. 69) have a short hemipenial body and slightly bilobed lobes (from 8 to 11 subcaudals long; Thomas, 1976). The organ is semicalyculate and noncapitate. The capitula are formed from papillate calyces. Both capitula are almost totally confluent in the broad intrasulcar region, forming an almost uninterrupted calyculate area restricted to the sulcate side of the organ. The calyculate area is approximately the same length as the hemipenial body. The sulcus spermaticus divides at the base of the calyculate area, with the centrolinal branches terminating in a slightly centrifugal position on the distal region of the lobes, but not at their tip. The proximal half of the organ, which corresponds to the hemipenial body, is covered with numerous spines of moderate size on the sulcate and lateral surfaces. In both species the more lateral rows of spines are significantly larger than the others, extending distally to the middle of the organ in *P. viridissima* and to the lateral side of the distal region of the lobes in *P. olfersii*. These medium-sized spines have the same topographic position as the enlarged lateral spines and are thus viewed as the homologue of the well-developed enlarged lateral spines present in the other species of the genus. The asulcate surface of the organ is ornamented with two parallel rows of large, weakly papillate, body calyces extending from the tip of the lobes and lobular crotch to the base of the hemipenial body. The description and figures of the hemipenis of *P. cordata* provided by Donnelly and Myers (1991) clearly show that this species has the same hemipenial pattern as *P. viridissima* and *P. olfersii*.

Philodryas aestiva (fig. 65), *P. burmeisteri*

(fig. 66), *P. chamissonis* (fig. 64), *P. livida* (fig. 67), *P. mattogrossensis* (fig. 68), *P. nattereri* (fig. 65), *P. patagoniensis* (fig. 68), and *P. psammophidea* (fig. 66) have a long hemipenial body and moderately long lobes (from 7 to 25 subcaudals long; Thomas, 1976). The most striking difference between this pattern and the one present in *P. olfersii* and *P. viridissima* is the length of the hemipenial body as compared to the length of the capitulate region of the lobes. The hemipenial body represents at least two-thirds of the length of the organ in the former, whereas the latter two species have an organ with a much stockier body that is more or less the same length as the capitulate region of the lobes. All eight species have a deeply bilobed, semicalyculate, slightly semicapitate hemipenis. The sulcus spermaticus divides on the proximal region of the body, with the centrolinal branches taking a slight centrifugal position on the distal region of the lobes. All eight species have two main rows of enlarged lateral spines extending from the base of the lobes along at least half of the length of the hemipenial body on its lateral surface. These rows of spines tend to divide in several rows of smaller spines that invade the sulcate surface on the proximal half of the body. The lobes are ornamented with papillate capitular calyces on their sulcate and lateral surfaces, and by large, shallow papillate body calyces on their medial and asulcate surfaces. These calyces extend in two or more parallel rows on the lobular crotch and distal half of the hemipenial body, being more or less pronounced in the latter area. In *P. livida* each lobe terminates in a sharp "awn-like" tip. *Philodryas burmeisteri* and *P. nattereri* have only the medial surface of the lobes ornamented with body calyces, with the rest of the lobular surface being covered with papillate capitular calyces. *Philodryas psammophidea* bears a row of moderately enlarged spines on the edge of each capitulum in the asulcate side. Each spine emerges from the lateral wall of the capitular calyces that form the edge of the capitulum, thus being topographically related to the latter structure. For this reason such spines are here viewed as derived from papillae instead of being true enlarged lateral spines as proposed by Thomas (1976: 242; his hemipenial

type 3). Indeed, such a configuration is also present in *Antillophis parvifrons*, where the "spines" arranged along the edge of each capitulum are clearly enlarged calcified papillae when examined carefully.

Phimophis

Figures 70–72

SPECIES EXAMINED: *P. guerini* (IB 63973, 26726, 54241), *P. guianensis* (AMNH 108791), *P. vittatus* (USNM 319628).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Rhinostoma nasuum* (= *P. guianensis*). Jenner and Dowling (1985) figured the sulcate side of the organ of *P. guianensis*.

HEMIPENIAL MORPHOLOGY: All three species have a deeply bilobed, bicalyculate, bicapitate hemipenis with well-developed enlarged lateral spines arranged in one to four major rows. The sulcus spermaticus divides on the proximal region of the hemipenial body, with each branch taking a centrifugal position that ends on the lateral tip of the lobes. The lobes are ornamented with papillate calyces, which form a laterally placed capitulum. The medial and asulcate surfaces of the lobes are ornamented with a papillate crest that runs from the distal tip of the enlarged lateral spine rows to the distal edge of the capitulum. The proximal two-thirds of each crest is inflated and bears several series of enlarged papillae and one row of enlarged lateral spines, whereas the distal one-third turns into a thin fringelike papillate crest. Papillate body calyces occur on each side of the crest distally, sharing the crest as their vertically directed medial wall. Each row is formed by one to three body calyces in *P. guerini* (fig. 70) and *P. vittatus* (fig. 71), whereas *P. guianensis* (fig. 72) has only vestiges of one pair of body calyces just below the distal edge of the capitulum. The remaining surface of the lobes (below the rows of calyces) is always nude. In all three species there is a large lobular crotch that bears a pair of nude pockets. The large intrasulcar region bears one row of three vertically directed enlarged intrasulcar spines on each side (one or two spines may be lacking in one of the rows). The distal region of the intrasulcar region tends to be nude along its

midline. The enlarged lateral spines are restricted to the lateral surface of the hemipenial body on its distal half, except for the extension of one row onto each lobular crest. The asulcate surface of the hemipenial body (below the pair of pockets) and the whole proximal region of the body are ornamented only by spinules. In *P. vittatus* the proximal region of the hemipenial body bears a large nude pocket on its lateral side. This pocket is less developed in *P. guerini* and seems to be absent in *P. guianensis*.

Pseudablables

Figure 69

SPECIES EXAMINED: (monotypic) *P. agassizi* (MNHN 1890.107, 1892.69).

REFERENCES AND REMARKS: *Pseudablables agassizi* has a hemipenial morphology very similar to that of *Philodryas aestiva*, corresponding to the "very long" hemipenial pattern present in *Philodryas* (hemipenial morphology suggests that this species may well belong to the genus *Philodryas*; see also remarks under *Philodryas*).

HEMIPENIAL MORPHOLOGY: This species has an organ with a long body and short lobes (less than a third of the total length) (fig. 69). However, the organ still retains a well-defined bilobation, and it is semicalyculate and slightly semicapitate. The semicapitation of the lobes is very weak, leading to an almost uniform outline of the organ laterally. The sulcus spermaticus divides in the proximal region of the hemipenial body, with the branches retaining a centrolateral position until they reach the distal tip of each lobe. The lateral surface of the hemipenial body has two main rows of enlarged lateral spines extending from the base of the organ to the base of the lobes. One of these rows is confluent with a row of spines, of somewhat smaller size, located on the lateral walls of the calyces that form the noncapitate edge of each capitulum, similar to the condition found in *Philodryas psammophidea* and *P. aestiva*. Adjacent calyces bear some less conspicuous spines or enlarged and calcified papillae. However, most of the calyces forming each capitulum are simply papillate. The capitula are restricted to the sulcate and lateral surfaces of the lobes. The lobular crotch and

asulcate surface of the lobes are ornamented with two parallel rows of large, shallow papillate body calyces. Both rows of calyces extend to the distal half of the hemipenial body to the middle of the organ, being more pronounced in the region of the lobes. The proximal half of the asulcate surface is covered with spinules. The proximal half of the sulcate side between the sulcus and the enlarged lateral spines is covered with medium-sized spines and spinules.

Pseudoboa

Figures 70–73

SPECIES EXAMINED: *P. coronata* (AMNH 134205; MNHN 1986.1488), *P. haasi* (IB 18245), *P. nigra* (CEPLAC 678; IB 48674, 54379; MNHN 1993.1619; MNRJ 4497), *P. neuwiedii* (AMNH 85942; MNHN 1955.48, 1978.2638, 1989.3187).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Scytale coronatum* (= *P. coronata*). Jenner and Dowling (1985) figured the sulcate side, and Zaher and Caramaschi (1992) provided drawings of both sides of the organ of *P. coronata*. Morato et al. (1995) figured both sides of the organ of *P. serrana*.

HEMIPENIAL MORPHOLOGY: All four species show a similar hemipenial pattern, with deeply bilobed, bicalyculate, bicapitate organs. The enlarged lateral spines are well developed and distributed in two to four major rows mostly restricted to the distal half of the hemipenial body. The sulcus spermaticus divides on the proximal region of the hemipenial body, with each branch taking a centrifugal position and ending on the lateral tip of the lobes. The lobes are ornamented with papillate calyces that form a capitulum, which is mostly restricted to the lateral and sulcate surfaces of the lobes. The medial and asulcate surfaces of the lobes are ornamented with a weakly papillate crest that runs from the distal tip of the row of enlarged lateral spines to the distal edge of the capitulum. The proximal two-thirds of each crest is inflated and bears some dispersed and weakly developed papillae. The same inflated portion of the crest is invaded by one row of enlarged lateral spines. The distal one-third of each crest turns into a thin papillate fringelike structure. In *P. haasi*

(fig. 71) the crest is inflated only on its proximal one-third; the remaining two-thirds have the thin papillate fringelike condition. All of the region on each side of the crest (i.e., the medial and asulcate surfaces of the lobes) is nude except for the presence of one or two weakly developed papillate body calyces on each side of the crest distally. The lobular crotch bears a pair of nude pockets, which are weakly papillate dorsally. The large intrasulcar region bears a row of three to six enlarged intrasulcar spines on each side. The asulcate surface of the hemipenial body below the pair of pockets and the whole proximal region of the body are ornamented only by spinules. *Pseudoboa neuwiedii* (fig. 70), *P. coronata* (fig. 72), and *P. nigra* (fig. 73) have an unusually long and narrow proximal region of the hemipenial body, just below the bifurcation of the sulcus. *Pseudoboa coronata* tends to have an enlargement of the area of the lobular crotch, thus forcing the capitula to occupy a ventral position with respect to their inflated crests.

Pseudoeryx

Figure 73

SPECIES EXAMINED: (monotypic) *P. plicatilis* (AMNH 53740; IB 51924; MNHN 1989.3290).

REFERENCES AND REMARKS: Rossman (1973) figured the sulcate side of the hemipenis of *P. plicatilis* and compared it with that of *Helicops* and *Hydrops*.

HEMIPENIAL MORPHOLOGY: *Pseudoeryx plicatilis* has a simplified hemipenial pattern, with only papillate flounces and calyces and moderately large spines but with high intra-specific variability, suggesting that some populations may well represent distinct species (fig. 73). Indeed, the three hemipenes examined show differences in the degree of bilobation, presence or absence of calyces, and degree of reduction of the flounces in the lobular crotch and hemipenial body. However, all three hemipenes show a slight bilobation. The sulcus spermaticus is centrolinal, bifurcating in the proximal region of the hemipenial body. The lobes, the lobular crotch, and the distal region of the hemipenial body are ornamented almost exclusively by papillate flounces. The flounces are always equal in

length. The hemipenial body is covered with moderately large spines, which decrease in length from the middle of the body to its base. Enlarged lateral spines are lacking. Two of the available hemipenes (AMNH 53740 and IB 51924) retain well-developed papillate calyces on both lobes, in a bicalyculate and non-capitate condition, followed by several rows of longitudinally directed papillate flounces (but transversely directed in Rossman, 1973: fig. 1). The pattern shown by these specimens suggests that the hemipenial condition present in *P. plicatilis* derived from a typical South American xenodontine condition with papillate capitular calyces and body calyces, with the latter being represented in this species by the proximal flounces on the asulcate surface of the lobular crotch and distal surface of the hemipenial body. The third hemipenial preparation (MNHN 1989.3290) shows only longitudinally directed papillate flounces on the lobes and on the distal region of the hemipenial body. The lobes are weakly defined. The flounces tend to disappear on the lobular crotch and midline of the body.

Psomophis

Figure 74

SPECIES EXAMINED: *P. genimaculatus* (IB 12590), *P. joberti* (IB 36437).

REFERENCES AND REMARKS: Myers and Cadle (1994) figured both sides of the organ of *P. genimaculatus* and described the hemipenial morphology of the three species placed in this genus. They discussed separately various hemipenial structures and their respective terminology. Both everted organs I examined conform with the descriptions given by Myers and Cadle (1994). The hemipenis of *P. joberti* also shows in both lobes "a single spine interspersed with the spinulate papillae about midway along one edge of the calyculate overhang" (Myers and Cadle, 1994: 12). This character is likely to be diagnostic of the species. The large papillae in *Psomophis* are unique in having a mineralized tip (Myers and Cadle, 1994). However, I interpret these "spinulate papillae" as true papillae (i.e., the same ornamenting the capitular calyces), with the mineralized tip being a synapomorphy of the genus. All of the capitulum has vestiges of calyces, except for

the distal region of the capitulum and for the large overhanging wall of tissue forming the distal edge of the capitulum (with both bearing very large unconnected papillae).

HEMIPENIAL MORPHOLOGY: Both species examined have very similar hemipenes, differing mostly by the presence in *P. joberti* of a single spine interspersed with the spinulate papillae about midway along the lateral edge of the capitulum (fig. 74). Their hemipenes are deeply bilobed, bicalyculate, and slightly bicapitate. The enlarged lateral spines are well developed and arranged in two parallel rows. The sulcus spermaticus divides on the proximal region of the hemipenial body, with each branch running in a centrolateral position and ending just above the middle of the lobes in their distal half. The lobes are twice as long as wide. The capitula are mostly restricted to the sulcate surface of the organ. Each capitulum is formed by numerous large papillae that show some vestiges of their supporting calyces. The calycular walls connecting the papillae on the proximal sulcate surface of the capitula are almost vestigial, whereas the same calycular walls are clearly visible proximally near the medial edge of each capitulum. The distal tip of each papillae is mineralized, forming a minute spinule. The distal region of each lobe has, on its lateral edge, a large overhanging fringe of tissue acting as an expansion of the capitulum. This fringelike structure, as well as the distal region of the capitulum, bears distinctly larger papillae than the rest of the capitulum. These larger papillae are not interconnected by calycular walls. The fringe turns medially on the distal tip of each lobe, differentiating itself from the capitulum and invading the nude medial surface of the lobes, on its distal third. The rest of the asulcate and medial surfaces of the lobes are completely nude (except from some slight vertically directed folds). The asulcate surface of the hemipenial body is covered with spinules.

Rhachidelus

Figure 75

SPECIES EXAMINED: (monotypic) *R. brazili* (IB 53558).

REFERENCES AND REMARKS: None.

HEMIPENIAL MORPHOLOGY: The hemipenis

is deeply bilobed, bicalyculate, and bicapitate (fig. 75). The enlarged lateral spines are well developed and distributed in four major rows mostly restricted to the distal half of the hemipenial body. The sulcus spermaticus divides on the proximal region of the hemipenial body, with each branch taking a centrifugal position and ending on the lateral tip of a lobe. The lobes are ornamented with papillate calyces, forming a capitulum that is mostly laterally directed on the lobes. The medial and asulcate surfaces of the lobes are ornamented with a weakly papillate crest that runs along the midline of the region from the distal edge of the capitulum to the distal tip of the rows of enlarged lateral spines. The proximal third of each crest is inflated and bears some dispersed and weakly developed papillae. The same inflated portion of the crest is invaded by one row of enlarged lateral spines. The distal third of each crest corresponds to a thin papillate fringelike structure. The region along each side of the crest on the medial and asulcate surfaces of the lobes is nude except for the presence of two to four weakly developed papillate body calyces on each side of the crest distally. The lobular crotch bears a pair of nude calycular pockets and is only weakly papillate dorsally. The large intrasulcar region bears a row of six to seven enlarged intrasulcar spines on each side. The asulcate surface of the hemipenial body (below the pair of pockets) and the whole proximal region of the body are ornamented only by spinules. This species has an unusually long and narrow proximal region of the hemipenial body just below the bifurcation of the sulcus.

Saphenophis

Figure 76

SPECIES EXAMINED: *S. tristriatus* (AMNH 129609), *S. boursieri* (AMNH 109500; USNM 233050).

REFERENCES AND REMARKS: Maglio (1970) and Myers (1969, 1973) figured the dissected organ of *S. boursieri*. Myers also furnished drawings of the dissected organ of *S. tristriatus*.

HEMIPENIAL MORPHOLOGY: *Saphenophis boursieri* and *S. tristriatus* have apparently highly divergent hemipenial patterns (fig.

76); however, both species present various common traits viewed as synapomorphies.

The hemipenis of *S. tristriatus* (fig. 76) is slightly bilobed, bicalyculate, and semicapitate, with short lobes and a deeply forked sulcus spermaticus dividing at the level of the proximal half of the body. Each branch of the sulcus extends centrolineally to the base of the capitula where they diverge to take a centrifugal position on the lobes that end on the distal region. The enlarged lateral spines are numerous and of moderate size on all the sulcate and lateral surfaces of the body, with the enlarged lateral spines of the asulcate surface being larger than those on the sulcate side. The large intrasulcar region is almost completely nude except for some sparse moderate-sized papillae that are mostly restricted to the edge of each spermatic branch. The capitulum of each lobe is restricted to the sulcate side and is formed by papillate calyces. The asulcate surface of each lobe bears a papillate crest that extends from the lobular crotch to the distal edge of the capitulum. The crest is inflated on its proximal half, whereas its distal half turns into a thin fringelike papillate crest. Both crests fail to meet on the midline of the lobular crotch. An inflated expansion bearing a row of enlarged lateral spines meets each lobular crest on its middle, there interspersing with the proximal wall of the crest. A pair of large nude pockets is present on the distal region of the asulcate side of the hemipenial body just below the lobular crests. The distal half of the hemipenial body bears a vertically oriented row of papillae and spinules on its midline. The proximal region of the asulcate surface of the body, as well as the narrow area between the pockets, is ornamented with spinules and medium-sized spines.

The hemipenis of *S. boursieri* (fig. 76) is deeply bilobed, bicalyculate, and semicapitate, with long lobes and a deeply forked sulcus spermaticus dividing at the level of the proximal half of the body. Each branch of the sulcus extends centrolineally and takes a centrifugal position on the lobes, ending on the lateral surface of the distal tips. The enlarged lateral spines are well developed and arranged in three main rows, with one row invading and reaching the middle of each

lobe. There is a row of weakly developed papillae extending from the lobular crotch to the distal edge of the capitulum on both lobes. The tissue sustaining both the row of papillae and the expanded row of enlarged lateral spines is slightly or poorly inflated. The distal region of the hemipenial body shows a pair of weakly developed depressions or pockets. The intrasulcar region is almost completely nude. The capitulum of each lobe is mostly restricted to the sulcate and lateral sides and is formed by papillate calyces. The asulcate surfaces of the lobes are almost completely nude except for the weakly developed rows of papillae extending from the lobular crotch to the distal edges of the capitula. The distal half of the hemipenial body bears a vertically oriented row of papillae and spinules on its midline. The rest of the hemipenial body lacks spinules.

Siphlophis

Figures 77, 78

SPECIES EXAMINED: *S. cervinus* (MNHN 1978.2513), *S. leucocephalus* (CEPLAC 993), *S. pulcher* (IB 13937, 22398), *S. worontzowi* (one uncatalogued specimen).

REFERENCES AND REMARKS: Jenner and Dowling (1985) figured the sulcate side of the organ of *S. cervinus*.

HEMIPENIAL MORPHOLOGY: All species have a deeply bilobed, bicalyculate, bicapitate hemipenis with well-developed enlarged lateral spines distributed in three or four rows (figs. 77, 78). The sulcus spermaticus divides on the proximal half of the hemipenial body, with each branch extending to the lateral sides of the organ where they take a centrifugal position. The lobes are ornamented with papillate calyces that tend to be spinulate on the edges of the capitulum. The capitulum is directed externally in a lateral position, whereas the noncapitulate surfaces of the lobes retain a nearly medial position. The proximal region of the intrasulcar area of each lobe bears one row of three enlarged intrasulcar spines, with the rest of the intrasulcar surface being covered with spinules. *Siphlophis pulcher* (fig. 77) is the only exception in lacking enlarged intrasulcar spines. The medial surface of each lobe is ornamented with an inflated crest proximally,

which reduces to a thin papillate crest that ends on the distal edge of the capitulum. The crest on each lobe is invaded by a row of enlarged lateral spines on its inflated proximal region. In all species the capitula are formed by numerous small calyces and tend to have a rounded condition.

All species bear a pair of nude pockets in the lobular crotch. Apart from the presence of a pair of crests and pockets, the region of the lobular crotch and asulcate surface of the lobes are nude. *Siphlophis cervinus* and *S. pulcher* show the smallest organs, with small lobes bearing distinctly rounded capitula (fig. 77). The lobes and the short hemipenial body show a T-shaped disposition, as in *Oxyrhopus clathratus* (fig. 57). This peculiar condition is due to the enlargement of the distal surface of the hemipenial body and lobular crotch, forcing the lobes and their capitula to be in the same horizontal plane as the lobular crotch. On the other hand, *S. worontzowi* (fig. 78) and *S. leucocephalus* (fig. 78) show a less derived condition with a longer organ bearing an enlarged lobular crotch but still having prominent lobes and capitula. All species have the hemipenial body mostly covered with spinules.

Tripanurgos

Figure 79

SPECIES EXAMINED: (monotypic) *T. compressus* (IB 52912, 53341; CEPLAC 520; LSUMZ 27352).

REFERENCES AND REMARKS: Jenner and Dowling (1985) figured the sulcate side of the organ of this species.

HEMIPENIAL MORPHOLOGY: The organ is deeply bilobed, bicalyculate, and bicapitate with well-developed enlarged lateral spines distributed in three or four rows (fig. 79). The sulcus spermaticus divides on the proximal half of the hemipenial body, with the branches extending to the lateral sides of the organ where they take a centrifugal position. The lobes are ornamented with papillate calyces that tend to be spinulate on the edges of the capitulum. The capitulum is directed externally in a lateral position. The noncapitulate surfaces of the lobes nearly face one another. The proximal region of the intrasulcar area of each lobe bears one row of three

enlarged intrasulcar spines. The rest of the intrasulcar surface is covered with spinules. The medial surface of the lobes is ornamented with an inflated crest proximally, which turns into a thin papillate crest distally; the thin crest ends on the distal edge of the capitulum. The whole inflated region of the crests is invaded by a row of enlarged lateral spines. The capitula are formed by numerous small calyces and tend to show a rounded condition on each lobe. The lobular crotch is ornamented with a pair of nude pockets. The lobular crotch and asulcate surface of the lobes are entirely nude except for the presence of the lobular crests and pockets. Two of the specimens examined (IB 52912, 53341) have small lobes bearing distinctly rounded capitula as well as a short hemipenial body in a T-shaped condition similar to that present in *Siphlophis*. As suggested above (see *Siphlophis* account), this peculiar condition is due to the enlargement of the distal surface of the hemipenial body and lobular crotch, forcing the lobes and their capitula to be in the same horizontal plane as the lobular crotch. One specimen (LSUMZ 27352) retains the less derived condition with a longer organ bearing an enlarged lobular crotch with prominent lobes. The fourth specimen (CEPLAC 520) shows an intermediate condition between the two described above, with an enlarged lobular crotch and only slightly prominent lobes being almost on the same plane as the lobular crotch. The rest of the hemipenial body is mostly covered with spinules.

Tropidodryas

Figure 79

SPECIES EXAMINED: *T. striaticeps* (IVB 1139; MNHN 3846, 1993.1622).

REFERENCES AND REMARKS: Thomas and Dixon (1977) compared the hemipenial pattern of this genus with that of *Philodryas* and figured both sides of the organ of *Tropidodryas striaticeps* and *P. nattereri*.

HEMIPENIAL MORPHOLOGY: The organ is deeply bilobed, bicalyculate, and noncapitate with well-developed enlarged lateral spines distributed in three or four rows (fig. 79). The sulcus spermaticus divides at the middle of the hemipenial body, with the branches

turning abruptly to the lateral sides of the organ where they take a centrifugal position. The lobes are ornamented with small papillate calyces. The capitulum is directed externally and is restricted to a lateral position. The noncapitate surfaces of the lobes face one another. The intrasulcar area bears two parallel rows of numerous enlarged intrasulcar spines that extend along the edges of the capitula on the sulcate side from the base of the intrasulcar area to the tip of each lobe. However, the two rows tend to fuse, forming one unique row on the distal region of each lobe. The capitula are also edged by two rows of enlarged lateral spines that extend along the asulcate side of the lobes until reaching their tip. The rows of intrasulcar and enlarged lateral spines do not meet at the level of the tip of the lobes. The medial surfaces of the lobes are completely nude with the exception of a discrete crest ornamented with a row of small papillae that runs up the middle of the medial surface from the lobular crotch to the tip of each lobe. The lobular crotch is nude except for the presence of some sparse papillae. The lobes are about as long as the hemipenial body and tend to be directed laterally, giving the organ a Y-shaped appearance. The asulcate surface of the hemipenial body is covered with spinules.

Uromacer

Figure 80

SPECIES EXAMINED: *U. catesbyi* (MPMH 18887; MNHN 8671), *U. frenatus* (MPMH 20135), *U. oxyrhynchus* (MNHN 1680, 8672).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Uromacer oxyrhynchus*.

HEMIPENIAL MORPHOLOGY: All species have a deeply bilobed, semicalyculate, semicapitate hemipenis with numerous well-developed enlarged lateral spines concentrated on the lateral surface of the proximal half of the hemipenial body (fig. 80). The sulcus spermaticus divides at the middle of the hemipenial body. Both branches run centrolinially throughout the lobes, taking a slightly centrifugal position only on the distal regions of the capitula. The capitula, formed by small

papillate calyces, are mostly confined to the sulcate and lateral sides of the lobes. The lobes comprise a third of the length of the organ, whereas the capitula represent half of the entire length since they extensively invade the sulcate surface of the hemipenial body. The body is relatively stocky rather than elongate. The medial and asulcate surfaces of the lobes are completely nude except for the presence of a spinulate and slightly inflated crest on the asulcate surface that reaches the distal tip of the lobes, touching the edge of the capitulum. In all three species the crest is invaded by a row of enlarged lateral spines that reaches the tip of the lobes in *U. frenatus* and *U. oxyrhynchus* (fig. 80), but is confined to the basal half of the lobes in *U. catesbyi* (fig. 80). In *catesbyi* the remaining surface of the crest ornamenting the other half of each lobe is covered with a row of thin spinules, a condition also present in *Hypsirhynchus* and part of *Alsophis* (see accounts above). The lobular crotch and asulcate surface of the hemipenial body are mostly nude. All three species share a peculiar capitular overhanging edge comprised of a thin fringe of tissue. This condition is also present in *Hypsirhynchus* and part of *Alsophis*.

Uromacerina

Figure 81

SPECIES EXAMINED: (monotypic) *U. ricardinii* (AMNH 71309).

REFERENCES AND REMARKS: Lema (1973) figured a partly everted hemipenis.

HEMIPENIAL MORPHOLOGY: The strongly bilobed hemipenis has enlarged lateral spines and a deeply forked sulcus spermaticus dividing proximally on the hemipenial body, with each branch extending centrolaterally up to the tip of a lobe (fig. 81). The organ is semicapitate and semicalyculate. It has long lobes (twice as long as wide) ornamented with papillate calyces on the sulcate surface that extend largely to the asulcate surface on its medial, lateral, and distal regions, thus ornamenting almost all the distal half of the asulcate side of the lobes. The proximal half of the lobes is almost nude, whereas the lobular crotch bears vestiges of what may have been one or two pairs of large papillate body

calyces. There are nine enlarged lateral spines distributed circularly on the body instead of restricted to a lateral position. The two most proximal pairs meet each other on the asulcate side, approximately at the middle of the hemipenial body.

Waglerophis

Figure 82

SPECIES EXAMINED: (monotypic) *W. merremi* (AMNH 140198; MNRJ 3236, 4496).

REFERENCES AND REMARKS: Romano and Hoge (1972) published a photograph of the sulcate side of the hemipenis of this species.

HEMIPENIAL MORPHOLOGY: This species shows a characteristically long and slender organ (fig. 82). The ornamentations are reduced to spines of varying size and apical disks. The organ is deeply bilobed, with the lobes being twice as long as the hemipenial body, which is short and stocky. The whole configuration of the organ superficially resembles the crotaline pattern. The forked sulcus spermaticus divides more or less in the middle of the hemipenial body. There is no vestige of calyculation or capitulation. The tip of each lobe is ornamented with a large, clearly convex, nude apical disk. Both branches of the sulcus diverge to a centrifugal position, being clearly centrifugal on the distal region of the lobes, where they enter the apical disk. Each branch ends well into the disk. The lobes are covered with many rows of medium-sized spines except for the distal region, just below the apical disk, which is covered with spinules. The hemipenial body bears numerous rows of enlarged lateral spines. The base of the organ and the middle of the asulcate surface of the hemipenial body are nude.

Xenodon

Figures 81–83

SPECIES EXAMINED: *X. severus* (AMNH 142634; IB 51997), *X. rabdocephalus* (AMNH 140265), *X. neuwiedii* (MNRJ 2880, 4782).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Xenodon severus* and *Acanthophallus colubrinus* (= *Xenodon rabdocephalus*?). Romano and Hoge (1972) published a photograph of the sulcate

side of *X. severus*. Jenner (1981) and Jenner and Dowling (1985) figured the sulcate side of the organ of the same species. V. L. F. Yuki (1993) described and figured both sides of the organ of *X. werneri* (the allocation of this species to a new genus by this author is not followed here; see discussion).

HEMIPENIAL MORPHOLOGY: All three species have reduced ornamentation, having only lateral and enlarged intrasulcar spines, spinules, and apical disks. There is no vestige of calyculation and capitation on the lobes. Two distinctly different patterns are present in the species analyzed. *Xenodon neuwiedii* (fig. 81) and *X. severus* (fig. 83) have hemipenes similar to the genera *Liophis*, *Lystrophis*, and *Erythrolamprus*, whereas *X. rabdocephalus* (and *X. werneri*; see V. L. F. Yuki, 1993) have a hemipenial morphology similar to that of *Waglerophis merremi* (fig. 82).

The former two species have a slightly bilobed organ with a deeply forked sulcus spermaticus dividing more or less in the middle of the hemipenial body. *Xenodon neuwiedii* has a pair of three or four slightly enlarged intrasulcar spines, which are lacking in *X. severus*. Both species have the branches of the sulcus diverging almost directly to a centrifugal position, being clearly centrifugal where they enter the apical disks. Each branch ends on the distal region of the disk. The disk's surface is highly plicate in *X. neuwiedii* and slightly plicate to smooth in *X. severus*. The hemipenial body of both species has moderately large enlarged lateral spines arranged in two to four rows. In *X. neuwiedii* one of these rows extends to the lobular crotch and proximal surface of the lobes on the asulcate side, whereas in *X. severus* the enlarged lateral spines are confined to the hemipenial body. However, *X. severus* has one isolated enlarged spine on the proximal surface of each lobe on the asulcate side. The rest of the lobular surface is nude in *X. severus* and is covered with spinules in *X. neuwiedii*. In both species the middle of the asulcate surface of the hemipenial body and its base are covered with diminutive spinules.

Xenodon rabdocephalus has a characteristically long and slender organ. The ornamentations are also reduced to spines and a pair of apical disks. The organ is deeply bi-

lobed. The lobes are relatively narrow and very long. The hemipenial body is also elongate, as in most Xenodontinae. The sulcus spermaticus divides proximally on the hemipenial body. Calyculation and capitation are absent. The tip of each lobe is ornamented with a narrow but recognizable convex, nude apical disk. Both branches of the sulcus diverge to a centrifugal position, being clearly centrifugal on most of the lobular surface and within the area of the apical disk. Each branch ends on the distal region of the disk. The lobes are completely covered with several rows of medium-sized spines. The hemipenial body bears two rows of enlarged lateral spines. Most of the asulcate surface of the hemipenial body, its base, and the lobular crotch are nude. This species shares with *Waglerophis merremi* and *X. werneri* the derived condition of long and slender lobes covered with rows of medium-sized spines.

Xenoxybelis

Figure 83

SPECIES EXAMINED: *X. argenteus* (MNHN 1978.2678, 1994.7000).

REFERENCES AND REMARKS: Machado (1993) figured both sides of the hemipenis of this species.

HEMIPENIAL MORPHOLOGY: The organ is slightly bilobed, semicalyculate, and slightly semicapitate (fig. 83). The capitula are comprised of papillate calyces. Both capitula are almost totally confluent in the broad intrasulcar region, forming an almost uninterrupted calyculate area restricted to the sulcate side of the organ. The calyculate area occupies approximately two-thirds of the sulcate side of the organ. The lobes and hemipenial body are completely confluent, without clear delimitation, except for the presence of a capitulum on the sulcate side. The organ has the same peculiar heart-shaped conformation as some species of *Philodryas* (see account of this genus and Donnelly and Myers, 1991). The sulcus spermaticus divides within the capitulum just above its basal edge. The centrolateral branches terminate on the distal tip of the lobes. The proximal one-third of the organ, which corresponds to the hemipenial body, is covered with three to four rows of enlarged lateral spines of moderate

size that are arranged on the sulcate and lateral surfaces. The two more lateral rows of spines (on each side) are significantly larger than the others, extending distally to the tips of the lobes along the lateral surface of the organ. The asulcate surface of the organ is ornamented with two parallel rows of large, weakly papillate body calyces extending from the tip of the lobes to the base of the hemipenial body. A papillate crest runs at the middle of the asulcate surface between the two rows of body calyces. The condition of a sulcus spermaticus dividing within the capitulum is here viewed as due to the shortening of the whole organ instead of reflecting a dipsadine pattern. Indeed, except for this characteristic, the hemipenis of *X. argenteus* conforms completely to the Xenodontinae pattern described herein.

"XENODONTINES" INCERTAE SEDIS

Carphophis

Figure 84

SPECIES EXAMINED: *C. amoenus* (AMNH 99112; MNHN 93).

REFERENCES AND REMARKS: Clark, Jr. (1970) figured both sides of an everted organ of *C. vermis*.

HEMIPENIAL MORPHOLOGY: The organ is poorly bilobed, unicalyculate, and noncapitate (fig. 84). The unique capitulum is clearly derived from the fusion of the lobes and their distinct capitula. The single calyculate area is mostly restricted to the sulcate and lateral sides of the distal one-third of the organ. The capitulum expands to the asulcate side only on the distal tip of the organ. The capitulum is formed by papillate calyces. The papillae are well developed whereas the calycular walls are reduced or vestigial on almost all the capitular surface. The distal region of the organ on the asulcate surface bears vestiges of some larger calyces. A lobular crotch is absent due to the poorly developed condition of the lobes. The sulcus spermaticus bifurcates at the base of the capitulum, and the branches run centrolineally to the tip of each rudimentary lobe. The proximal two-thirds of the organ represents the hemipenial body, which is uniformly covered with rows of small spines.

Contia

Figure 84

SPECIES EXAMINED: *C. tenuis* (UMMZ 133370).

REFERENCES AND REMARKS: None.

HEMIPENIAL MORPHOLOGY: The organ is unilobed, unicalyculate, and noncapitate (fig. 84). The capitulum covers the distal third of the organ and is formed of poorly developed papillate calyces. The calycular walls tend to be very reduced in most of the capitular surface. The distal region of the organ on the asulcate surface bears vestiges of some larger calyces. The sulcus spermaticus bifurcates at the base of the capitulum, and the short branches run centrolineally to the distal region of the lobe. The hemipenial body represents the proximal two-thirds of the organ and is uniformly covered with rows of small spines.

Diadophis

Figure 85

SPECIES EXAMINED: *D. dugesi* (MNHN 1975.171), *D. punctatus* (AMNH 3711; MNHN 1897.170).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Diadophis regalis* (= *D. punctatus*).

HEMIPENIAL MORPHOLOGY: Both species show essentially the same hemipenial morphology. The organ is slightly bilobed, unicalyculate and noncapitate (i.e., without a capitular groove) (fig. 85). However, the outer walls of the calyces forming the edge of the capitulum tend to be shallower on the sulcate and lateral sides of the organ, suggesting an almost semicapitate condition. The unique capitulum is clearly derived from the fusion of the basal region of the lobes. For this reason, both capitula are totally confluent on the lobular crotch and on the intrasulcar region, forming a single calyculate area ornamenting the sulcate, lateral, and asulcate sides of the distal one-third of the organ. The capitulum is formed by papillate calyces. The papillate calyces ornamenting the lobular crotch and lobes on the asulcate surface are larger than the papillate calyces of the lateral and sulcate surfaces, gradually increasing in size from the tip of the lobes to the base of the capitulum. This state is viewed here as represent-

ing an intermediate condition between undifferentiated calyces and distinctly larger body calyces on the asulcate surface of the lobes and lobular crotch. The papillae are poorly developed or almost absent whereas the calyces are well developed over most of the capitulum. The sulcus spermaticus bifurcates at the base of the capitulum, and the branches run centrolineally to the tip of each lobe. The proximal two-thirds of the organ constitute the hemipenial body, which is uniformly covered with rows of small spines.

Echinanthera

Figures 85, 86

SPECIES EXAMINED: *E. amoena* (IB 9569, 26406), *E. melanostigma* (IB 855, 8322), *E. undulata* (IB 54234, 55676).

REFERENCES AND REMARKS: Cope (1895) figured the dissected hemipenis of *Echinanthera cyanopleura*, and Di-Bernardo (1992) figured the sulcate, asulcate, and lateral surfaces of the organ of this species. Myers and Cadle (1994) discussed some relevant hemipenial features of the genus.

HEMIPENIAL MORPHOLOGY: *Echinanthera amoena* (fig. 86) and *E. melanostigma* (fig. 86) have a similar hemipenial pattern, distinct from the pattern in *E. undulata* (fig. 85) and *E. cyanopleura* (see Di-Bernardo, 1992: fig. 1). Indeed, these two groups of species can be promptly distinguished by their hemipenial morphology. However, peculiar characteristics in both groups are also present in the species of *Taeniophallus* examined, suggesting that these features may well be diagnostic of a more inclusive group encompassing both genera (see below).

All species of *Echinanthera* have a unilobed, unicalyculate, noncapitate hemipenis. The sulcus spermaticus is divided for nearly half its length, with branches bifurcating at the very base of the capitulum and running almost parallel centrolineally to the tip of the organ. The distal half of the sulcate and lateral sides of the organ have a capitulum formed by small papillate calyces. The capitulum is restricted to the distal one-third of the organ on the asulcate side due to the invasion of a pronounced nude interspinal area ("interspinal asulcal gap" sensu Myers and Cadle, 1994: 5) onto the middle of the capitular area. The invasion by this nude

area is more or less extensive on each species, being restricted to the basal region of the capitulum in *E. melanostigma*, extending to the middle of the capitular region in *E. amoena*, and reaching the tip of the organ in *E. undulata* (and *E. cyanopleura*; see Di-Bernardo, 1992: fig. 1). In the species examined, the edges of the capitulum around this nude area are ornamented with enlarged flaplike papillae. The upper half of the hemipenial body just below the capitulum is ornamented with many parallel rows of small spines that converge distally, when passing to the asulcate side, to form a straight pack of spines. The more basal row of spines is the only one extending to the base of the organ, bordering the nude interspinal area on each side of the body. At their distal end, the rows of spines are confluent with the enlarged flaplike papillae edging the capitulum. A few enlarged flaplike papillae are present in the distal tip of the lobe of *E. undulata*. The proximal half of the sulcate surface of the hemipenial body is almost completely nude, with only a few sparse, medium-sized spines. The nude interspinal area on the asulcate surface is ornamented on its midline with a row of small papillae that is conspicuous in *E. amoena* and weakly developed in *E. melanostigma*. A row of small spines is present in the same topographical position in *E. undulata*, extending from the base of the nude area to the distal tip of the hemipenial body, without reaching the tip of the area. All three species show a differentiated row of larger spines running along the edge of the interspinal area on both sides. In *E. amoena* these spines are significantly larger than the other medium-sized spines of the organ and are responsible for the "flounced" appearance on each side of the median row of papillae on the interspinal area. The flounced appearance may be the result of differential tissue expansion due to the accommodation of the spines (see also Myers and Cadle, 1994: 5). In *E. undulata* only the four most proximal spines of the pair of differentiated rows are conspicuously larger than the rest. In *E. melanostigma* the two differentiated rows bear only slightly larger spines.

The examined species of *Echinanthera* and *Taeniophallus* have strikingly similar hemipenial morphologies. They share the presence of a nude interspinal area on the asulcate side that is edged on each side by a

differentiated row of medium-sized spines; some have a row of papillae or spines on the midline of this gap. The two rows of spines correspond to the more basal rows of medium spines (originally ornamenting the distal half of the hemipenial body) which diverge from the main block of spines to run downward along the edges of the nude area. Among the species examined, *Echinanthera undulata* and *Taeniophallus occipitalis* are the only species of their genera that lack a row of papillae on the midline of the nude area, with the former presenting a row of spines and the latter showing only one enlarged spine basally. However, both the row of spines and the unique enlarged spine are here viewed as homologous to the row of papillae present in the remaining species of *Echinanthera* and *Taeniophallus*, because of their same topographical position.

Di-Bernardo (1992) emphasized a similarity between the hemipenes of *Echinanthera* and some species of the *brevirostris* group [= *Taeniophallus*], namely the presence of a nude asulcal area (or gap). However, Myers and Cadle (1994; pers. commun.) indicated that this character is absent in the species *nicaeus* (the generic type) and in *brevirostris*. Myers and Cadle (1994: 5) also pointed out that a nude asulcal area "is not confined to the *brevirostris* group nor is it universal within that group," citing *Rhadinaea hansteini* as an example supporting their view.

Although it is suggested that the nude areas present in some species of *Rhadinaea* and *Echinanthera/Taeniophallus* may not be homologous, evidence supporting this view is tenuous and a more thorough review of the hemipenial morphology of these genera is needed before the nude area edged by rows of spines can be interpreted as a synapomorphy of an *Echinanthera/Taeniophallus* clade (the hemipenial morphology of *T. occipitalis* being especially puzzling).

Gomesophis

Figure 87

SPECIES EXAMINED: (monotypic) *G. brasiliensis* (IB 12191, 51001).

REFERENCES AND REMARKS: None.

HEMIPENIAL MORPHOLOGY: *Gomesophis* shows a general hemipenial pattern very sim-

ilar to the one present in the other "tachymenines." The organ is slightly bilobed, unicalyculate, and noncapitate, with a capitulum covering the distal third of the organ and the short lobular crotch (fig. 87). The capitulum is formed by spinulate calyces. The calyces are very reduced and the spinules enlarged. The capitulum on the sulcate and lateral surfaces is ornamented only by vestigial calyces, with the enlarged spinules tending to form horizontal rows. On the asulcate surface the calyces are shallower and larger than the ones ornamenting the lateral and sulcate surfaces, and thus they are still easily distinguished. The sulcus spermaticus divides distally at the base of the capitulum, with both branches running centrolineally to end at the tip of each lobe. The hemipenial body, representing two-thirds of the organ, is uniformly covered with several vertically directed rows of small spines. The spines gradually increase in size from the distal region of the hemipenial body to the base; the distalmost ones have almost the same size as the enlarged spinules ornamenting the capitulum. The base of the hemipenis is nude.

Nothopsis

Figure 88

SPECIES EXAMINED: (monotypic) *N. rugosus* (QCAZ 1089; USNM 142306).

REFERENCES AND REMARKS: Dunn and Dowling (1957) furnished a drawing of a dissected hemipenis of the species. As already pointed out by McDowell (1987), this genus is not related to the "xenodermatines." Indeed, its hemipenial morphology is typically dipsadine, with a sulcus spermaticus dividing inside a capitulum.

HEMIPENIAL MORPHOLOGY: The hemipenis is unilobed, unicalyculate, and slightly capitate (fig. 88). The capitulum is restricted to the sulcate side of the organ, covering nearly three-fourths of its surface except for the very base, which is mostly spinulate. The very base of the organ, which may be considered as the hemipenial body, also bears a series of medium-sized spines that tend to be in a more lateral position. From this group of basal spines on both lateral sides of the hemipenis emerges a row of medium-sized spines that extends parallel to the capitulum

and terminates on the distal region of the organ. The spines forming these rows gradually reduce in size distally. The basal region of the asulcate surface is inflated and bears a vertically directed row of five medium-sized spines. The three more distal spines are larger than the other two. The remaining two-thirds of the asulcate surface is completely nude. The edge of the capitulum bears on its distal region a fringe of thin, nude translucent tissue folded toward the asulcate surface. The sulcus spermaticus is deeply divided and centrolineal, bifurcating well within the capitulum and on the proximal half of the organ. Both branches run parallel to terminate on the distal region of the lobe just below its tip.

Ptychophis

Figure 87

SPECIES EXAMINED: (monotypic) *P. flavovirgatus* (AMNH 71312; IB 12316).

REFERENCES AND REMARKS: None.

HEMIPENIAL MORPHOLOGY: The general hemipenial pattern of *P. flavovirgatus* is very similar to the one found in the other "tachymenines." However, the organ is completely devoid of any ornamentation other than spinules and small-sized spines (fig. 87). The hemipenis is slightly bilobed, noncalyculate, and noncapitate. The lobes are reduced and covered with spinules. There is a slight constriction at the base of the lobes that marks the limit between the lobes and the hemipenial body. The sulcus spermaticus divides on the distal region of the organ just below the lobes and at the level of the constriction. Both branches run centrolineally, ending at the tip of each lobe. The hemipenial body is uniformly covered with several vertically directed rows of small spines. The spines gradually increase in size from the distal region of the hemipenial body to the base, with the most distal ones being almost the same size as the enlarged spinules ornamenting the capitulum.

Sordellina

Figure 89

SPECIES EXAMINED: *S. punctata* (IB 55703).

REFERENCES AND REMARKS: None.

HEMIPENIAL MORPHOLOGY: The organ is poorly bilobed, with only the tip of both lobes being present (fig. 89). The distal third of the organ is ornamented with several rows of papillae distributed along the sulcate (intrasulcar) and lateral sides, forming a "capitulum." These papillae, which may have some interconnection of tissue, are regarded as vestiges of calyces. The asulcate surface, corresponding to the level of the lobular region (i.e., the distal third of the organ), is nude except for the presence of three vertically directed papillate crests. The capitulum does not extend to the asulcate surface of the organ. The lateral sides are constricted just below the edges of the capitulum in a typically semicapitate condition. A lobular crotch is absent due to the poorly developed condition of the lobes. The sulcus spermaticus bifurcates just below the capitulum, and the branches run centrolineally on each lobe to end below their tips. The hemipenial body comprises the proximal two-thirds of the organ. The distal half of the hemipenial body is completely covered with numerous rows of small spines. Just below this region the hemipenial body constricts in a twisted fashion. This constriction causes the sulcus to change its direction abruptly by turning around the organ to reach its base in a lateral position. This region of the hemipenial body is mostly nude except for a few small spines.

Synophis

Figures 88, 89

SPECIES EXAMINED: *S. bicolor* (QCAZ 452), *S. lazallei* (USNM 233062).

REFERENCES AND REMARKS: Bogert (1964) described succinctly the dissected hemipenis of both species of *Synophis*, as well as that of *Diaphorolepis wagneri*, furnishing a comparison between them and the genera usually placed in the subfamily "Xenodermatinae." The hemipenes of both species are almost identical and differ markedly from the hemipenial morphology found in the "xenodermatines" examined. Their hemipenial pattern is dipsadinelike since it has a centrolineal sulcus dividing on the proximal half of the organ and lobes ornamented with papillate calyces. These two conditions are absent in the "xenodermatines" (see section on the

hemipenial morphology of the other colubroid snakes).

HEMIPENIAL MORPHOLOGY: In both species the hemipenis is slightly bilobed, semicalyculate, and semicapitate (figs. 88, 89). The capitular grooves are very pronounced on the asulcate surface, with the edge of each capitulum forming an arch on the proximal region of the lobes. The edge of each capitulum is ornamented on the asulcate side by a row of calcified medium-sized papillae that meet on the lobular crotch. However, the capitula are mostly formed by diminutive papillate calyces that cover all the sulcate, medial, and lateral surfaces and most of the asulcate surface. The papillae on the asulcate surface are larger than those ornamenting the sulcate side. On the sulcate surface the capitulum extends far down the hemipenial body. The sulcus spermaticus divides on the proximal half of the body at the edge of the capitulum. The branches run centrolineally to end on the distal tip of the lobes. The sulcate, asulcate, and lateral surfaces of the hemipenial body are covered with medium-sized spines.

Tachymenis

Figures 90, 91

SPECIES EXAMINED: *T. attenuata* (AMNH 36024), *T. chilensis* (AMNH 64941; MNHN 209), *T. peruviana* (AMNH 5256).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *T. peruvianus*. Walker (1945) described the hemipenial pattern of the genus, discussed intrageneric variations, and presented photographs of dissected organs of *T. peruviana*, *T. attenuata*, and *T. chilensis*. Vellard (1955) figured both sides of the hemipenis of *T. peruviana*.

HEMIPENIAL MORPHOLOGY: All three species have essentially the same general hemipenial morphology; however, there are some important differences that are stressed below. The organs are poorly bilobed in *T. chilensis* (fig. 90) and *T. attenuata* (fig. 91) and slightly bilobed in *T. peruviana* (fig. 90). In all three species, the organ is unicalyculate and noncapitate (i.e., with a capitulum covering the distal third of the organ but lacking capitular grooves). The unicalyculate condition is due to the almost complete fusion of the

lobes. As a consequence, the lobular crotch is almost lacking. However, *T. peruviana* has a short lobular crotch. All three species have capitula formed by papillate calyces. However, the calyces are very reduced and the papillae are enlarged in *T. peruviana*, with some of them bearing spinules instead of papillae; in *T. attenuata* and *T. chilensis*, however, the calyces are developed and the papillae reduced in size. In the three species the more proximal calyces ornamenting the distal surface of the hemipenial body on its asulcate surface are mostly ornamented with spinules and tend to be larger than the rest of the calyces composing the capitula. The sulcus spermaticus divides very distally in *T. attenuata* (at the middle of the capitulum), with both branches running centrolineally a short distance to end at the tip of the poorly developed lobes. In *T. chilensis* the sulcus bifurcates at the base of the capitulum, and in *T. peruviana* the sulcus divides at the middle of the hemipenial body. In both of the latter species the branches extend centrolineally to the tip of the lobes. In all three species the hemipenial body comprises two-thirds of the organ. In *T. peruviana* the hemipenial body is uniformly covered with several vertically directed rows of small spines. In *T. attenuata* and *T. chilensis* the hemipenial body is also covered with medium-sized spines. However, in the latter two species the spines gradually increase in size from the distal region of the hemipenial body to the base. In *T. chilensis* the six most basalmost spines are greatly enlarged. The base of the hemipenis in all three species is nude.

Taeniophallus

Figures 92, 93

SPECIES EXAMINED: *T. affinis* (IB 27970), *T. bilineatus* (IB 23607, 26182), *T. occipitalis* (IB 22538, 55699), *T. persimilis* (IB 9504).

REFERENCES AND REMARKS: Cope's (1895) illustration of the dissected hemipenes of *Taeniophallus nicagus* was really based on *T. brevirostris* according to Myers (1974: 208), who figured the retracted organs of three species in his *Rhadinaea brevirostris* group. Di-Bernardo (1992) mentioned hemipenes under the genus *Echinanthera*. Myers

and Cadle (1994) resurrected *Taeniophallus* for the *brevirostris* group and further discussed their hemipenial pattern, summarizing some of the diversity in the genus.

HEMIPENIAL MORPHOLOGY: The four species examined have a unilobed and unicalyculate hemipenis. The organ is noncapitate in *Taeniophallus persimilis* and *T. bilineatus*, slightly unicapitate in *T. affinis*, and deeply unicapitate in *T. occipitalis*. The sulcus spermaticus is divided, with branches bifurcating at the base of the capitulum and running almost parallel and in a centrolineal position to the tip of the organ (*T. nicagus* has a single sulcus spermaticus, presumably derived by loss of one branch; see Myers and Cadle, 1994: 4). The distal half of the sulcate and lateral sides of the organ are ornamented with a capitulum formed by small papillate calyces. The capitulum is invaded by a pronounced nude interspinal area ("interspinal asulcal gap" sensu Myers and Cadle, 1994: 5) on the asulcate side of the organ. In all species the nude interspinal area approaches closely (*T. occipitalis*) or reaches (the other species) the tip of the organ. *Taeniophallus affinis* (fig. 92), *T. persimilis* (fig. 93), and *T. bilineatus* (fig. 93) show a very similar hemipenial morphology, whereas *T. occipitalis* (fig. 92) has a slightly different pattern. The edges of the capitulum around the nude interspinal area are ornamented with enlarged flaplike papillae. The upper half of the hemipenial body just below the capitulum is ornamented with two or three parallel rows of small spines that converge distally when passing to the asulcate side. At their distal end, the rows of spines are confluent with the enlarged flaplike papillae edging the capitulum. The proximal region of the sulcate surface of the hemipenial body is almost completely nude, having only a few sparse, medium-sized spines. The nude interspinal area is ornamented on its midline with a row of small papillae that runs from its base to the distal tip of the hemipenial body (except in *T. occipitalis* which has only one enlarged spine proximally). All four species have a differentiated row of larger spines extending along the edge of the interspinal area on both sides. In *T. occipitalis* there are two parallel rows of spines extending along the edges of the nude area. In *Taeniophallus affinis*, *T.*

persimilis, and *T. bilineatus* the nude area is ornamented with a series of horizontally directed "flounces" on each side of the median row of papillae. As in *Echinanthera*, this condition is the result of differential tissue expansions due to the accommodation of the enlarged spines edging the nude area. The nude area in *T. occipitalis* lacks flounces. In *T. affinis*, *T. persimilis*, and *T. bilineatus* the two most basal spines of the differentiated rows are larger than the others, conspicuously more so in *T. bilineatus*.

Thamnodynastes

Figure 94

SPECIES EXAMINED: *T. pallidus* (IB 50614), *T. strigatus* (IB 22541, 53789, 53790).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Thamnodynastes strigatus* and *T. nattererii* (= *T. strigilis*). Hoge (1952) figured the sulcate side of the hemipenis of *T. strigatus*. Myers and Donnelly (1996) illustrated both sulcate and asulcate sides of the hemipenis of *T. yavi* and also the retracted organs of *T. duida* and *T. chimanta*.

HEMIPENIAL MORPHOLOGY: The general hemipenial pattern of *Thamnodynastes* is very similar to that found in the other "tachymenines." The two available species have essentially the same hemipenial morphology (fig. 94). The hemipenis is poorly bilobed (single in *T. yavi*; see Myers and Donnelly, 1996), unicalyculate, and noncapitate. It has a capitulum distributed on most of the distal half of the organ and a short lobular crotch. The capitulum is formed by papillate calyces distally and spinulate calyces proximally. Proximally, the calyces are very reduced or almost absent and the spinules enlarged and tend to form horizontally directed rows. On the proximal region of the asulcate surface of the capitulum, the calyces are shallower and larger than those ornamenting the rest of the capitulum. The sulcus spermaticus divides distally at the base of the capitulum. Both branches extend centrolineally to end at the tip of each lobe. The hemipenial body is uniformly covered with many rows of small to medium-sized spines. The spines gradually increase in size from the distal region of the hemipenial body to the base. Among the

most basal spines, two spines on each side of the sulcus are conspicuously larger. The base of the hemipenis is nude.

Tomodon

Figure 91

SPECIES EXAMINED: *T. dorsatus* (IB 21957; MNHN 1991.230).

REFERENCES AND REMARKS: Cope (1895) figured the dissected organ of *Tomodon ocellatus*.

HEMIPENIAL MORPHOLOGY: The general hemipenial pattern of this species is very similar to that of the other "tachymenines." The organ is slightly bilobed, unicalyculate, and noncapitate, with a capitulum distributed on most of the distal half of the organ and the short lobular crotch (fig. 91). The capitulum is single (= unicalyculate) due to the nearly complete fusion of the lobes. The capitulum is formed by papillate calyces. Both calyces and papillae are developed throughout the capitulum. The more proximal calyces of the capitulum are conspicuously larger and shallower than are the other calyces composing the capitulum. The calyces are also mostly ornamented with spinules instead of papillae. The sulcus spermaticus divides distally on the organ at the base of the capitulum. Both branches extend centrolineally to the tip of the lobes. The hemipenial body constitutes approximately half of the organ's length and is uniformly covered with vertically directed rows of medium-sized spines. The spines gradually increase in size from

the distal region of the hemipenial body to the base. The base of the hemipenes is nude.

Xenopholis

Figure 95

SPECIES EXAMINED: *X. scalaris* (AMNH 52170, 52870; CEPLAC 377), *X. undulatus* (one uncatalogued specimen).

REFERENCES AND REMARKS: Dowling and Duellman (1978) figured the sulcate side of the hemipenis of *X. scalaris*. *Xenopholis* has a typically dipsadine hemipenial morphology.

HEMIPENIAL MORPHOLOGY: Both species show similar hemipenial morphologies, although *X. undulatus* has a more slender, longer organ than does *X. scalaris* (fig. 95). In both species the hemipenis is unilobed, unicalyculate, and noncapitate on the sulcate and lateral surfaces, but with a series of arched capitular grooves at the edge of the capitulum on the asulcate side. The capitulum is formed by small papillate calyces. These calyces are mostly uniform in size in *X. scalaris*. In *X. undulatus* they are larger on the asulcate side. The sulcus spermaticus bifurcates on the distal half of the organ within the capitulum, and the short branches run centrolineally to end on the tip of the lobe. The hemipenial body comprises a third (*undulatus*) or two-thirds (*scalaris*) of the entire length of the organ and is more or less uniformly ornamented with medium-sized spines, which tend to be concentrated on the distal part of the body.

CONCLUSION

The present study proposes a monophyletic Xenodontinae supported by two hemipenial synapomorphies: (1) the presence of enlarged lateral spines, and (2) the presence of two distinctly ornamented regions on the lobes, with the medial and/or asulcate surfaces bearing generally a series of weakly or well-developed body calyces or being completely nude when such calyces are absent.

This proposed monophyly of the Xenodontinae excludes various New World genera, placed here in incertae sedis. Their pre-

cise relationships within the "colubrids" represent a puzzling problem that remains to be evaluated. Additionally, because only two synapomorphies, both derived from one single morphological complex, are proposed in support of this group, this hypothesis should be viewed as tentative. An issue perhaps remaining to be elucidated by additional evidence is the exact level of applicability for the two proposed synapomorphies, since some of the genera delineated as incertae sedis may have secondarily lost these structures.

Cadle (1984a, 1984b, 1984c, 1985, 1988) and Dessauer et al. (1987) stated that the New World genera *Carphophis*, *Conophis*, *Contia*, *Heterodon*, *Farancia*, and *Diadophis* did not show immunological affinity either to the South or Central American assemblages or to one another. Cadle (1984c) thus concluded that these genera were distinct "xenodontine" lineages related only remotely to the Central and South American assemblages. However, the present study suggests that the genera *Conophis*, *Heterodon*, and *Farancia* do belong to the Xenodontinae (Cadle's South American assemblage). Crother and Hillis (1995) have recently shown, based on an analysis of the nuclear rDNA repeat region of several West Indian and South American xenodontines, that *Farancia* does belong to the South American radiation.

The Xenodontinae are a clade comprised of 41 genera (table 1; appendix 1) for which several presumed monophyletic suprageneric groups are redefined or proposed. These groups are the Pseudoboini; the Elapomorhini; the clade formed by *Darlingtonia haetiana*, *Arrhyton exiguum*, and *Antillophis parvifrons*; the clade formed by *Alsophis cantherigerus* and *A. vudii*; the clade formed by *Conophis* and *Manolepis*; the Cuban species of *Arrhyton*; the Jamaican species of *Arrhyton*; the clade formed by the Galapagos species of *Alsophis*, *Alsophis elegans*, and *Saphenophis*. Additionally, hemipenial evidence suggests that the genera *Alsophis*, *An-*

tillophis, *Arrhyton*, *Clelia*, *Oxyrhopus*, and *Philodryas* are polyphyletic or, at least, paraphyletic (see discussion). The genera *Hydrops* and *Pseudoeryx* lack the two derived character states of the Xenodontinae. However, they are placed in the Xenodontinae because they share with *Helicops* (a clear member of the Xenodontinae) at least one non-hemipenial synapomorphy.

Twenty-seven genera of New World xenodontines (Xenodontinae + Dipsadinae) were considered of problematical assignment and are here placed in incertae sedis (table 1; appendix 1). Although the available hemipenial evidence suggests a dipsadine relationship for most of these taxa, they are here retained as incertae sedis pending more work.

Apart from the inclusion of the genera *Heterodon*, *Farancia*, and *Conophis* within the Xenodontinae, the above conclusions are consistent with Cadle's (1984a, 1984b, 1984c) immunological results.

Several suprageneric groups of "colubrids" are here recognized (appendix 1). Although some of them may represent paraphyletic assemblages, such arrangement of genera furnished a framework in which "colubrid" hemipenial morphology could be investigated. Previously known or newly proposed hemipenial synapomorphies are presented for the Caenophidia, Colubroidea, Natricinae, Colubrinae, Dipsadinae, part of the Calamariinae, and for a possible clade formed by the "Pseudoxyrhophiinae" and "Homalopsinae."

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APPENDIX 1

List of Genera Placed in the Families Atractaspididae and "Colubridae"

Although various tribes of "colubrid" snakes are now well corroborated (e.g., Pseudoboini, Xenodontini, Elapomorphini, Thamnophiini, Sonorini, Sibynophiini, Dasypeltini), tribal arrangements are not shown here. Suprageneric taxa that may not represent monophyletic units, but that were used in the present paper, are enclosed within quotation marks. Underwood and Kochva's (1993) Atractaspididae is included in this list (see text for explanation).

I have taken as a starting point the lists of Dowling and Duellman (1978), McDowell (1987), Williams and Wallach (1989), and Meirte (1992). Genera for which hemipenial material was available for study are noted with an asterisk (see also list of specimens in appendix 2). Order of suprageneric taxa follows the order of appearance in the text.

Atractaspididae	<i>Bothrolycus</i> *	<i>Chionactis</i> *
<i>Aparallactus</i> *	<i>Bothrophthalmus</i>	<i>Chironius</i>
<i>Atractaspis</i> *	<i>Chamaelycus</i>	<i>Chrysopelea</i> *
<i>Amblyodipsas</i> *	<i>Cryptolycus</i>	<i>Coluber</i> *
<i>Brachyophis</i>	<i>Dendrolycus</i>	<i>Conopsis</i> *
<i>Chilorhinophis</i>	<i>Dipsina</i>	<i>Coronella</i>
<i>Elapocalamus</i>	<i>Dromophis</i>	<i>Crotaphopeltis</i> *
<i>Elapotinus</i>	<i>Gonionotophis</i>	<i>Cyclophiops</i>
<i>Hypoptophis</i>	<i>Grayia</i> *	<i>Dasypeltis</i> *
<i>Macrelaps</i> *	<i>Homonotus</i>	<i>Dendrelaphis</i> *
<i>Micrelaps</i>	<i>Lamprophis</i> *	<i>Dendrophidion</i>
<i>Polemon</i> *	<i>Lycodonomorphus</i> *	<i>Dinodon</i> *
<i>Xenocalamus</i>	<i>Lycophidion</i> *	<i>Dipsadoboa</i> *
	<i>Macroprotodon</i>	<i>Dispholidus</i> *
"COLUBRIDAE"	<i>Mehelya</i> *	<i>Drymarchon</i>
"Xenodermatinae"	<i>Pseudaspis</i> *	<i>Drymobius</i>
<i>Achalinus</i>	<i>Pseudoboodon</i>	<i>Drymoluber</i>
<i>Fimbrios</i>	<i>Pythonodipsas</i>	<i>Dryocalamus</i>
<i>Oxyrhabdium</i> *	<i>Scaphiophis</i>	<i>Dryophiops</i>
<i>Stoliczkaia</i>		<i>Eirenis</i>
<i>Xenodermus</i> *	"Boodontinae" incertae sedis	<i>Elachistodon</i>
<i>Xylophis</i>	<i>Buhoma</i>	<i>Elaphe</i> *
	<i>Dromicodryas</i> *	<i>Ficimia</i> *
Pareatinae	<i>Duberria</i> *	<i>Gastropyxis</i>
<i>Aplopeltura</i>	<i>Montaspis</i>	<i>Geagras</i> *
<i>Internatus</i>		<i>Gonyophis</i>
<i>Pareas</i> *	"Pseudoxyrhophiinae"	<i>Gonyosoma</i> *
Calamariinae	<i>Alluaudina</i> *	<i>Gyalopion</i> *
<i>Calamaria</i> *	<i>Compsophis</i>	<i>Hapsidophrys</i> *
<i>Calamorphabidium</i>	<i>Dityophis</i>	<i>Lampropeltis</i> *
<i>Collorhabdium</i>	<i>Geodipsas</i> *	<i>Leptodrymus</i>
<i>Etheridgeum</i>	<i>Heteroliodon</i>	<i>Leptophis</i>
<i>Macrocalamus</i> *	<i>Ithycyphus</i> *	<i>Lepturophis</i>
<i>Pseudorhabdion</i>	<i>Langaha</i> *	<i>Liochlorophis</i>
<i>Rabdion</i>	<i>Leioheterodon</i> *	<i>Liopeltis</i>
	<i>Liophidium</i> *	<i>Lycodon</i> *
"Homalopsinae"	<i>Liopholidophis</i> *	<i>Lytrochynchus</i>
<i>Bitia</i> *	<i>Lycodryas</i>	<i>Masticophis</i>
<i>Cantoria</i> *	<i>Madagascarophis</i> *	<i>Mastigodryas</i>
<i>Cerberus</i>	<i>Micropisthodon</i>	<i>Meizodon</i>
<i>Enhydris</i>	<i>Pararhadinaea</i>	<i>Oligodon</i> *
<i>Erpeton</i>	<i>Perinettia</i>	<i>Opheodrys</i>
<i>Fordonia</i> *	<i>Pseudoxyrhopus</i> *	<i>Oxybelis</i> *
<i>Gerarda</i> *	<i>Stenophis</i> *	<i>Philothamnus</i> *
<i>Heurnia</i>	Colubrinae	<i>Phyllorhynchus</i> *
<i>Homalopsis</i> *	<i>Aeluroglena</i>	<i>Pituophis</i>
<i>Myron</i>	<i>Ahaetulla</i> *	<i>Prosymna</i>
	<i>Argyrogena</i>	<i>Pseudocyclophis</i>
"Homalopsinae" incertae sedis	<i>Arizona</i> *	<i>Pseudoficimia</i> *
<i>Brachyorrhos</i> *	<i>Bogertophis</i> *	<i>Pseustes</i>
	<i>Boiga</i> *	<i>Ptyas</i> *
"Boodontinae"	<i>Cemophora</i> *	<i>Rhamnophis</i>
<i>Boaedon</i>	<i>Chilomeniscus</i> *	<i>Rhinobothryum</i>

APPENDIX 1

Continued.

<i>Rhinocheilus*</i>	<i>Sinonatrix*</i>	Xenodontinae
<i>Rhynchocalamus*</i>	<i>Storeria*</i>	<i>Alsophis*</i>
<i>Rhynchophis</i>	<i>Thamnophis*</i>	<i>Antillophis*</i>
<i>Salvadora*</i>	<i>Tropidoclonion</i>	<i>Apostolepis*</i>
<i>Sacaphiodontophis*</i>	<i>Tropidonophis*</i>	<i>Arrhyton*</i>
<i>Scolecophis</i>	<i>Virginia*</i>	<i>Boiruna*</i>
<i>Senticolis*</i>		<i>Clelia*</i>
<i>Sibynophis*</i>	Natricinae incertae sedis	<i>Conophis*</i>
<i>Simophis</i>	<i>Amplorhinus*</i>	<i>Darlingtonia*</i>
<i>Sonora*</i>	<i>Limnophis*</i>	<i>Ditaxodon*</i>
<i>Spalerosophis*</i>	<i>Natriciteres*</i>	<i>Drepanoides*</i>
<i>Spilotes</i>	<i>Psammodynastes*</i>	<i>Elapomorphus*</i>
<i>Stegonotus*</i>	<i>Xenochrophis*</i>	<i>Erythrolamprus*</i>
<i>Stenorrhina*</i>		<i>Farancia*</i>
<i>Stilosoma</i>	Dipsadinae	<i>Helicops*</i>
<i>Symphimus</i>	<i>Adelphicos*</i>	<i>Heterodon*</i>
<i>Sympholis*</i>	<i>Amastridium*</i>	<i>Hydrodynastes*</i>
<i>Tantilla</i>	<i>Atractus*</i>	<i>Hydrops*</i>
<i>Tantillita</i>	<i>Chersodromus*</i>	<i>Hypsirhynchus*</i>
<i>Telescopus*</i>	<i>Coniophanes*</i>	<i>Ialtris*</i>
<i>Thelotornis*</i>	<i>Cryophis</i>	<i>Liophis*</i>
<i>Thrasops*</i>	<i>Dipsas*</i>	<i>Lystrophis*</i>
<i>Toluca</i>	<i>Eridiphas</i>	<i>Manolepis*</i>
<i>Trimorphodon*</i>	<i>Geophis*</i>	<i>Oxyrhopus*</i>
<i>Xenelaphis</i>	<i>Hypsiglena*</i>	<i>Phalotris*</i>
<i>Zaocys*</i>	<i>Imantodes*</i>	<i>Philodryas*</i>
	<i>Leptodeira*</i>	<i>Phimophis*</i>
Psammophiinae	<i>Ninia*</i>	<i>Pseudablades*</i>
<i>Hemirhagerris</i>	<i>Pliocercus*</i>	<i>Pseudoboa*</i>
<i>Malpolon</i>	<i>Pseudoleptodeira</i>	<i>Pseudoeryx*</i>
<i>Mimophis*</i>	<i>Rhadinaea*</i>	<i>Psomophis*</i>
<i>Psammophis*</i>	<i>Sibon*</i>	<i>Rhachidelus*</i>
<i>Psammophylax*</i>	<i>Sibynomorphus*</i>	<i>Saphenophis*</i>
<i>Rhamphiophis*</i>	<i>Tretanorhinus*</i>	<i>Siphlophis*</i>
	<i>Trimetopon</i>	<i>Tripanurgos*</i>
Pseudoxenodontinae	<i>Tropidodipsas*</i>	<i>Tropidodryas*</i>
<i>Plagiopholis</i>	<i>Urotheca*</i>	<i>Umbrivaga</i>
<i>Pseudoxenodon*</i>		<i>Uromacer*</i>
Natricinae	Dipsadinae incertae sedis	<i>Uromacerina*</i>
<i>Adelophis</i>	<i>Calamodontophis</i>	<i>Waglerophis*</i>
<i>Afronatrix*</i>	<i>Carphophis*</i>	<i>Xenodon*</i>
<i>Amphiesma*</i>	<i>Contia*</i>	<i>Xenoxybelis*</i>
<i>Amphiesmoides</i>	<i>Crisantophis</i>	
<i>Anoplohydrus</i>	<i>Diadophis*</i>	Xenodontinae incertae sedis
<i>Aspidura*</i>	<i>Diaphorolepis</i>	<i>Cercophis</i>
<i>Atretium*</i>	<i>Echinanthera*</i>	<i>Lioheterophis</i>
<i>Balanophis</i>	<i>Emmochliophis</i>	<i>Sordellina*</i>
<i>Clonophis*</i>	<i>Enuliophis</i>	
<i>Hologerrhum</i>	<i>Enulius</i>	"Colubridae" incertae sedis
<i>Hydraclabes</i>	<i>Gomesophis*</i>	<i>Blythia</i>
<i>Hydraethiops*</i>	<i>Hydromorphus</i>	<i>Cercaspis</i>
<i>Iguanognathus</i>	<i>Nothopsis*</i>	<i>Cyclocorus</i>
<i>Lycognathophis*</i>	<i>Opisthoplus</i>	<i>Elapoidis</i>
<i>Macropisthodon*</i>	<i>Pseudotomodon</i>	<i>Gongylosoma</i>
<i>Natrix*</i>	<i>Ptycophis*</i>	<i>Haplocercus</i>
<i>Nerodia*</i>	<i>Rhadinophanes</i>	<i>Helophis</i>
<i>Opisthotropis*</i>	<i>Synophis*</i>	<i>Myersophis</i>
<i>Parahelicops</i>	<i>Tachymenis*</i>	<i>Oreocalamus</i>
<i>Pararhabdophis</i>	<i>Taeniophallus*</i>	<i>Rhabdops</i>
<i>Pseudagkistrodon</i>	<i>Tantalophis</i>	<i>Poecilopholis</i>
<i>Regina*</i>	<i>Thamnodynastes*</i>	<i>Tetralepis</i>
<i>Rhabdophis*</i>	<i>Tomodon*</i>	<i>Thermophis</i>
<i>Seminatrix*</i>	<i>Xenopholis*</i>	<i>Trachischium</i>

APPENDIX 2

Colubroid Specimens Examined for Hemipenial Morphology

TROPIDOPHOIDAE: *Tropidophis canus* (AMNH 93001); *Tropidophis melanurus* (AMNH 82882); *Tropidophis pardalis* (AMNH 78605).

ACROCHORDOIDAE: *Acrochordus javanicus* (AMNH 115651; LSUMZ 34406).

ELAPIDAE: *Bungarus caeruleus* (AMNH 86910); *Calliophis calligaster* (AMNH 73415); *Calliophis gracilis* (AMNH 2870); *Calliophis japonicus* (AMNH 67190); *Dendroaspis jamesonii* (AMNH CROCK-17); *Demansia olivacea* (AMNH 82479); *Elapsoidea sundevalli* (AMNH 63777); *Homoroselaps dorsalis* (AMNH 94690); *Hydrelaps darwiniensis* (AMNH 86172); *Hydrolaps gracilis* (AMNH 87680).

VIPERIDAE: *Agkistrodon piscivorus* (AMNH 67168); *Atheris squamiger* (AMNH 11867); *Causus maculatus* (AMNH 142435); *Cerastes cerastes* (AMNH 62248); *Crotalus basiliscus* (AMNH 64253, 64254).

ATRACTASPIDIDAE: *Amblyodipsas polylepis* (AMNH 82408); *Aparallactus capensis* (AMNH 18214); *Atractaspis fallax* (AMNH 102298); *Atractaspis irregularis* (AMNH 82076); *Macrelaps microlepidota* (AMNH 57636; FMNH 205863); *Polemon acanthias* (AMNH 142421); *Polemon christyi* (FMNH 219912).

"COLUBRIDAE": *Adelphicos quadrivirgatus* (LSUMZ 22518, 28325, 28344); *Afronatrix anoscopus* (AMNH 50524, 142404); *Ahaetulla fasciolata* (AMNH 2918); *Alluaudina bellyi* (UMMZ 201607, 209239); *Amastri-dium veliferum* (AMNH 114310; KU 190897; USNM 46509); *Amphiesma stolata* (AMNH 85501); *Amplorhinus multimaculatus* (FMNH 206311); *Arizona elegans* (AMNH 72402); *Aspidura trachyprocta* (AMNH 120248); *Atractus latifrons* (AMNH 64900); *Atretium schistosum* (AMNH 96075); *Bitia hydroides* (FMNH 229568); *Bogertophis subocularis* (AMNH 117741); *Boiga dendrophila* (AMNH 116014); *Boiga irregularis* (AMNH 134140); *Bothrolycus ater* (AMNH 11971); *Brachyorrhos albus* (CNHM 142324); *Calamaria lin-naei* (AMNH 31943); *Calamaria septentrionalis* (AMNH 24535); *Calamaria virgulata* (AMNH 31944); *Cantoria violacea* (FMNH 250117); *Cemophora coccinea* (AMNH 99044); *Chersodromus liebmanni* (USNM 109932); *Chilomeniscus stramineus* (AMNH 5578); *Chionactis occipitalis* (AMNH 63896, 66129); *Chrysopelea ornata* (AMNH 43380); *Clonophis kirtlandii* (LSUMZ WGE-062672-3); *Coluber constrictor* (AMNH 77108, 91689); *Coluber viridiflavus* (AMNH 90454); *Coniophanes bipunctatus* (LSUMZ 46841); *Coniophanes fissidens* (LSUMZ 33724); *Coniophanes imperialis* (LSUMZ 36769, 48401); *Conopsis nasus* (AMNH 93410); *Crotaphopeltis hotamboeia* (AMNH 12301); *Dasyopeltis scabra* (AMNH 12198); *Dendrelaphis pa-puensis* (AMNH 107175); *Dinodon flavozonatum* (AMNH 34372); *Dinodon rufozonatum* (AMNH 28256, 34372, 61597); *Dipsadoboa unicolor* (AMNH 50554); *Dipsas indica* (AMNH 52940); *Dispholidus typus*

(AMNH 12498); *Dromicodryas bernieri* (AMNH 24768; UMMZ 218166, 218167); *Dromicodryas quad-rilineatus* (UMMZ 209290, 209291); *Duberria lutrix* (AMNH 62876, 115639); *Elaphe moellendorffi* (AMNH 99694); *Elaphe obsoleta* (AMNH 69624); *Ficimia oli-vacea* (AMNH 99149); *Foronia leucobalia* (AMNH 86240); *Geagras redimitus* (AMNH 66793); *Geodipsas heimi* (UMMZ 197141); *Geodipsas infralineata* (UMMZ 209316); *Geophis anocularis* (KU 200975); *Geophis brachycephalus* (KU 63802); *Geophis dubius* (AMNH 102954); *Geophis rhodogaster* (KU 187272); *Geophis zeledoni* (KU 63822); *Gerarda prevostiana* (CNHM 179111); *Gonyosoma oxycephalum* (AMNH 90095); *Grayia smithii* (AMNH 12156); *Gyalopion can-um* (AMNH 115590); *Hapsidophrys lineatus* (AMNH 12132); *Homalopsis buccata* (AMNH 62802); *Hydrae-thiops melanogaster* (AMNH 11952, 11959); *Hypsi-glena torquata* (AMNH 111181); *Imantodes cenchoa* (KU 148316, 190964); *Imantodes inornatus* (KU 75706, 110215); *Imantodes lentiferus* (KU 121898); *Ithycyphus miniatus* (UMMZ 201615); *Ithycyphus oursi* (UMMZ 218188); *Lampropeltis getulus* (AMNH 93761); *Lam-propheis geometricus* (UMMZ 144458); *Lampropheis oli-vaceus* (AMNH 12001); *Langaha madagascariensis* (UMMZ 218209, 218210); *Leioheterodon madagascari-ensis* (UMMZ 201618); *Leioheterodon modestus* (UMMZ 191916, 218228); *Leptodeira annulata* (AMNH 107291; KU 62102); *Leptodeira maculata* (KU 62489); *Leptodeira nigrofasciata* (KU 174245); *Lepto-deira septentrionalis* (KU 187325); *Limnophis bicolor* (AMNH 50533); *Liophidium apperti* (UMMZ 197154); *Liophidium rhadinaea* (UMMZ 197155, 209471); *Lio-phidium rhodogaster* (UMMZ 209424); *Liophidium tor-quatus* (UMMZ 191923, 209430, 209431, 209437, 209443, 209451, 209457); *Liophidium vaillantii* (UMMZ 191934, 209465); *Liopholidophis lateralis* (UMMZ 218241); *Liopholidophis sexlineatus* (UMMZ 209492, 218261); *Liopholidophis stumppfi* (UMMZ 197183); *Lio-pholidophis thieli* (UMMZ 191963); *Lycodon aulicus* (AMNH 31967, LSUMZ 44673); *Lycodon laoensis* (LSUMZ 37500); *Lycodonomorphus rufulus* (AMNH 140278); *Lycognathophis seychellensis* (UMMZ 167994, 195836); *Lycophidion capense* (AMNH 60109); *Macrocalamus lateralis* (CNHM 109943); *Macropistho-don rudis* (LSUMZ 33681); *Madagascarophis colubri-nus* (UMMZ 197210, 197215); *Mehelya capensis* (LSUMZ 14477); *Mehelya poensis* (AMNH 12053); *Mimophis mahfalensis* (UMMZ 209655); *Natriciteres olivacea* (AMNH 11915); *Natrix natrix* (AMNH 89822); *Nerodia erythrogaster* (AMNH 88758); *Nerodia fascia-ta* (AMNH 85988); *Nerodia sipedon* (AMNH 123211); *Ninia diademata* (AMNH 102976); *Oligodon arnensis* (AMNH 94501); *Oligodon cinereus* (AMNH 27879); *Oligodon formosanus* (AMNH 33813); *Oligodon taeni-olatus* (AMNH 84018); *Opisthotropis kuatunensis*

(AMNH 34438); *Oxybelis brevirostris* (AMNH 108936); *Oxyrhabdion modestum* (CNHM 68907); *Pareas margaritophora* (AMNH 27770, 27773); *Pareas stanleyi* (AMNH 34606); *Philothamnus angolensis* (AMNH 67753); *Philothamnus carinatus* (AMNH 12076); *Phyllorhynchus browni* (LSUMZ 37959); *Pliocercus elapoides* (AMNH 102489); *Pliocercus euryzonus* (USNM 15634); *Psammodynastes pulverulentus* (AMNH 84547); *Psammophis schokari* (AMNH 87475); *Psammophylax multisquamis* (AMNH 16899); *Pseudaspis cana* (AMNH 49948); *Pseudoficimia frontalis* (AMNH 71359); *Pseudoxenodon bambusicola* (AMNH 35143); *Pseudoxenodon fukiensis* (AMNH 34648, 34649); *Pseudoxenodon karlschmidti* (AMNH 34660); *Pseudoxenodon striaticaudatus* (AMNH 34673, 34675); *Pseudoxyrhopus microps* (UMMZ 195849, 203646); *Pseudoxyrhopus quinquelineatus* (UMMZ 203662); *Pseudoxyrhopus tritaeniatus* (UMMZ 195854); *Ptyas mucosus* (AMNH 27821, 62826, 96227); *Regina alleni* (AMNH 103207); *Rhabdophis tigrinum* (LSUMZ 24364, 24372); *Rhadinaea calligaster* (KU 107820); *Rhadinaea decipiens* (KU 112440); *Rhadinaea decorata* (KU 112446); *Rhadinaea flavilata* (AMNH 63434); *Rhadinaea fulvivittis* (AMNH 100899); *Rhadinaea godmani* (KU 214783); *Rhadinaea taeniata* (AMNH 102985); *Rhamphiophis oxyrhynchus* (LSUMZ 30402, one uncatalogued specimen); *Rhinocheilus lecontei*

(AMNH 60091, 62243); *Rhynchocalamus melanocephalus* (AMNH 68155); *Salvadora mexicana* (AMNH 58363); *Scaphiodontophis annulatus* (KU 191073); *Seminatrix pygaea* (AMNH 27628, 44955); *Senticolis triaspis* (AMNH 110625); *Sibon nebulata* (AMNH 97068); *Sibynomorphus mikani* (AMNH 6495, 14540); *Sibynophis chinensis* (AMNH 34102); *Sinonatrix annularis* (AMNH 33837, 84530); *Sinonatrix percarinata* (AMNH 34390); *Sonora semiannulata* (AMNH 88428); *Spalerosophis diadema* (AMNH 21793); *Stegonotus cucullatus* (AMNH 134134); *Stenophis arctifasciatus* (UMMZ 209547); *Stenophis gaimardi* (UMMZ 218290); *Stenophis variabilis* (UMMZ 218298); *Stenorrhina degenhardtii* (AMNH 119885); *Stenorrhina freminvillei* (AMNH 100645); *Storeria dekayi* (AMNH 130730); *Sympholis lippiens* (AMNH 106579); *Thamnophis elegans* (AMNH 62051); *Thamnophis marcianus* (AMNH 58365); *Telescopus fallax* (AMNH 21803); *Thelotornis kirtlandi* (AMNH 12281); *Thrasops flavigularis* (AMNH 50574); *Tretanorhinus variabilis* (AMNH 83657); *Trimorphodon tau* (AMNH 96652); *Tropidodipsas fasciata* (AMNH 65160); *Tropidonophis aenigmaticus* (AMNH 95538); *Urotheca decipiens* (KU 103892); *Urotheca fulviceps* (KU 112455); *Virginia valeriae* (AMNH 81916); *Xenochrophis piscator* (LSUMZ 14479, 36792); *Xenodermus javanicus* (CNHM 138678); *Zaocys dhumnades* (AMNH 24621).

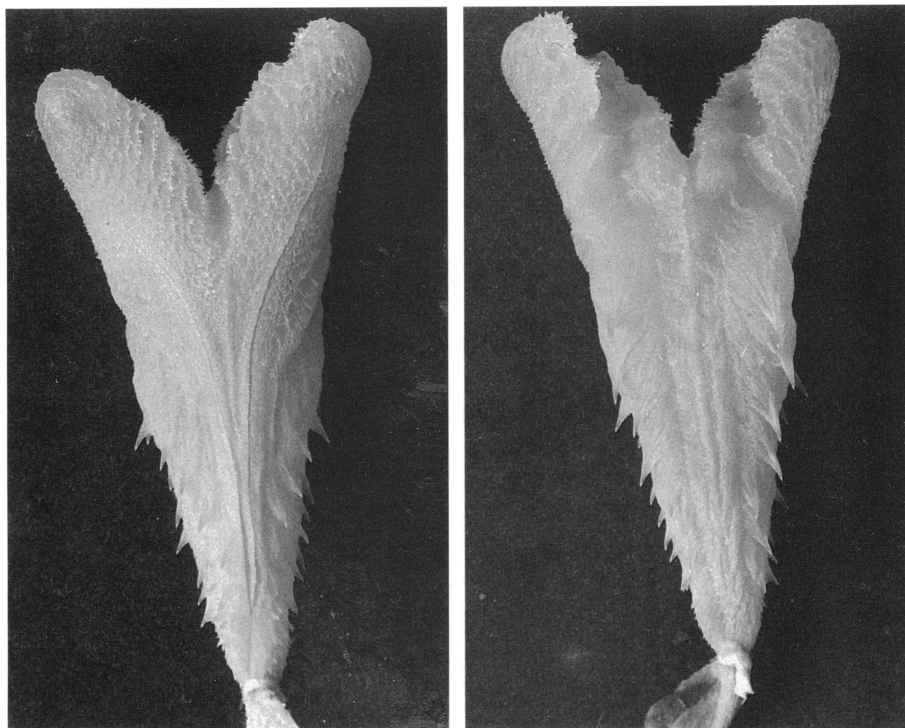


Fig. 21. Hemipenis of *Alsophis cantherigerus* (MNHN 1883.385). Sulcate (left) and asulcate (right) views.

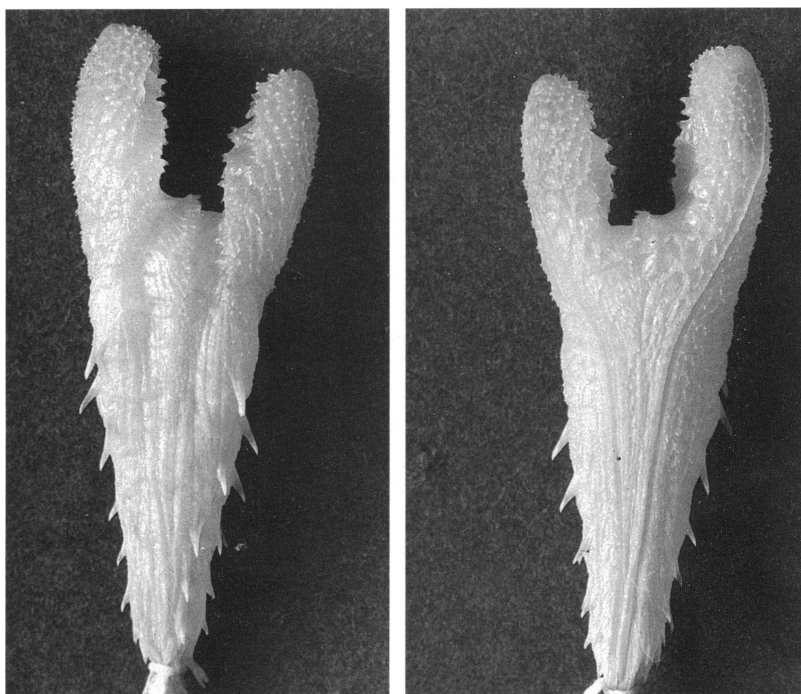


Fig. 22. Hemipenis of *Alsophis ater* (MNHN 497). Asulcate (left) and sulcate (right) views.

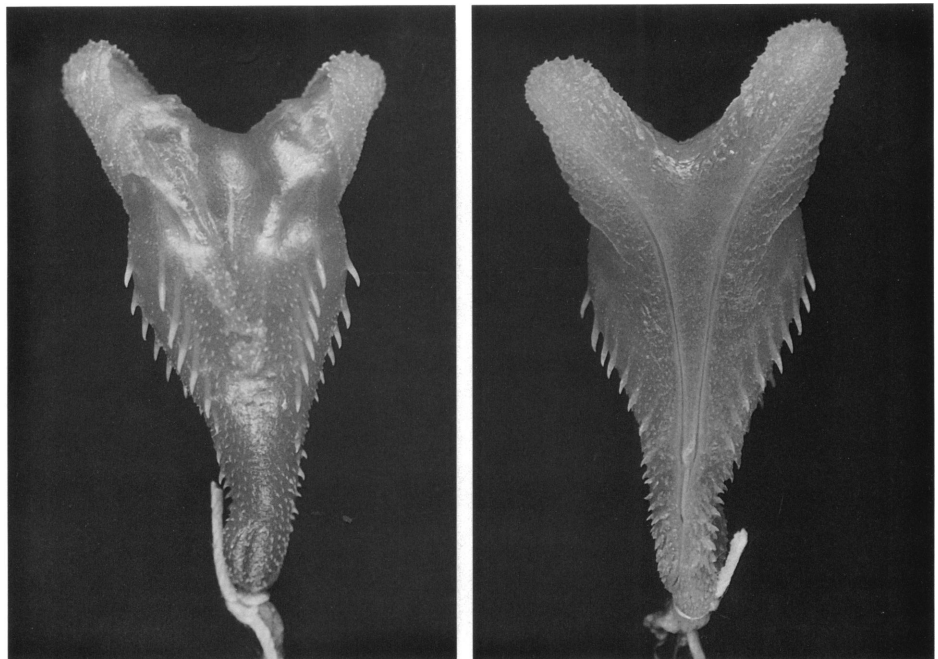


Fig. 23. Hemipenis of *Alsophis portoricensis* (AMNH 99545). Asulcate (left) and sulcate (right) views.

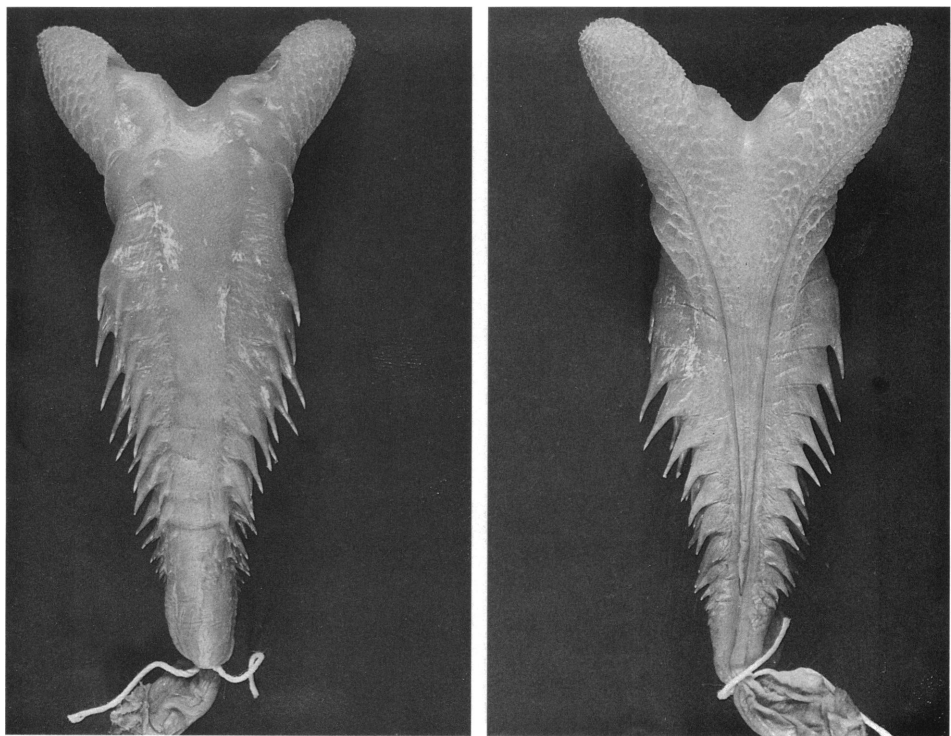


Fig. 24. Hemipenis of *Alsophis anomalus* (AMNH 44839). Asulcate (left) and sulcate (right) views.

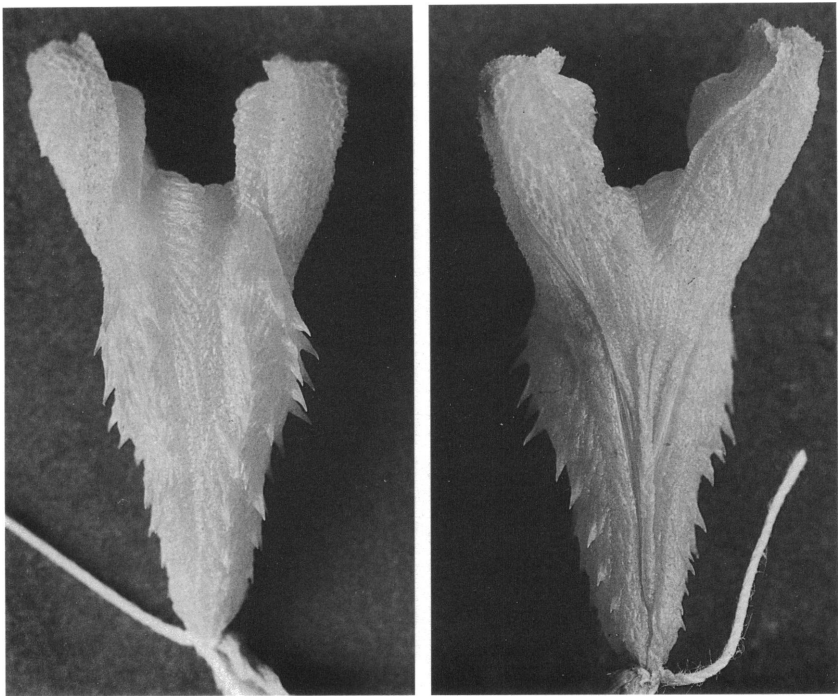


Fig. 25. Hemipenis of *Alsophis rufiventris* (MNHN 3560). Asulcate (left) and sulcate (right) views.

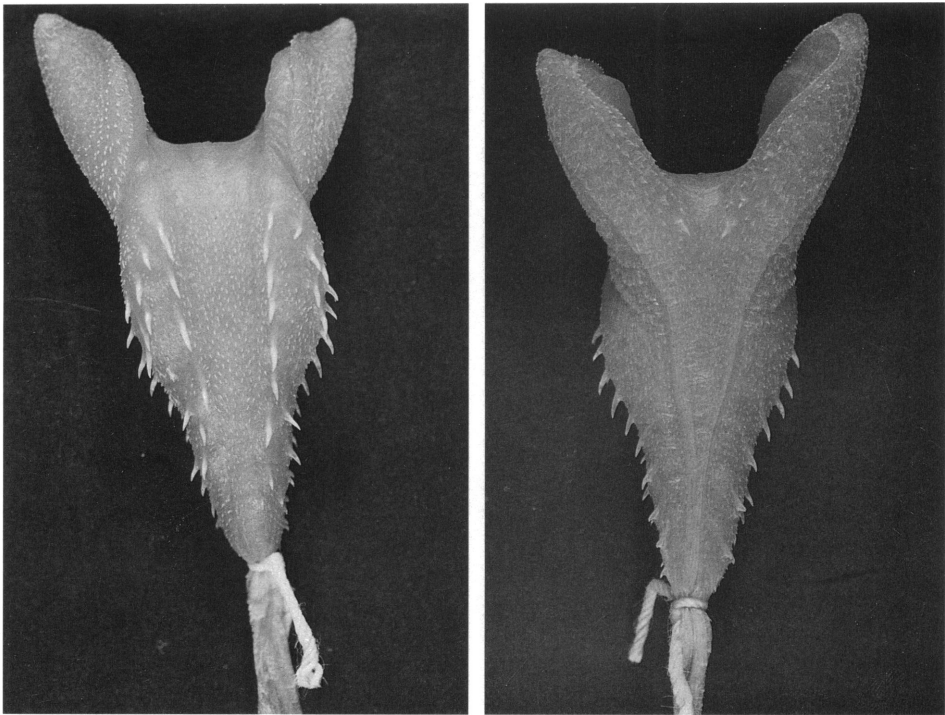


Fig. 26. Hemipenis of *Alsophis antiguae* (AMNH 2832). Asulcate (left) and sulcate (right) views.

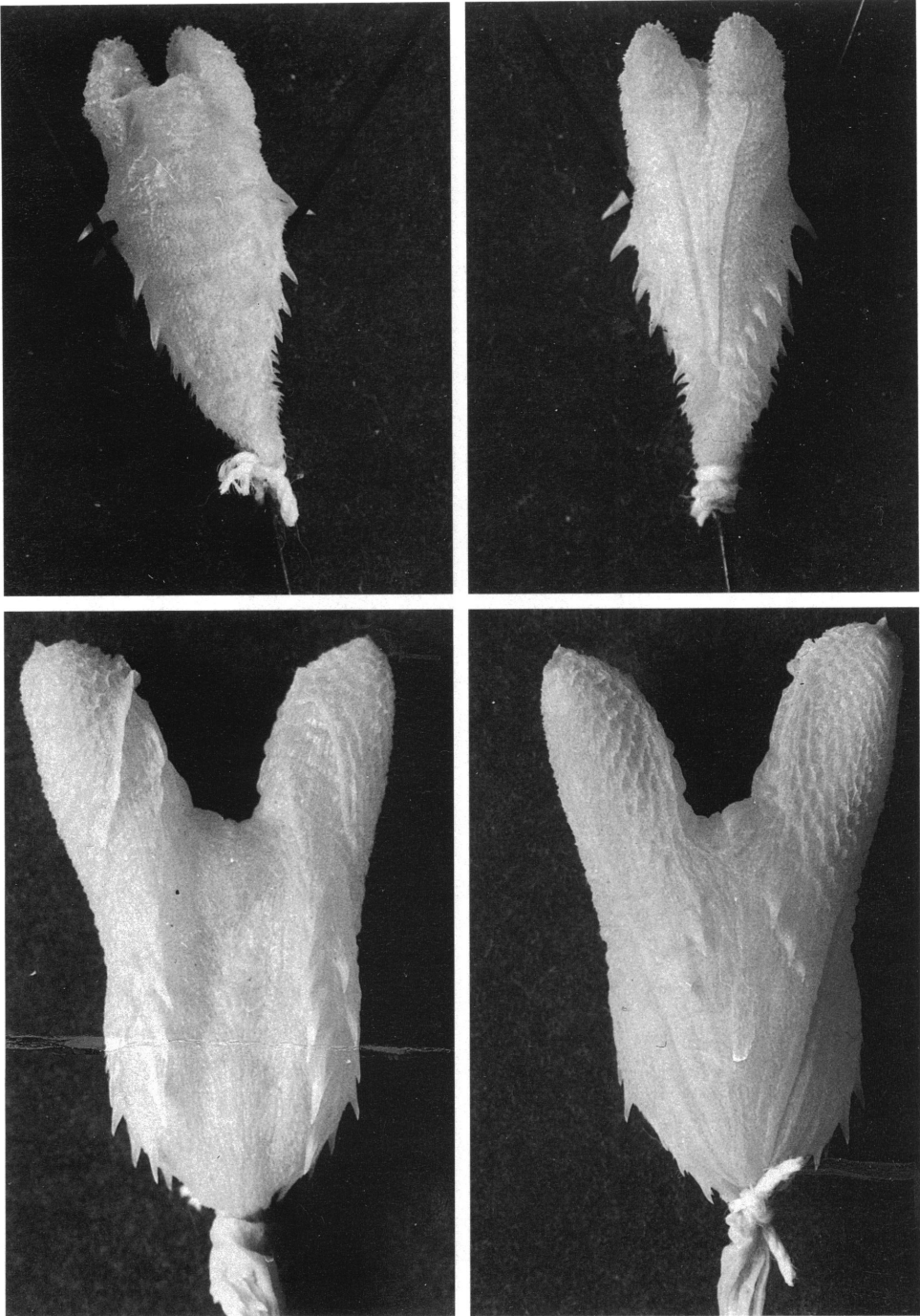


Fig. 27. Hemipenes of *Alsophis vudii* (upper; MPMH 22048) and *Alsophis rijersmai* (lower; MNHN 1991.439). Asulcate (left) and sulcate (right) views.

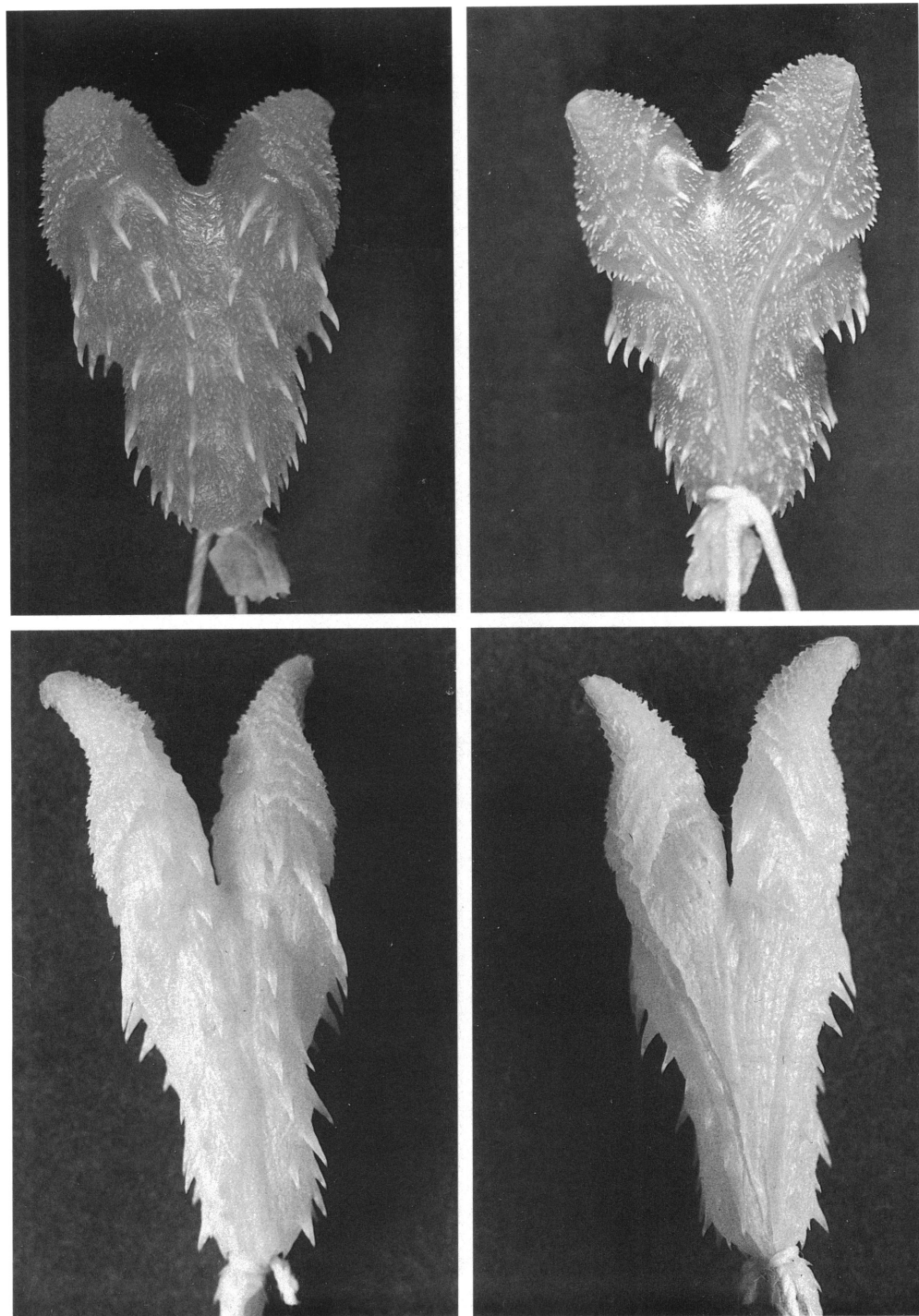


Fig. 28. Hemipenes of *Alsophis sibonius* (upper; USNM 325085) and *Alsophis danforthi* (lower; MNHN 1991.1487). Asulcate (left) and sulcate (right) views.

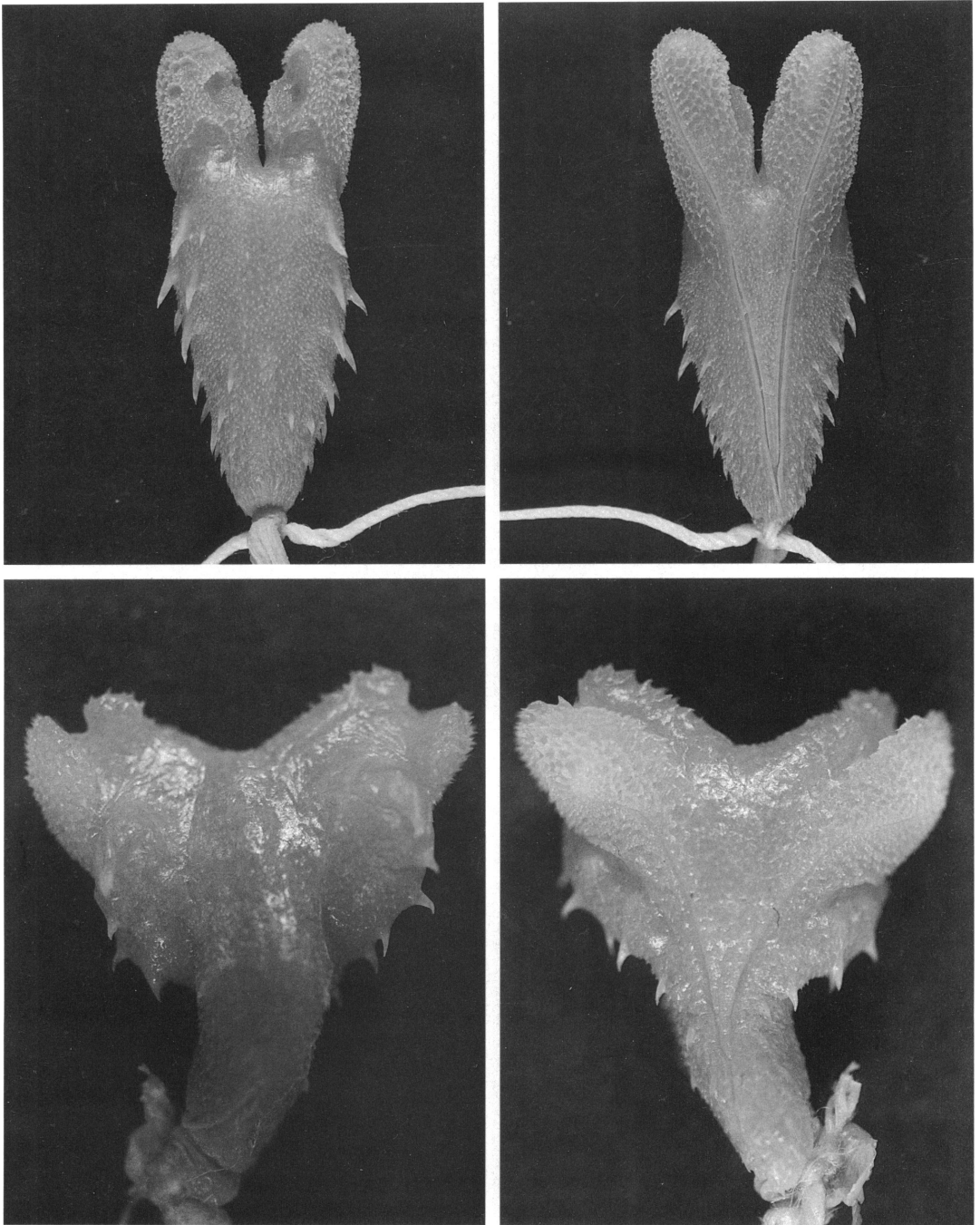


Fig. 29. Hemipenes of *Alsophis hoodensis* (upper; USNM 96005) and *Alsophis elegans* (lower; uncatalogued specimen). Asulcate (left) and sulcate (right) views.

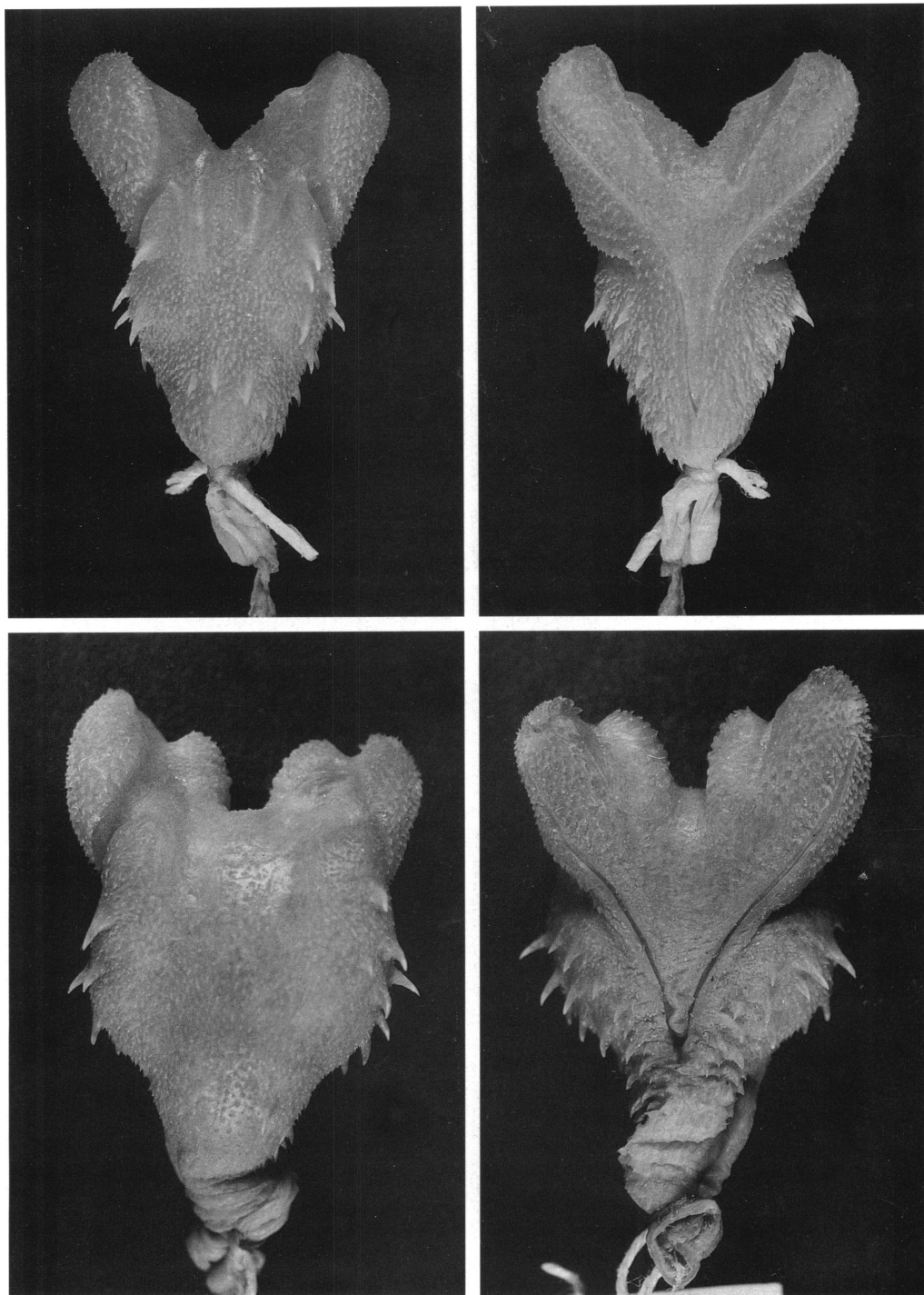


Fig. 30. Hemipenes of *Alsophis dorsalis* (upper; USNM 115614) and *Alsophis occidentalis* (lower; AMNH 91474). Asulcate (left) and sulcate (right) views.

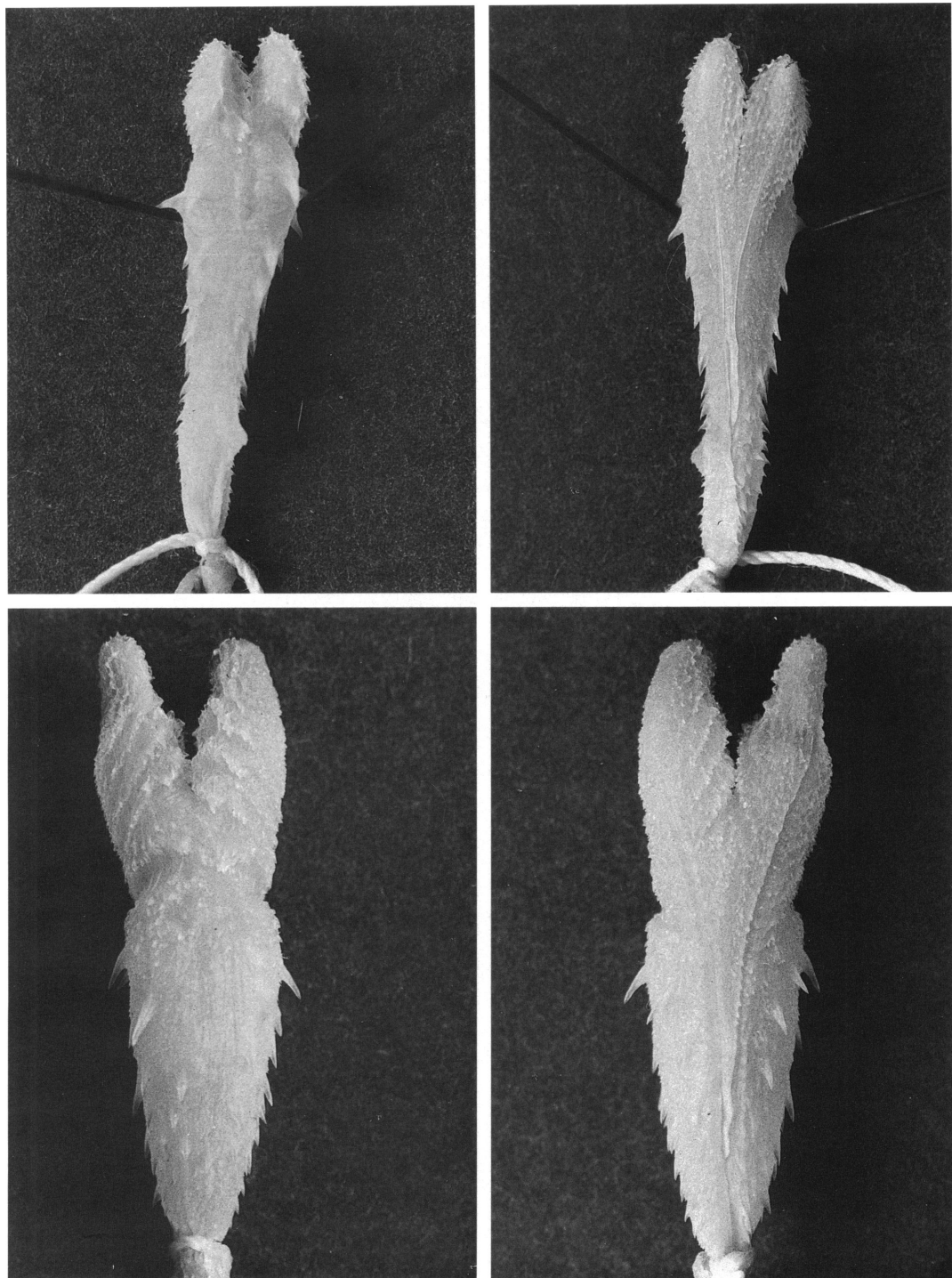


Fig. 31. Hemipenes of *Antillophis parvifrons* (upper; MPMH 18878) and *Antillophis andreae* (lower; MNHN 1883.387). Asulcate (left) and sulcate (right) views.

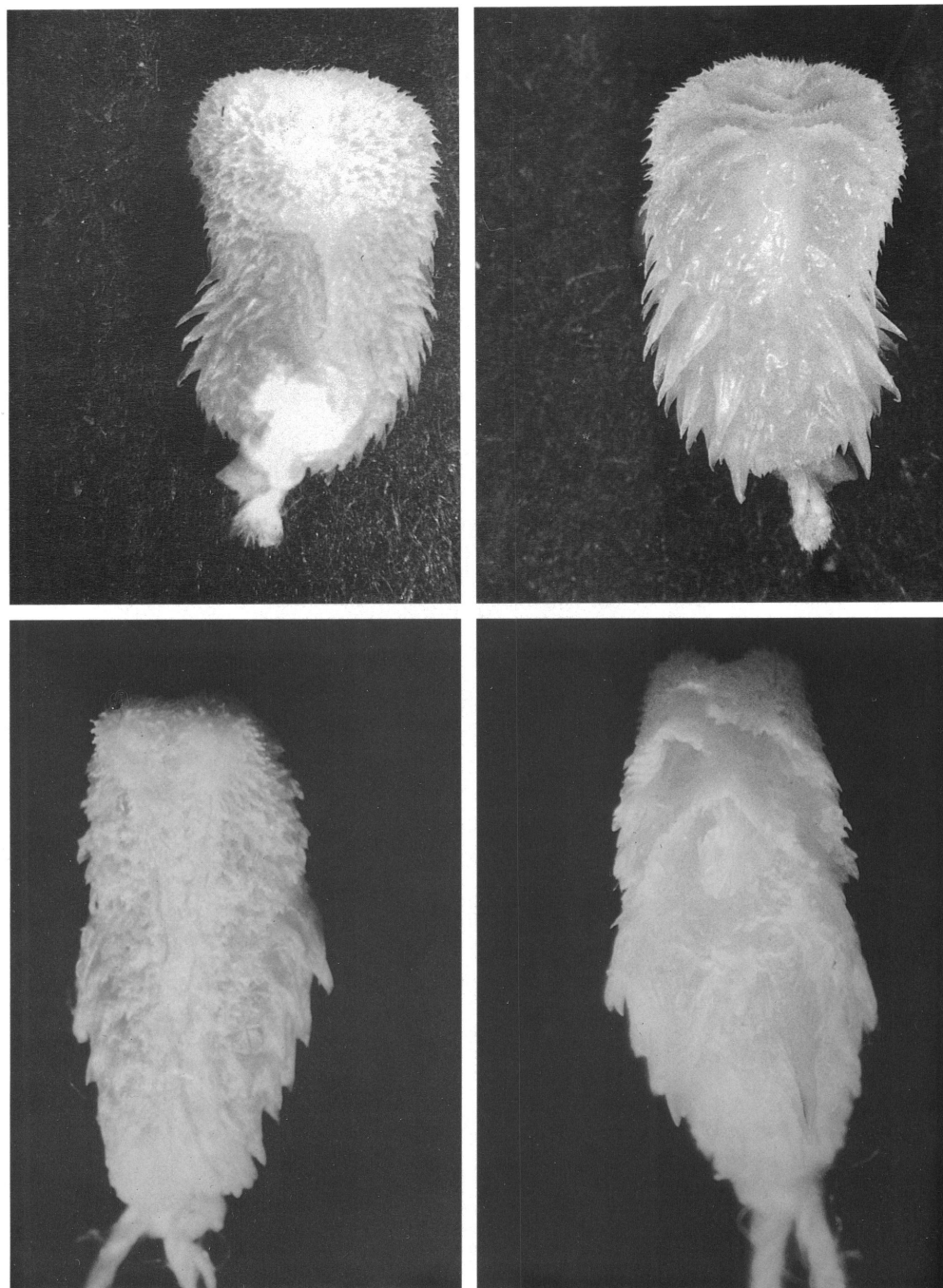


Fig. 32. Hemipenes of *Apostolepis assimilis* (upper; IB 54071) and *Apostolepis dimidiata* (lower; uncatalogued specimen). Sulcate (left) and asulcate (right) views.

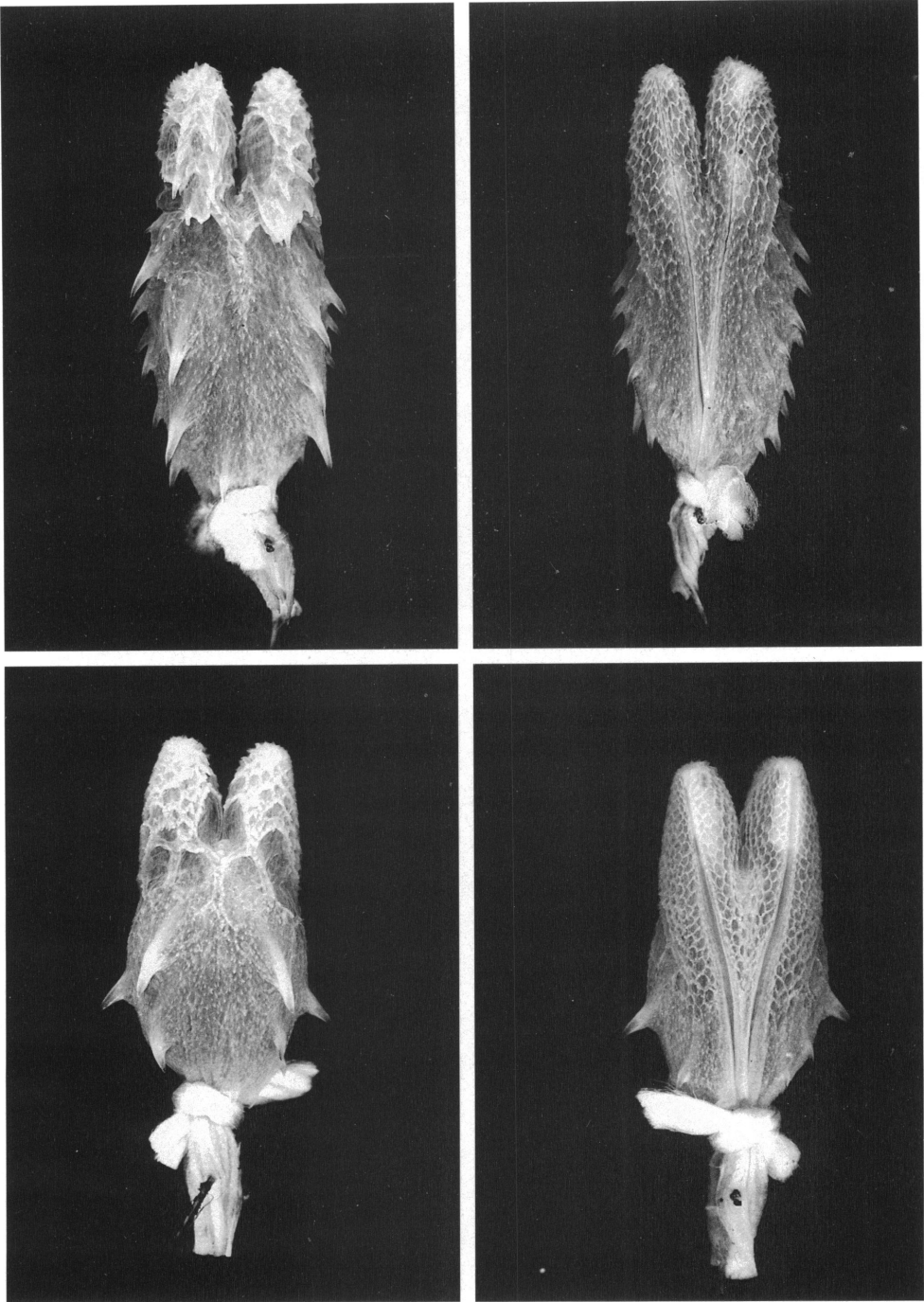


Fig. 33. Hemipenes of *Arrhyton vittatum* (upper; AMNH 46727) and *Arrhyton landoi* (lower; AMNH 36703). Asulcate (left) and sulcate (right) views.

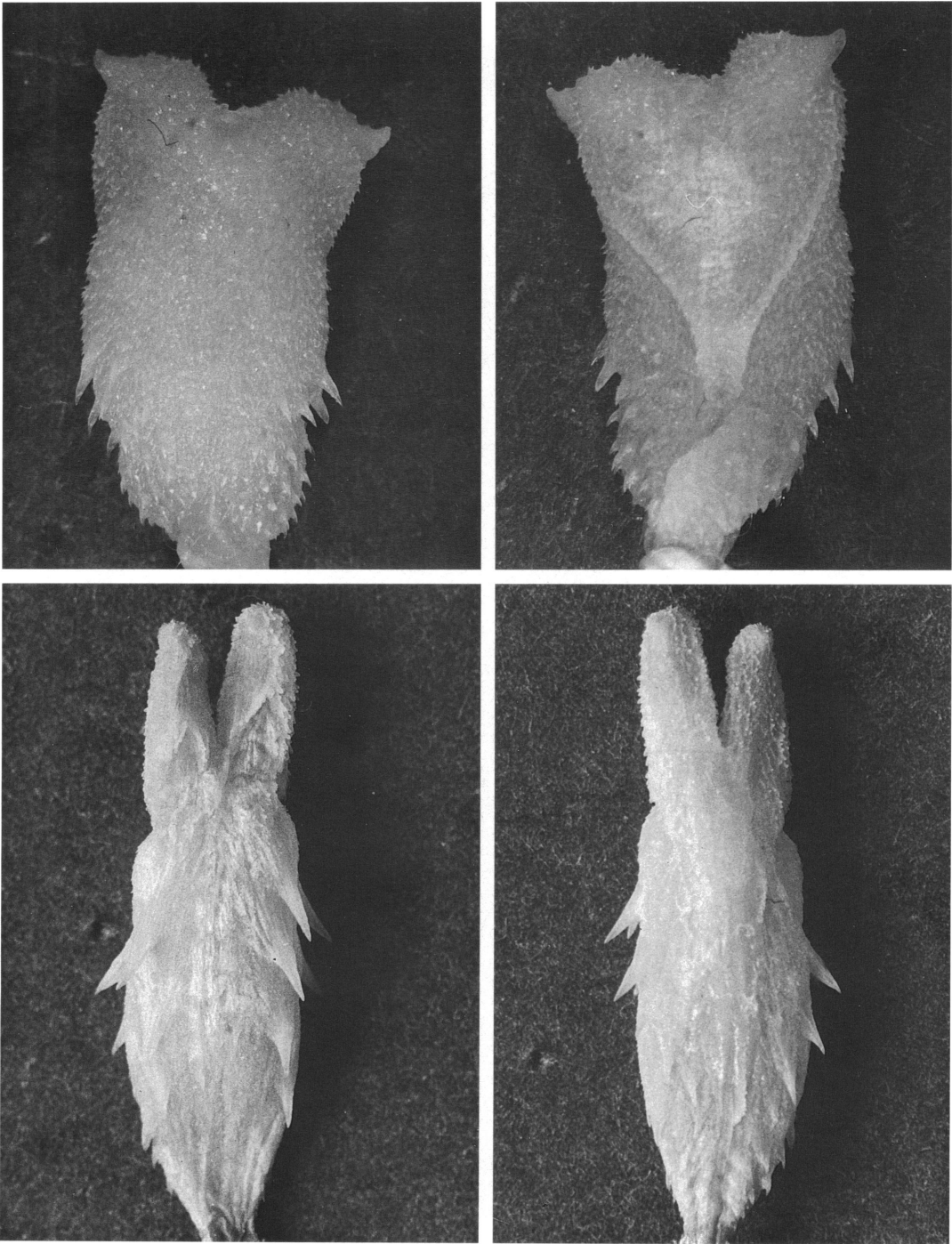


Fig. 34. Hemipenes of *Arrhyton callilaemum* (upper; MPMH 22707) and *Arrhyton taeniatum* (lower; MNHN 695). Asulcate (left) and sulcate (right) views.



Fig. 35. Hemipenis of *Arrhyton funereum* (MPMH 22789). Asulcate (left) and sulcate (right) views.

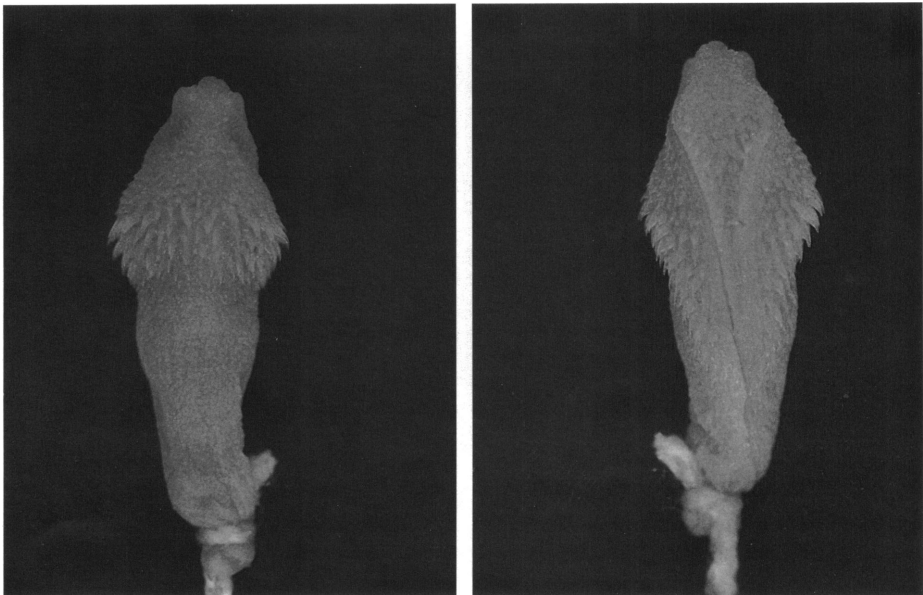


Fig. 36. Hemipenis of *Arrhyton polylepis* (lower; MPMH 22703). Asulcate (left) and sulcate (right) views.

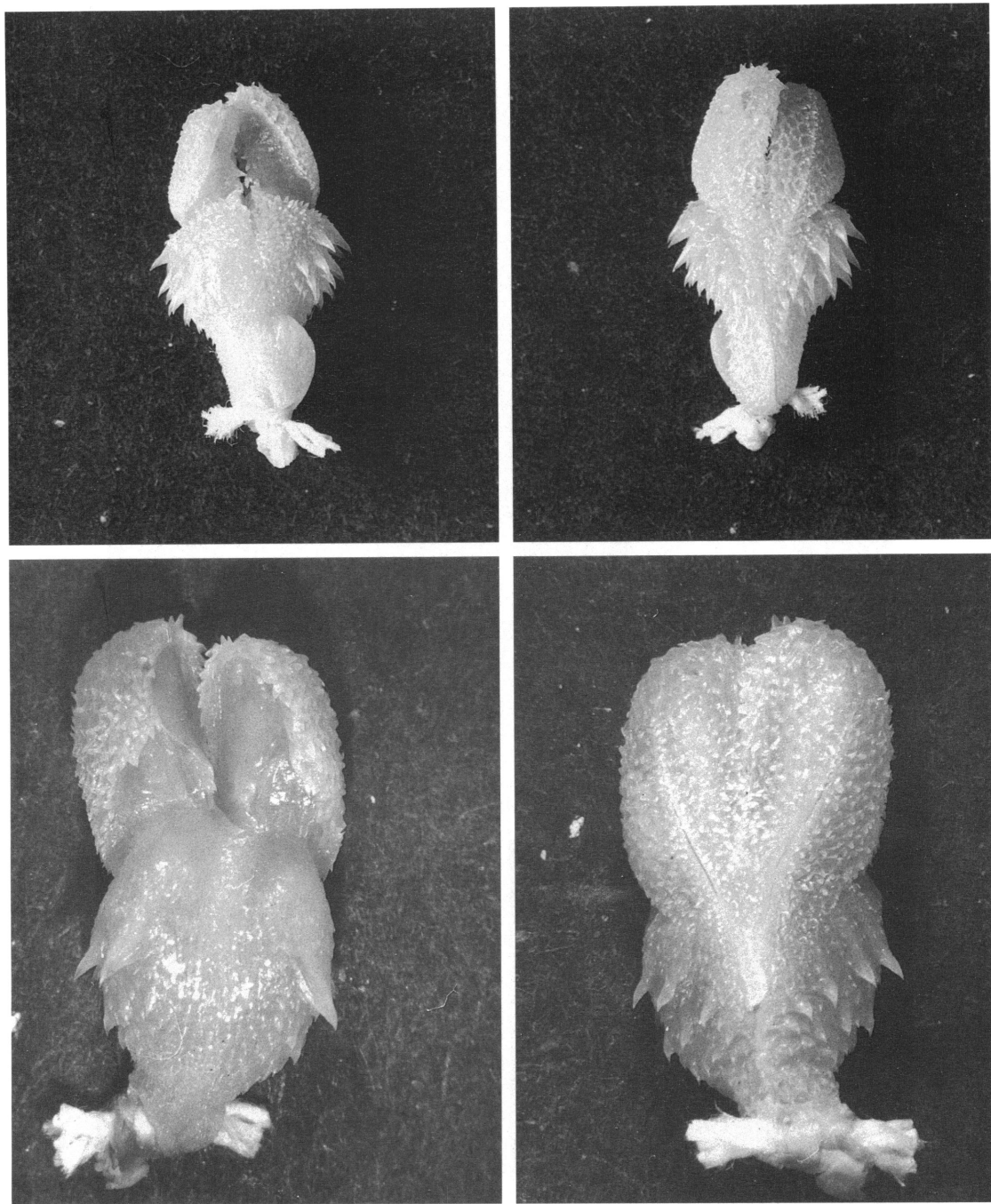


Fig. 37. Hemipenes of *Arrhyton exiguum* (upper; RT 10079) and *Darlingtonia haetiana* (lower; RT 6141). Asulcate (left) and sulcate (right) views.

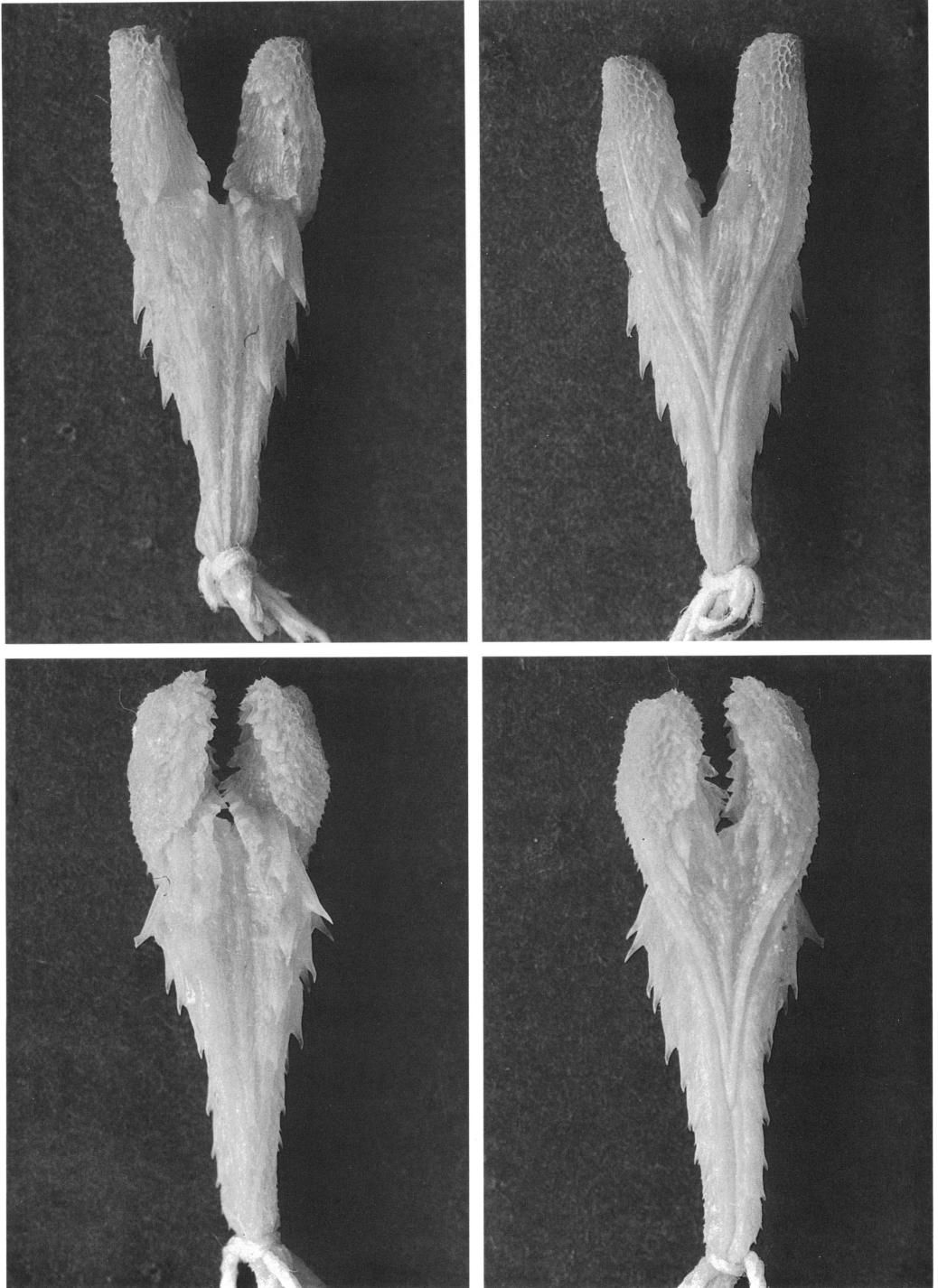


Fig. 38. Hemipenes of *Clelia quimi* (upper; IB 1350) and *Clelia bicolor* (lower; MRSN R1802). Asulcate (left) and sulcate (right) views.



Fig. 39. Hemipenis of *Clelia montana* (IB 43072). Asulcate view of the lobes and crotch.

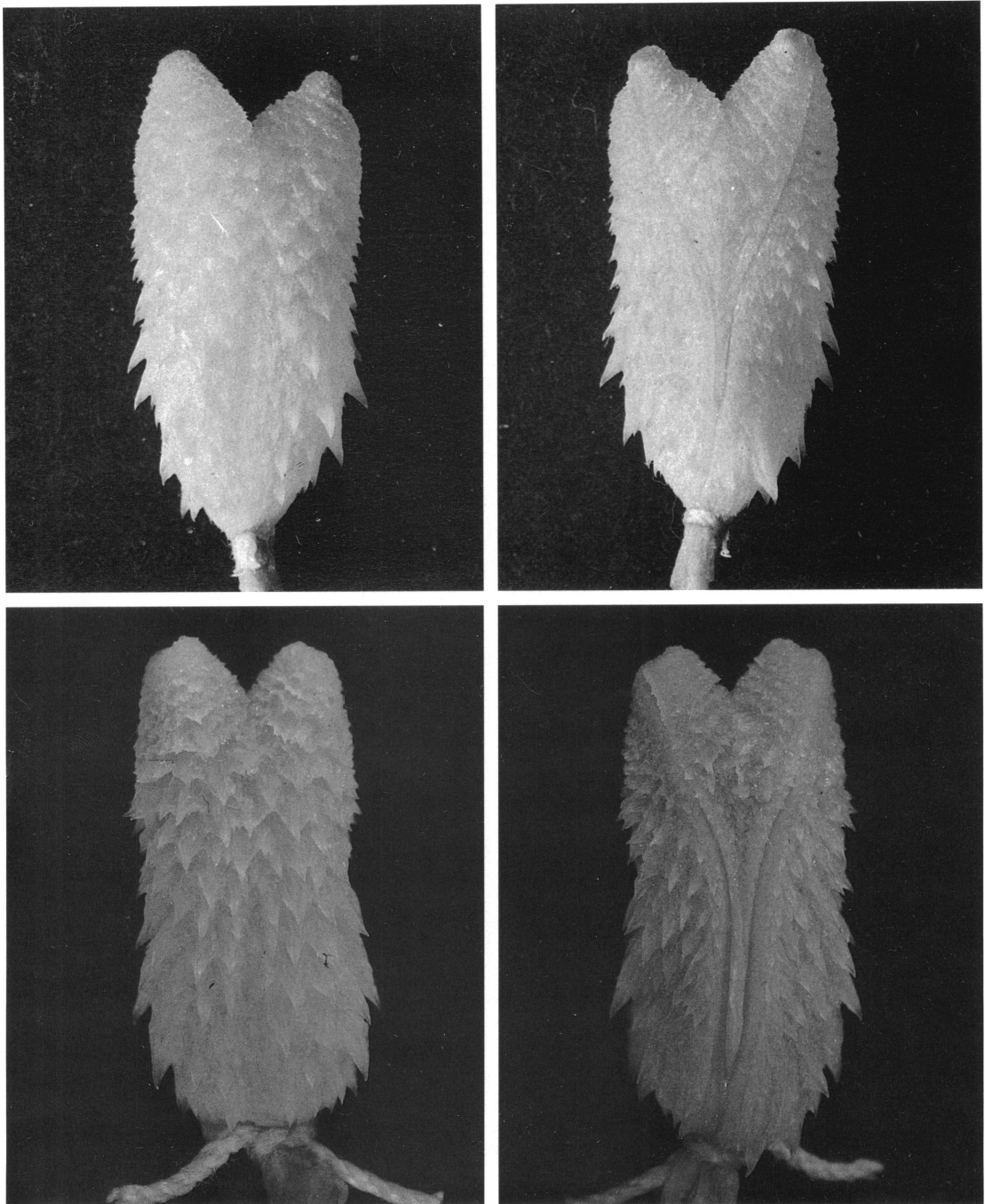


Fig. 40. Hemipenes of *Conophis pulcher* (upper; MNHN 5981) and *Conophis lineatus* (lower; MNHN 3740). Asulcate (left) and sulcate (right) views.

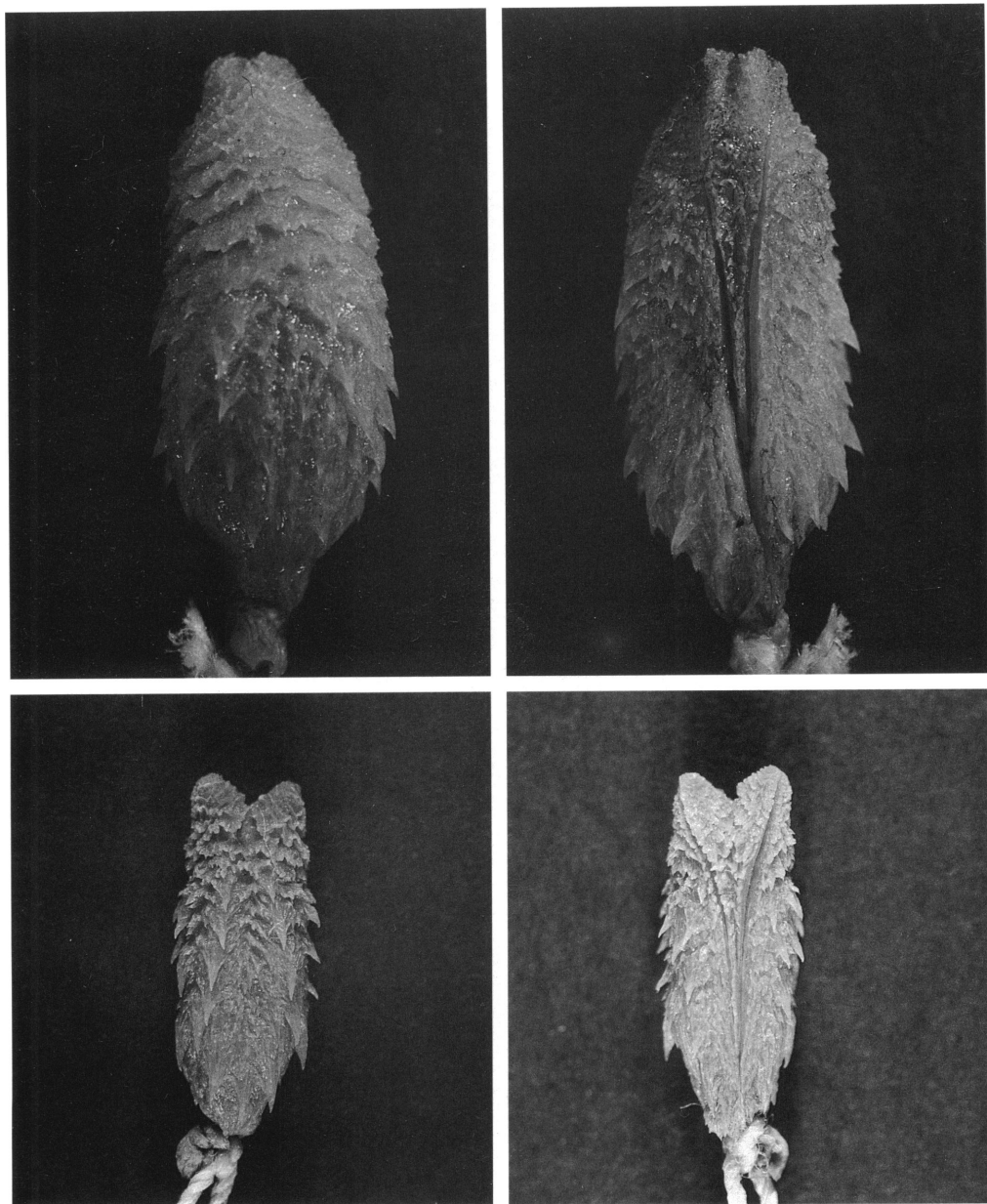


Fig. 41. Hemipenes of *Conophis vittatus* (upper; AMNH 66337) and *Manolepis putnami* (lower; AMNH 66824). Asulcate (left) and sulcate (right) views.

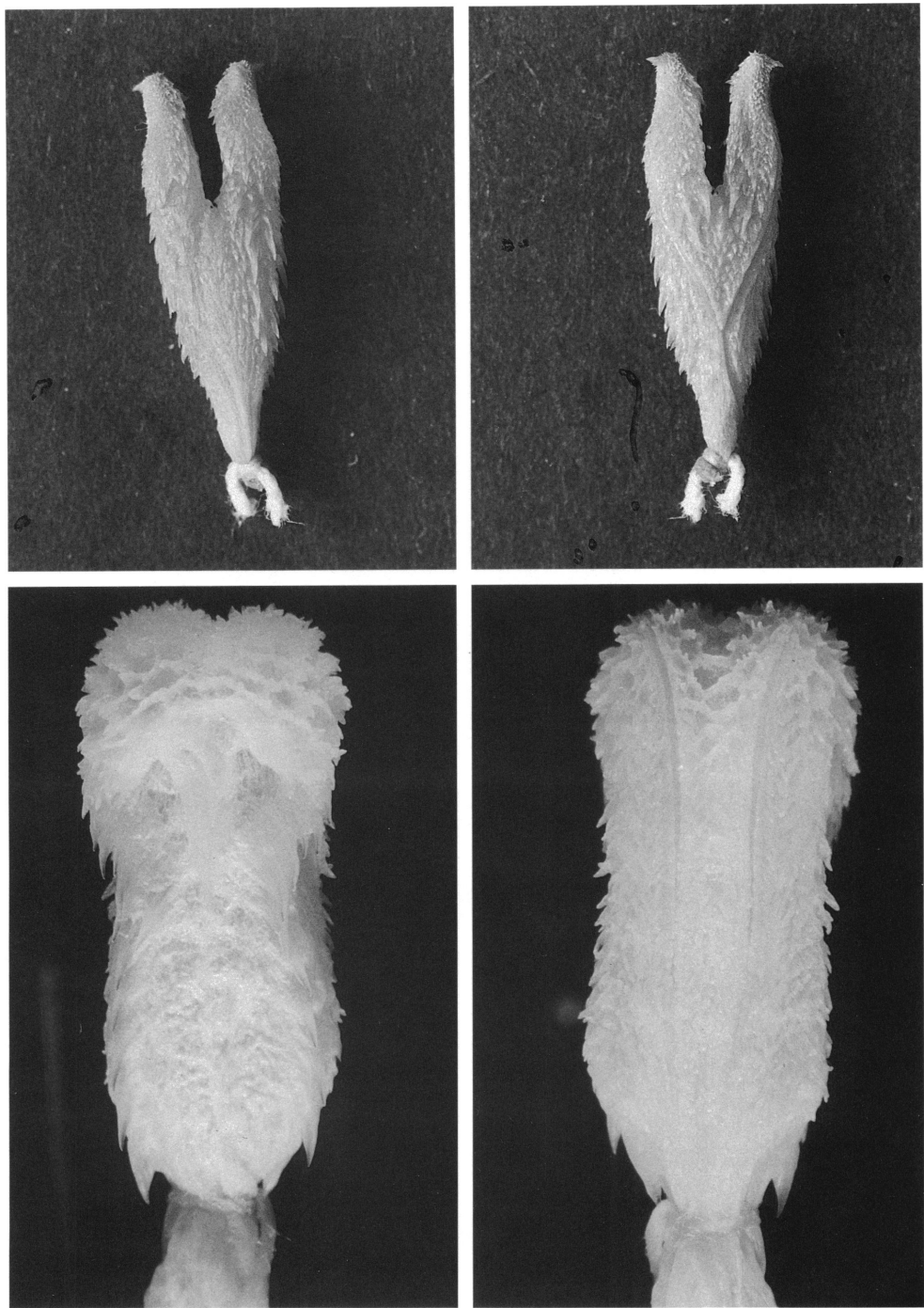


Fig. 42. Hemipenes of *Drepanoides anomalus* (upper; MNRJ 2989) and *Ditaxodon taeniatus* (lower; IB 40751). Asulcate (left) and sulcate (right) views.

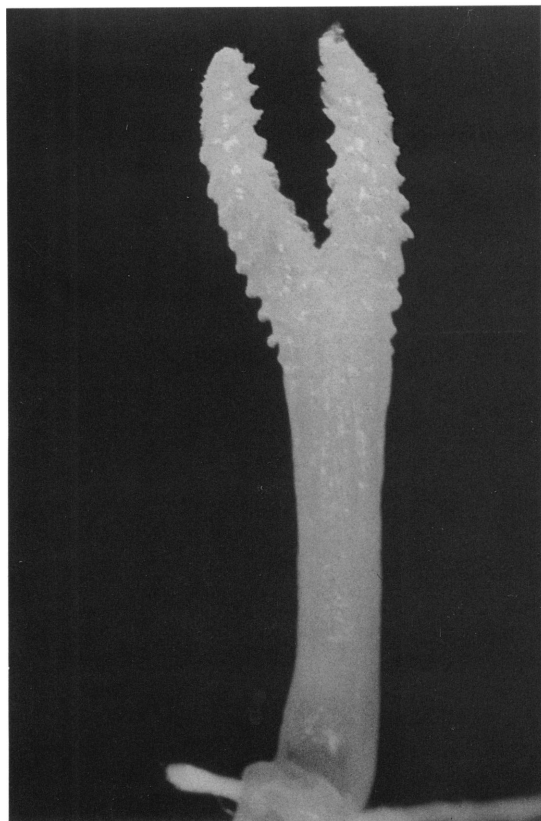


Fig. 43. Hemipenis of *Elapomorphus quinquelineatus* (IB 52713). Asulcate (left) and sulcate (right) views.

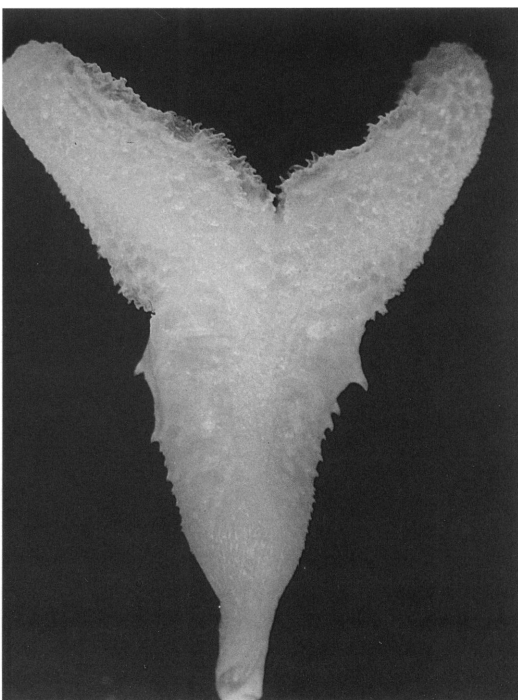
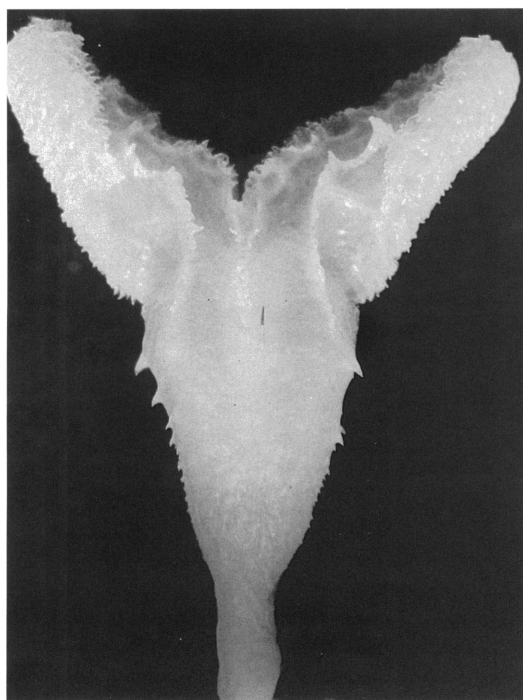


Fig. 44. Hemipenis of *Elapomorphus lepidus* (CEPLAC 748). Asulcate (left) and sulcate (right) views.

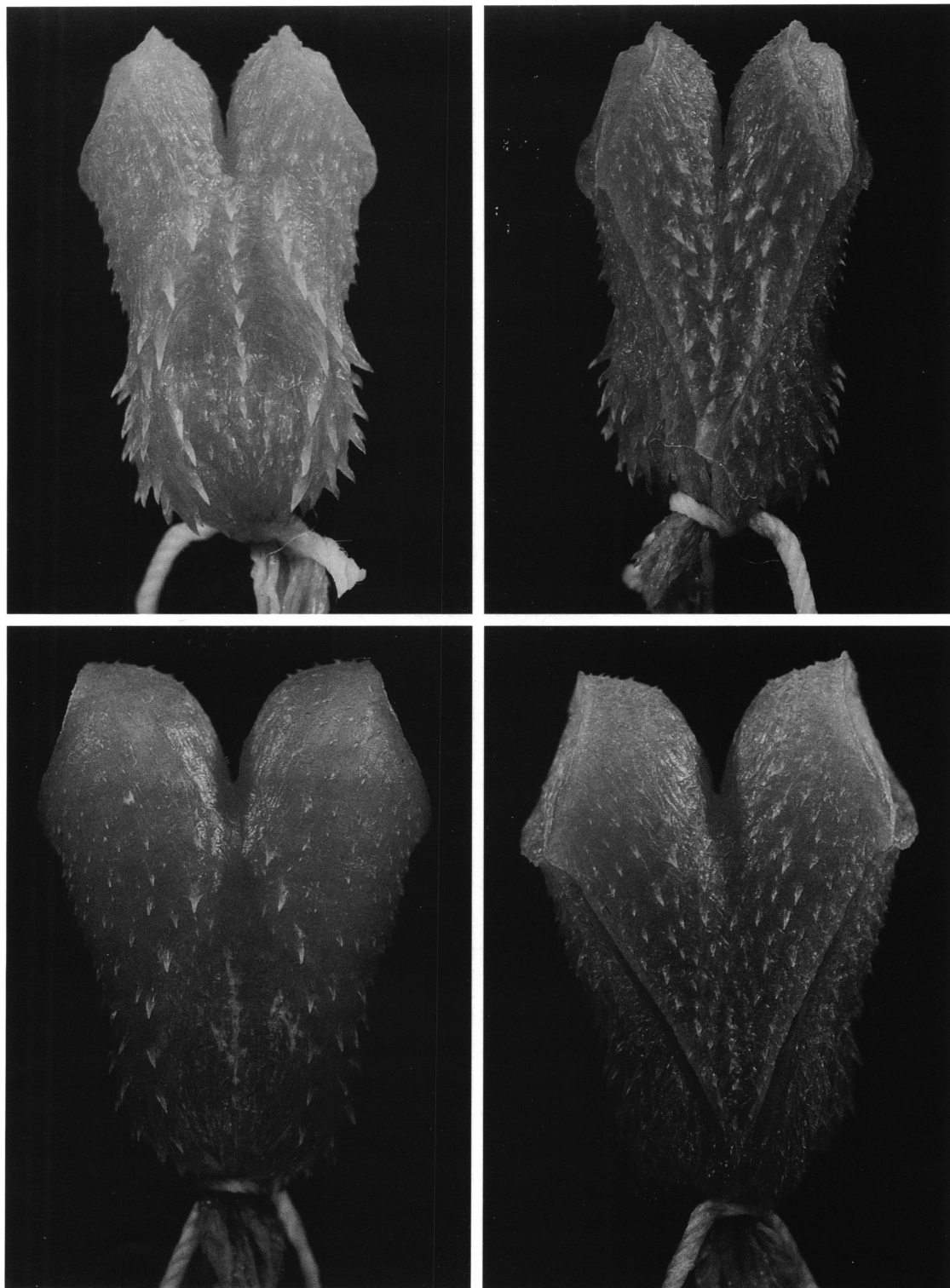


Fig. 45. Hemipenes of *Erythrolamprus mimus* (upper; AMNH 12697) and *Erythrolamprus bizona* (lower; AMNH 35576). Asulcate (left) and sulcate (right) views.



Fig. 46. Hemipenes of *Farancia erytrogramma* (upper; AMNH 126497) and *Farancia abacura* (lower; MNHN 1903.325). Asulcate (left) and sulcate (right) views.

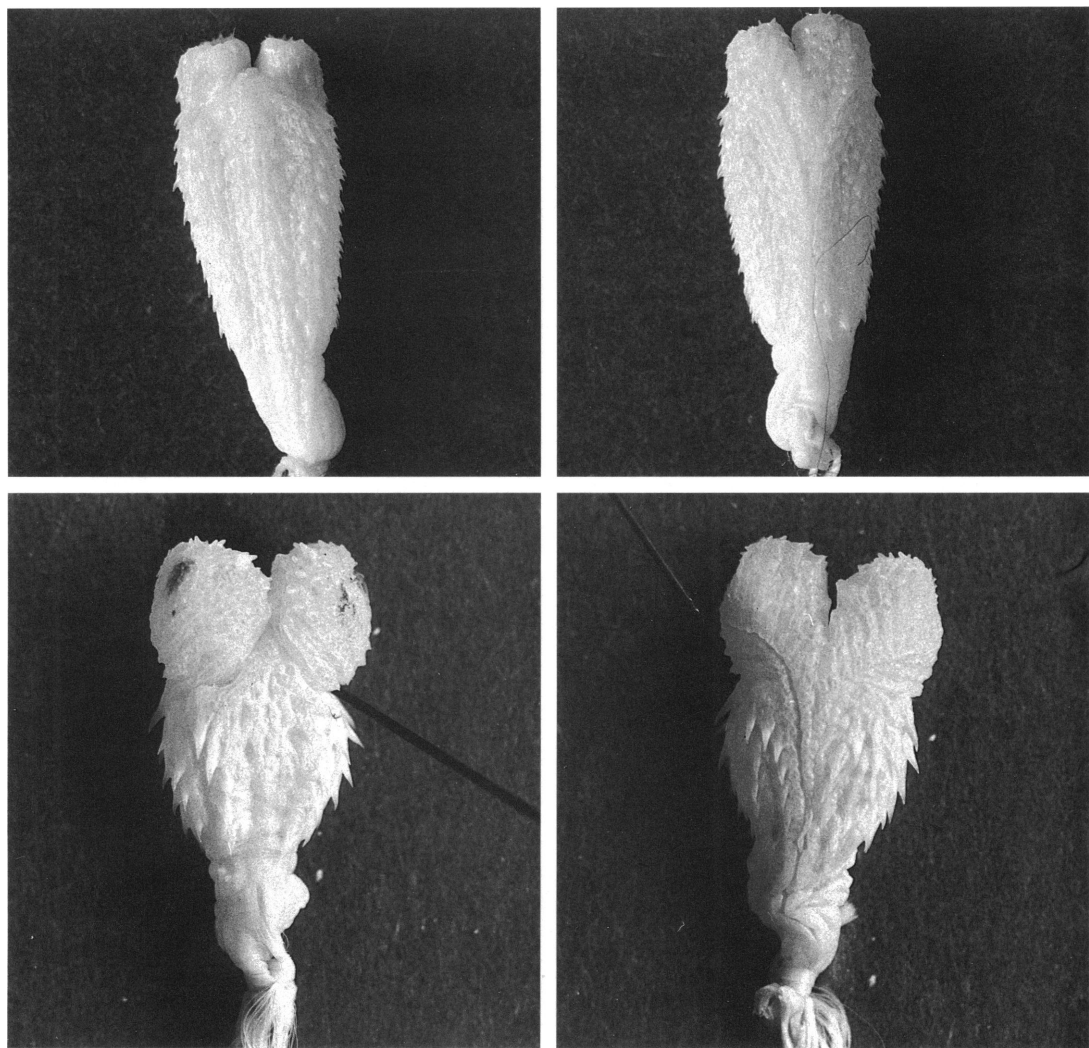


Fig. 47. Hemipenes of *Helicops leopardinus* (upper; LSUMZ 40470) and *Helicops angulatus* (lower; uncatalogued specimen). Asulcate (left) and sulcate (right) views.

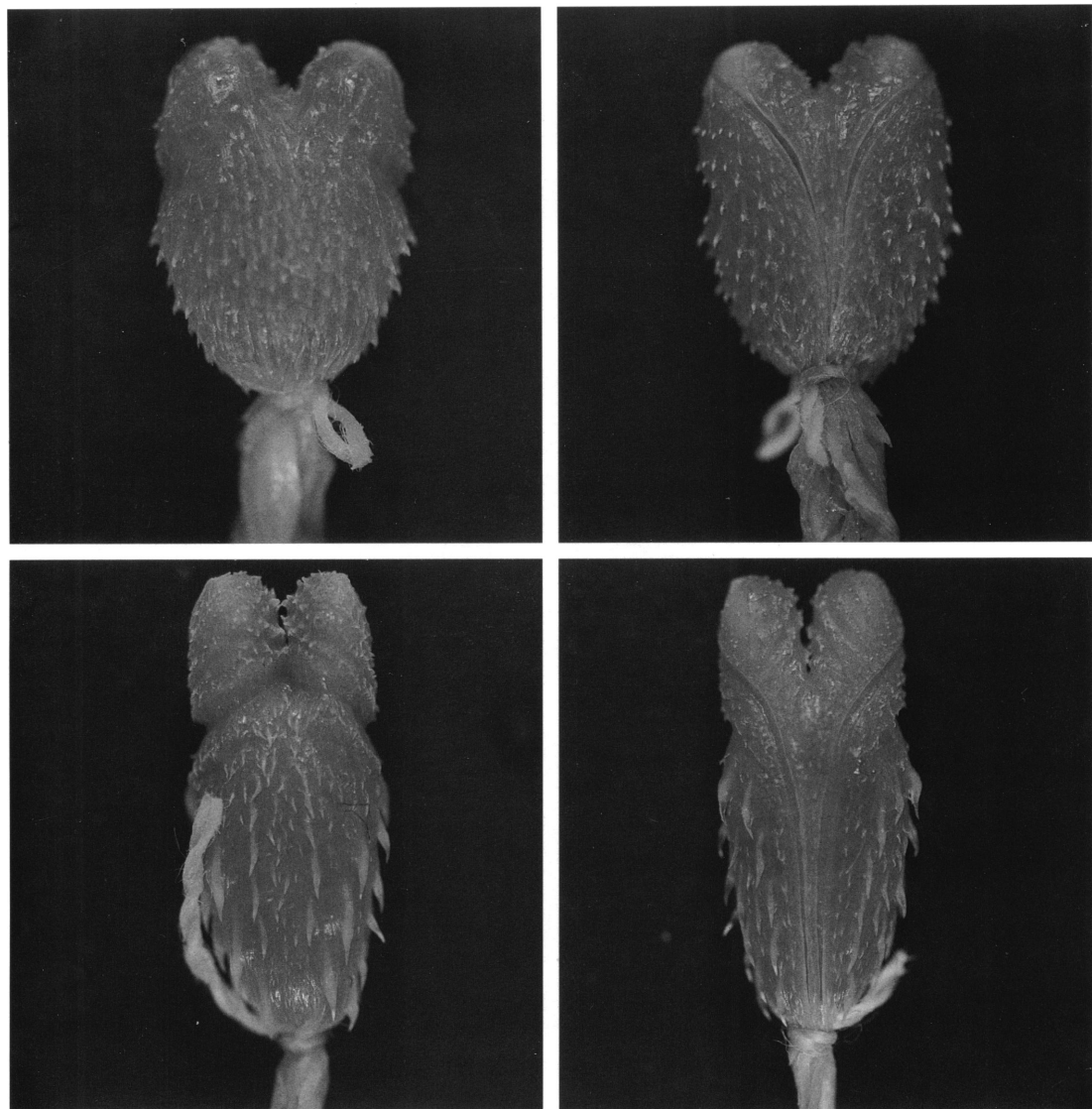


Fig. 48. Hemipenes of *Helicops modestus* (upper; AMNH 5741) and *Helicops pastazae* (lower; AMNH 57342). Asulcate (left) and sulcate (right) views.

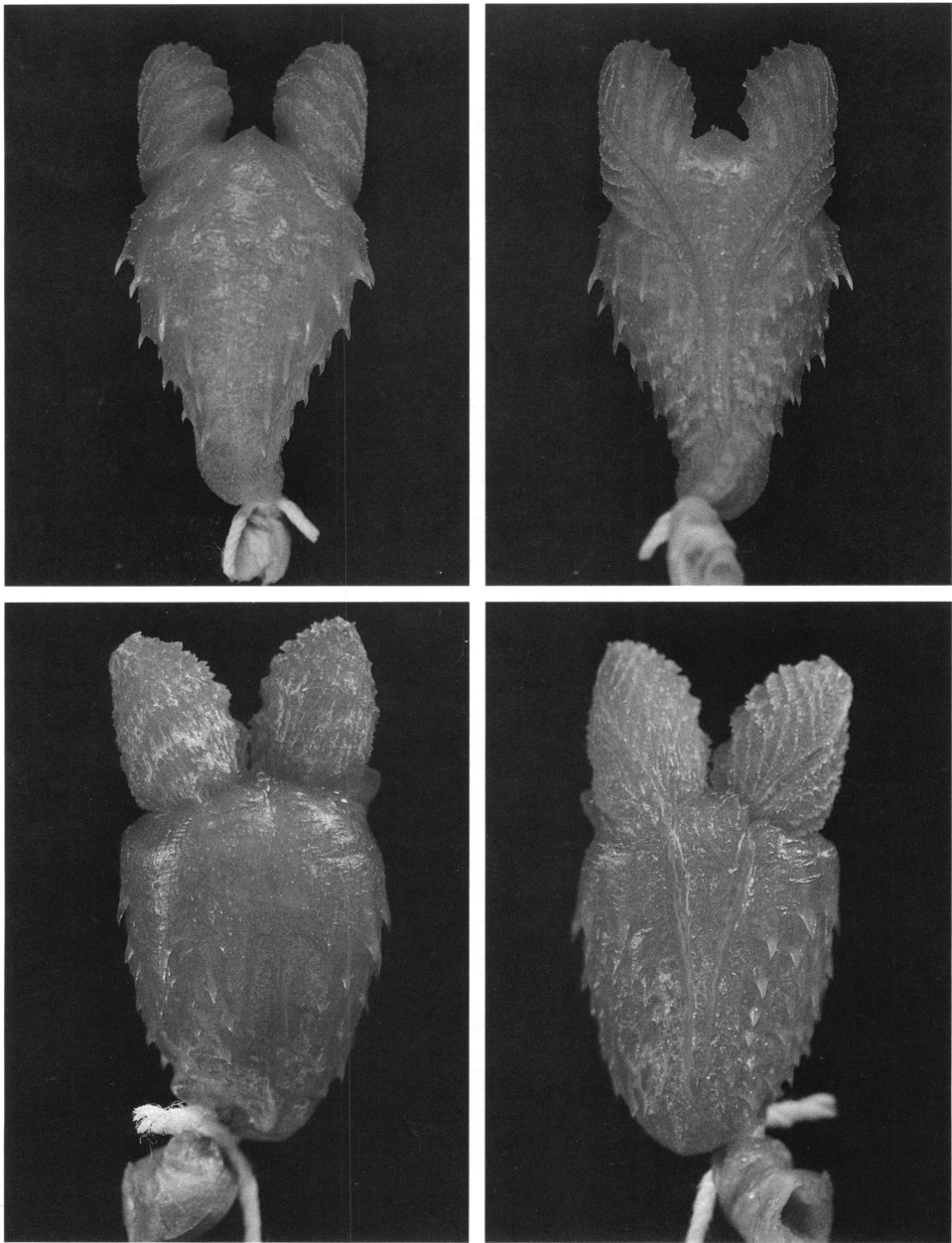


Fig. 49. Hemipenes of *Helicops danieli* (upper; AMNH 97461) and *Helicops polylepis* (lower; AMNH 101856). Asulcate (left) and sulcate (right) views.

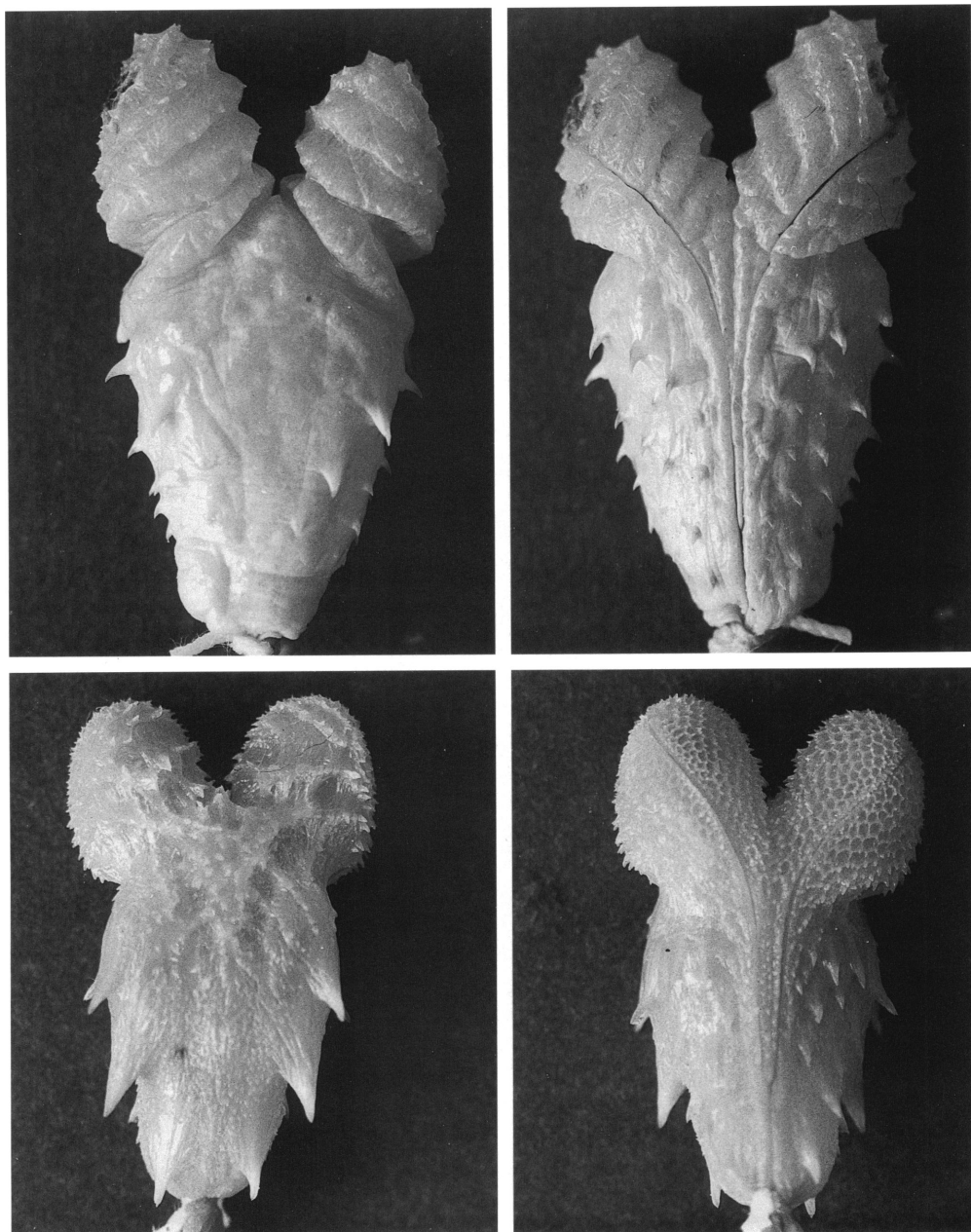


Fig. 50. Hemipenes of *Helicops carinicaudus* (upper; MNRJ 4299) and *Heterodon nasicus* (lower; MNHN 3636). Asulcate (left) and sulcate (right) views.

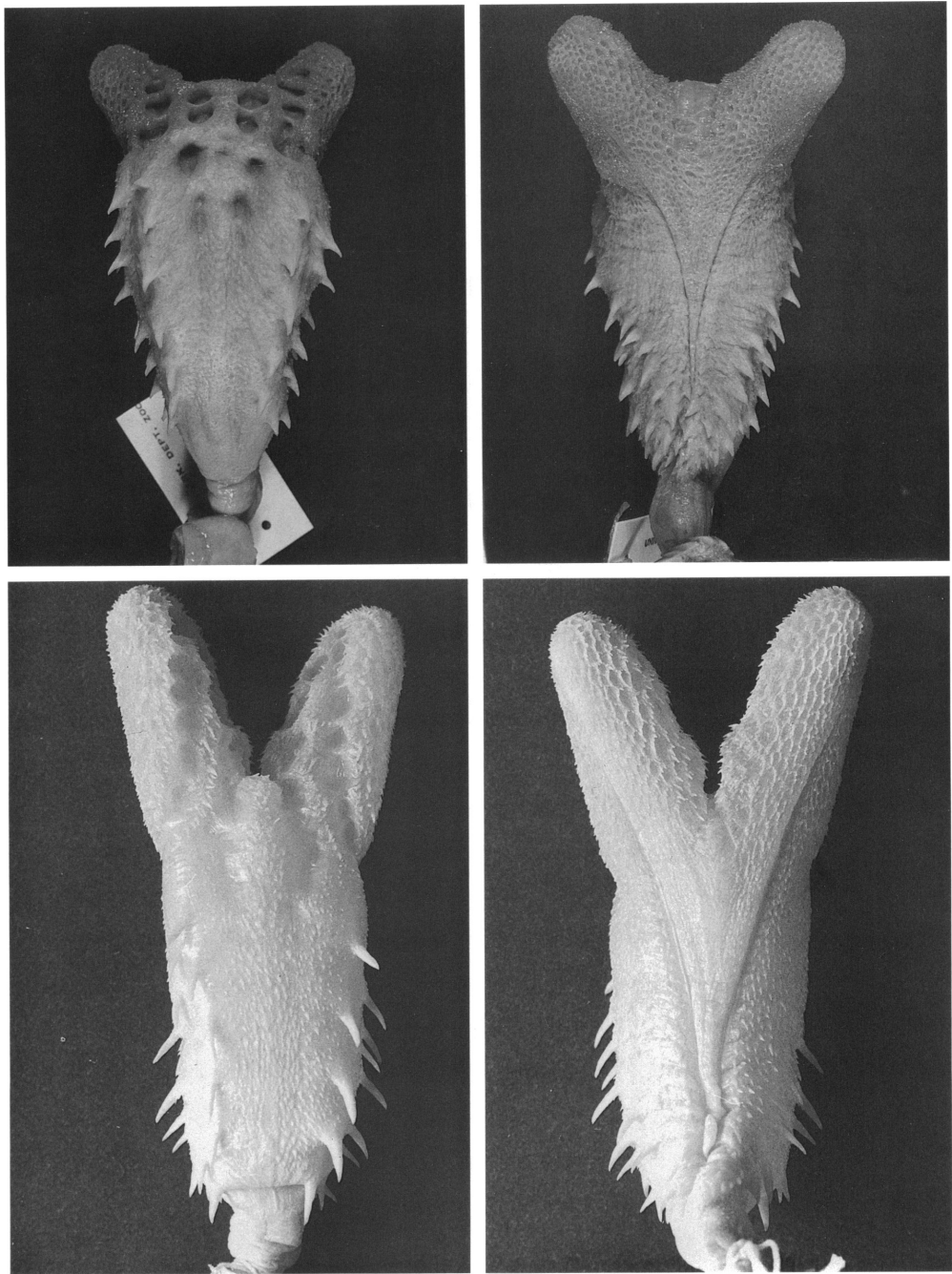


Fig. 51. Hemipenes of *Hydrodynastes gigas* (upper; AMNH 57956) and *Hydrodynastes bicinctus* (lower; MNHN 1993.1618). Asulcate (left) and sulcate (right) views.

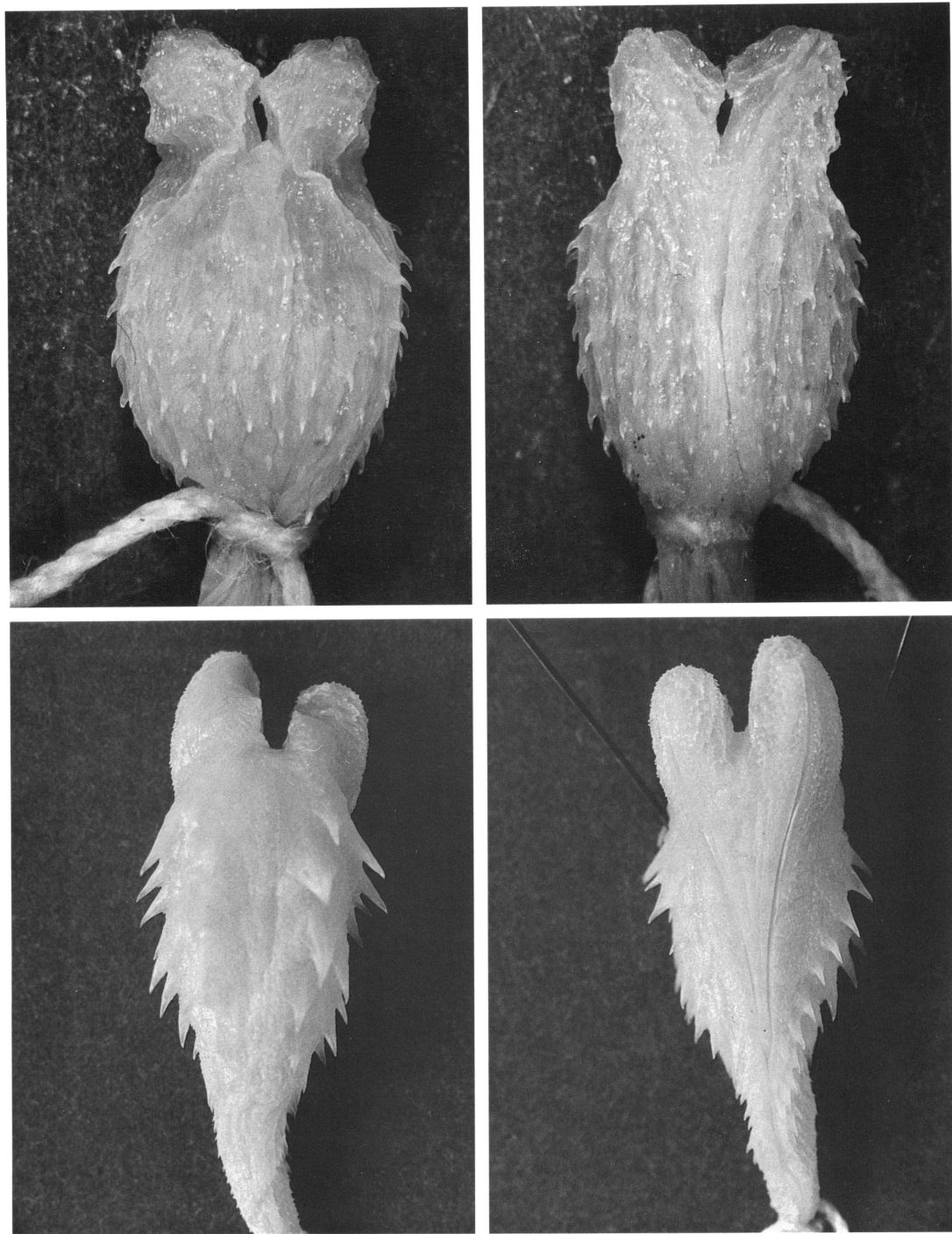


Fig. 52. Hemipenes of *Hydrops martii* (upper; MNHN 5349) and *Hypsirhynchus ferox* (lower; MPMH 23385). Asulcate (left) and sulcate (right) views.

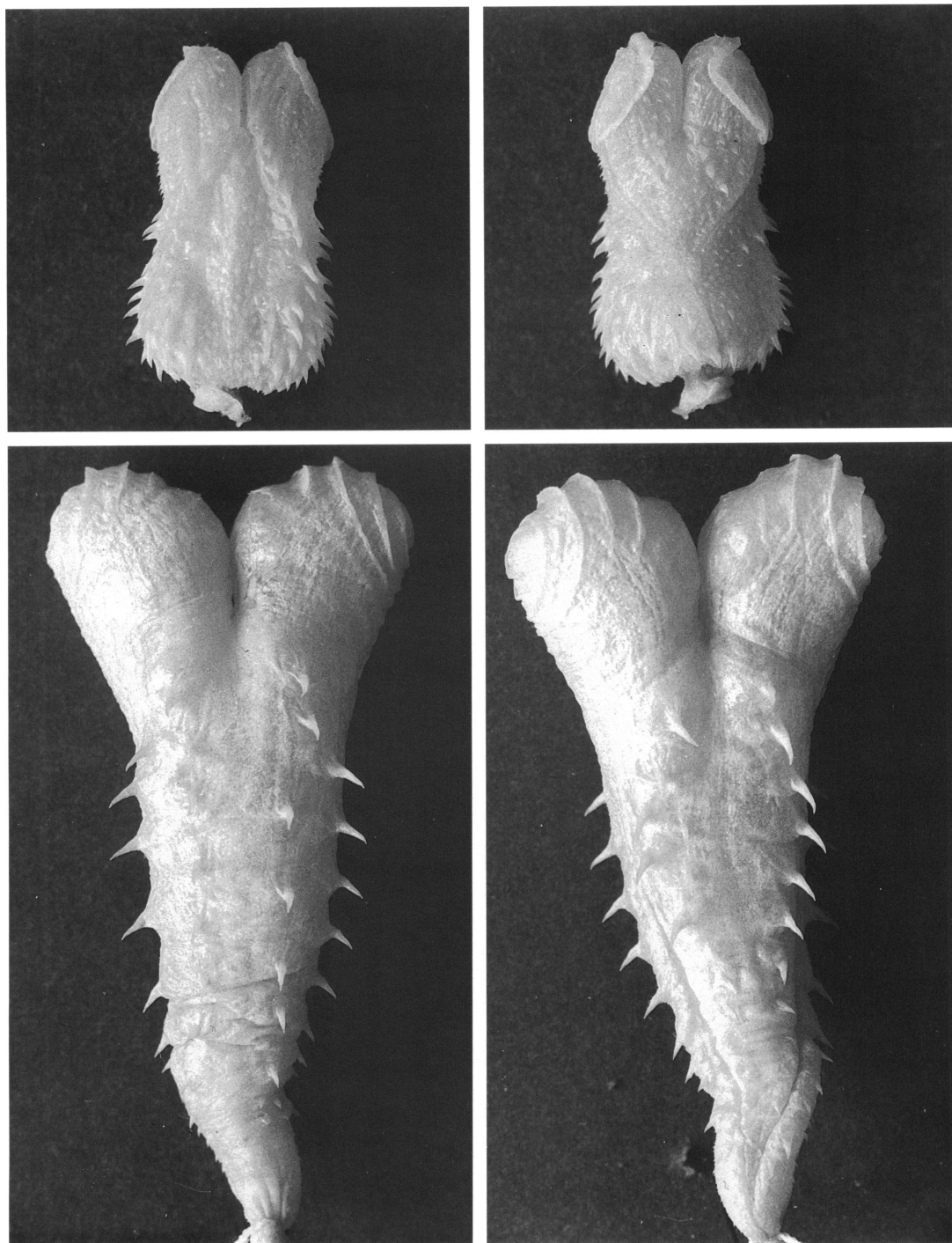


Fig. 53. Hemipenes of *Liophis reginae* (upper; uncatalogued specimen) and *Laltris dorsalis* (lower; KU 268621). Asulcate (left) and sulcate (right) views.

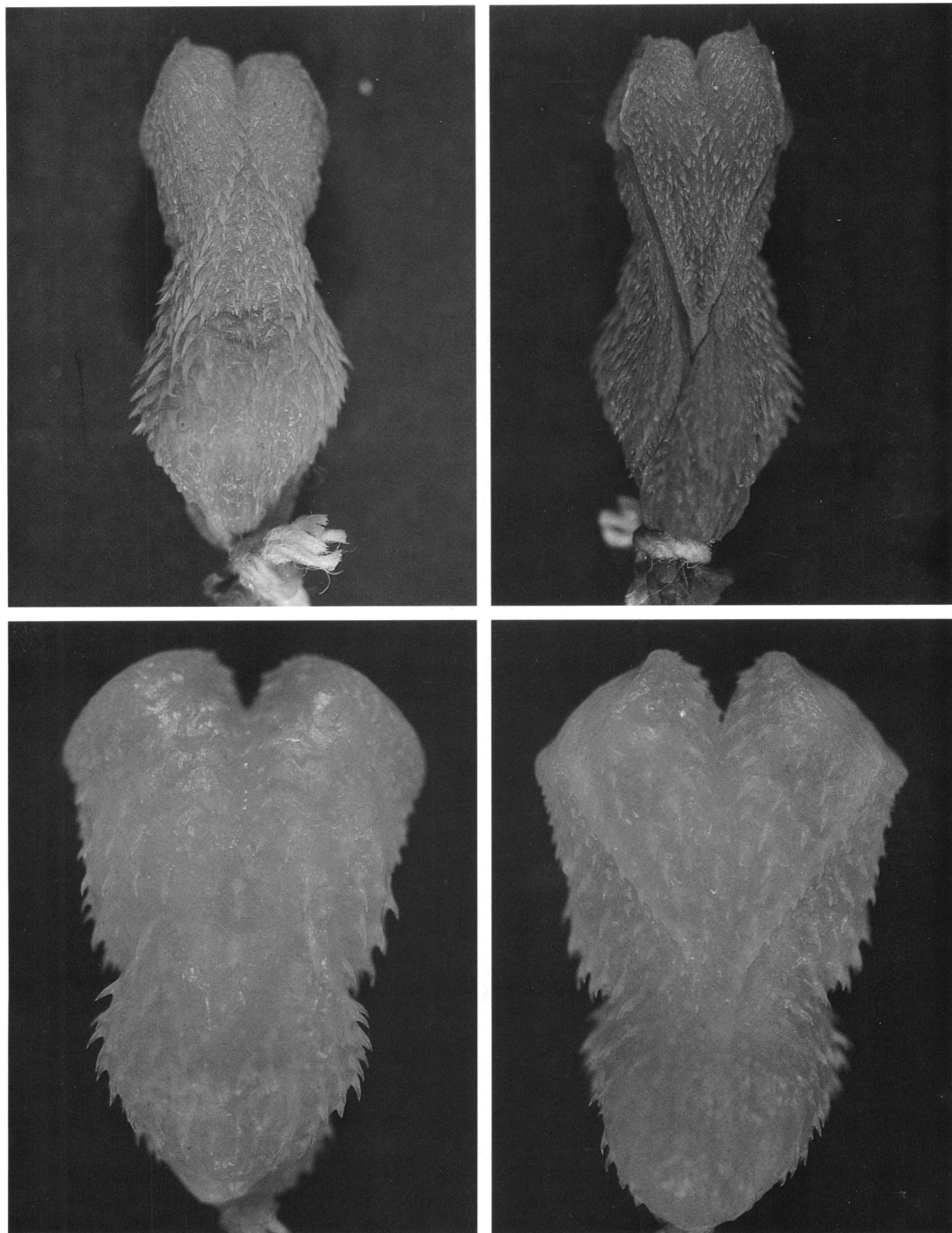


Fig. 54. Hemipenes of *Liophis almadensis* (upper; AMNH 22458) and *Liophis frenata* (lower; uncatalogued specimen). Asulcate (left) and sulcate (right) views.

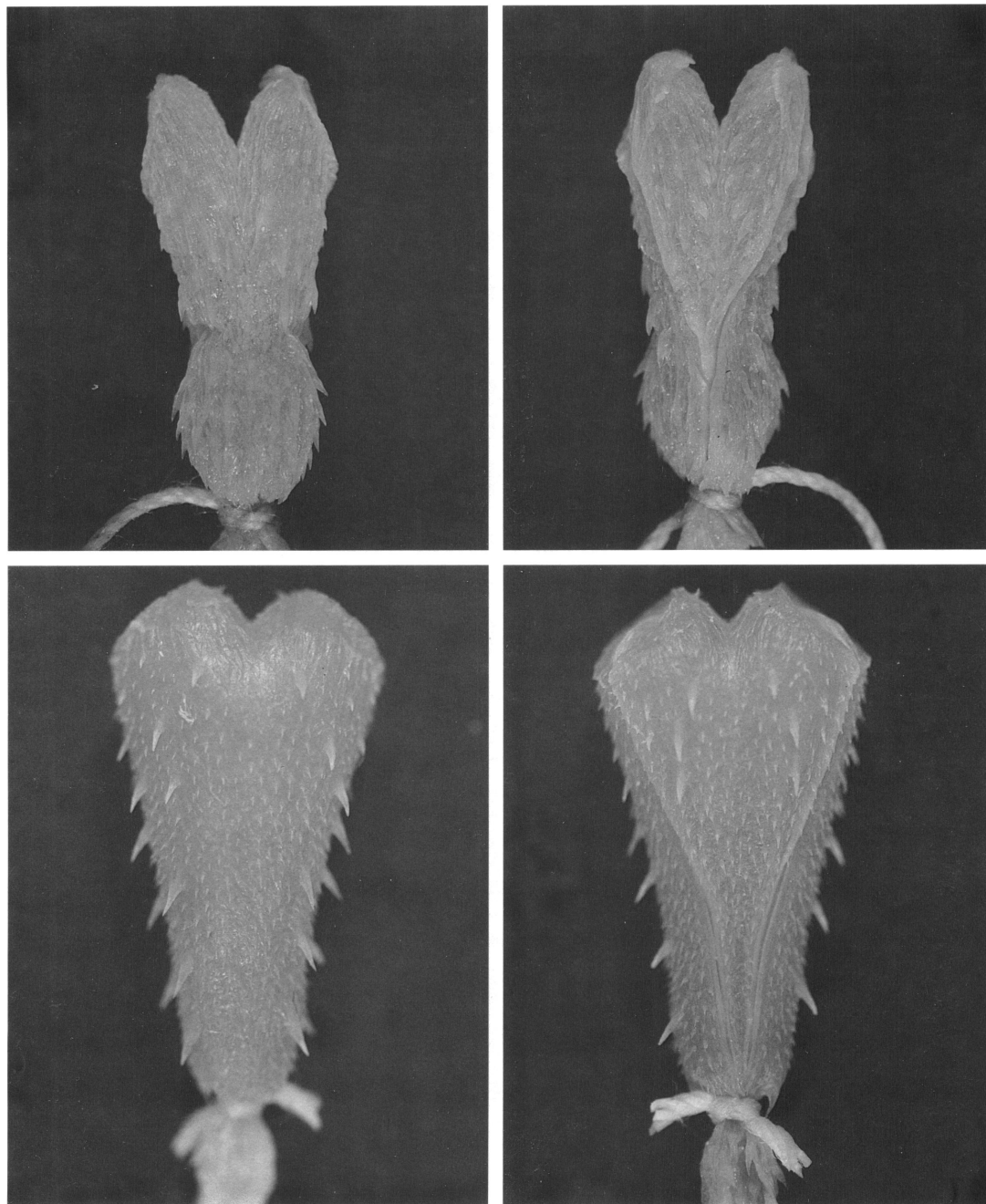


Fig. 55. Hemipenes of *Liophis juliae* (upper; MNHN 1977.1617) and *Liophis dilepis* (lower; MNHN 1967.147). Asulcate (left) and sulcate (right) views.

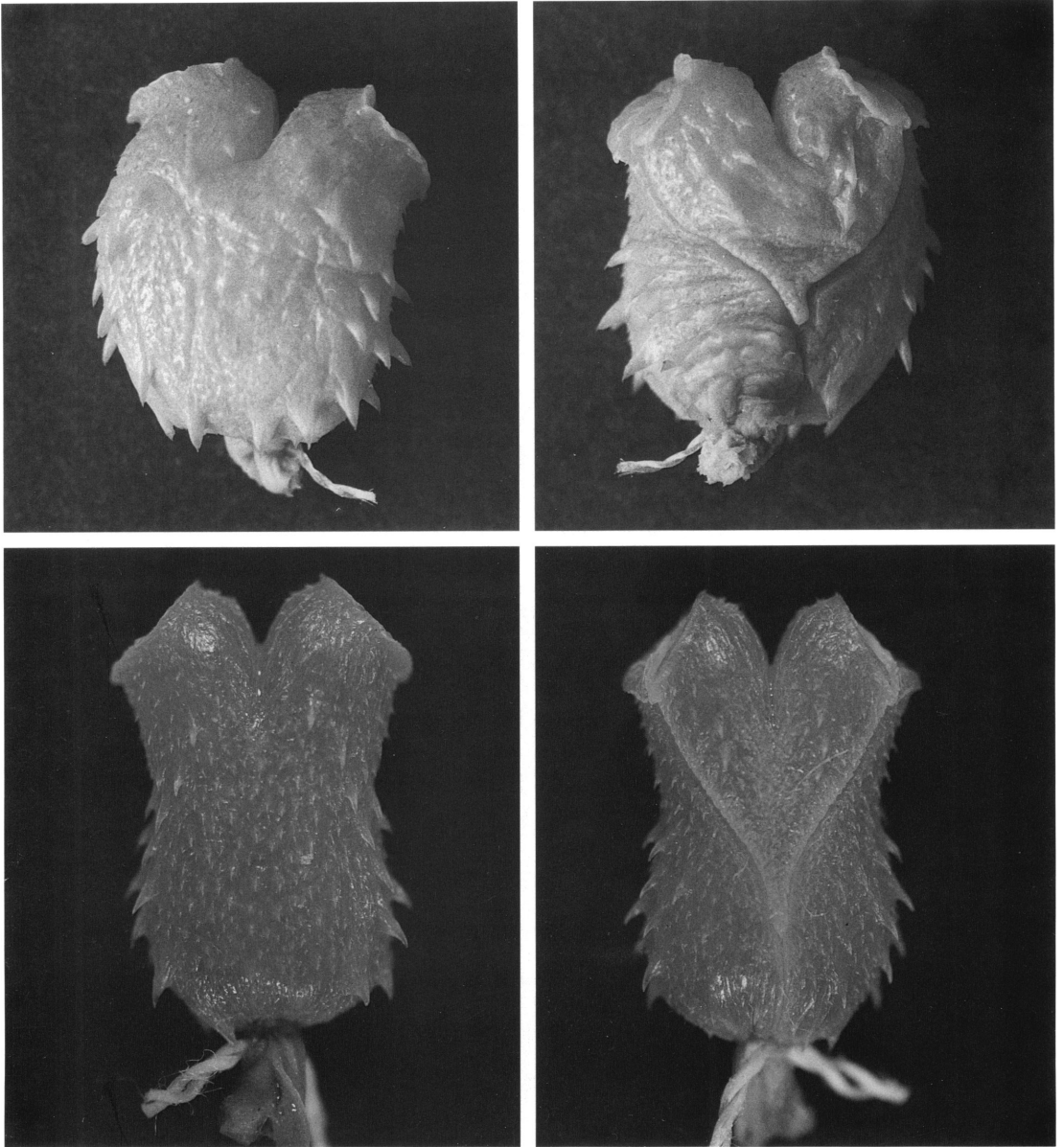


Fig. 56. Hemipenes of *Lystrophis dorbignyi* (upper; uncatalogued specimen) and *Lystrophis histricus* (lower; MNRJ 4615). Asulcate (left) and sulcate (right) views.

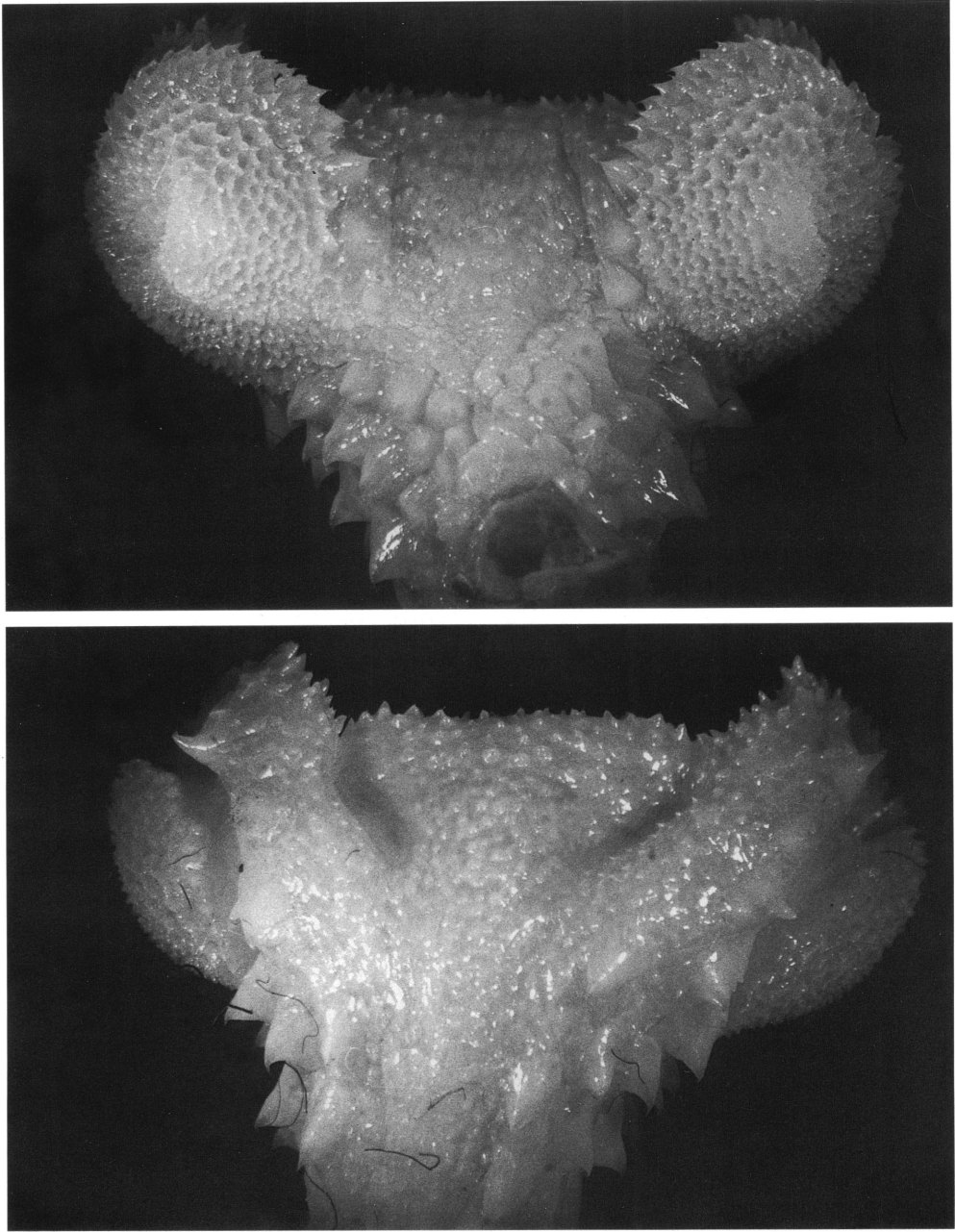


Fig. 57. Hemipenis of *Oxyrhopus clathratus* (MN RJ 3895). Sulcate (upper) and asulcate (lower) views.

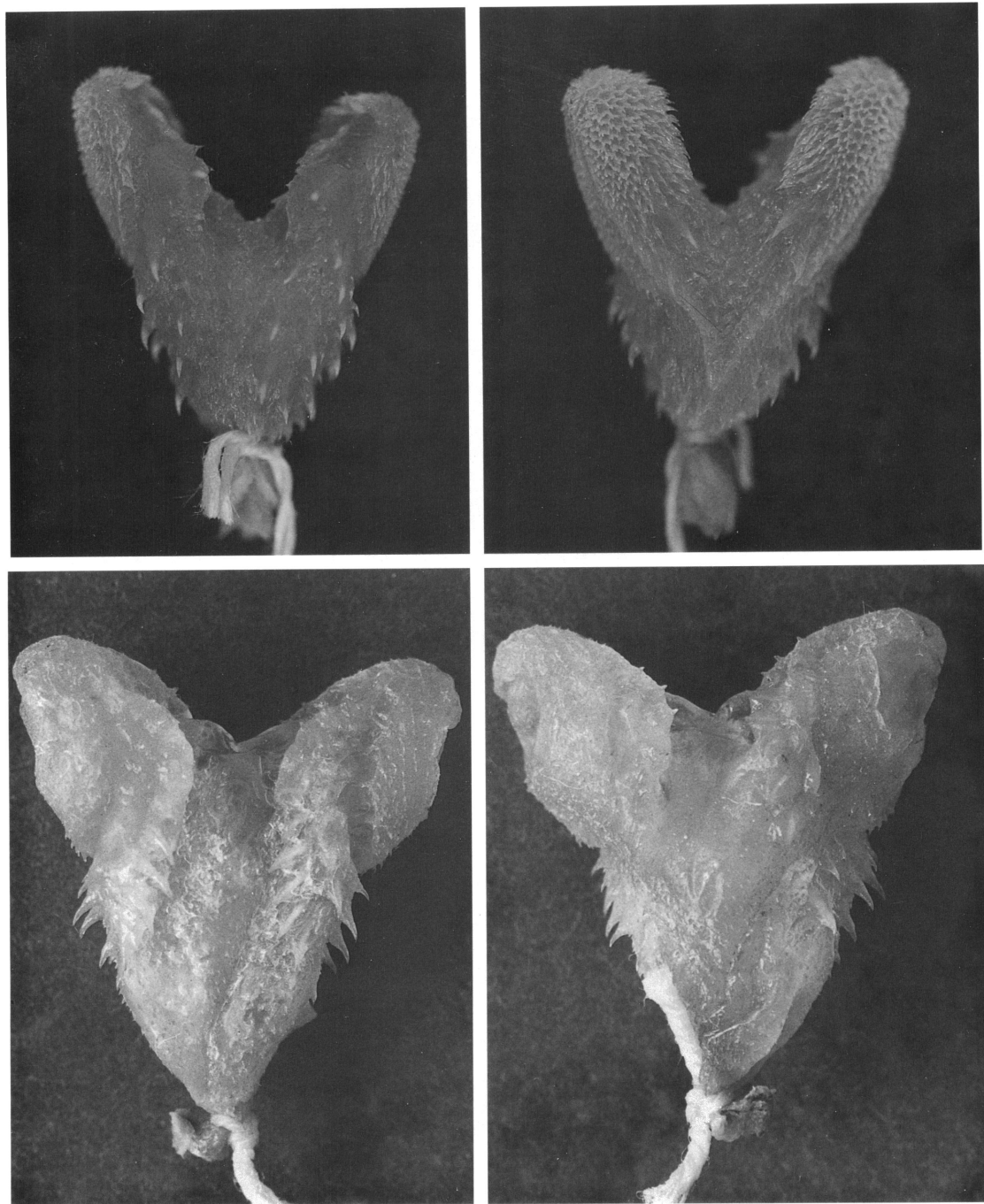


Fig. 58. Hemipenes of *Oxyrhopus leucomelas* (upper; AMNH 44922) and *Oxyrhopus trigeminus* (lower; IB 53968). Asulcate (left) and sulcate (right) views.

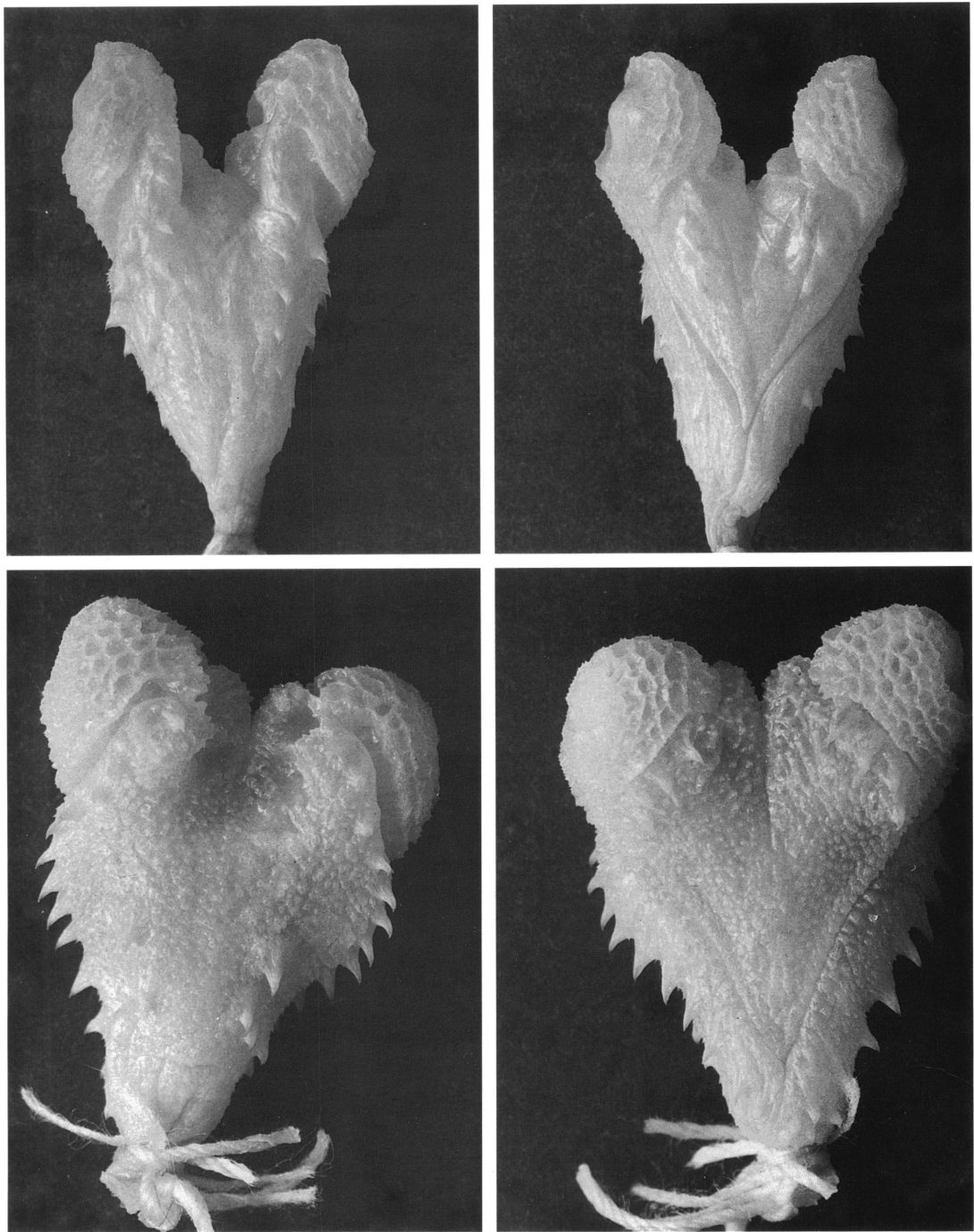


Fig. 59. Hemipenes of *Oxyrhopus rhombifer* (upper; IB 16559) and *Oxyrhopus erdisii* (lower; LSUMZ 26872). Asulcate (left) and sulcate (right) views.

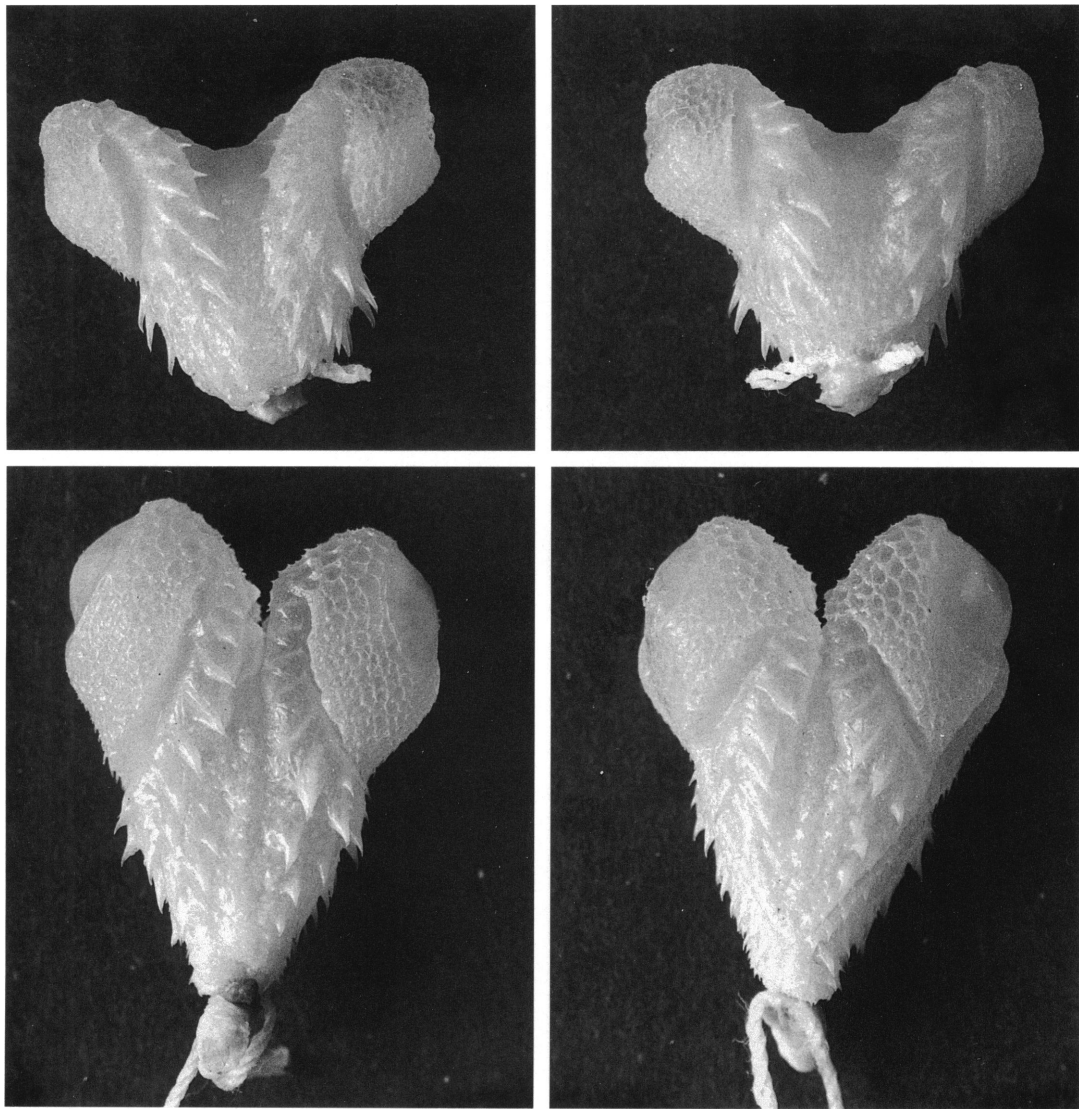


Fig. 60. Hemipenes of *Oxyrhopus melanogenys* (upper; IB 52863) and *Oxyrhopus petola* (lower; MNHN 1989.3787). Asulcate (left) and sulcate (right) views.

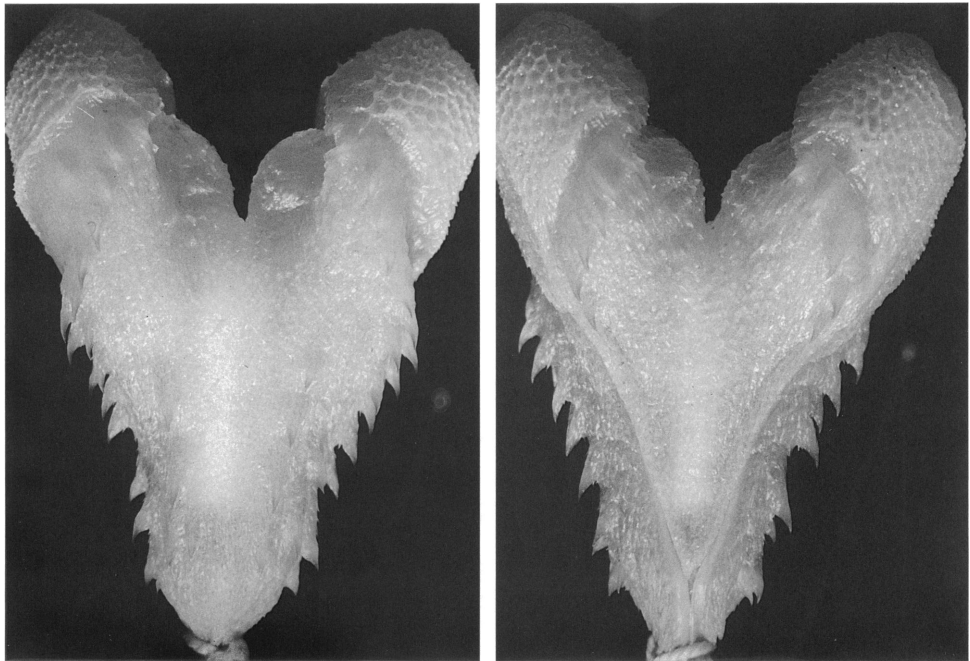


Fig. 61. Hemipenis of *Oxyrhopus formosus* (AMNH 55620). Asulcate (left) and sulcate (right).

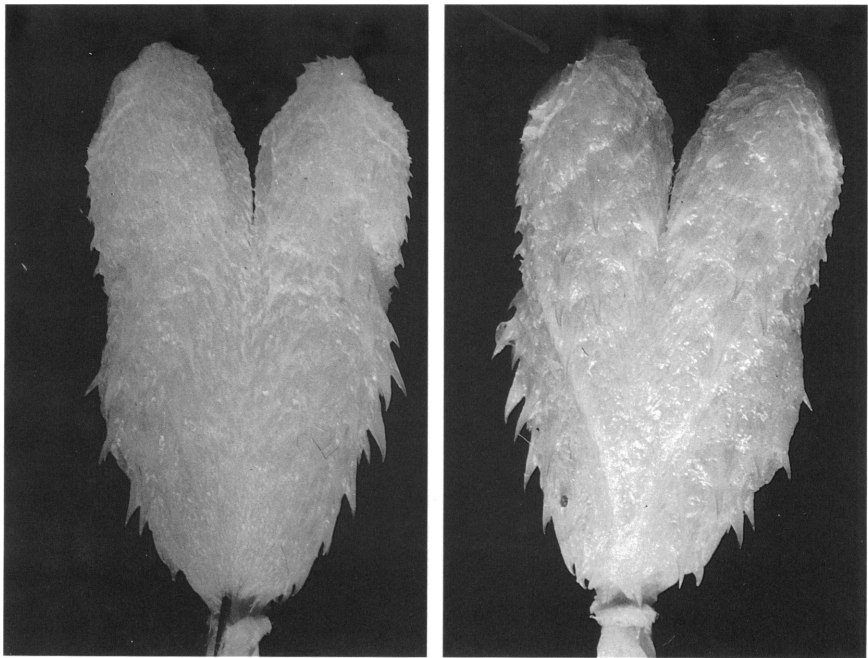


Fig. 62. Hemipenis of *Oxyrhopus fitzingeri* (BMNH 46.1.14.27). Asulcate (left) and sulcate (right).

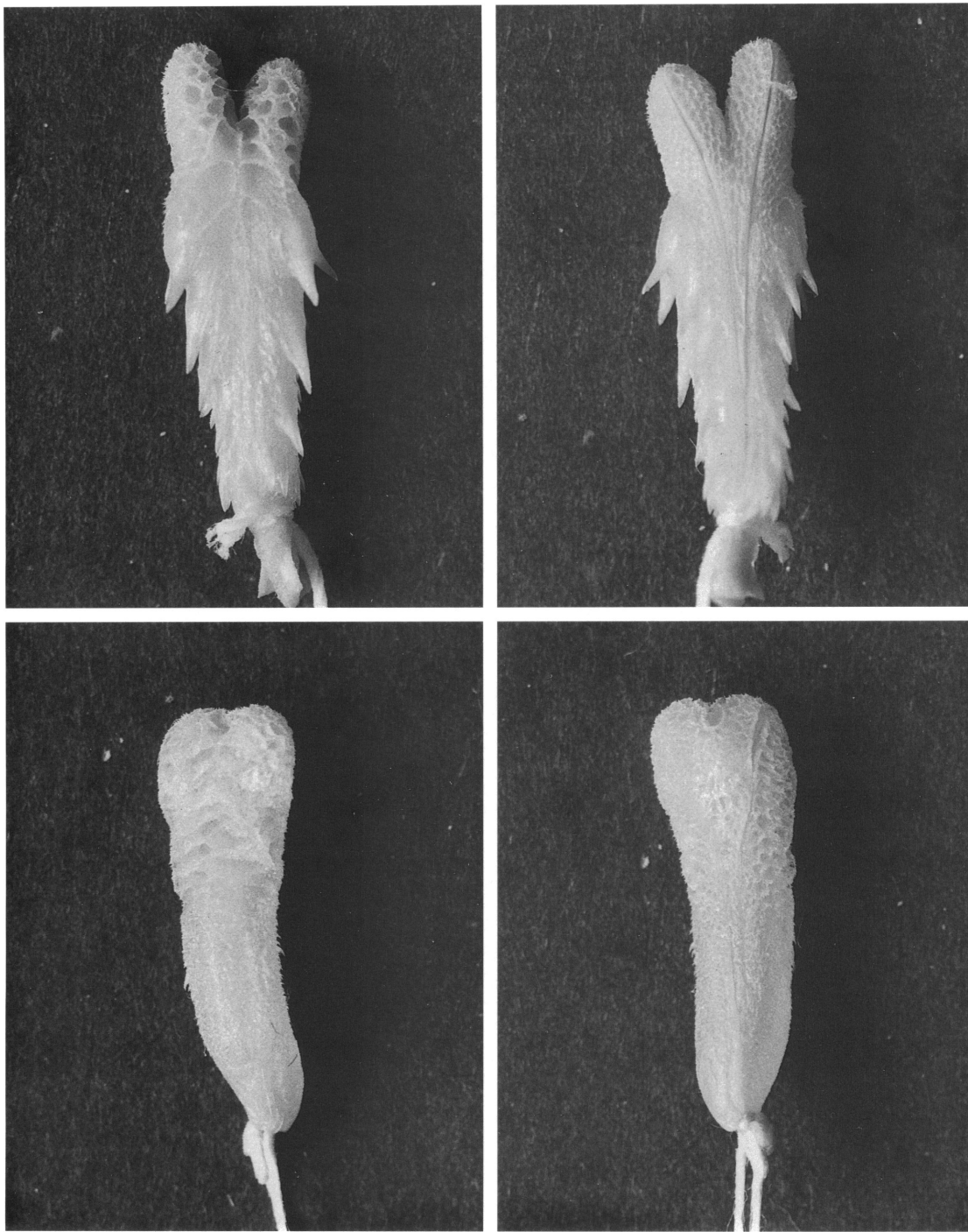


Fig. 63. Hemipenes of *Phalotris nasutus* (upper; IB 28950) and *Phalotris mertensi* (lower; MNHN 1993.1621). Asulcate (left) and sulcate (right) views.

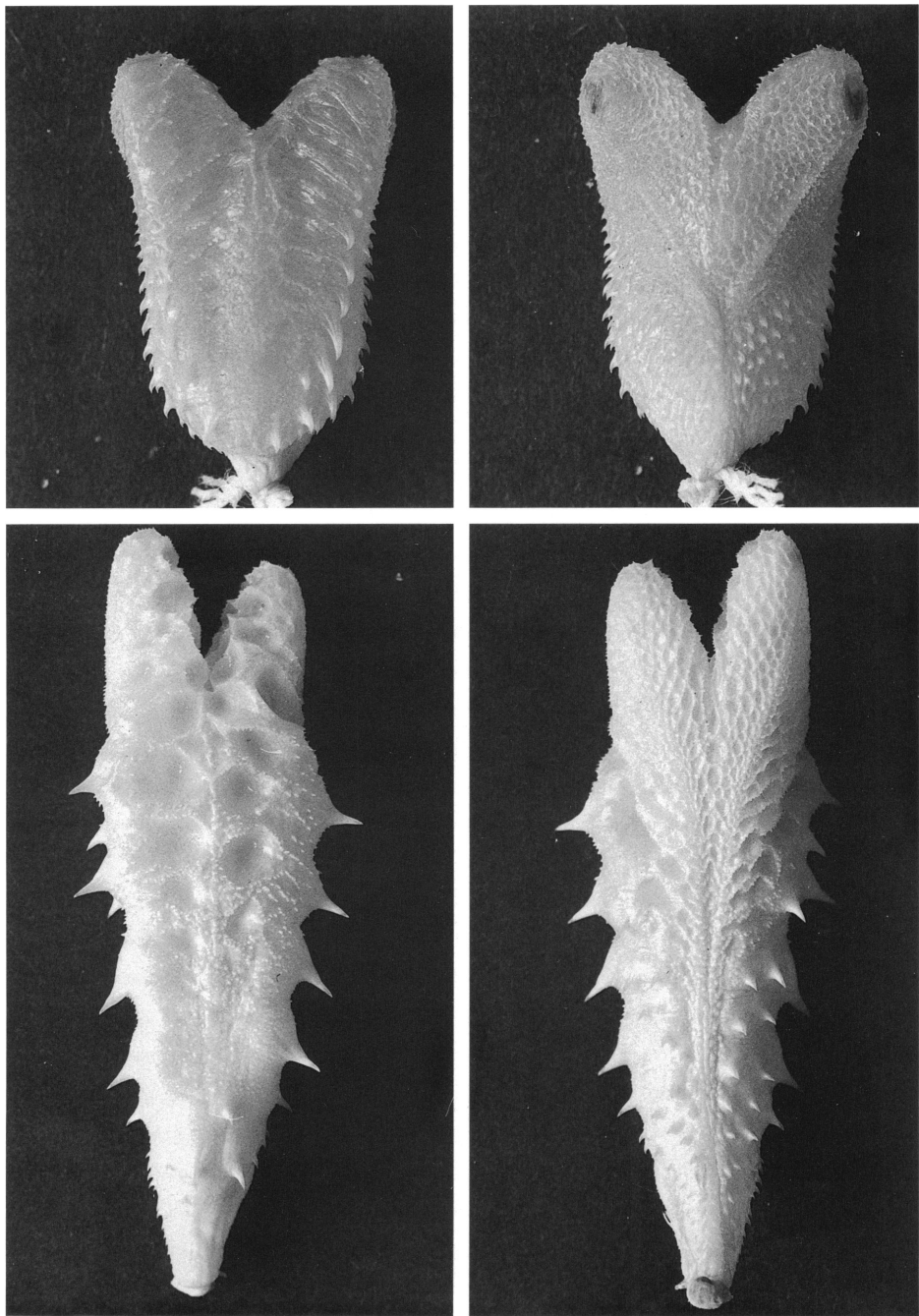


Fig. 64. Hemipenes of *Philodryas olfersii* (upper; CEPLAC 1016) and *Philodryas chamissonis* (lower; MNHN 1991.429). Asulcate (left) and sulcate (right) views.

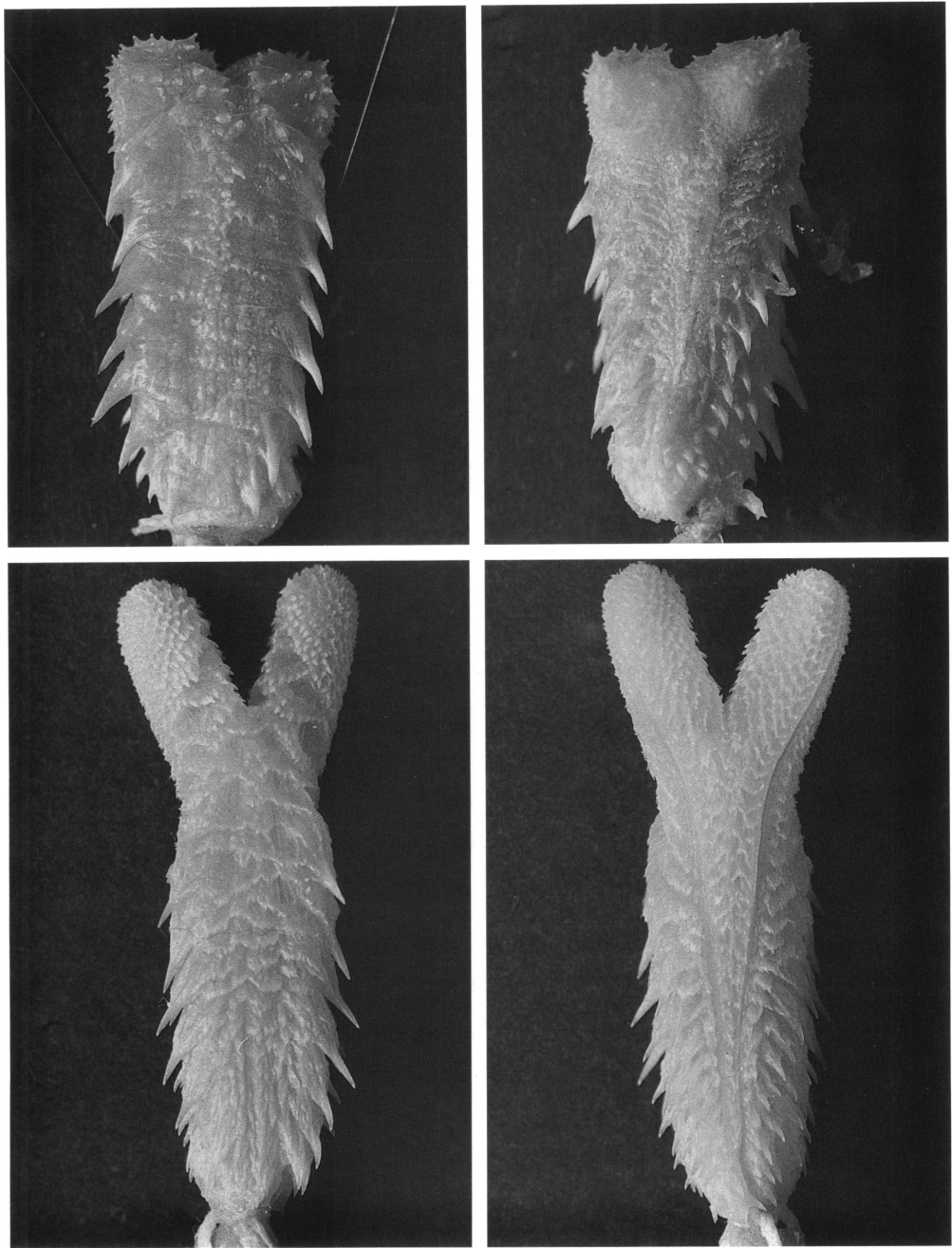


Fig. 65. Hemipenes of *Philodryas aestiva* (upper; IB 54407) and *Philodryas nattereri* (lower; IB 48404). Asulcate (left) and sulcate (right) views.

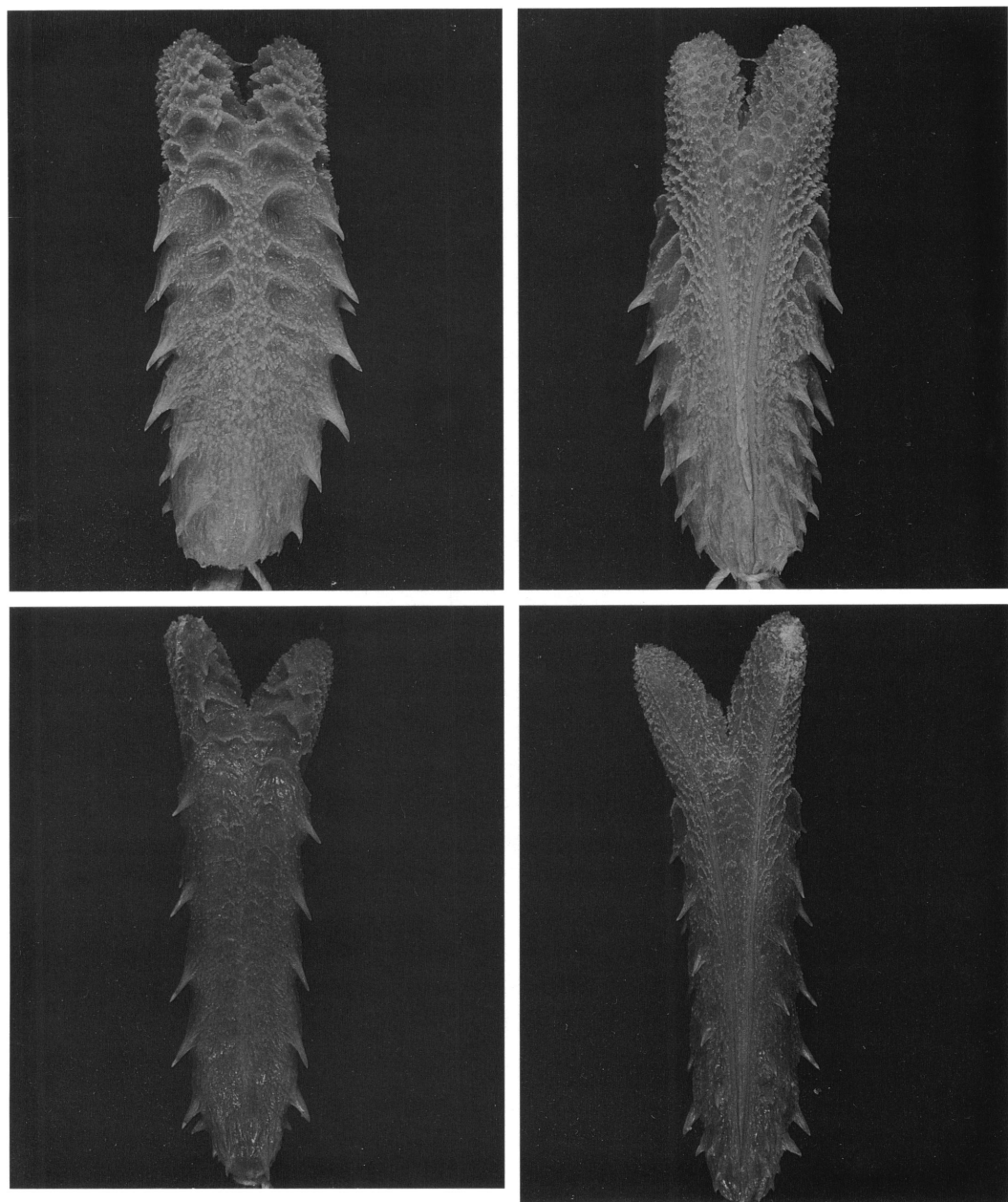


Fig. 66. Hemipenes of *Philodryas burmeisteri* (upper; USNM 52961) and *Philodryas psammophidea* (lower; AMNH 36203). Asulcate (left) and sulcate (right) views.

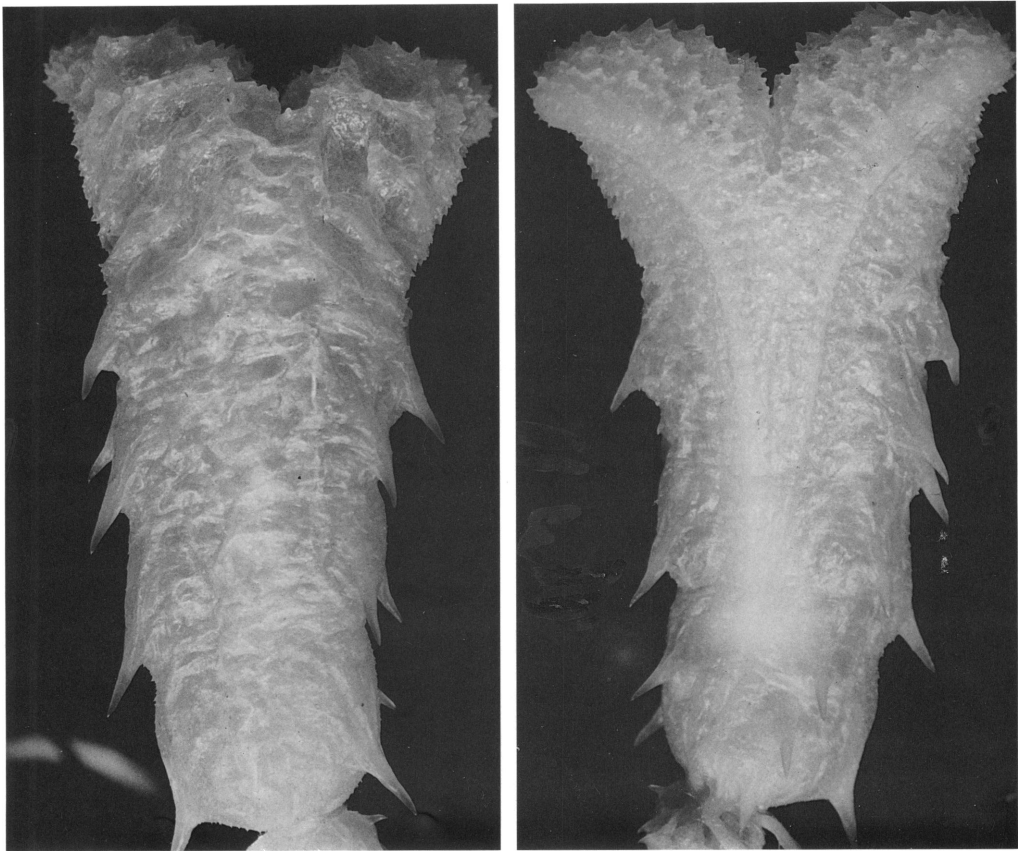


Fig. 67. Hemipenis of *Philodryas livida* (IB 40953). Asulcate (left) and sulcate (right) views.

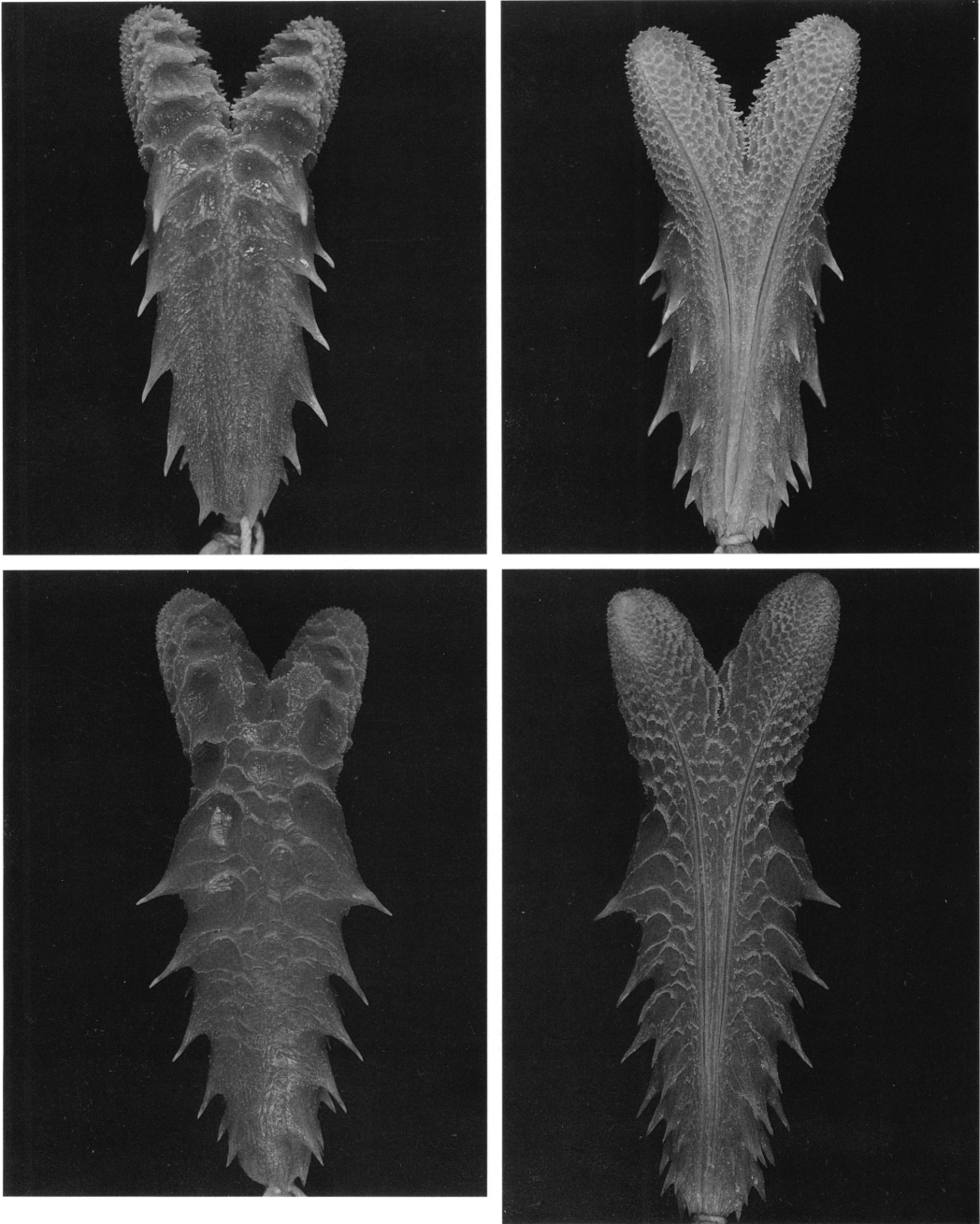


Fig. 68. Hemipenes of *Philodryas patagoniensis* (upper; MNHN 7641) and *Philodryas mattogrossensis* (lower; AMNH 141663). Asulcate (left) and sulcate (right) views.

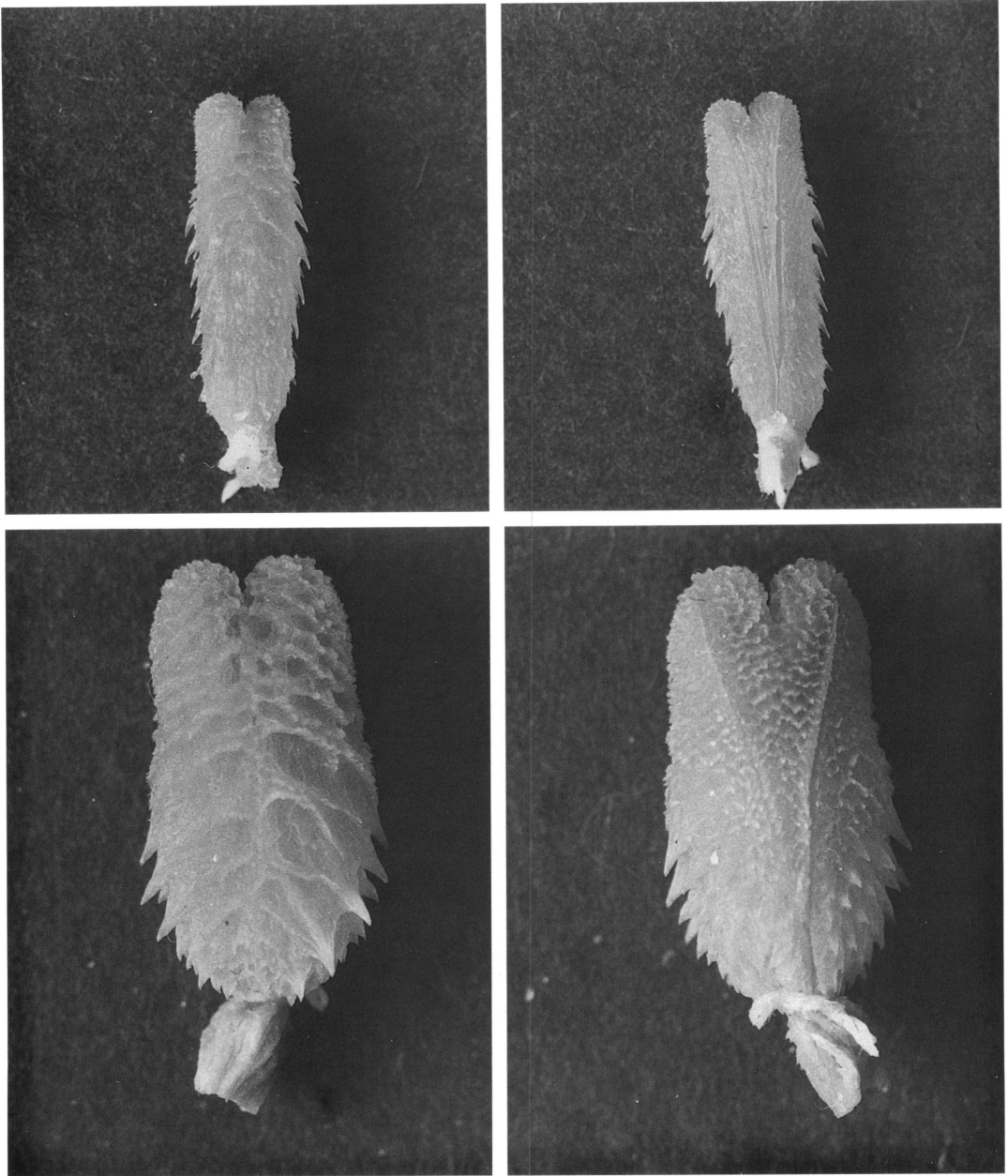


Fig. 69. Hemipenes of *Pseudablabes agassizi* (upper; MNHN 1892.69) and *Philodryas viridissima* (lower; MNHN 3837). Asulcate (left) and sulcate (right) views.

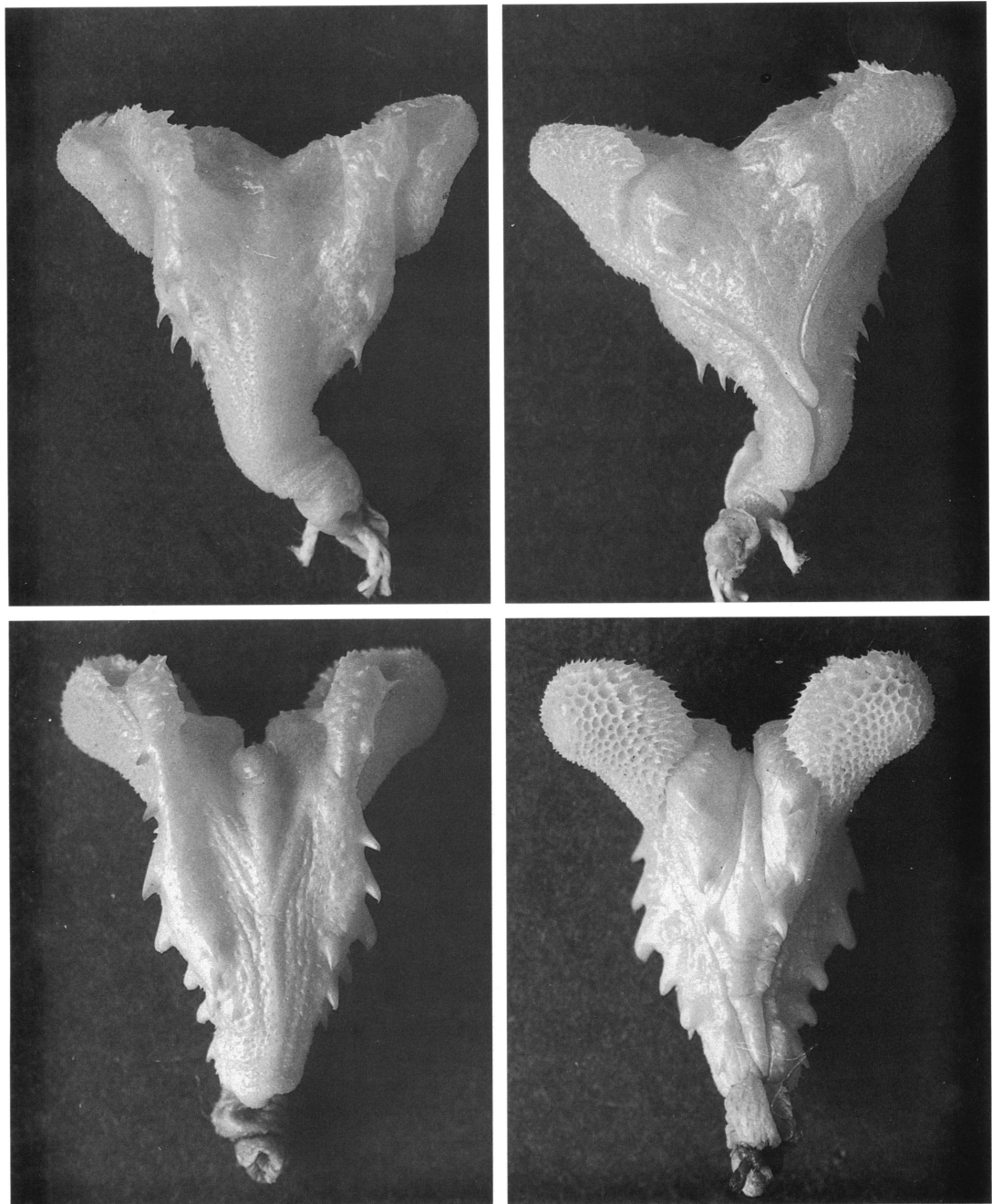


Fig. 70. Hemipenes of *Phimophis guerini* (upper; IB 54241) and *Pseudoboa newwiedii* (lower; MNHN 1989.3187). Asulcate (left) and sulcate (right) views.

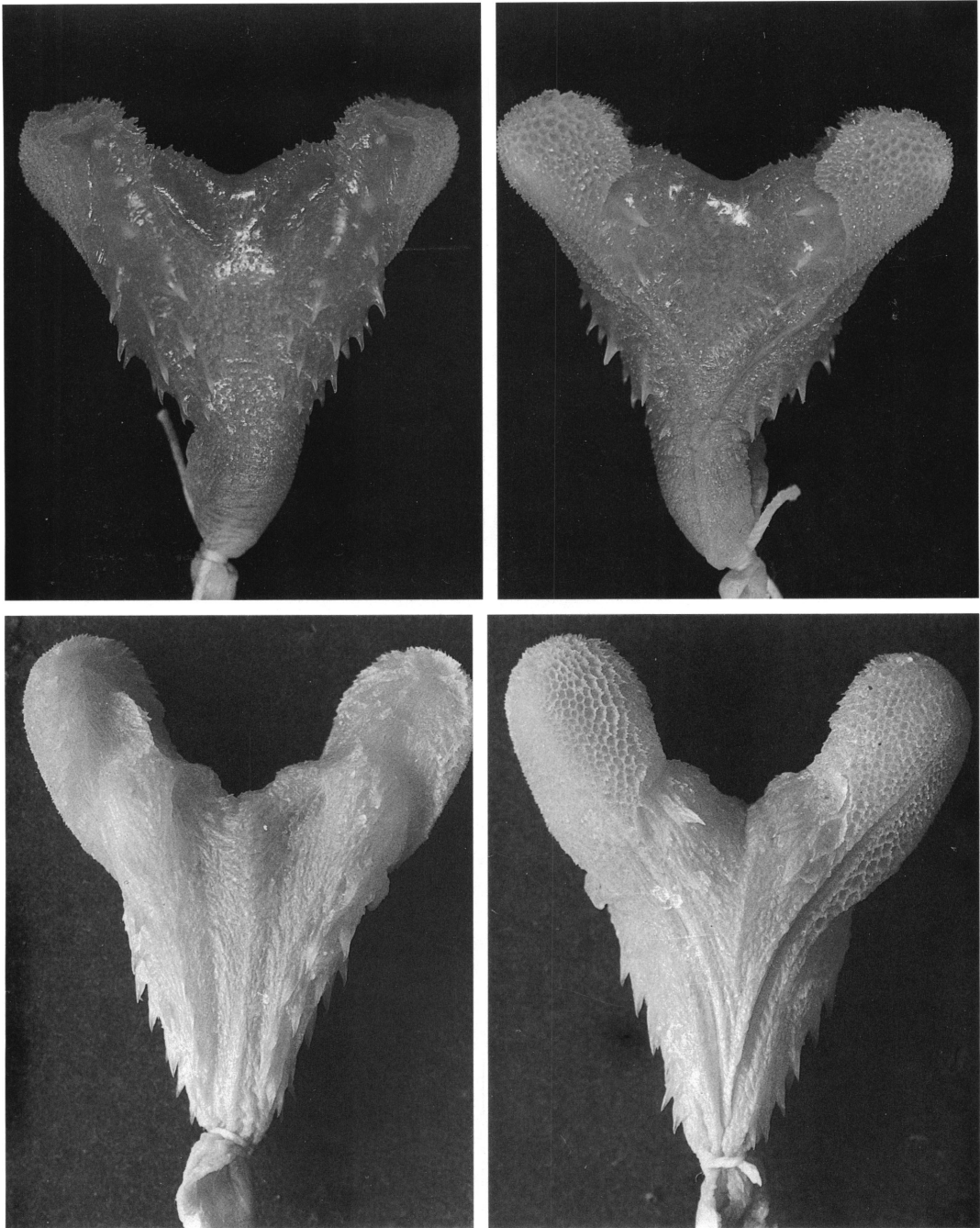


Fig. 71. Hemipenes of *Phimophis vittatus* (upper; USNM 319628) and *Pseudoboa haasi* (lower; IB 18245). Asulcate (left) and sulcate (right) views.

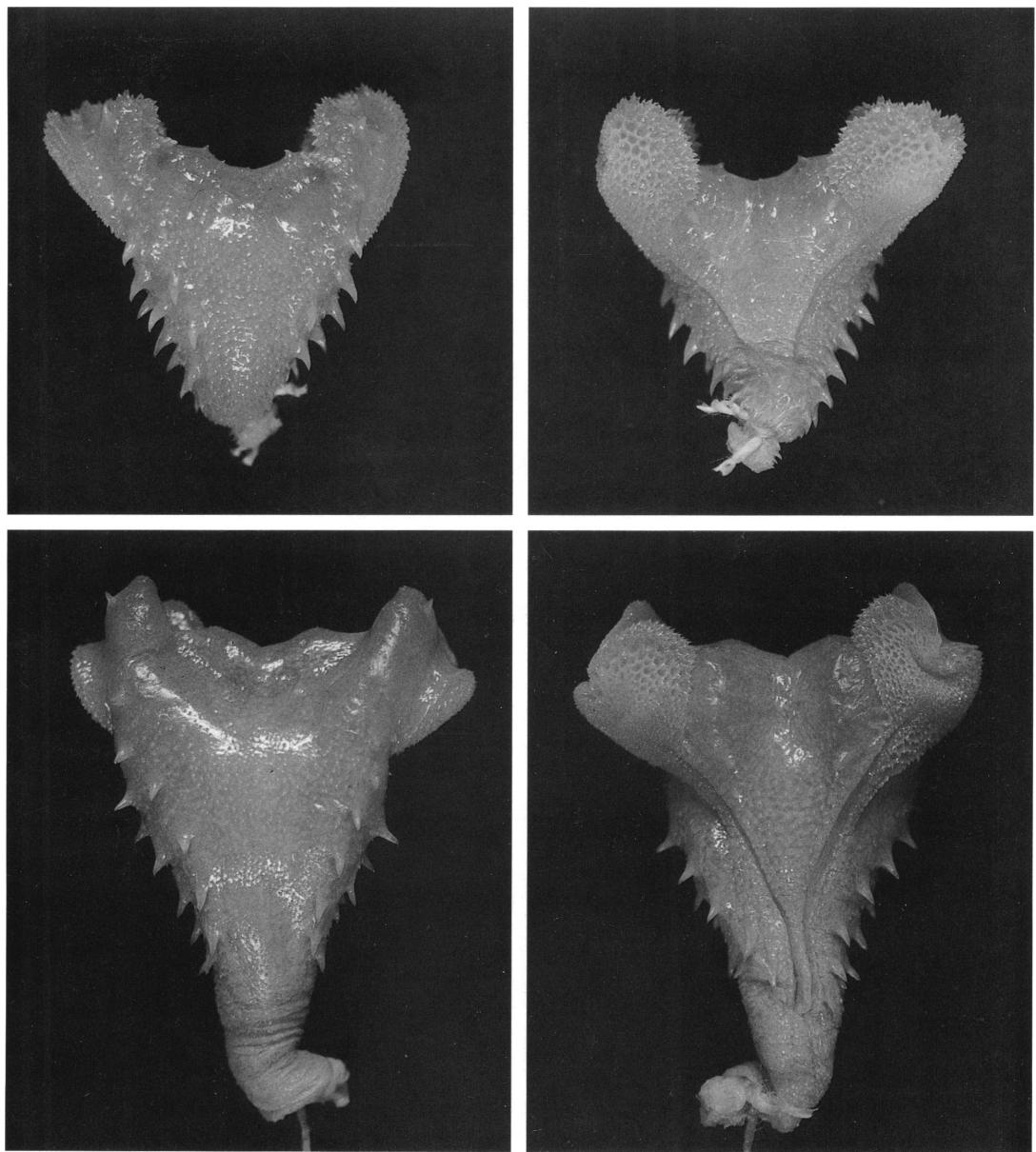


Fig. 72. Hemipenes of *Phimophis guianensis* (upper; AMNH 108791) and *Pseudoboa coronata* (lower; AMNH 134205). Asulcate (left) and sulcate (right) views.

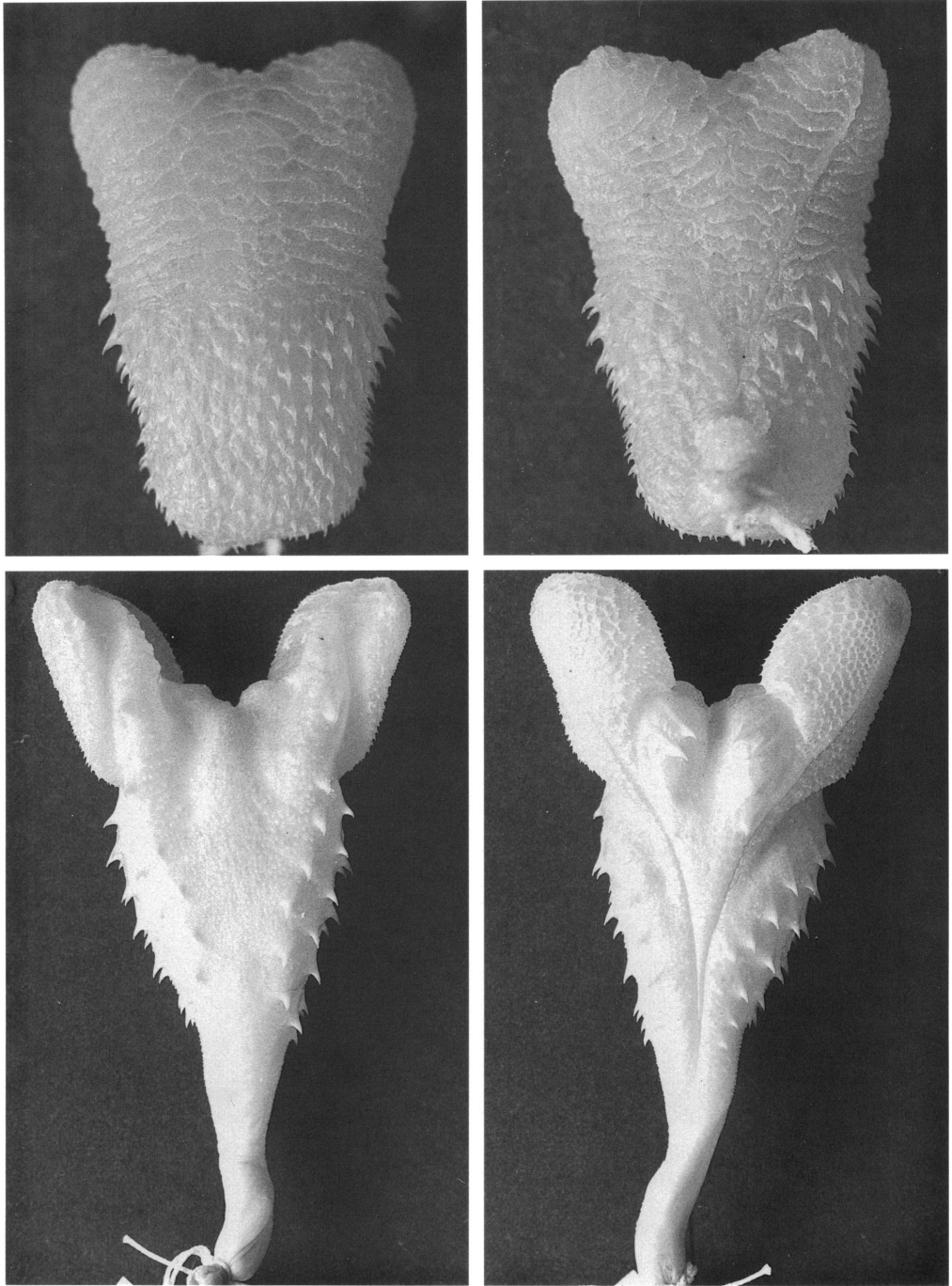


Fig. 73. Hemipenes of *Pseudoeryx plicatilis* (upper; IB 51924) and *Pseudoboa nigra* (lower; MNHN 1993.1619). Asulcate (left) and sulcate (right) views.

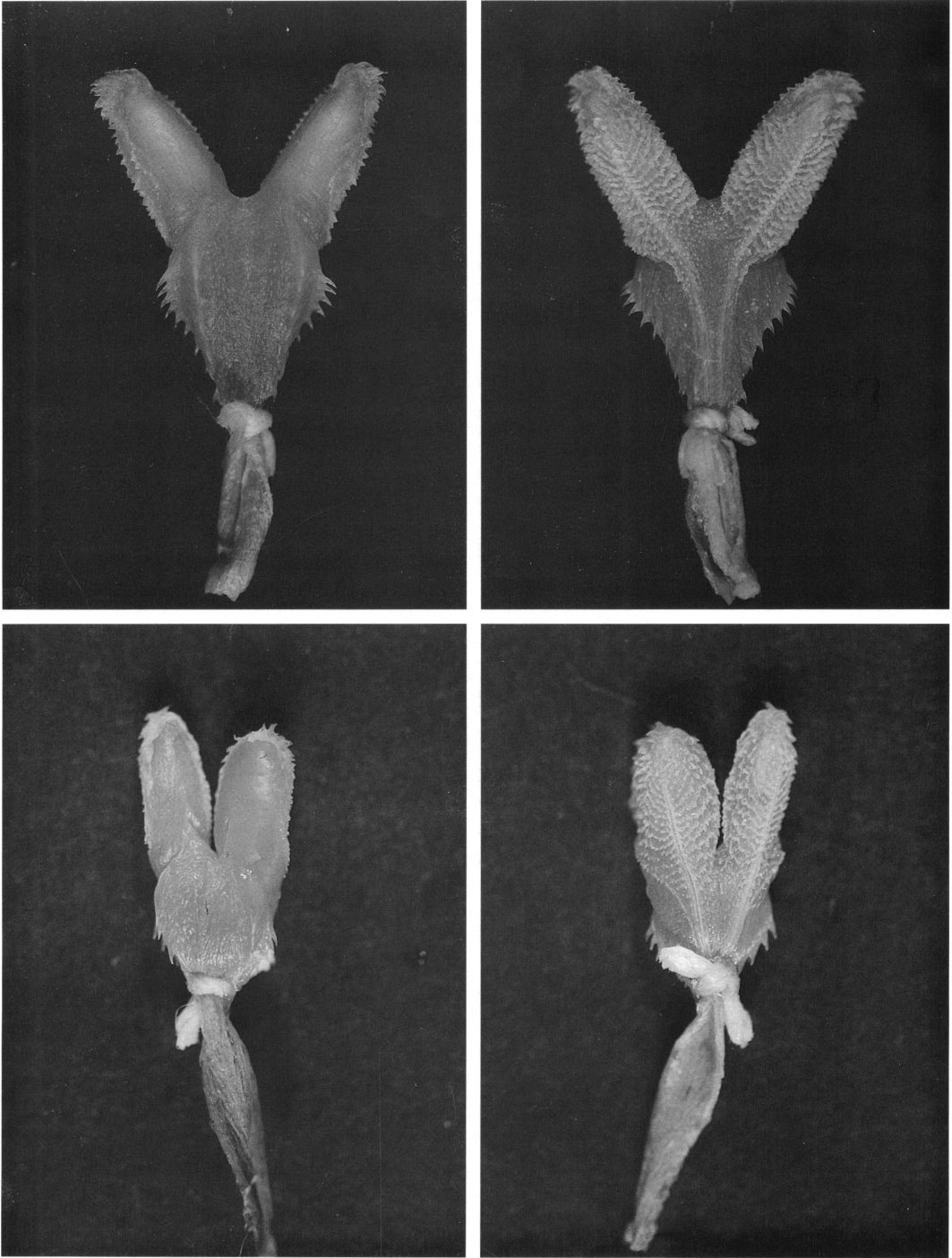


Fig. 74. Hemipenes of *Psomophis joberti* (upper; IB 36437) and *Psomophis genimaculatus* (lower; IB 12590). Asulcate (left) and sulcate (right) views.

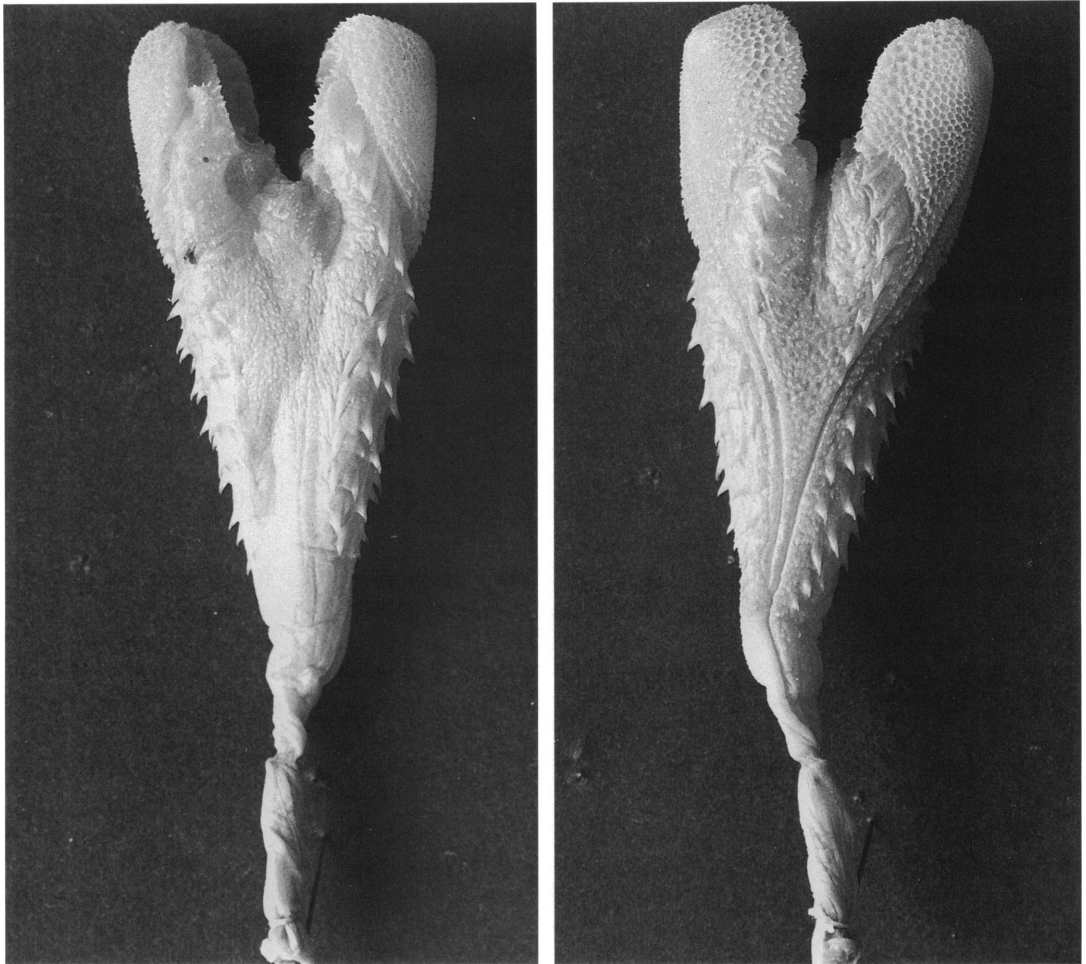


Fig. 75. Hemipenis of *Rhachidelus brazili* (IB 53558). Asulcate (left) and sulcate (right) views.

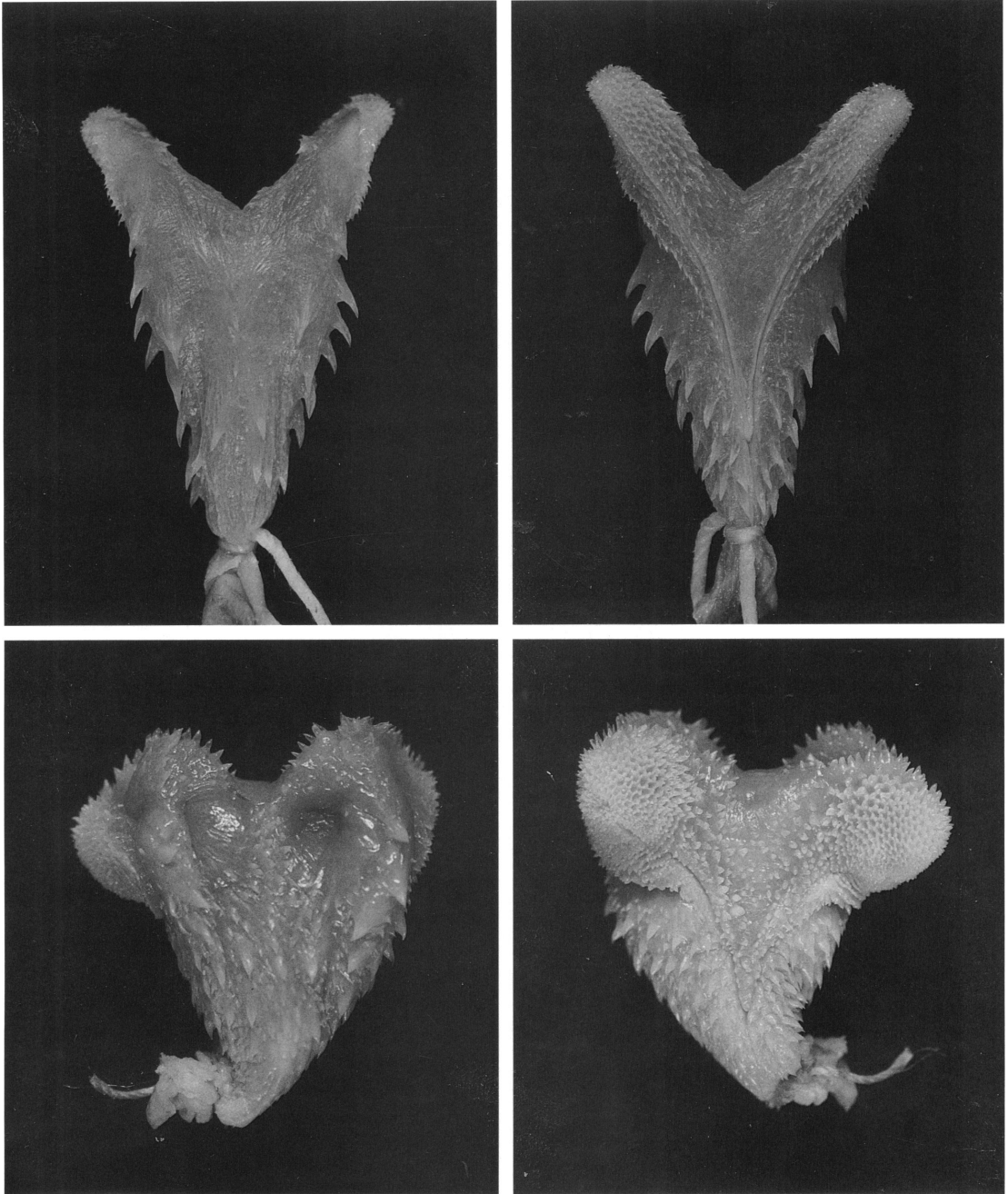


Fig. 76. Hemipenes of *Saphenophis boursieri* (upper; AMNH 109500) and *Saphenophis tristriatus* (lower; AMNH 129609). Asulcate (left) and sulcate (right) views.

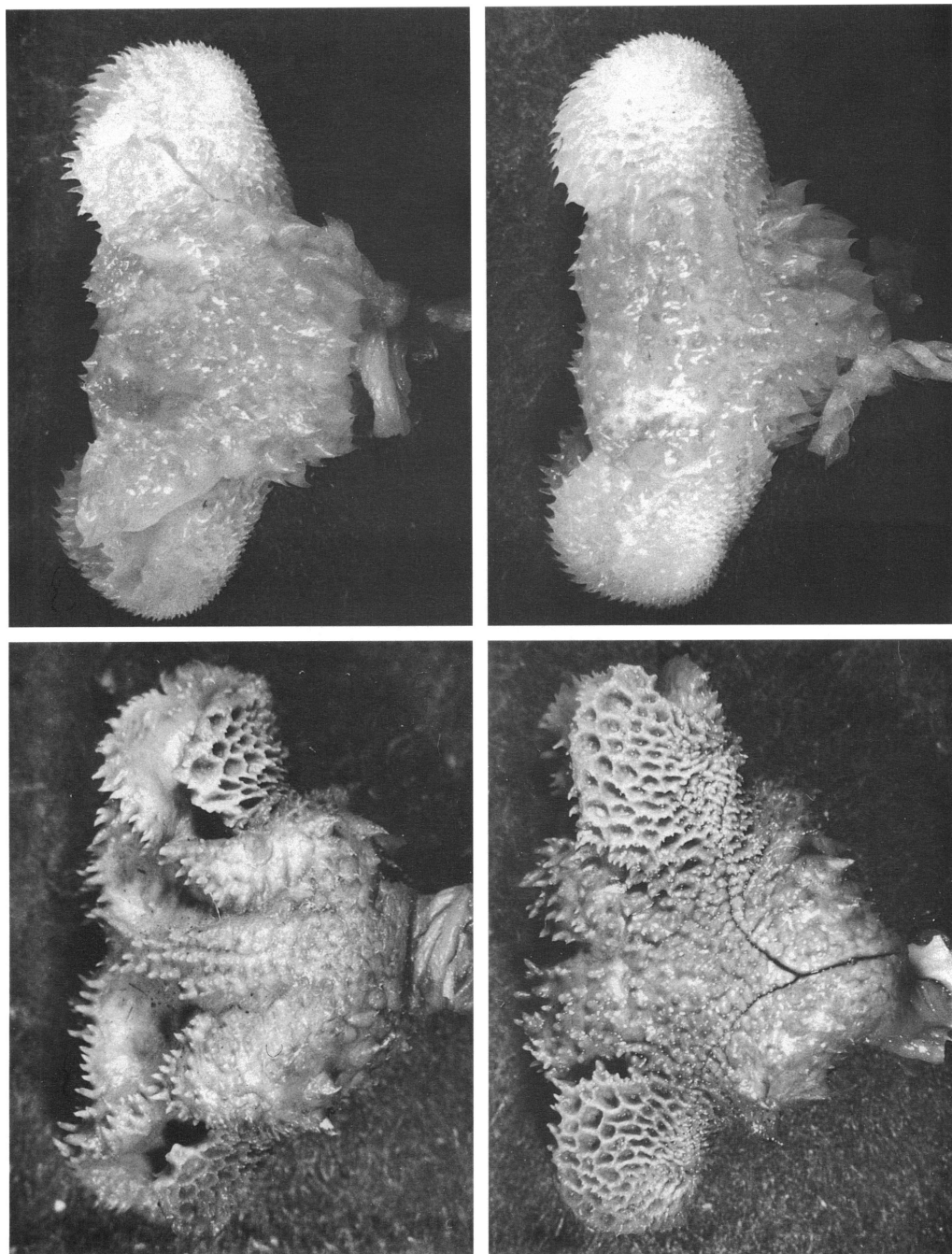


Fig. 77. Hemipenes of *Siphlophis cervinus* (upper; MNHN 1978.2513) and *Siphlophis pulcher* (lower; IB 22398). Asulcate (left) and sulcate (right) views.

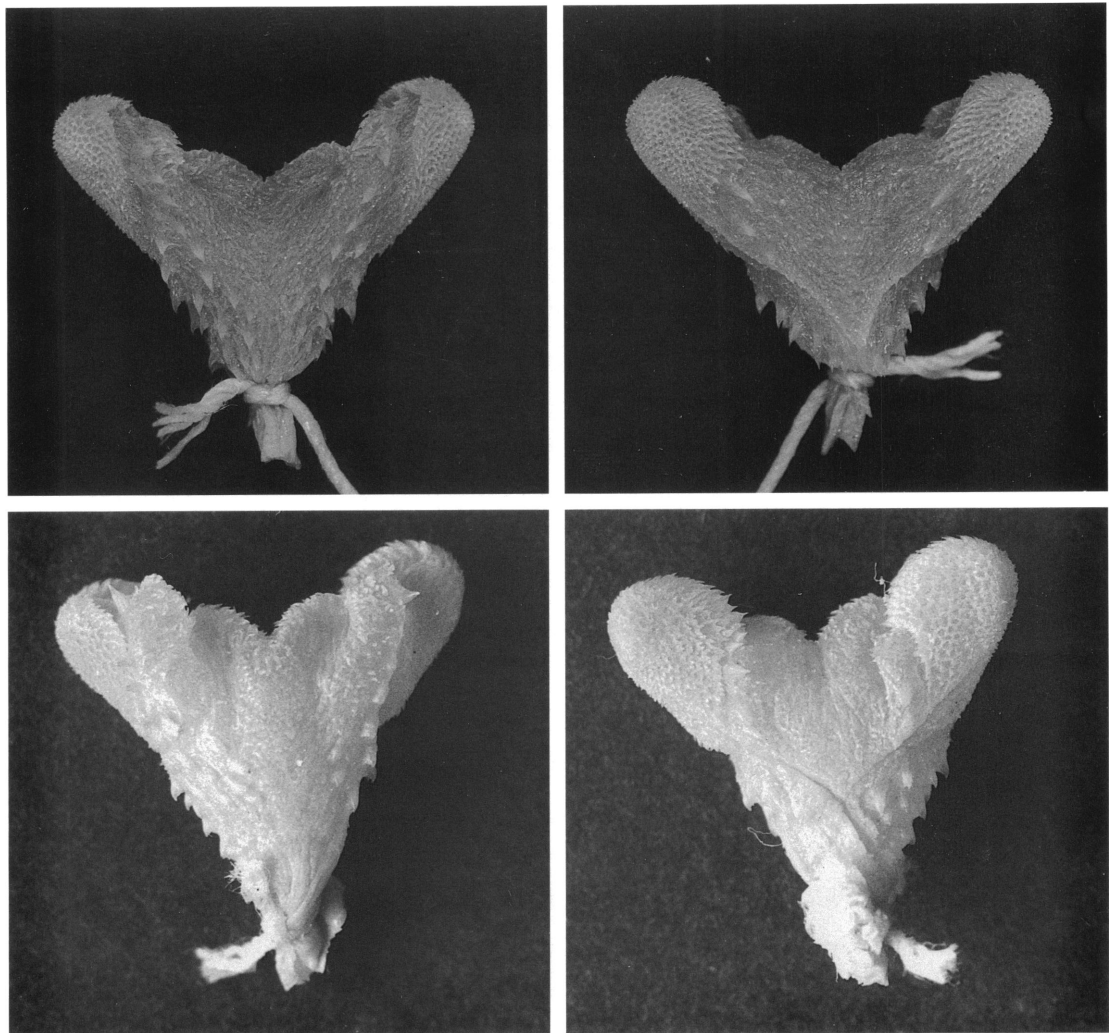


Fig. 78. Hemipenes of *Siphlophis worontzowi* (upper; uncatalogued specimen) and *Siphlophis leucocephalus* (lower; CEPLAC 993). Asulcate (left) and sulcate (right) views.

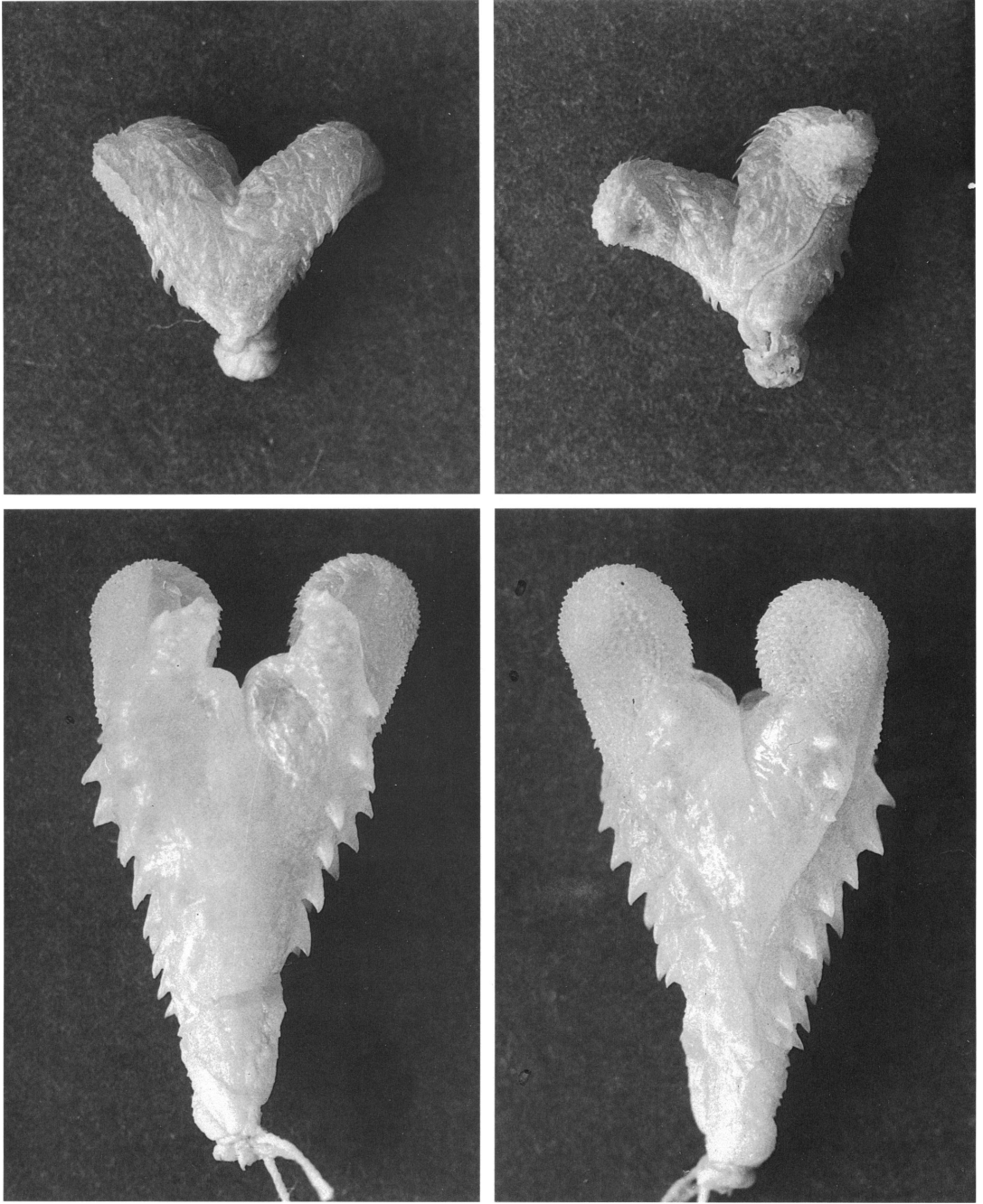


Fig. 79. Hemipenes of *Tropidodryas striaticeps* (upper; MNHN 1993.1622) and *Tripanurgos compressus* (lower; LSUMZ 27352). Asulcate (left) and sulcate (right) views.

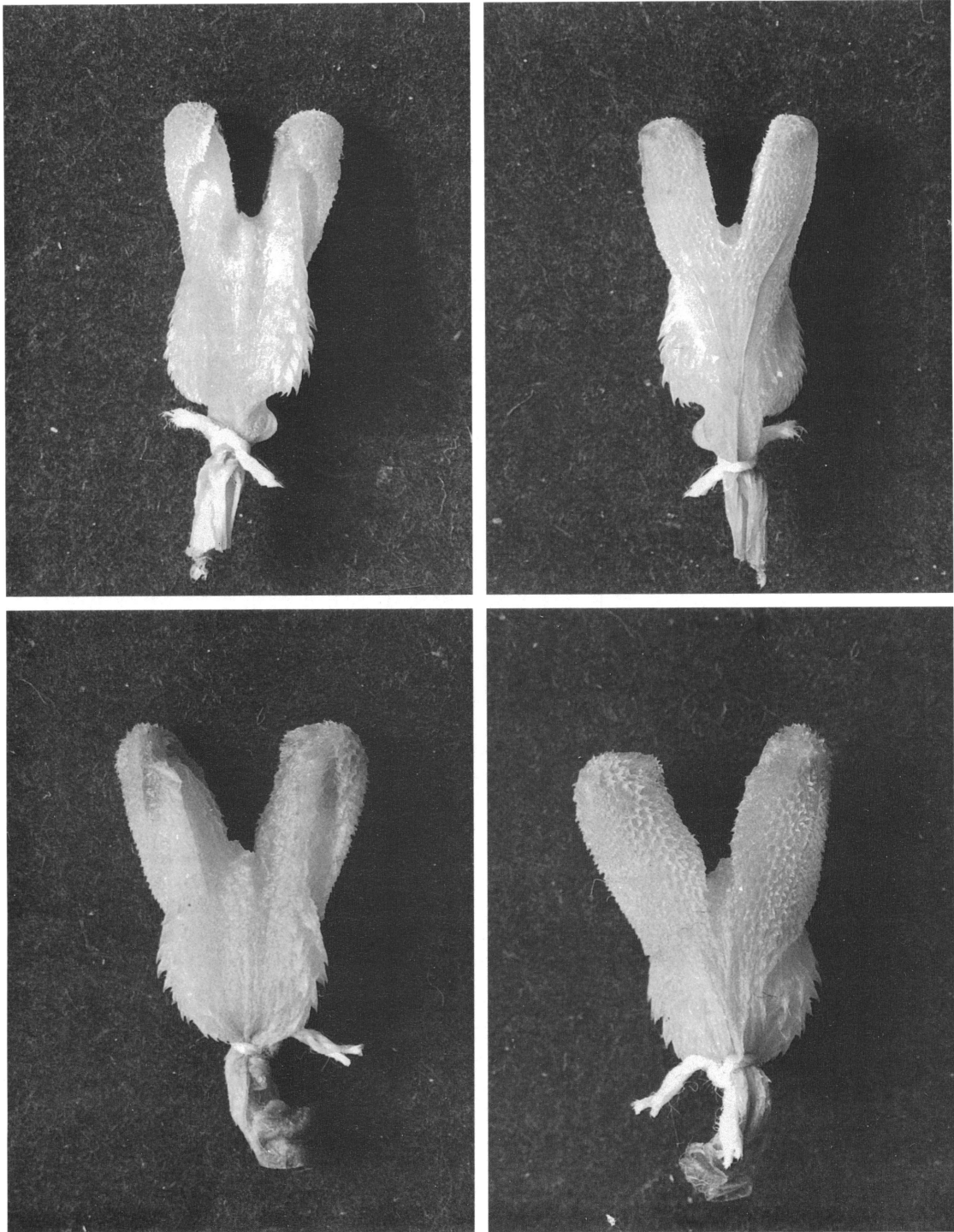


Fig. 80. Hemipenes of *Uromacer catesbyi* (upper; MNHN 8671) and *Uromacer oxyrhynchus* (lower; MNHN 8672). Asulcate (left) and sulcate (right) views.

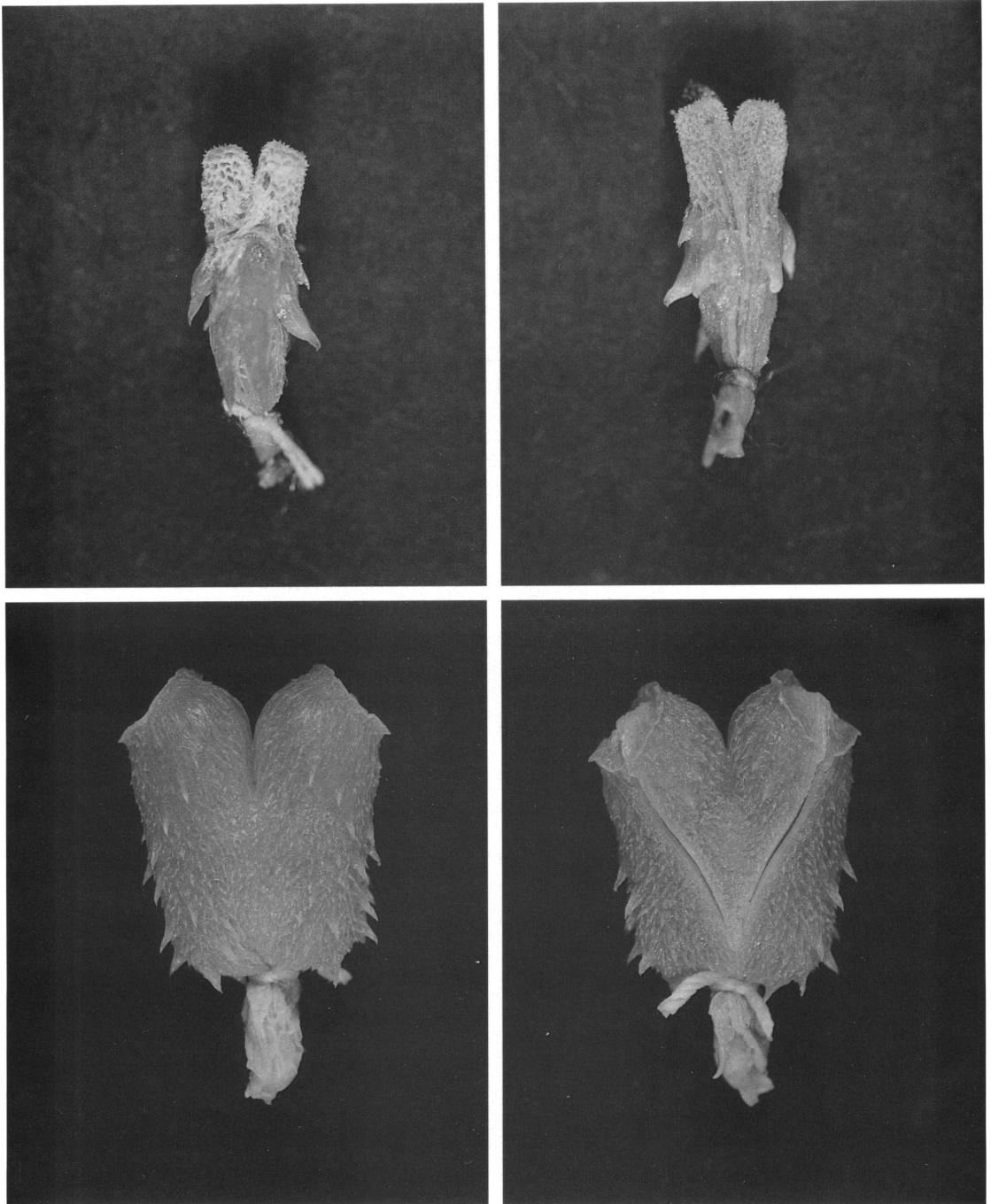


Fig. 81. Hemipenes of *Uromacerina ricardinii* (upper; AMNH 71309) and *Xenodon neuwiedii* (lower; MNRJ 2880). Asulcate (left) and sulcate (right) views.

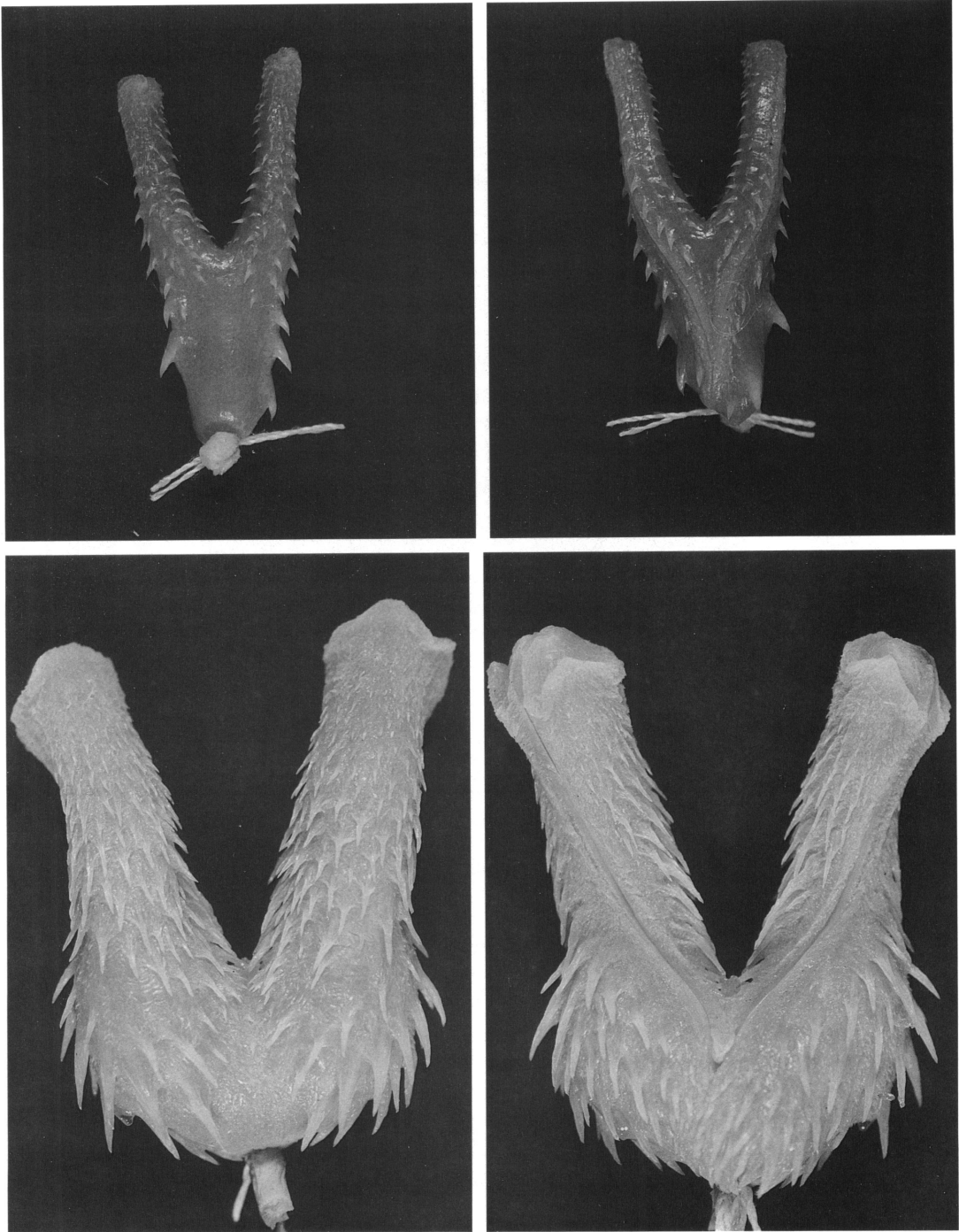


Fig. 82. Hemipenes of *Xenodon rabdocephalus* (upper; AMNH 140265) and *Waglerophis merremi* (lower; MNRJ 3236). Asulcate (left) and sulcate (right) views.

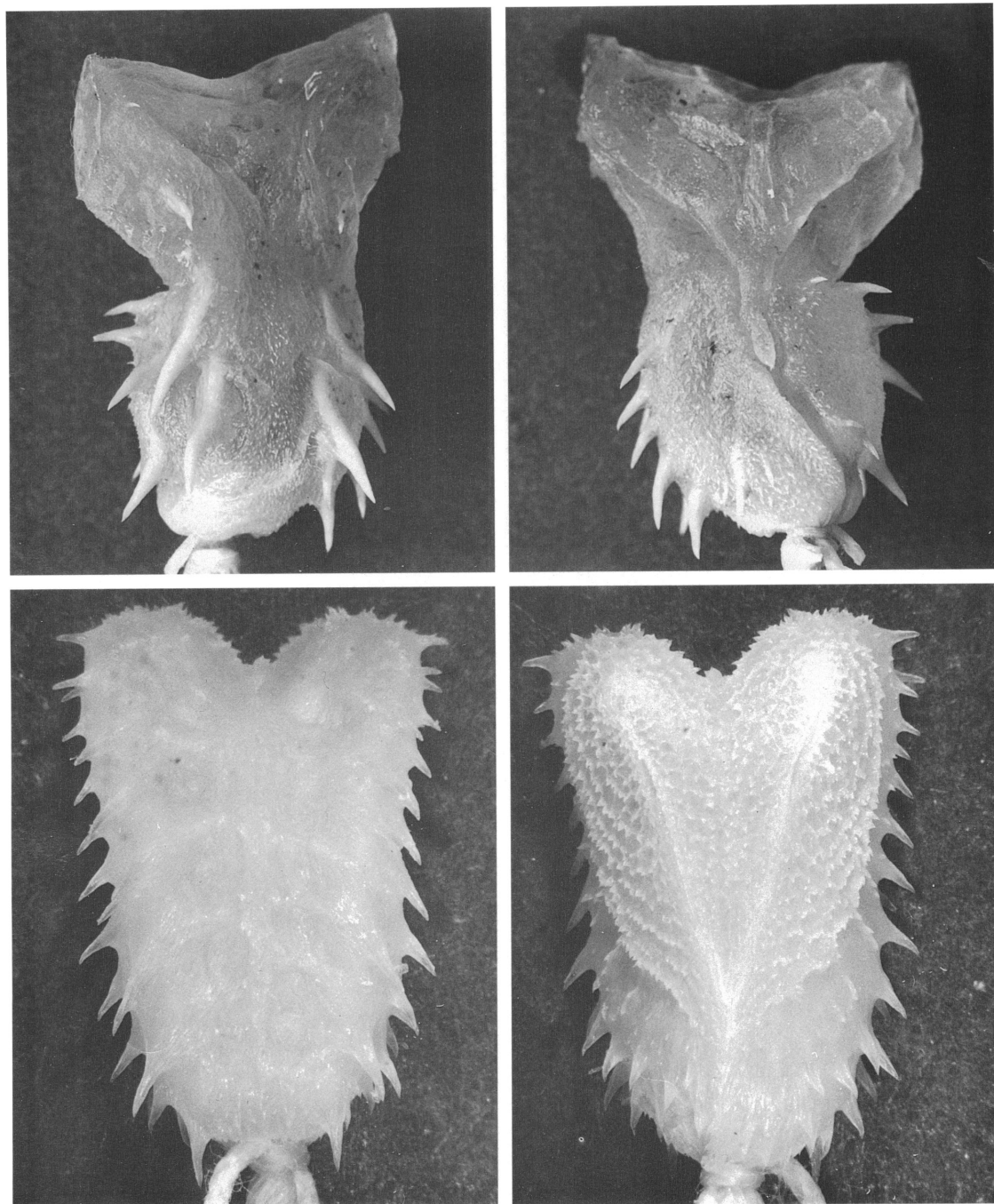


Fig. 83. Hemipenes of *Xenodon severus* (upper; IB 51997) and *Xenoxylis argenteus* (lower; MNHN 1978.2678). Asulcate (left) and sulcate (right) views.

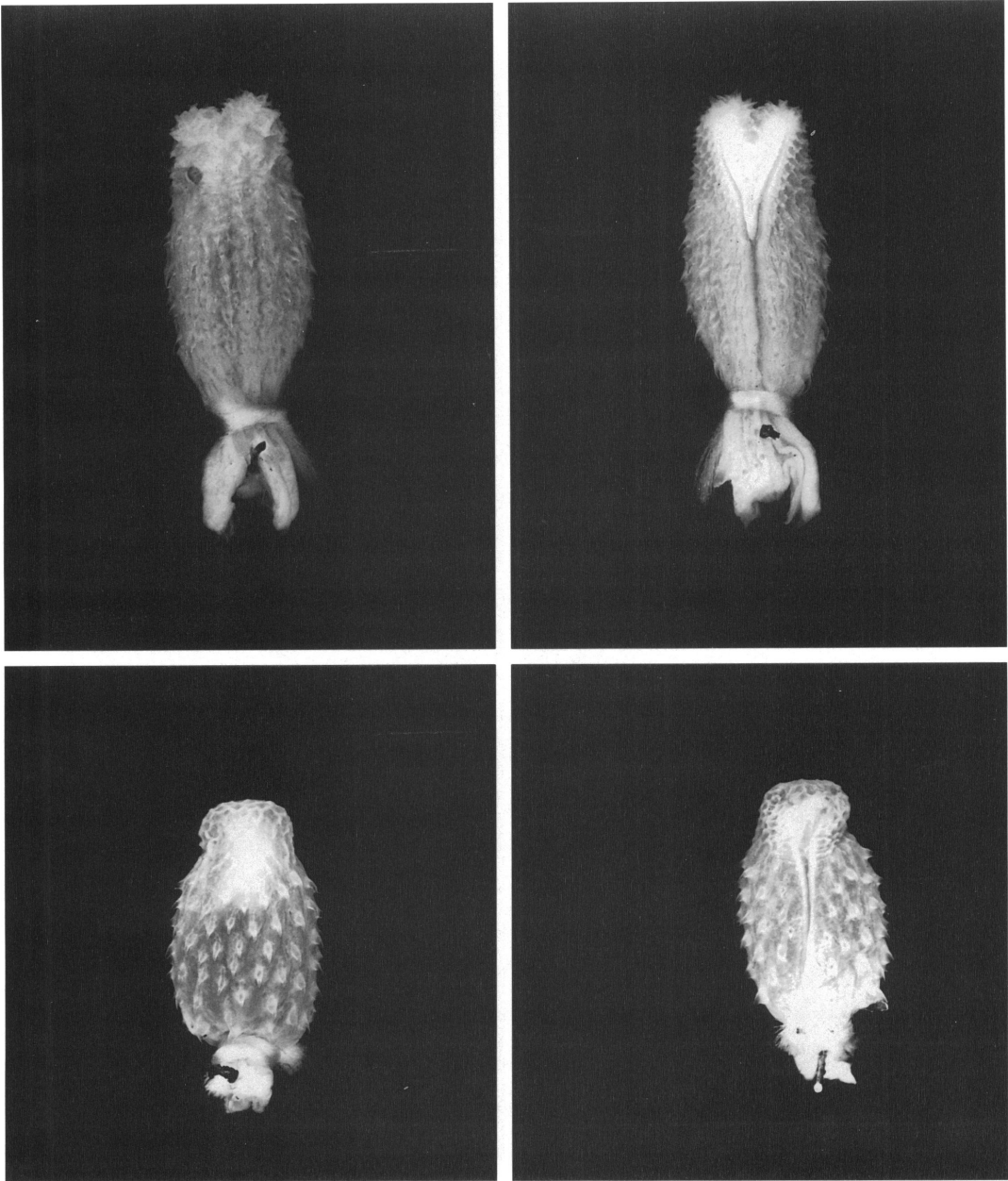


Fig. 84. Hemipenes of *Carphophis amoenus* (upper; MNHN 93) and *Contia tenuis* (lower; UMMZ 133370). Asulcate (left) and sulcate (right) views.

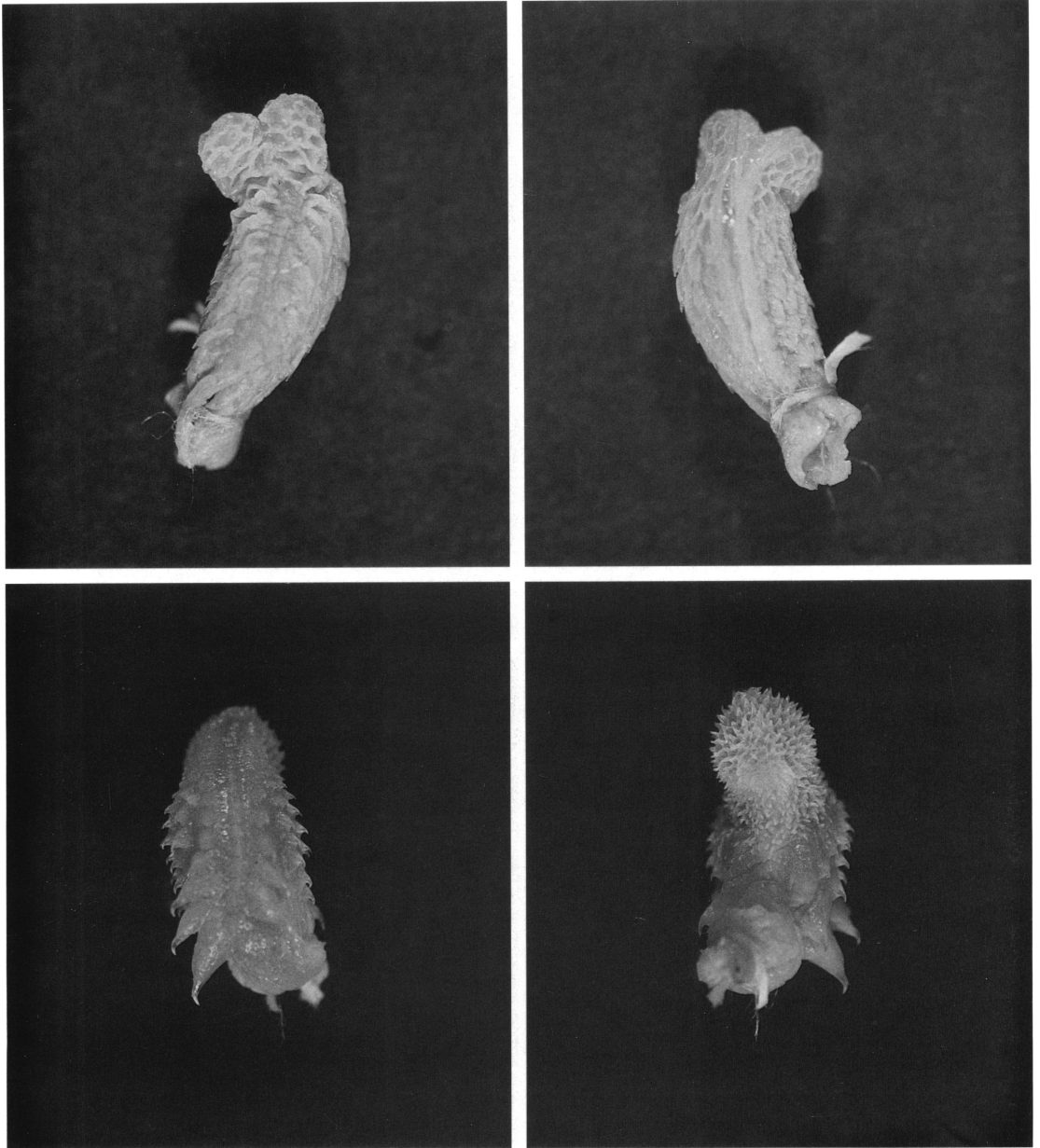


Fig. 85. Hemipenes of *Diadophis dugesi* (upper; MNHN 1975.171) and *Echinanthera undulata* (lower; IB 54234). Asulcate (left) and sulcate (right) views.

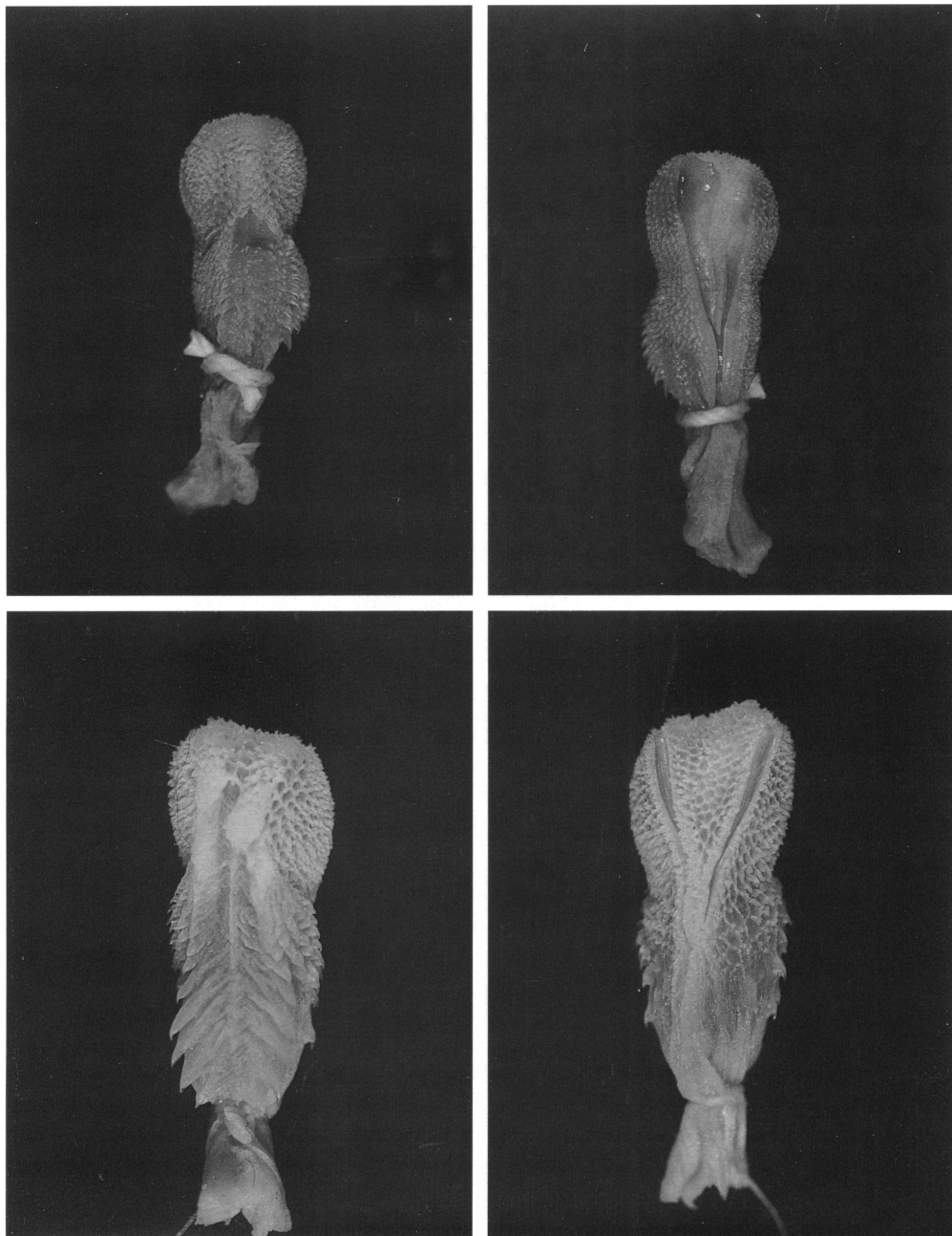


Fig. 86. Hemipenes of *Echinanthera melanostigma* (upper; IB 855) and *Echinanthera amoena* (lower; IB 26406). Asulcate (left) and sulcate (right) views.

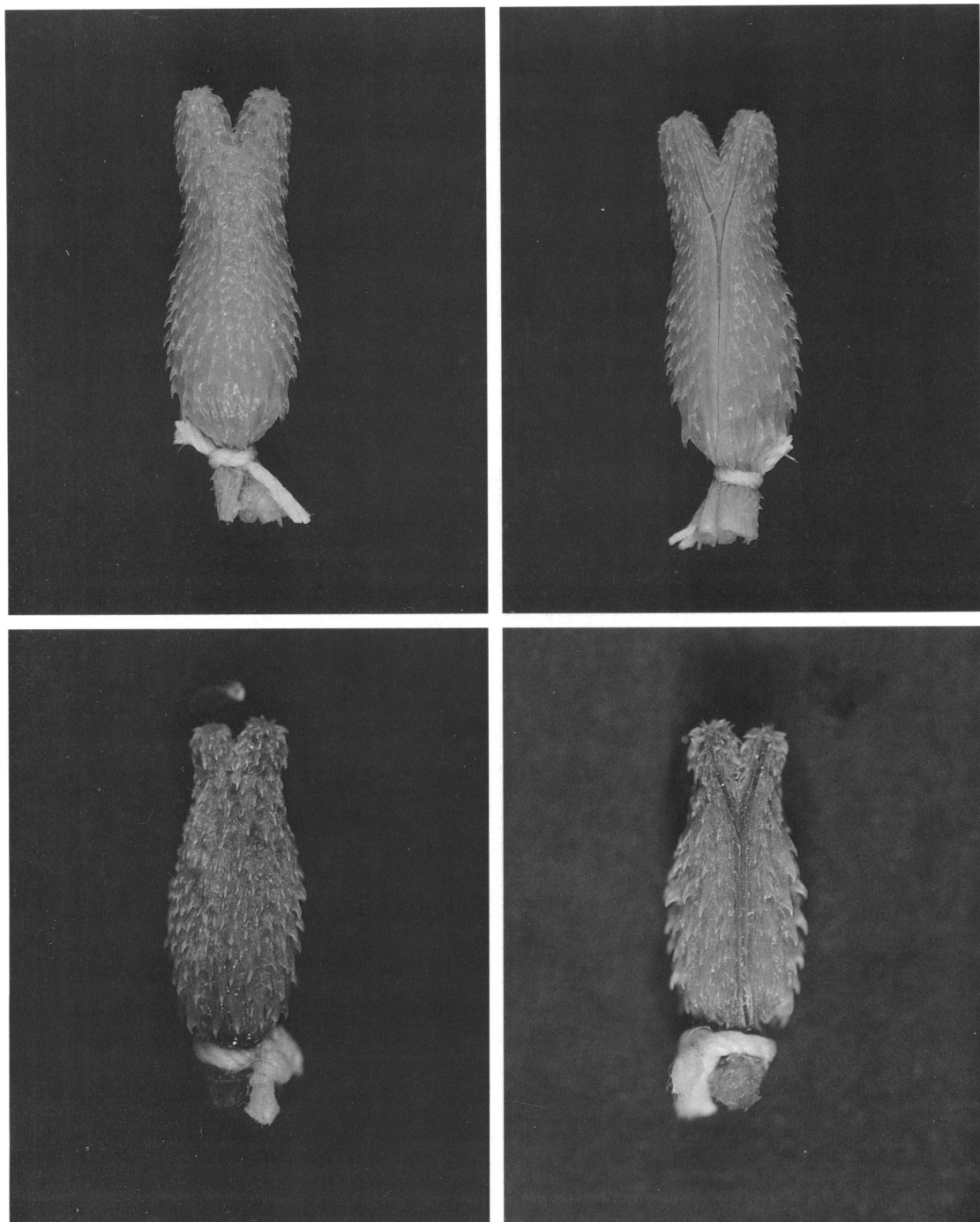


Fig. 87. Hemipenes of *Gomesophis brasiliensis* (upper; IB 12191) and *Ptycophis flavovirgatus* (lower; AMNH 71312). Asulcate (left) and sulcate (right) views.

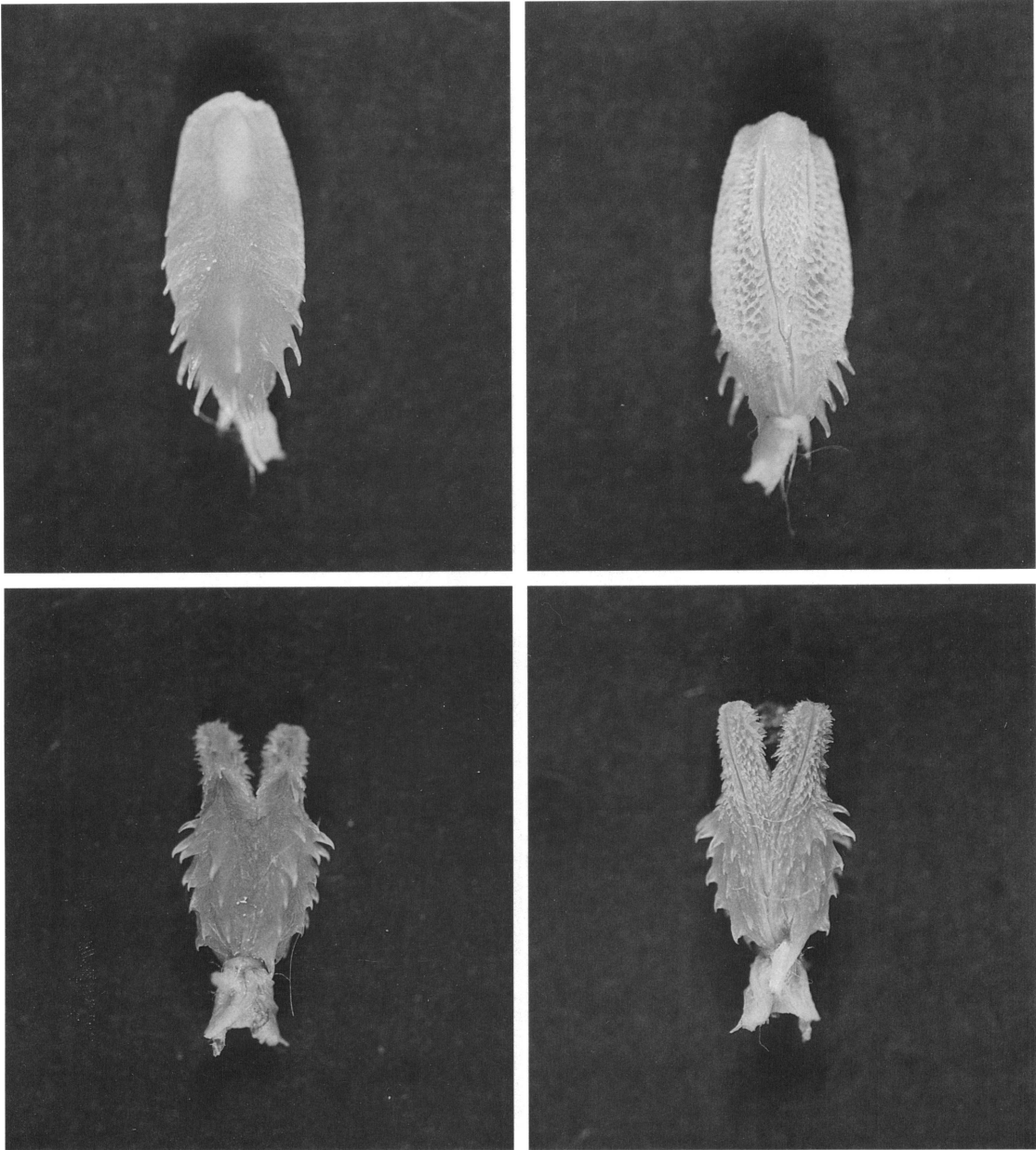


Fig. 88. Hemipenes of *Nothopsis rugosus* (upper; USNM 142306) and *Synophis lazallei* (lower; USNM 233062). Asulcate (left) and sulcate (right) views.

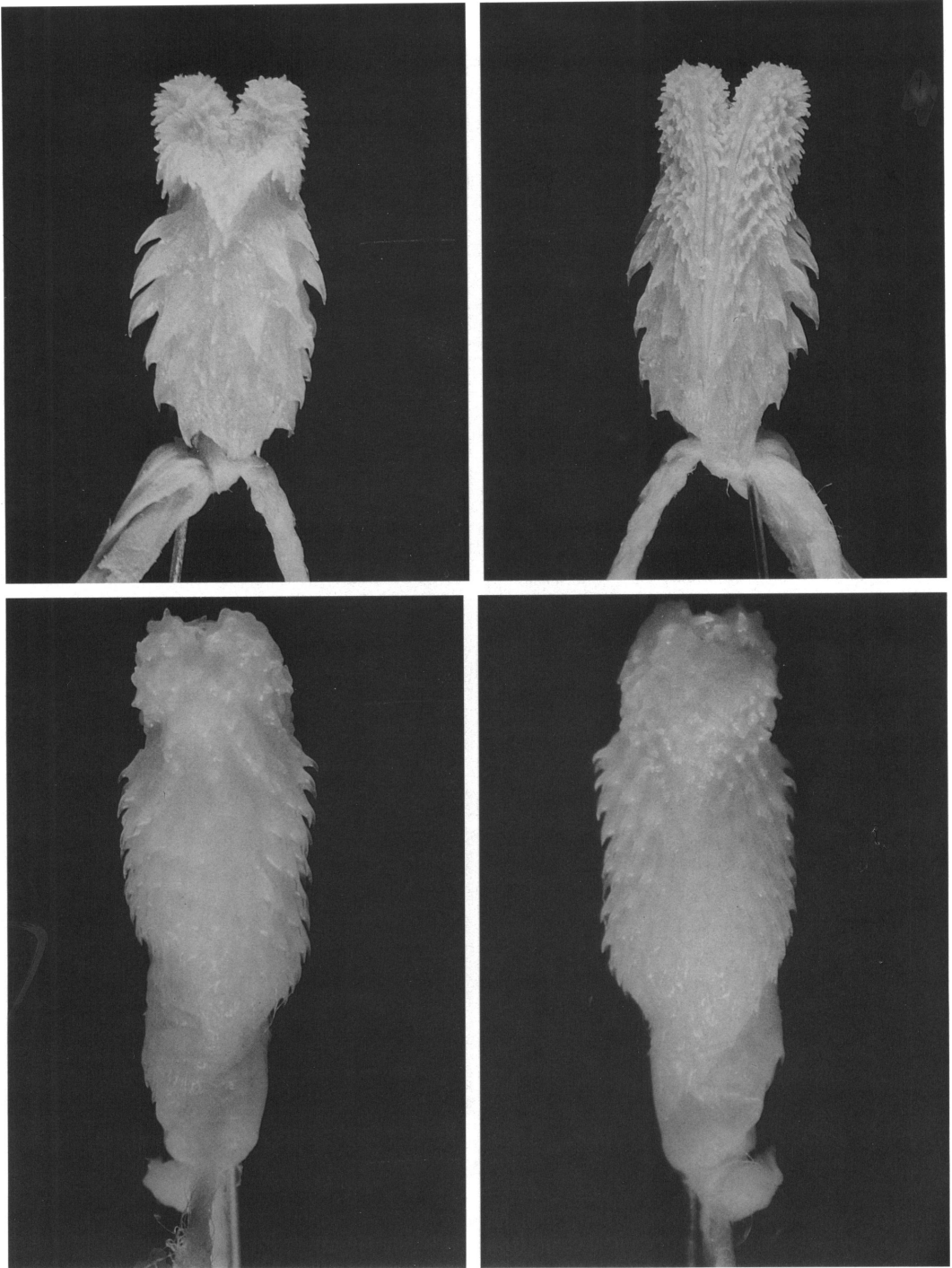


Fig. 89. Hemipenes of *Synophis bicolor* (upper; QCAZ 452) and *Sordellina punctata* (lower; IB 55703). Asulcate (left) and sulcate (right) views.

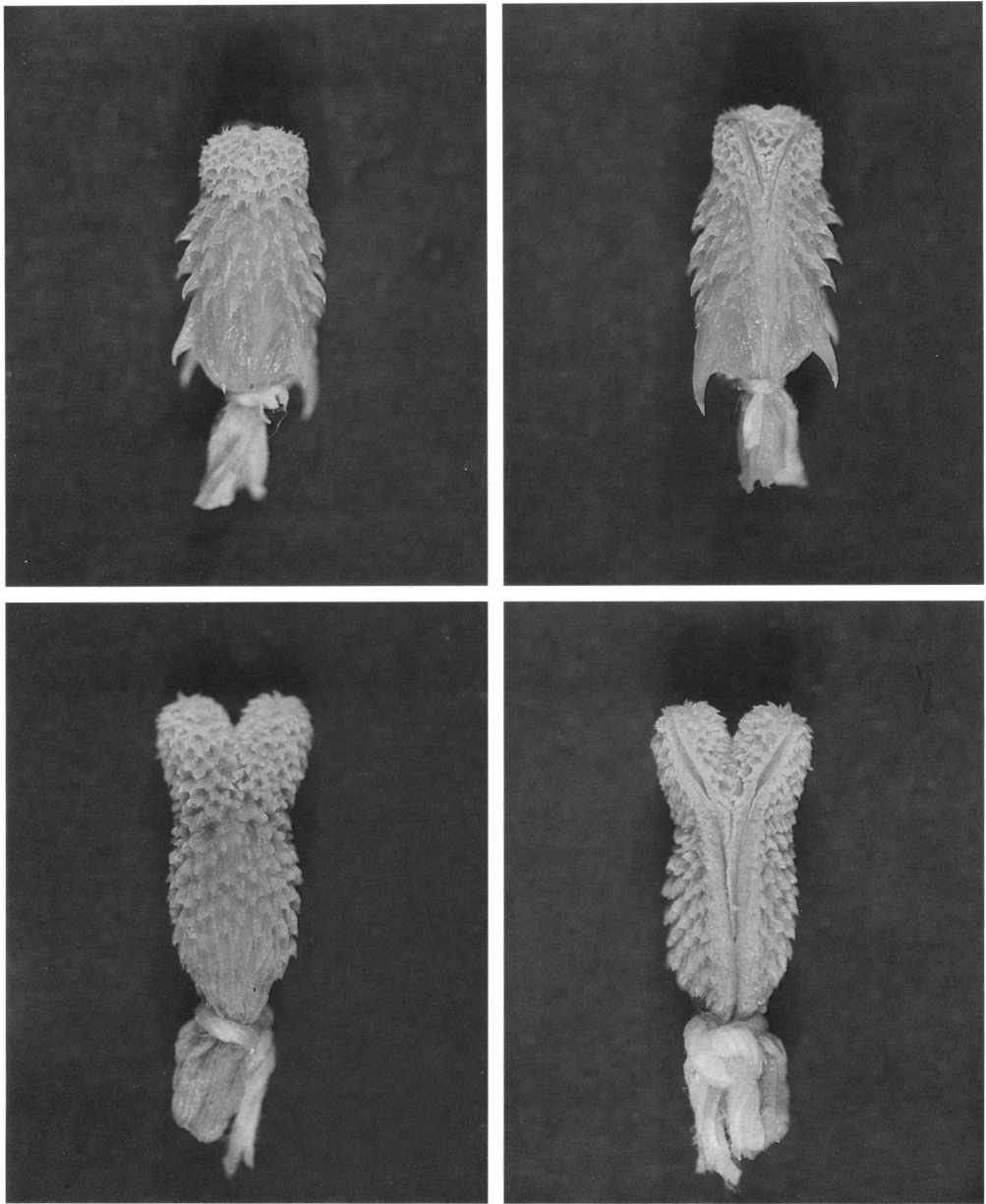


Fig. 90. Hemipenes of *Tachymenis chilensis* (upper; AMNH 64941) and *Tachymenis peruviana* (lower; AMNH 5256). Asulcate (left) and sulcate (right) views.

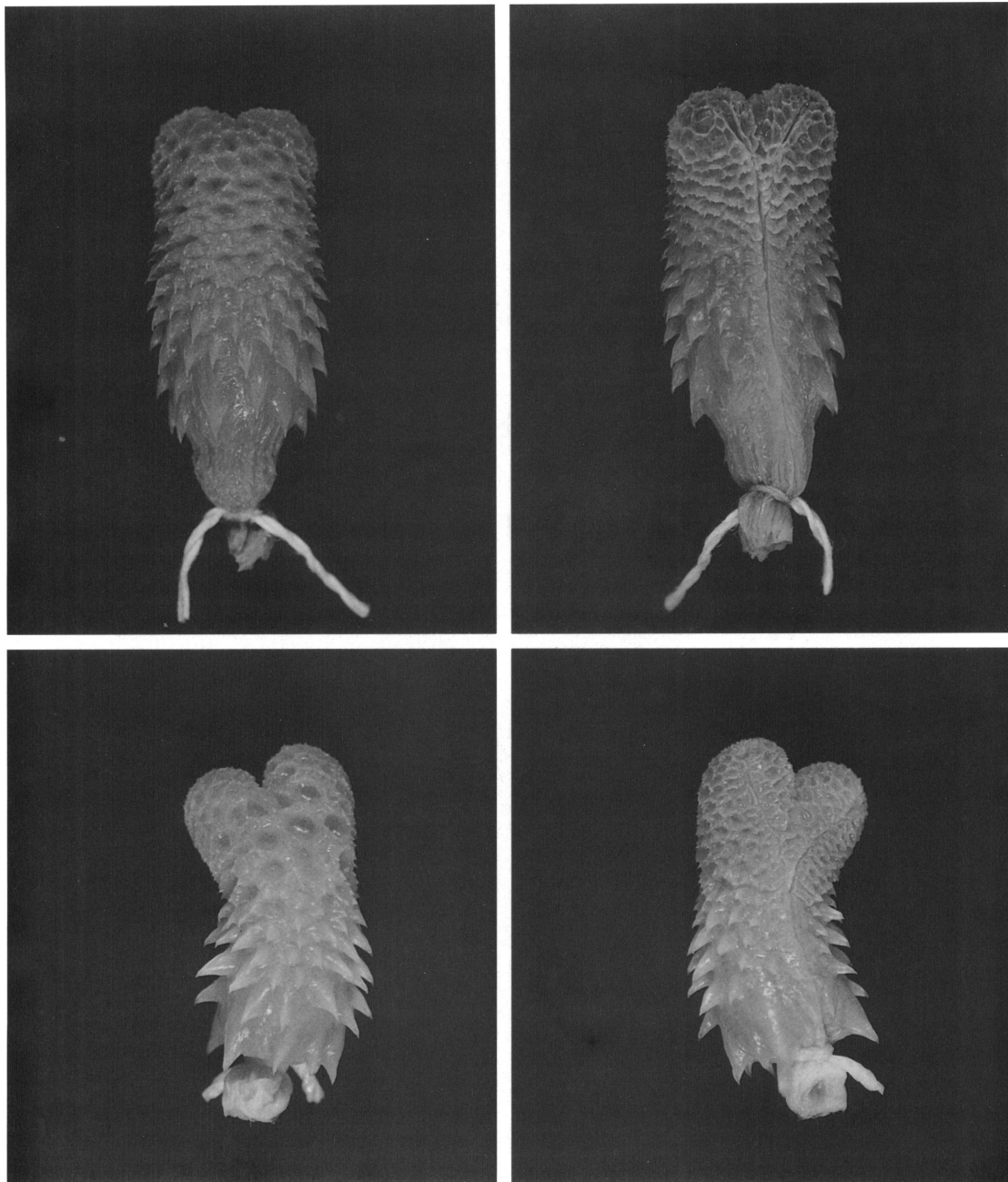


Fig. 91. Hemipenes of *Tachymenis attenuata* (upper; AMNH 36024) and *Tomodon dorsatus* (lower; IB 21957). Asulcate (left) and sulcate (right) views.

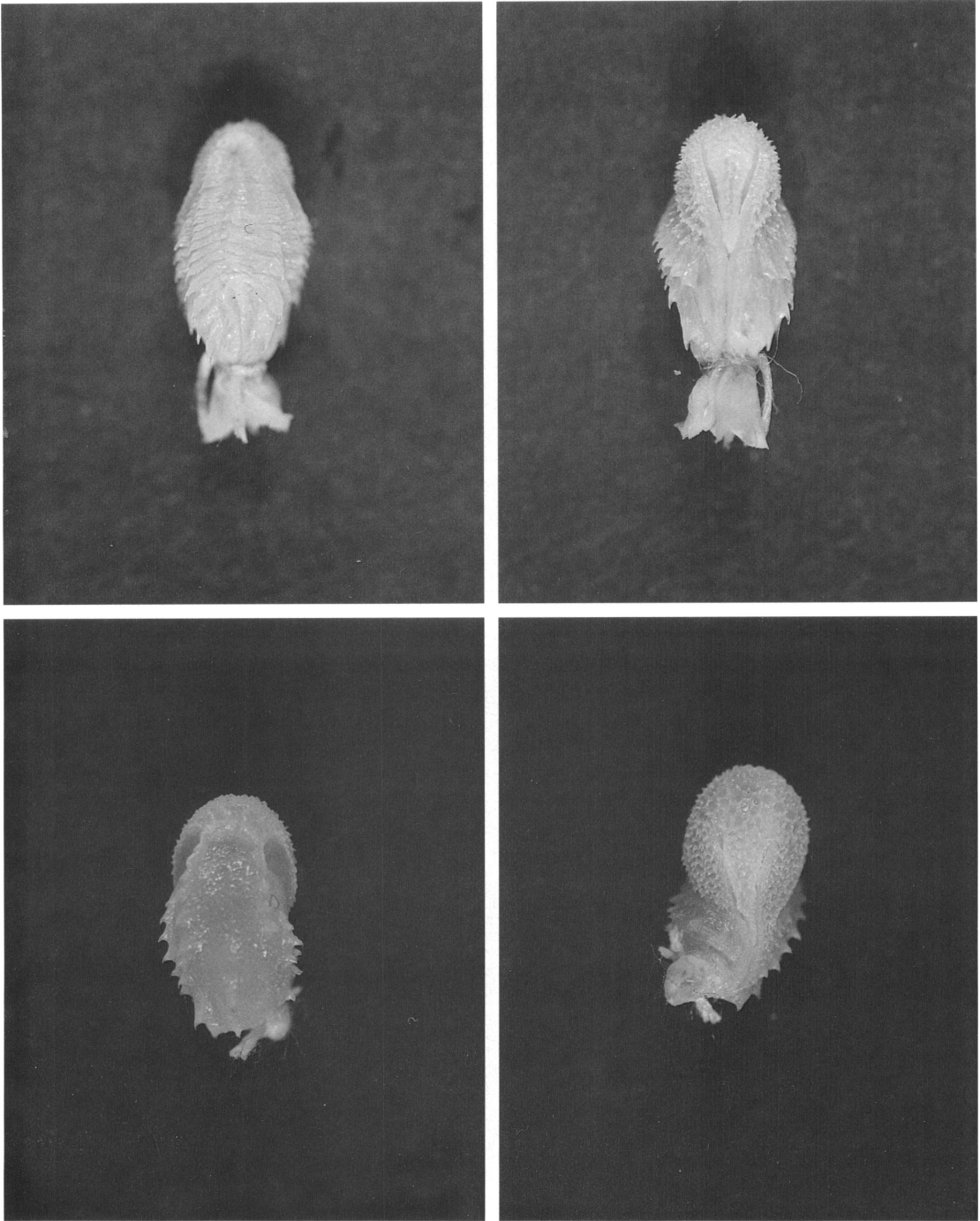


Fig. 92. Hemipenes of *Taeniophallus affinis* (upper; IB 27970) and *Taeniophallus occipitalis* (lower; IB 22538). Asulcate (left) and sulcate (right) views.

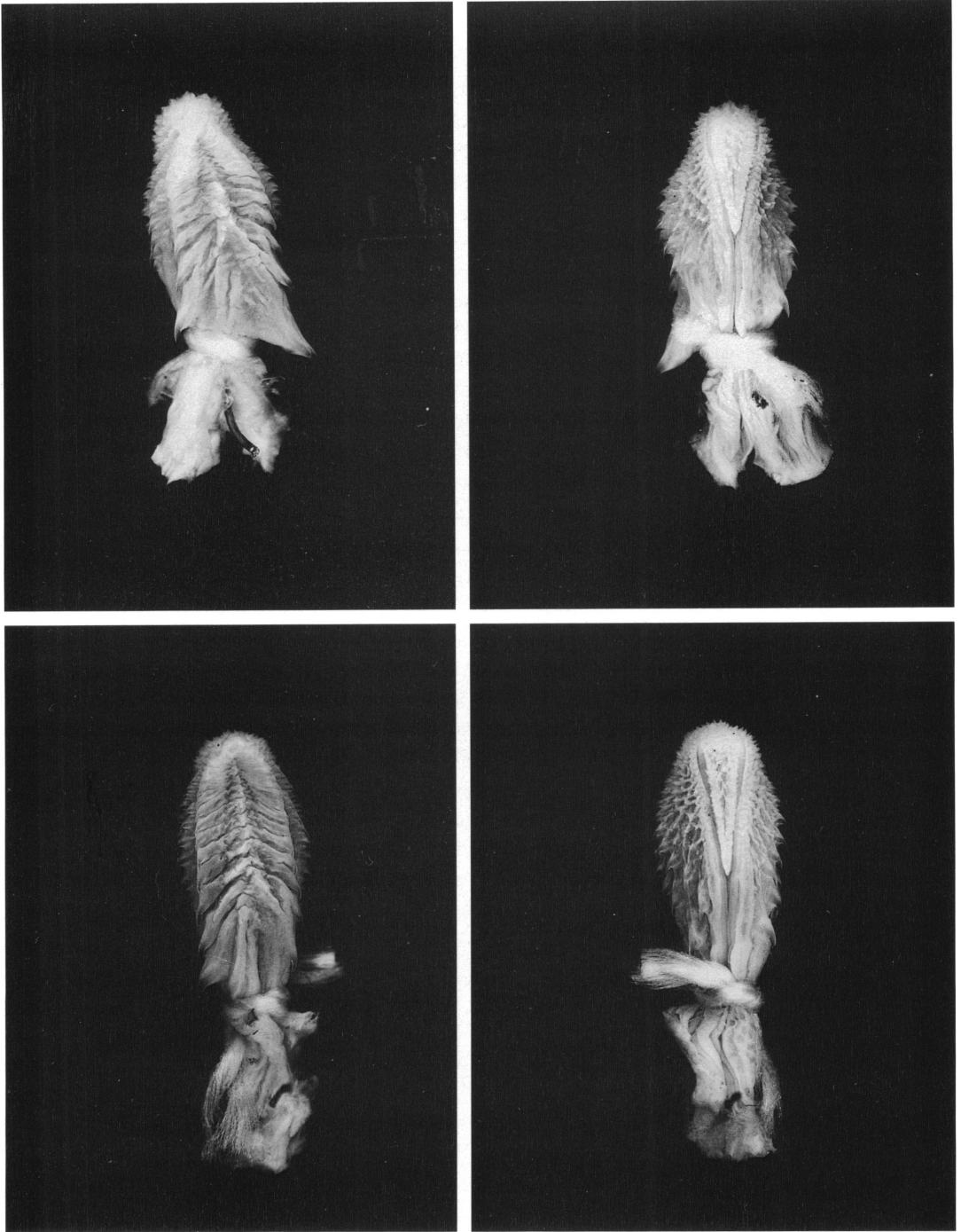


Fig. 93. Hemipenes of *Taeniophallus bilineatus* (upper; IB 26182) and *Taeniophallus persimilis* (lower; IB 9504). Asulcate (left) and sulcate (right) views.

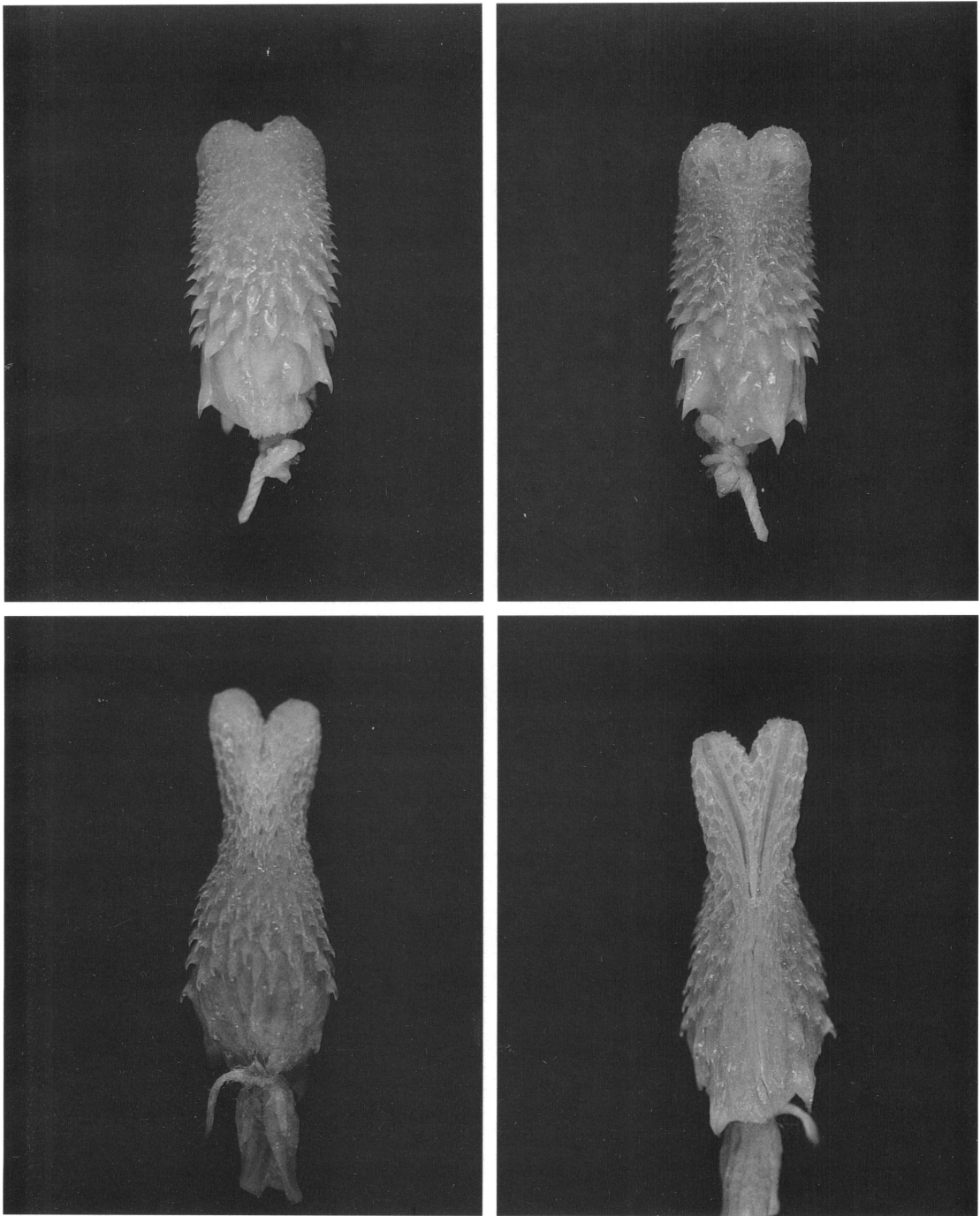


Fig. 94. Hemipenes of *Thamnodynastes strigatus* (upper; IB 53789) and *Thamnodynastes pallidus* (lower; IB 50614). Asulcate (left) and sulcate (right) views.

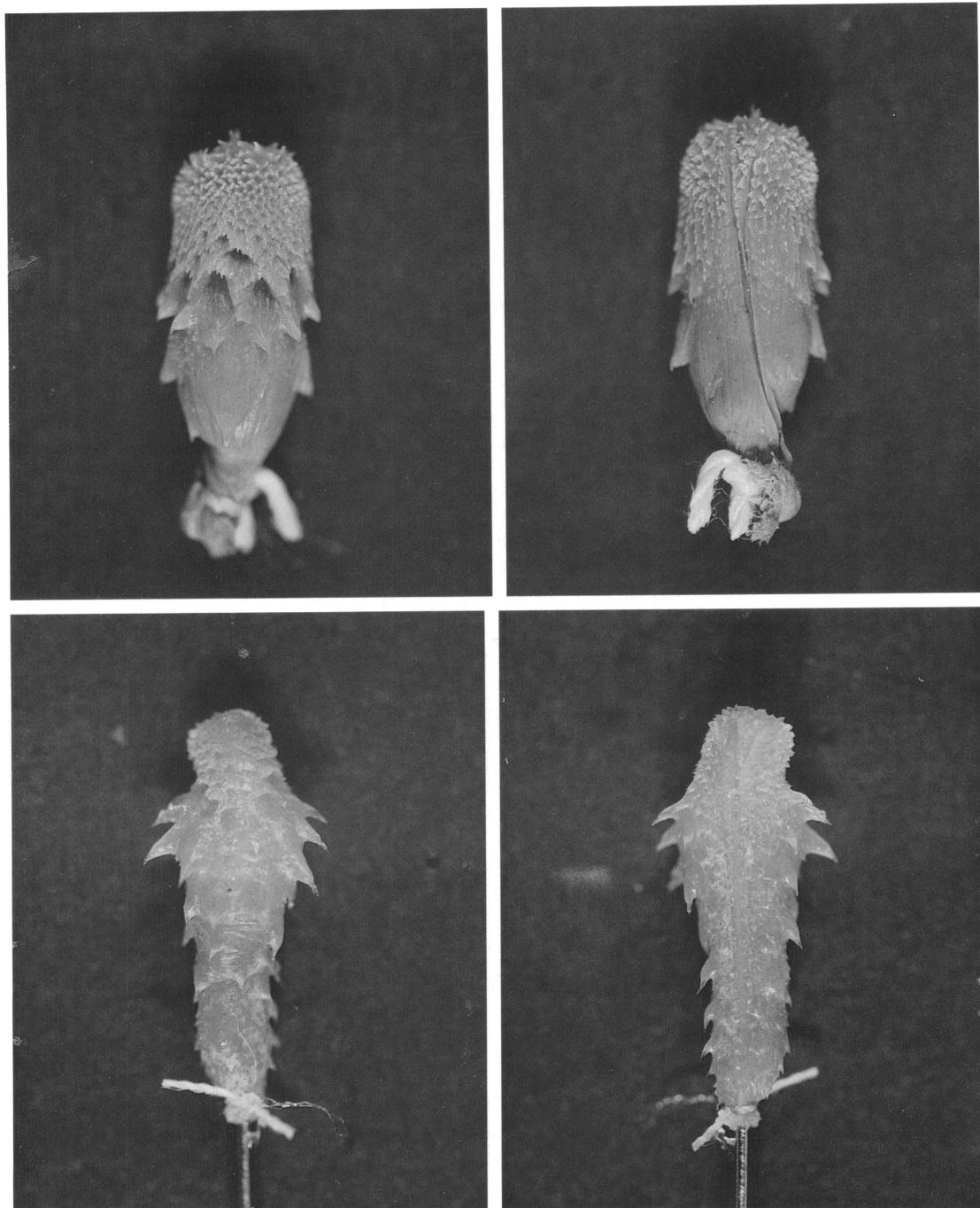


Fig. 95. Hemipenes of *Xenopholis scalaris* (upper; AMNH 52870) and *Xenopholis undulatus* (lower; uncatalogued specimen). Asulcate (left) and sulcate (right) views.

