Ichthyology & Herpetology 110, No. 2, 2022, 299–314

First Report of Hemipenial Variation among Some Genera and Species of Shieldtail Snakes (Serpentes: Uropeltidae) from India and Sri Lanka

R. Alexander Pyron[1], Vivek P. Cyriac[2], S. R. Ganesh[3], Ashok K. Mallik[2], Anslem de Silva[4], Achyuthan N. Srikanthan[2,5], and Kartik Shanker[2]

Hemipenial characteristics have historically provided a wealth of comparative morphological characters for the systematic classification of snakes. However, the organs remain poorly known in many groups, particularly tropical and burrowing lineages. Here, we report on hemipenial morphology for 12 species from five genera from the family Uropeltidae: *Melanophidium punctatum*, *M.* cf. *wynaudense*, *Plectrurus perrotetii*, *Rhinophis karinthandani*, *R. melanoleucus*, *R. saffragamus*, *R. sanguineus*, *Teretrurus* cf. *hewstoni*, *Uropeltis bhupathyi*, *U.* cf. *ceylanica*, *U. macrolepis*, and *U. rajendrani*. Many are photographed or illustrated here for the first time. In *Melanophidium*, the organ is bulbous and mushroom-shaped, with the sulcus spermaticus winding through numerous convoluted folds. In *Plectrurus* and *Teretrurus*, it is simple, smooth, and conical. In Sri Lankan *Rhinophis* and some *Uropeltis*, the organ generally resembles previously described hemipenes from other species in those genera in being simple, subcylindrical, and covered in fine spines. However, a median lobular process is observed in the Indian species *R. karinthandani*, *R. melanoleucus*, and *R. sanguineus*, seemingly representing a novel bilobate morphology. One species, *U. bhupathyi*, exhibits a novel, bulbous morphology, but this may be an artifact of preservation. The hemipenes of the Uropeltidae and their sister group Cylindrophiidae resemble some typhlopoid blindsnakes more than their henophidian relatives such as pythons and boas. Whether this is due to convergence related to microhabitat, a form of sexual selection unrelated to ecomorphology, or symplesiomorphy from an ancestral snake morphology is unclear. Gross hemipenial morphology can now serve to diagnose uropeltids to the genus level or species group, though more data and comparative series are needed to determine whether other characters, such as the number and location of spines, can potentially differentiate taxa at finer scales.

THE hemipenis of squamate reptiles has been recognized as an important indicator of systematic variation for over a century, particularly for snakes (Cope, 1893; Dunn, 1928; Zaher, 1999). Extensive systems of classification and terminology have been developed to characterize this information across lineages and standardize observations (Dowling and Savage, 1960; Savage, 1997; Zaher, 1999). Such observations continue to provide relevant sources of information for the higher-level classification of taxa and the recognition of new species (Schargel and Castoe, 2003; Jadin and Smith, 2010; Torres-Carvajal et al., 2015). However, incomplete observations in some lineages preclude complete descriptions of hemipenial morphology across snakes, as well as limiting the usefulness of these characters to classify known taxa. One such example is the South Asian shieldtail snake family Uropeltidae.

Uropeltidae comprises 62 currently recognized species from South Asia, with the greatest diversity centered in the Western Ghats–Sri Lanka biodiversity hotspot (Uetz and Hošek, 2021). Although recent studies have increased phylogenetic knowledge in the group using molecular data (Bossuyt et al., 2004; Pyron et al., 2013, 2016; Cyriac and Kodandaramaiah, 2017; Jins et al., 2018; Sampaio et al., 2020), little is known about hemipenial morphology beyond a few preliminary observations (see summary in Pyron et al., 2016). The organ is single with a simple sulcus spermaticus in the few species where the organs have been described thus far. Wall (1919) remarked on the timing of hemipenial eversion during embryonic development of a male *Plectrurus perrotetii* but did not describe it in detail. After examining the organs of a juvenile *Uropeltis woodmasoni* (then called *Silybura nigra*) from the Palni hills, Wall (1923: 389) commented that "genitalia are cylindrical organs that are rather larger in girth distally than basally, and are beset with minute villi." Smith (1943) noted two types: short and thick with the sulcus spermaticus winding through convoluted folds (*Melanophidium*), and longer and slenderer with fine spines (*Uropeltis grandis*). Rajendran (1985) reported on the female reproductive organs and their dissections but did not deal with the male organs.

Though the first uropeltid was described in 1801, everted hemipenes have only been illustrated for four recently described species. In the Indian *Uropeltis rajendrani*, the organ was reported to be fairly short and stout, extending to the 2nd subcaudal, unilobed and spiny, bearing tiny flounces, with a shallow sulcus spermaticus. In the Sri Lankan species *Rhinophis lineatus* (Gower and Maduwage, 2011: fig. 5; WHT 5208; see additional detail in Gower and Wickramasinghe, 2016: 210) and *R. dorsimaculatus* (Gower and Wickramasinghe, 2016: fig. 2; CAS 225842), the organ is simple, subcylindrical, covered in fine dense spines on most or all of the asulcate surface, with a shallow, straight sulcus spermaticus. In both, the sulcate surface is depauperate of spines, and the organ is long, representing roughly half the

[1] Department of Biological Sciences, The George Washington University, Washington, D.C.; Email: rpyron@colubroid.org. Send reprint requests to this address.
[2] Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India.
[3] Chennai Snake Park, Rajbhavan Post, Chennai, Tamil Nadu, India.
[4] Amphibia & Reptile Research Organization of Sri Lanka, 15/1 Dolosbage Road, Gampola, Sri Lanka.
[5] Department of Biology, Clark University, Worcester, Massachusetts.
Submitted: 17 February 2021. Accepted: 25 October 2021. Associate Editor: D. S. Siegel.
 DOI: 10.1643/h2021024 Published online: 20 May 2022

Table 1. Specimen information: snout–vent length (SVL) and tail length (TL) in mm, with counts of ventral (V) and subcaudal (SC) scales, following Gower and Ablett (2006). *adjacent body scales were counted as proxies where ventral scales damaged.

Species	Voucher	Locality	SVL	TL	V	SC
Melanophidium punctatum	SACON/S1	Top Slip	570	29	198*	13
M. cf. *wynaudense*	CESS 291	Kudremukh	340	17	199	13
Plectrurus perrotetii	CESS 324	Sispara	235	15	150	11
P. perrotetii	CESS 325	Sispara	185	13	158	11
Rhinophis karinthandani	BNHS 3545	Lakkidi	221	12	198	7
R. karinthandani	VPRS 0721121	Lakkidi	226	11	191	9
R. melanoleucus	BNHS 3537	Lakkidi	293	11	236	8
R. sanguineus	VPRS 0918093	Meppadi	268	12	199	9
R. saffragamus	—	Telijjawila	—	—	—	—
Teretrurus cf. *hewstoni*	VPTH 0721123	Mananthawadi	126	7	124	7
Uropeltis bhupathyi	SACON/S2	Anaikatti	293	12	205*	9
U. cf. *ceylanica*	CESS 266	Kudremukh	154	9	123	10
U. macrolepis "mahableshwarensis"	U12/3303	Panchgani	192	16	125*	12
U. rajendrani	BNHS 3359	Bodhamalai	221	13	148	11

length of the tail. In contrast, the hemipenis of the Indian species *R. melanoleucus* (Cyriac et al., 2020: figs. 5, 6) is short and blunt, and was interpreted as unilobate with a median asulcate lobular process.

Here, we provide opportunistic observations of partially everted hemipenes *in situ* for 14 specimens of 12 species from five genera: *Melanophidium punctatum*, *M.* cf. *wynaudense*, *Plectrurus perrotetii*, *Rhinophis karinthandani*, *R. melanoleucus*, *R. sanguineus*, *Teretrurus* cf. *hewstoni*, *Uropeltis bhupathyi*, *U.* cf. *ceylanica*, *U. macrolepis*, and *U. rajendrani* from India, and *R. saffragamus* from Sri Lanka. With a few noted exceptions, the organs of these taxa are photographed or illustrated here for the first time and provide an expanded overview of systematic variation in the group. We report two new, distinct hemipenial morphologies for Uropeltidae in *Plectrurus* and *Teretrurus* (simple and attenuate) and some Indian *Rhinophis*, (apparently bilobed while all other known uropeltids are unilobed). A single specimen of *U. bhupathyi* possesses a potential fifth distinct, bulbous morphology. We note the overall similarity of uropeltid hemipenes to those of some typhlopoid blindsnakes, rather than the more closely related henophidian snakes, such as pythons and boas. Additional work is needed to characterize variation in the remaining genera and species, and to determine which quantitative or qualitative characters are useful for diagnosing taxa at different phylogenetic scales.

MATERIALS AND METHODS

Personal observations in the field and a review of the uropeltid specimens in the snake collection (CESS and VP series) at the Centre for Ecological Science, Indian Institute of Science (CES-IISc) in Bangalore, the Bombay Natural History Society (BNHS) in Mumbai, and the Salim Ali Centre for Ornithology & Natural History (SACON) in Coimbatore allowed us to document the presence of everted hemipenes in several specimens (Table 1). All specimens are approaching or within the SVL range considered "adult" or sexually mature for each species (see Pyron et al., 2016), and we therefore assume the organs to be fully developed or nearly so. One hemipenis of *Rhinophis saffragamus* was illustrated from a low-resolution photograph taken in the field of an unvouchered animal, described in de Silva and Ukuwela (2020). For the CES specimens, the hemipenes were photographed *in situ* using a Leica dissecting microscope and high-resolution macro camera, which we reproduce along with illustrations. Our terminology is standardized from previous authors (Dowling and Savage, 1960; Savage, 1997). We did not observe any features that require the use of novel terms.

The representatives of *Melanophidium punctatum*, *Uropeltis bhupathyi*, and *U. macrolepis "mahableshwarensis"* are described from roadkill specimens. The specimen of *M. punctatum* had no injuries near the hemipenis. In the specimen of *U. bhupathyi*, the right half of the body was injured, and some internal tissues were damaged, protruding out of torn skin patches. Care was taken to ensure that it was not too damaged to permit an undistorted illustration of its hemipenis from low-resolution photographs. The hemipenis of *U. macrolepis* is also described from a roadkill specimen with the left side of the body injured with internal tissue protruding from tears in the skin at the midbody. Although this specimen has no injuries in the tail region, the hemipenis itself was slightly damaged. All other organs in other taxa are described from well-preserved specimens where the hemipenes were everted.

Many authors have suggested that a complete characterization of hemipenial morphology requires the organs to be studied in the retracted or inverted state, as well as prepared, stained, and dissected (see Cope, 1895; Myers, 1974; Pesantes, 1994; Dowling, 2002; Myers and Cadle, 2003; Zaher and Prudente, 2003). We did not attempt this here due to the small sample sizes. Our observations are based only on the partially to fully everted organs prepared during the initial preservation of the specimens. Thus, our description of apical morphology and basal portions that are adpressed to the body in some specimens are likely incomplete or may be altered once complete preparations become available. Given the relative paucity of information regarding even the external morphology of the everted uropeltid hemipenis, these observations nonetheless provide a valuable resource. Furthermore, they will serve as a guide for more thorough work in the future when additional preparation types are available from additional specimens. We provide both high-resolution photographs and labeled drawings for most specimens, though a few of our illustrations are based either on drawings of recently published photographs (which we cite) for specimens we examined but did not photograph

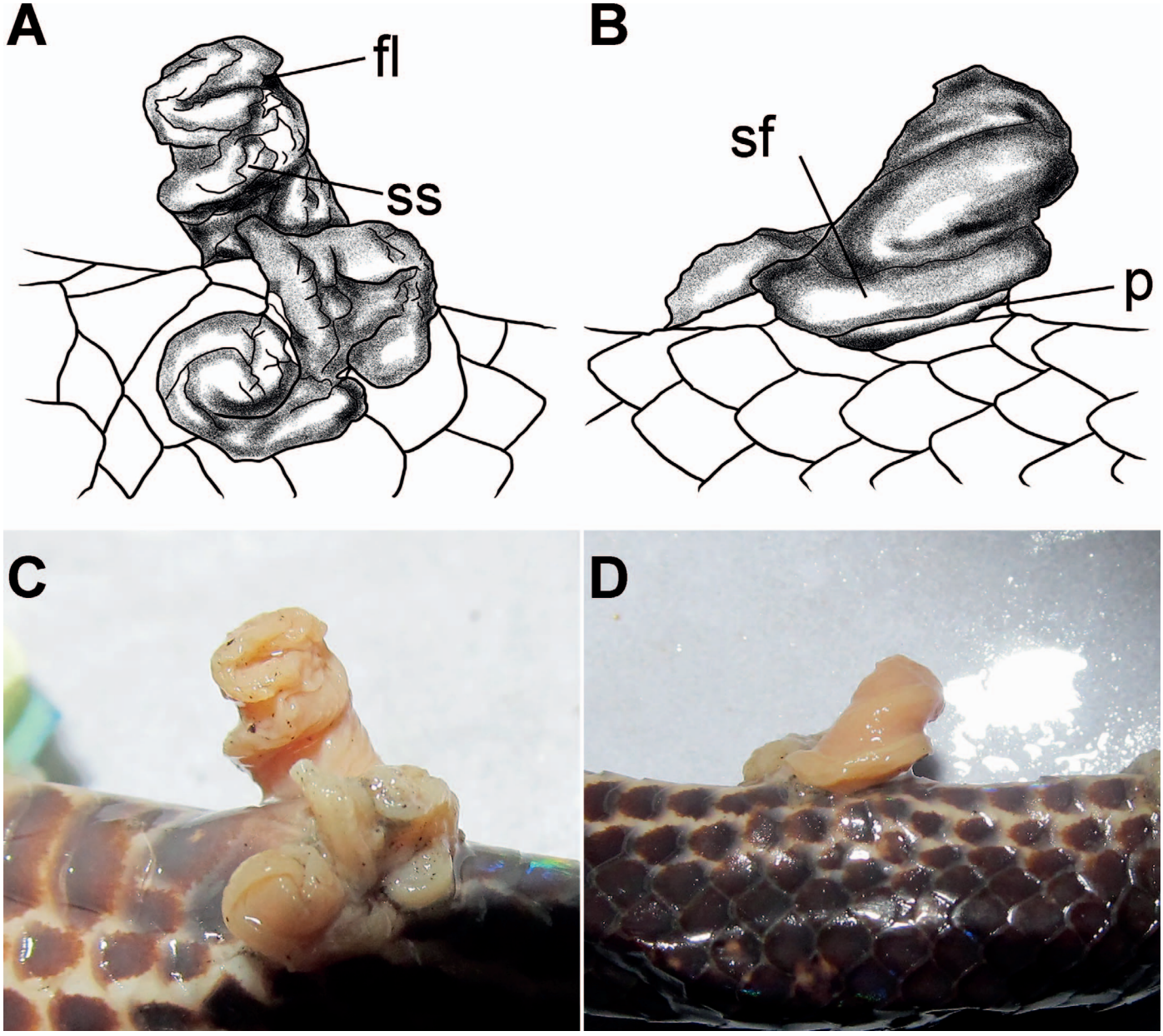

Fig. 1. Partially everted hemipenes of *Melanophidium punctatum* SACON/S1 in sulcate (A, C) and asulcate (B, D) view. No fixed scale bar available; organ ~7.7 mm (~27% of 29 mm TL; Table 1). Abbreviations: fl, lobular flounces; p, pedicel; sf, sulcal folds; ss, sulcus spermaticus.

ourselves, or on photographs which were of insufficiently high quality for presentation here.

RESULTS

We observed gross external morphology from 14 specimens, all of which had single (or possibly bilobed) hemipenes with a simple, smooth, shallow or deep sulcus spermaticus. Using existing terminology (see Dowling and Savage, 1960), we characterize the hemipenes as follows:

Melanophidium punctatum.—Length approximately 7.7 mm (~27% of 29 mm tail length [TL]); when adpressed posteriorly, reaching between 3rd and 4th subcaudal scales; shape subcylindrical and mushroom-like, with a series of convoluted raised sulcal folds; lobe head flounced with sulcal spirals; sulcal lips broad, almost as wide as lobe head; capitular groove at the end of lobe head obscure; sulcal spirals centrifugal, contributing to the equal width of lobe compared to the visible part of the pedicel; flounced lobe head unornamented, lacking spinules, awns, or any other structures; sulcus spermaticus raised, winding along the pedicel basally. Overall appearance is a long, cylindrical-to-conical organ that is smooth, with thick, winding sulcal folds resembling a corkscrew (Fig. 1).

Melanophidium* cf. *wynaudense.—Length approximately 4 mm (~24% of 17 mm TL), reaching subcaudals 3–4; shape clavate with numerous convoluted folds, similar to *M. punctatum*; sulcus spermaticus simple, shallow, and smooth, winding obliquely through folds of organ, terminating at apex; apex nude, forming a flattened circular surface comprising convoluted folds of tissue with a central depression. Convoluted folds on flattened apical cap may

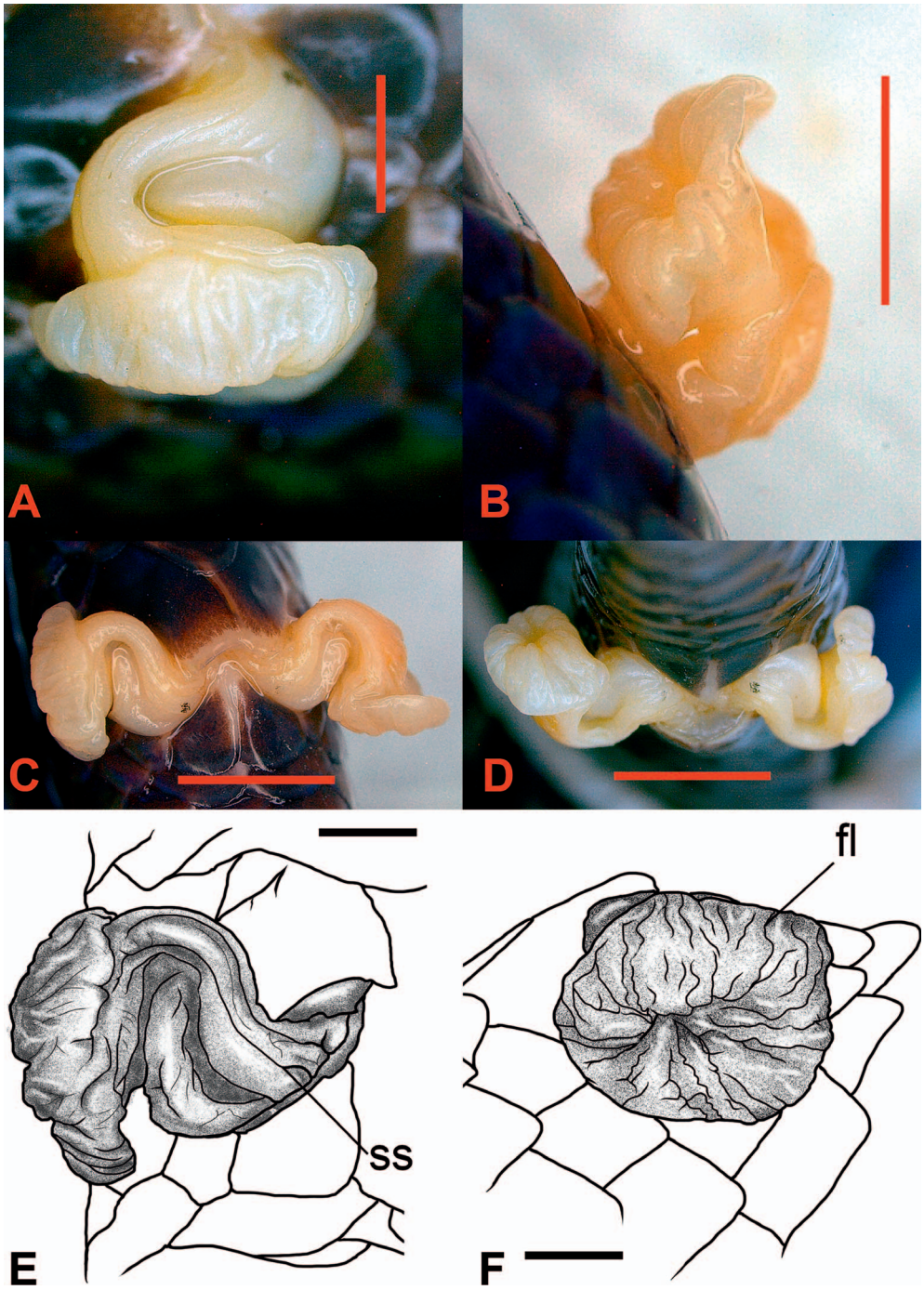

Fig. 2. Everted hemipenes of *Melanophidium* cf. *wynaudense* CESS 291 in photograph (A–D) and illustration (E, F). Views are sulcate (A, C, E) and asulcate (B, D, F). Scale bars in A, E, and F are 1 mm; B is 2 mm; and C and D are 3 mm. Abbreviations: fl, lobular flounces; ss, sulcus spermaticus.

be interpreted as flounces. Overall appearance is bulbous and mushroom-like (Fig. 2).

Plectrurus perrotetii.—Length approximately 2–2.5 mm (~15% of 13–15 mm TL); shape simple and attenuate; simple, straight, shallow, and smooth sulcus spermaticus terminating at apex; naked and undifferentiated; apex nude. Overall appearance is a very simple, elongate, coniform organ (Fig. 3).

Rhinophis karinthandani.—Two specimens; length approximately 2.0 mm (~16.6–18.2% of 11–12 mm TL); reaching up to the 1st subcaudal when adpressed posteriorly; hemipenes single, broad at the base (1.1–1.3 mm), appears asymmetrically bilobate, with a broad nude outer lobe and an inner lobe with a narrower apical projection or papilla; inner lobe of the right hemipenis having an apical depression or dimple in VPRS 0721121 (likely due to incomplete eversion); the lobes diverting approximately 1.4 mm from the base. The extended apical projection of the inner lobe cylindrical, short, with small papillae more prominent toward the apex. Base of the inner lobe with large globular folds in sulcate and asulcate view. Outer lobe irregularly shaped, wider than the inner lobe, and without prominent ornamentation. Sulcus spermaticus examined in VPRS 0721121 is simple, shallow, and narrow and terminating at the apical depression of the inner lobe. Base and body with obscure convoluted folds or flounces in asulcate view (Fig. 4).

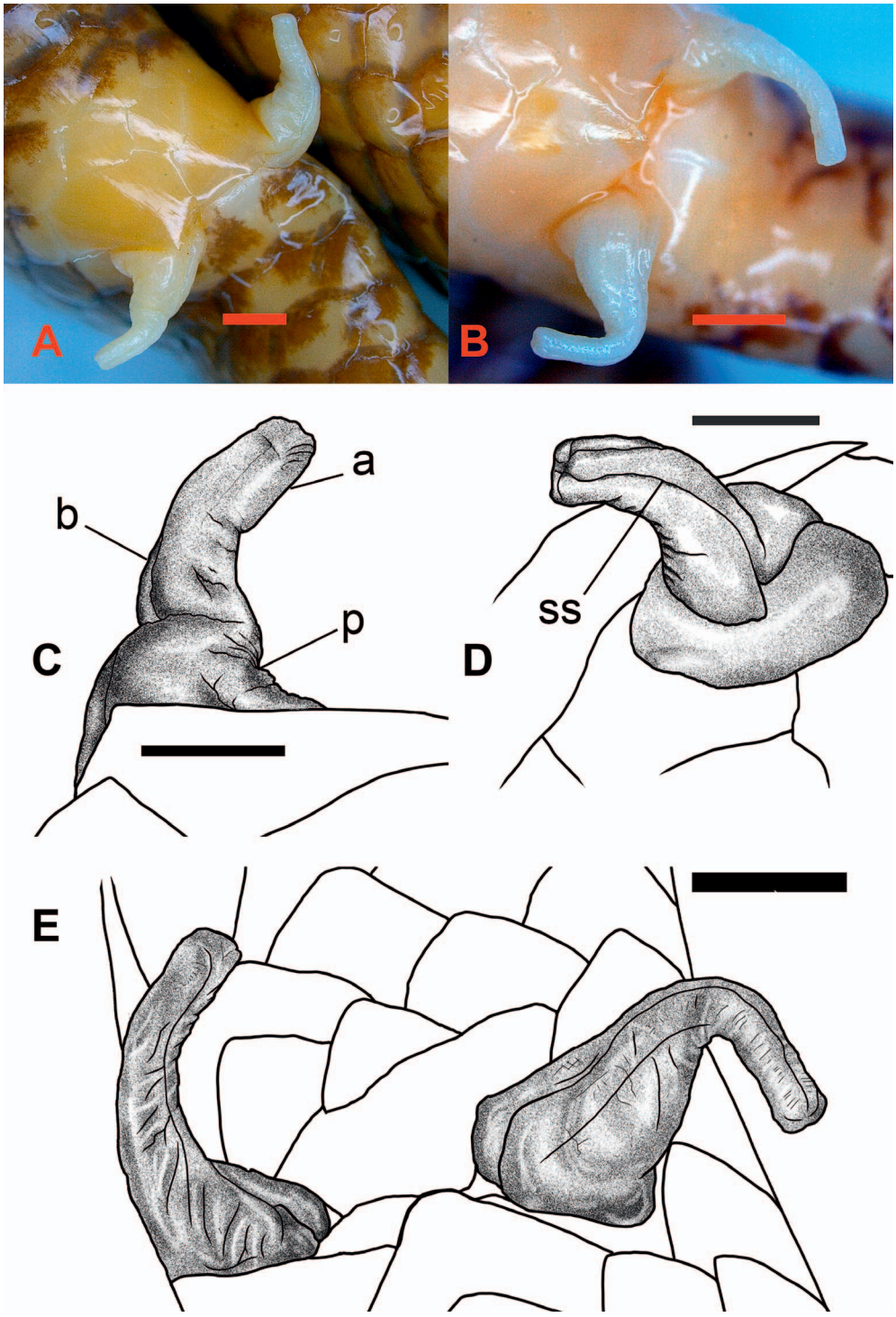

Fig. 3. Everted hemipenes (photograph [A, B] and illustration [C–E]) of *Plectrurus perrotetii* CESS 324 (A, C, and D) and CESS 325 (B and E). Organ is simple, cylindrical, elongate, and conical with an enlarged pedicel. Views are sulcate (A, B, D, E) and asulcate (C). All scale bars are 1 mm. Abbreviations: a, apex; b, body; p, pedicel; ss, sulcus spermaticus.

Rhinophis melanoleucus.—Organ originally figured in Cyriac et al. (2020: figs. 5, 6); updated description given here for everted organs of the paratype BNHS 3537. Length approximately 2.1 mm (~18% of 11.5 mm TL); reaching up to the 2nd subcaudal when adpressed posteriorly; hemipenes short and broad; organs appear asymmetrically bilobate (originally interpreted as unilobate with an asulcate median lobular process). Inner lobe subcylindrical, broad (~1.2 mm in width) and densely ornamented with small, prominent, spines throughout; outer lobe small (~0.8 mm in width), shorter than the inner lobe, and with irregularly arranged longitudinal folds; lobes extending ~1.5 mm from the base; straight, shallow, and smooth sulcus spermaticus covered by a large flap and several globular folds at the base of the lobes, and terminating at the apex of the inner lobe; basal portion with irregular large horizontal folds or flounces. Overall appearance is a bifurcated cylinder with asymmetrical lobes (Fig. 5).

Rhinophis saffragamus.—Field observations and low-resolution photographs gathered by one of us (AdS) for a live specimen show a simple, subcylindrical organ covered in fine spines or papillae, somewhat similar to the hemipenes of other Sri Lankan species of *Rhinophis* and *Uropeltis* described

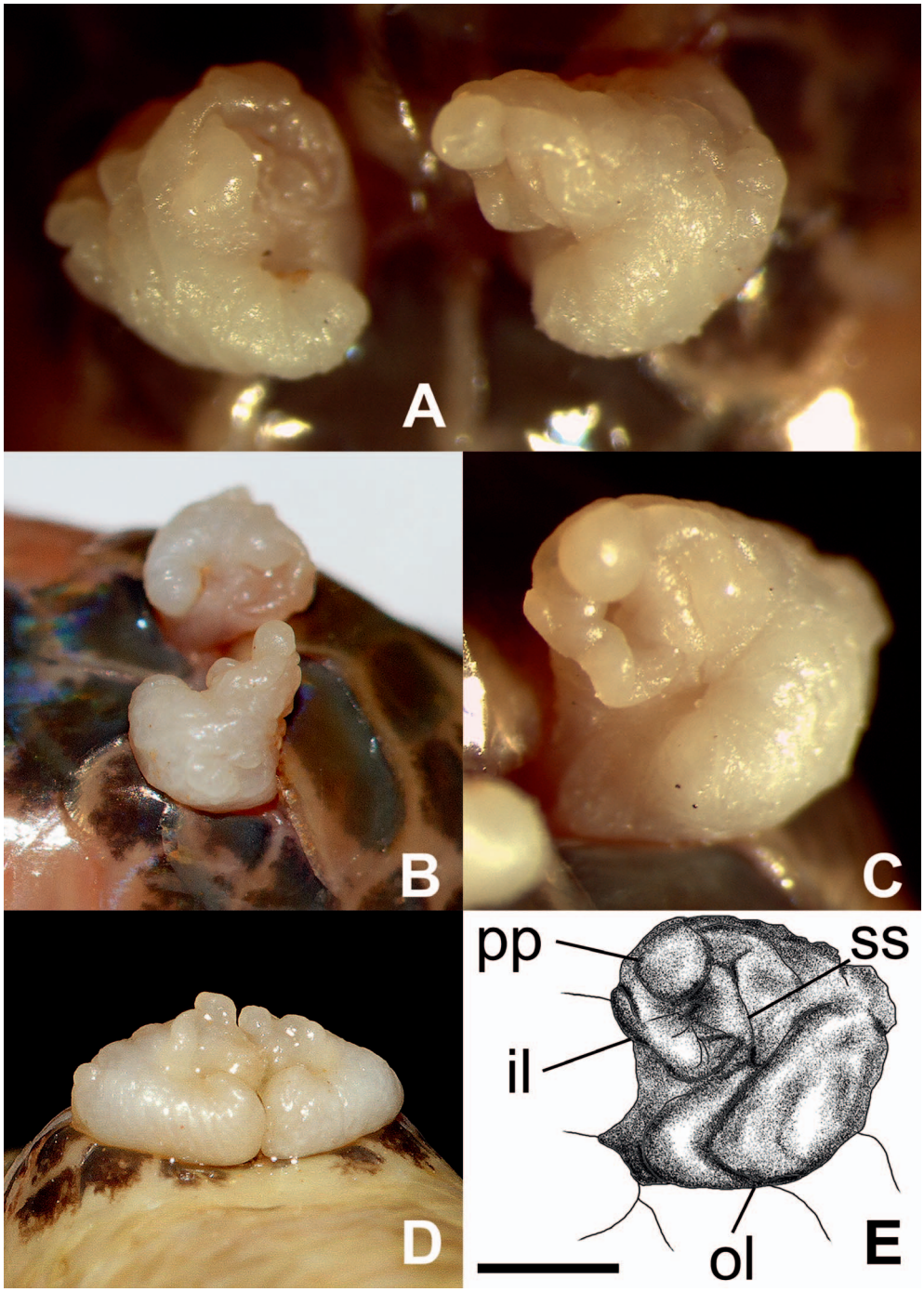

Fig. 4. Partially everted hemipenes of two specimens of *Rhinophis karinthandani*, VPRS 0721121 (A–C, E) and paratype BNHS 3545 (D), showing unusual, possibly bilobate condition. No fixed scale bar available for photos; both organs ~2 mm, ~16–18% TL. Scale bar for drawing 1 mm. Abbreviations: il, inner lobe; ol, outer lobe; pp, apical papilla; ss, sulcus spermaticus.

here and elsewhere. In contrast to the other species of *Rhinophis* and *Uropeltis*, the organs are long (~50–75% of TL; greater than any other species of *Rhinophis* or *Uropeltis* for which this is known), recurved and forming a complete half-circle, and possessing a red fleshy lobe on the proximal (interior or inner) surface of the sulcal lips in sulcate view (Fig. 6). Whether the curvature is an artifact of eversion and preservation is difficult to determine.

***Rhinophis sanguineus*.**—Length approximately 2.1 mm (~18% of 11.5 mm TL); reaching up to the 1st subcaudal when adpressed posteriorly, shape single, appears asymmetrically bilobate with a broad nude outer lobe and an inner lobe with a narrower apical projection; the lobes diverting approximately 1.2 mm from the base. Extended apical projection of the inner lobe cylindrical with small papillae at base in asulcate view and convoluted folds in sulcate view; short spines around the tip. Outer lobe irregularly shaped with large, convoluted folds. Sulcus spermaticus simple, straight, broad, and deep, terminating at the tip of the extended apical projection of the inner lobe. Base and body with small regular transverse flounces in asulcate view (Fig. 7).

***Teretrurus* cf. *hewstoni*.**—Length approximately 1.3 mm (~18.6% of 7 mm TL); shape simple with a broad base and a slightly truncated apex; base of the hemipenes with short, irregular folds or flounces; simple, straight, and shallow

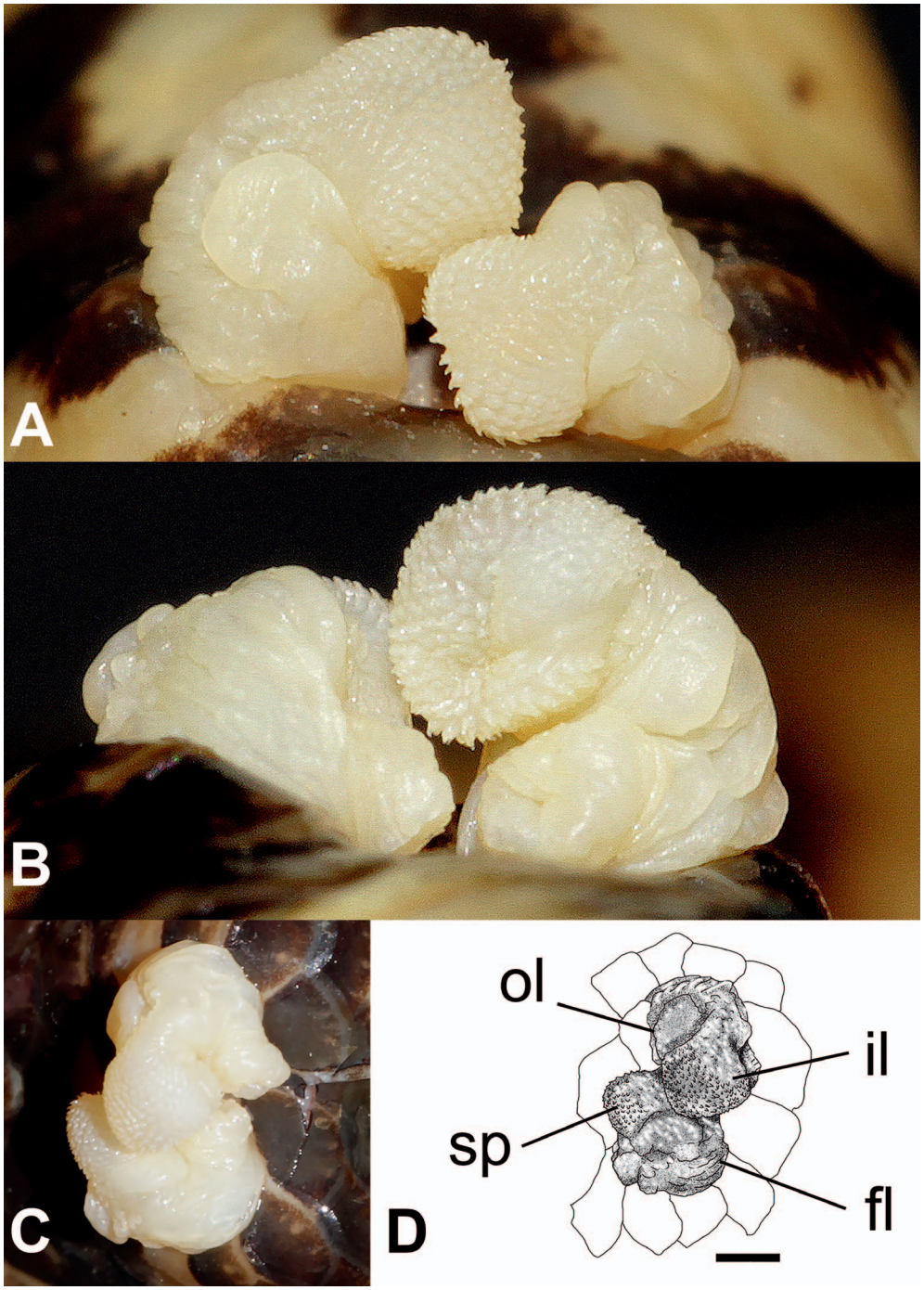

Fig. 5. Partially everted hemipenes of a paratype of *Rhinophis melanoleucus* (BNHS 3537; see Cyriac et al., 2020) in asulcate (A) and sulcate (B) views along with ventral aspect (C–D), showing unusual, possibly bilobate condition. Whether this is an artifact of preservation, a lobular process, or a truly distinct bilobed morphology requires additional study. No fixed scale bar available for photographs (A–C); 1 mm for illustration (D); organs ~2.1 mm, ~18% TL. Abbreviations: fl, basal flounces; il, inner lobe; ol, outer lobe; sp, fine lobular spines or hooks.

sulcus spermaticus terminating at apex; apex naked and undifferentiated. Overall appearance is a very simple, coniform organ (Fig. 8), somewhat similar to that of *Plectrurus* (see above).

Uropeltis bhupathyi.—Length approximately 4 mm (~30% of 13 mm TL); reaching 3rd to 4th subcaudal scales when adpressed posteriorly; shape subcylindrical (or possibly bulbous), simple, and lacking spines; lobular head visibly convex, not quite flounced; lobe width greater than pedicel width, sulcus spermaticus thin, not raised, short and simple, terminating at apex; sulcal lips naked, not easily discernible from surrounding parts of apex; capitular groove barely if at all visible; lateral body of lobe head smooth, lacking spines; sulcus spermaticus barely visible in sulcate view, being obscured by thick and muscular pedicel. The bulbous appearance of the organ may result in part from the damage accumulated from the vehicle strike. However, we are confident that this organ represents the hemipenis and not prolapsed viscera, as it is bilaterally paired and originates anterior to the vent. Overall appearance is a robust, smooth, and bulbous organ that is narrower basally and broader distally (Fig. 9).

Uropeltis* cf. *ceylanica.—Length approximately 1.5 mm (~16% of 9.1 mm TL); shape simple, subcylindrical; simple, straight, shallow, and smooth sulcus spermaticus terminating at apex; ornamented and differentiated, with recurved spines

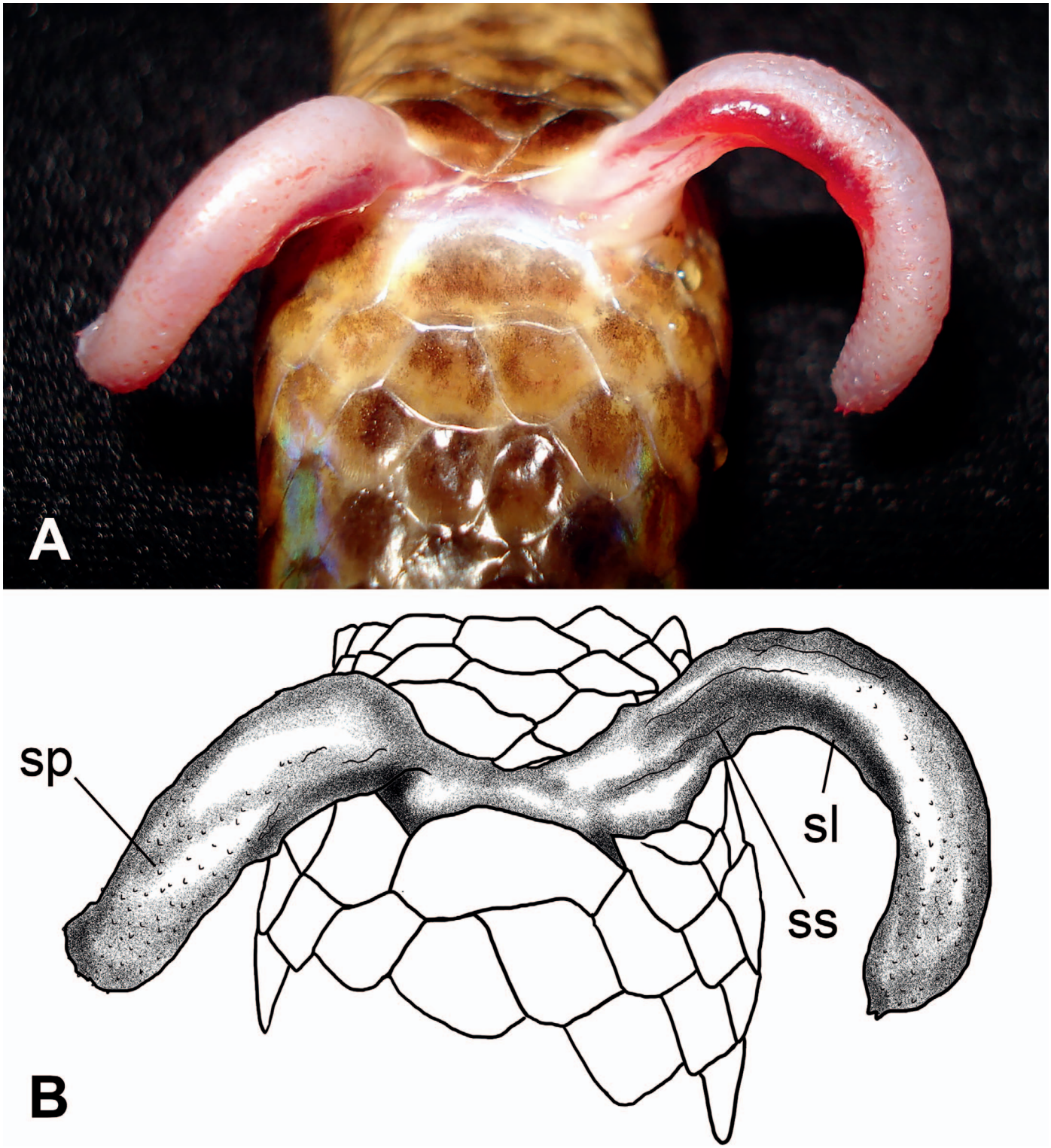

Fig. 6. Photograph (A) and drawing (B) of partially everted hemipenes of *Rhinophis saffragamus* in partial sulcate view. No fixed scale bar available; length of everted portion of organs ~50–75% of TL (see de Silva and Ukuwela, 2020 for extensive description of the full specimen). Abbreviations: sl, fleshy, lobular sulcal lips; sp, fine lobular spines or hooks; ss, sulcus spermaticus.

on the distal half, more prominent on the asulcate surface and near the apex; apex flattened and undifferentiated from immediately adjacent body of organ, with prominent spines. Overall appearance is of a cylinder or rod covered in fine spines or hooks (Fig. 10), similar to several other known species of *Rhinophis* and *Uropeltis* (Smith, 1943; Gower and Wickramasinghe, 2016; Ganesh and Achyuthan, 2020).

Uropeltis macrolepis "mahableshwarensis".—Length approximately 7.1 mm (~44% of 16.2 mm TL); reaching to the 5th subcaudal when adpressed posteriorly; hemipenis slightly

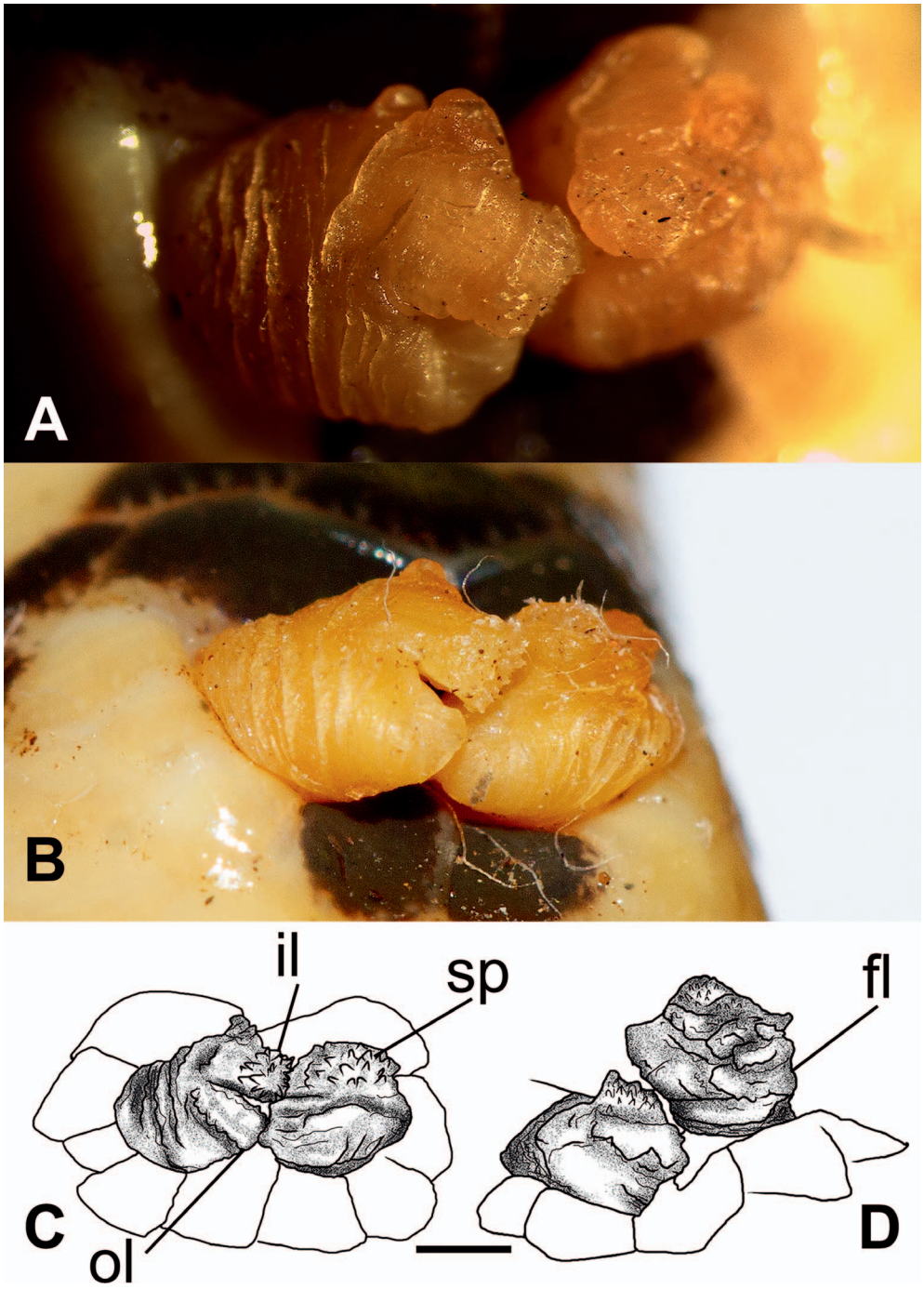

Fig. 7. Partially everted hemipenes of *Rhinophis sanguineus* (VPRS 0918093) in asulcate (A, B, C) and sulcate (D) view, showing short, stout organs with median lobular processes potentially representing a bilobate condition. No fixed scale bar available for photographs (A, B); 1 mm for illustrations (C, D); organs ~2.1 mm, ~18% TL. Abbreviations: fl, basal flounces; il, inner lobe; ol, outer lobe; sp, fine lobular spines or hooks.

damaged toward the tip. Shape simple, subcylindrical, narrower at the base; ornamented with small, recurved spines at the apex and body, more prominent on the asulcate surface. Overall appearance is a cylinder covered in spines and tapering toward the base of hemipenis with large horizontal folds or flounces. The damaged area of the organ is darkened for illustration (Fig. 11).

Uropeltis rajendrani.—Organ originally figured in Ganesh and Achyuthan (2020: img. 1H–I); updated description given here for everted organ of the holotype BNHS 3359. Length approximately 3 mm (~23% of 13 mm TL); extending to the 2nd subcaudal when adpressed posteriorly; organ fairly short and stout; unilobed and spiny, bearing tiny flounces; with a shallow sulcus spermaticus with rounded lip; plain and smooth pedicel in asulcate view (Fig. 12).

DISCUSSION

We provide initial descriptions of hemipenial morphology for 12 species from five genera. Of these, *Melanophidium* cf. *wynaudense*, *Plectrurus perrotetii*, and *Uropeltis* cf. *ceylanica* are the type species of their respective genera (McDiarmid et al., 1999). Since our observations were of opportunistically everted organs, we cannot yet present a comprehensive overview of uropeltid hemipenes or quantify intraspecific or intrageneric variation. However, some general statements

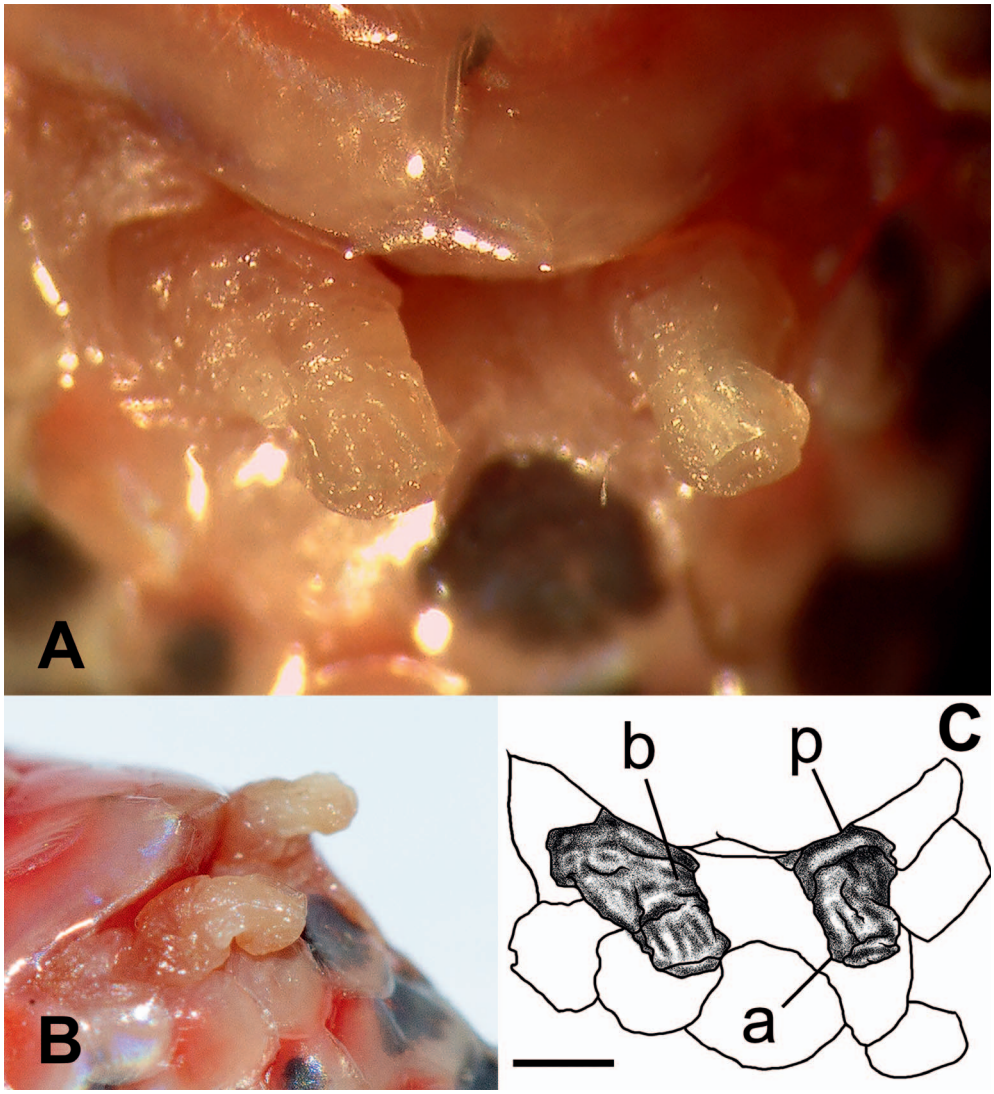

Fig. 8. Partially everted hemipenes of *Teretrurus* cf. *hewstoni* (VPTH 0721123) in asulcate view (A–C). Organ is simple, cylindrical, elongate, and conical with an enlarged pedicel. No fixed scale bar available for photographs (A, B); 1 mm for illustration (C); organs ~1.3 mm, ~19% TL. Abbreviations: a, apex; b, base; p, pedicel.

can be made in summary. We propose that there are four distinct, known types of hemipenis in uropeltids, with a possible fifth.

First are bulbous, mushroom-shaped organs with a winding sulcus spermaticus and numerous convoluted folds. In *Melanophidium*, all surfaces are uniform in character and lack obvious ornamentation such as calyces, papillae, and spines observed in other lineages. Thus, they may be considered naked and undifferentiated. However, the convoluted folds of the organ could be considered flounced ornamentation, particularly near the apex (Figs. 1, 2). Second are simple, undifferentiated, and unadorned cylindrical or coniform organs in *Plectrurus* and *Teretrurus* (Figs. 3, 8). Third are short, stout, subcylindrical organs covered in fine spines with a straight or sinuous sulcus spermaticus. This is the most common type, observed in most known *Uropeltis* and Sri Lankan *Rhinophis* (Figs. 6, 10–12).

All known uropeltid hemipenes have been previously considered to be single or unilobate. However, the hemipenes of three parapatric Indian species of *Rhinophis*, *R. karinthandandi*, *R. melanoleucus*, and *R. sanguineus*, described here (and previously) give the impression of being bilobate (Figs. 4, 5, 7), forming the fourth type. Specifically, the median lobular process described by Cyriac et al. (2020) seems to represent a second capitate lobe. This is a distinguishing characteristic from the other known Sri Lankan species, which are unilobed. We refrain from drawing a firm conclusion here pending more completely dissected and stained preparations that can be described in more detail. However, the preparations presented here and previously from four specimens of three species provide robust confirmation that hemipenial morphology in this species group differs from the simple, subcylindrical morphology of most *Uropeltis* and Sri Lankan *Rhinophis*. We observe a potential fifth morphology, a large, convoluted and bulbous organ, in one roadkill specimen of *U. bhupathyi* (Fig. 9). While the organ appeared intact, we cannot be certain it was undamaged or developmentally aberrant. Hopefully, future specimens can be observed to corroborate or reject the distinctiveness of this apparently novel morphology.

Hemipenes are still unknown in the majority of uropeltid species, and in the genera *Brachyophidium* (nested within *Teretrurus*), *Platyplectrurus*, and *Pseudoplectrurus*. Whether species in these three genera possess one of the five known types or a novel form remains to be seen. Based on the similarity between some species of *Rhinophis* and *Uropeltis* and *Plectrurus* and *Teretrurus* observed here, we can currently only identify characters specific to the genus level or above.

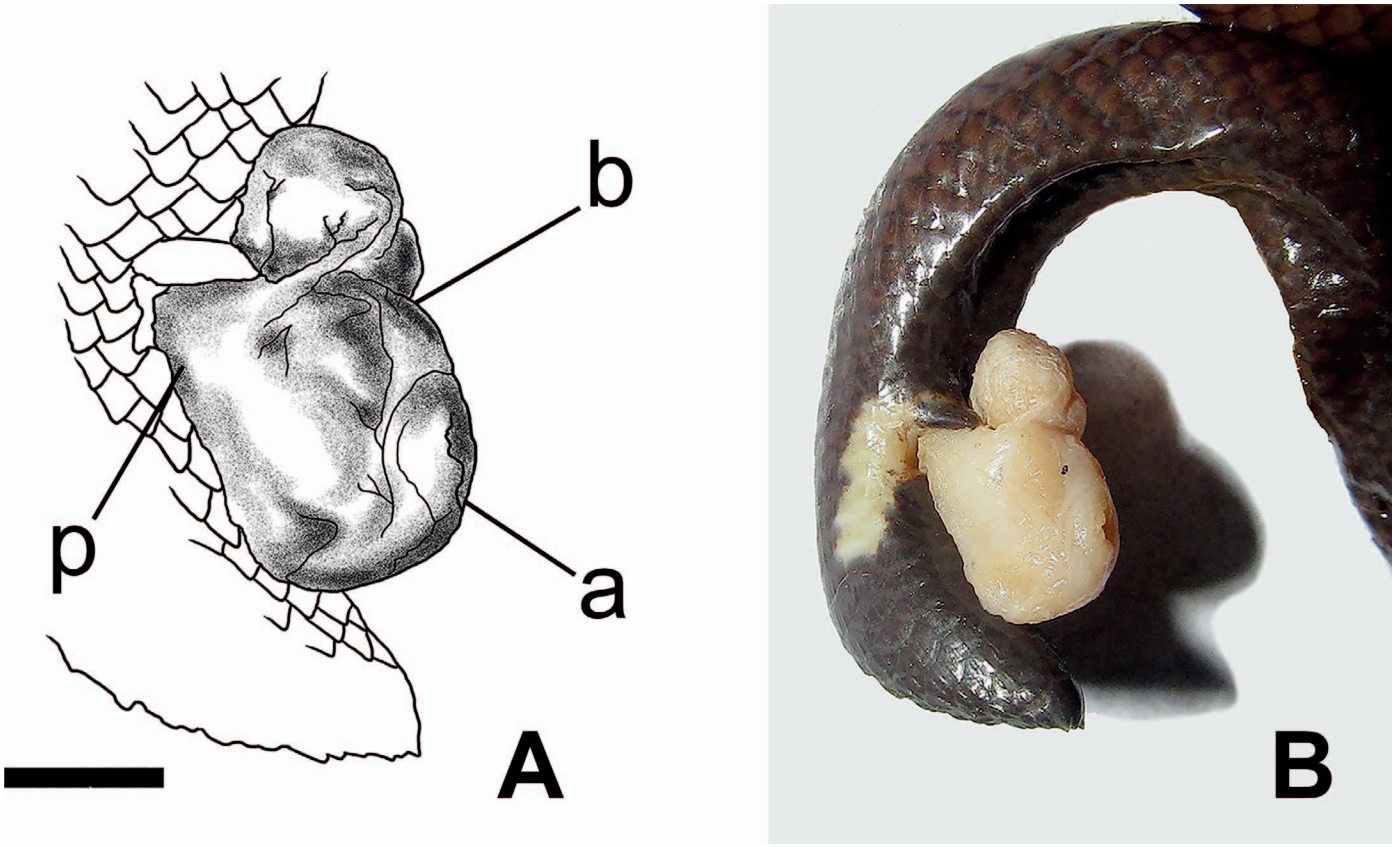

Fig. 9. Partially everted hemipenes of *Uropeltis bhupathyi* (SACON/S2) in lateral view illustrated (A) and photographed (B). Scale bar 1 mm; length of lower-most everted organ ~4 mm (~30% of 13 mm TL; Table 1). Abbreviations: a, apex; b, basal portion; p, pedicel.

However, we also find key differences in overall morphology and ornamentation in three closely related species of Indian *Rhinophis*, suggesting that these can serve as diagnostic characters for species groups in some genera. Additional study will be needed to quantify other areas of variation (such as degree of ornamentation) to determine whether hemipenes show taxonomically useful species-specific characteristics. For instance, the number and distribution of spines in subcylindrical unilobate *Rhinophis* + *Uropeltis*-type organs may provide a potential source of quantitative variation for diagnosing species.

Hemipenial incompatibility has been long known (Arnold, 1986; Köhler et al., 2012; Nunes et al., 2012) as a strong pre-zygotic barrier among snakes (David et al., 2001, 2002; Guo and Zhang, 2001) and other squamates (Maduwage et al., 2008). Among the taxa sampled here, *Melanophidium* cf. *wynaudense* and *Plectrurus perrotetii* are broadly sympatric in parts of the western Nilgiris (Wall, 1919; Pyron et al., 2016) after accounting for some elevational differences in their occurrence (SRG, pers. obs.) and show very distinct hemipenial morphologies. Additionally, the three closely related India *Rhinophis* (*R. karinthandani*, *R. melanoleucus*, and *R. sanguineus*), which are broadly parapatric or sympatric in the Wayanad region (Sampaio et al., 2020), have a seemingly bilobate organ but show several differences in the degree of ornamentation. Though we note in passing that the strongly incompatible hemipenial structures observed here support the prevailing notion of reinforced sexual incompatibility, our lack of data for typically allopatric congeneric species precludes us from commenting further. Given the phylogenetic distance between these genera, genital incompatibility may no longer be an important source of pre-zygotic isolation, though it may still be involved in speciation.

The hemipenes of uropeltids are highly modified and distinct from those of most of their henophidian relatives, the majority of which are at least partially bilobed, with a bifurcate sulcus spermaticus, and typically some degree of ornamentation or differentiation (Underwood, 1967; Branch, 1981). An exception is *Cylindrophis*, the sister group of Uropeltidae, in which the organ and sulcus are simple (Smith, 1943), and in *C. engkariensis* specifically resembles the *Plectrurus* organ in being coniform and smooth (Stuebing, 1994). In Uropeltidae, only in the three species of Indian *Rhinophis* examined do we observe a possibly bilobate condition, though interpretation of this median lobular process is unclear. Some uropeltids may indeed possess bilobate organs, or this structure observed in *R. karinthandani*, *R. melanoleucus*, and *R. sanguineus* may instead represent an additional novelty in the diverse morphological structure of snake hemipenes.

In contrast to the diversity and complexity of the hemipenes of other henophidian snakes and of alethinophidians more broadly, the hemipenes of cylindrophiids and some uropeltids appear to resemble most strongly those of typhlopoid blindsnakes. The organ in *Melanophidium* is highly similar to that of the African afrotyphlopines *Afrotyphlops* and *Rhinotyphlops* (Branch, 1986: fig. 2). Specifically, both taxa have short, bulbous, and mushroom-shaped organs with convoluted terminal folds or flounces. Similarly,

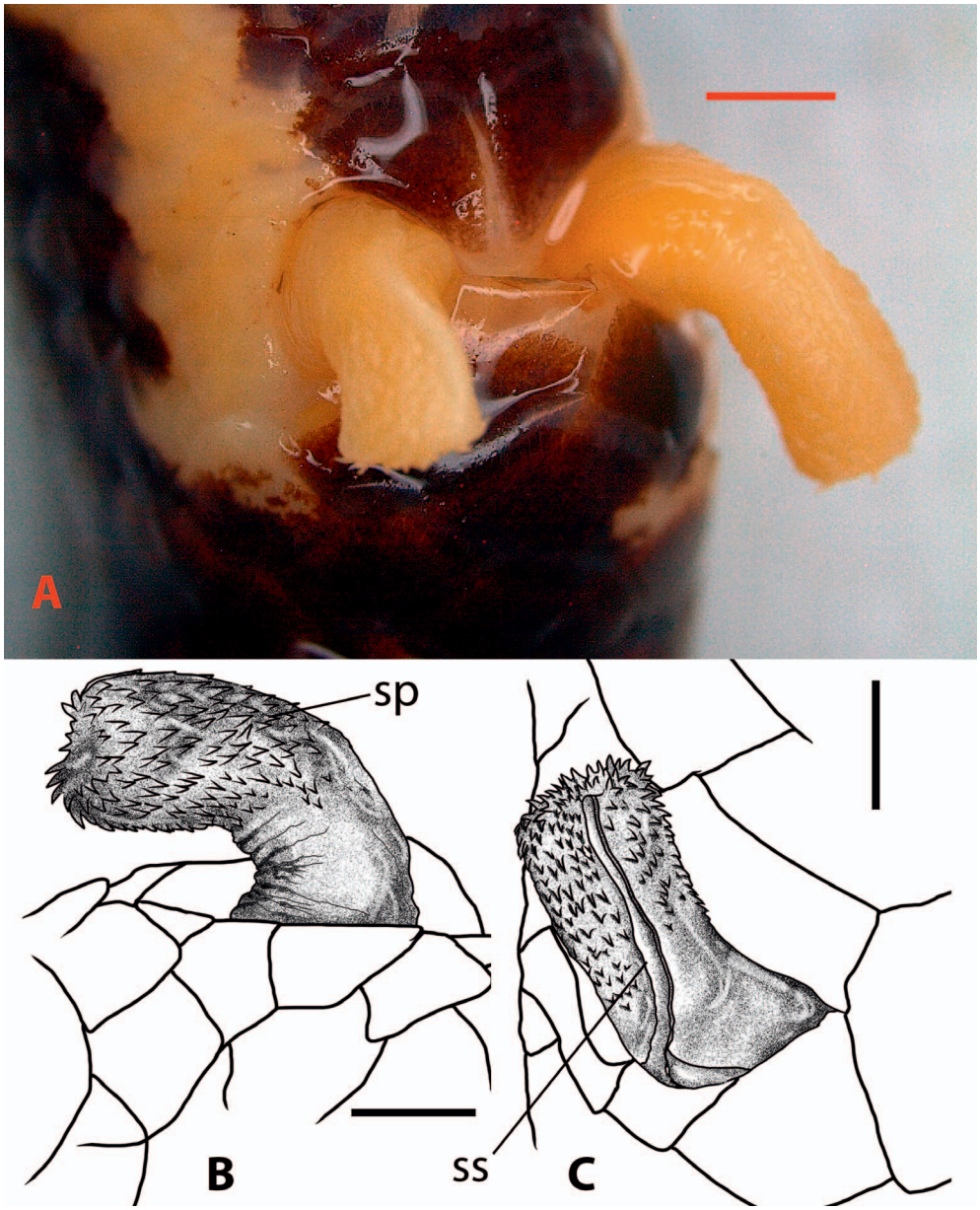

Fig. 10. Partially everted hemipenes of *Uropeltis* cf. *ceylanica* (CESS 266) in overhead (A), asulcate (B), and sulcate (C) views. Scale bars are 1 mm. Abbreviations: sp, fine lobular spines or hooks; ss, sulcus spermaticus.

the organ in *Cylindrophis* and *Plectrurus* resembles that of the African leptotyphlopids *Leptotyphlops conjunctus* and *L. nigricans* (Branch, 1986: fig. 1). In both groups, the organ is long, simple, and attenuate, with a broader, coniform base. However, Branch (1986) also reports a greater degree of ornamentation in many typhlopids (e.g., hooked terminal awns, calyces, and papillae) not seen here in uropeltids.

The subcylindrical hemipenis in Sri Lankan *Rhinophis* and some *Uropeltis* bears a gross resemblance to that of the West Indian typhlopids *Typhlops jamaicensis* and *T. richardi* illustrated and briefly described by Thomas (1966: fig. 5a). However, this comparison is not detailed, given the relative paucity of detail offered by Thomas (1966) and the overall scarcity of data on typhlopid hemipenes. The hemipenis of *T. jamaicensis* bears a resemblance to the rod-like organ of some *Rhinophis* and *Uropeltis*, but Thomas (1966) does not mention fine spines or hooks as in uropeltids. The attenuate and undifferentiated organ in *T. richardi* is also similar to that of *Plectrurus*, *Teretrurus*, and the African typhlopids described above by Branch (1986).

Among terrestrial alethinophidian and caenophidian snakes, the organ in *Cylindrophis*, *Plectrurus*, and *Teretrurus* (along with several typhlopids as noted above) also resembles that of the psammophiid caenophidian *Malpolon insignitus* (see Andonov et al., 2017). The organ in *Malpolon* is simple, cylindrical, undifferentiated, and unadorned, with a broad coniform base. This is a highly derived advanced snake that is nested within a group (Colubroides) possessing diverse and varied hemipenial morphologies, typically bilobated, highly differentiated, and heavily adorned. This suggests that the resemblance between typhlopids, cylindrophiids, uropeltids, and *Malpolon* is convergent, and further underscores the evolutionarily and ecologically labile nature of hemipenis structures across snakes.

Given the prevalence of convergence toward burrowing morphologies across squamates (Lee, 1998; Da Silva et al., 2018; Ebel et al., 2020), one potential hypothesis is that the

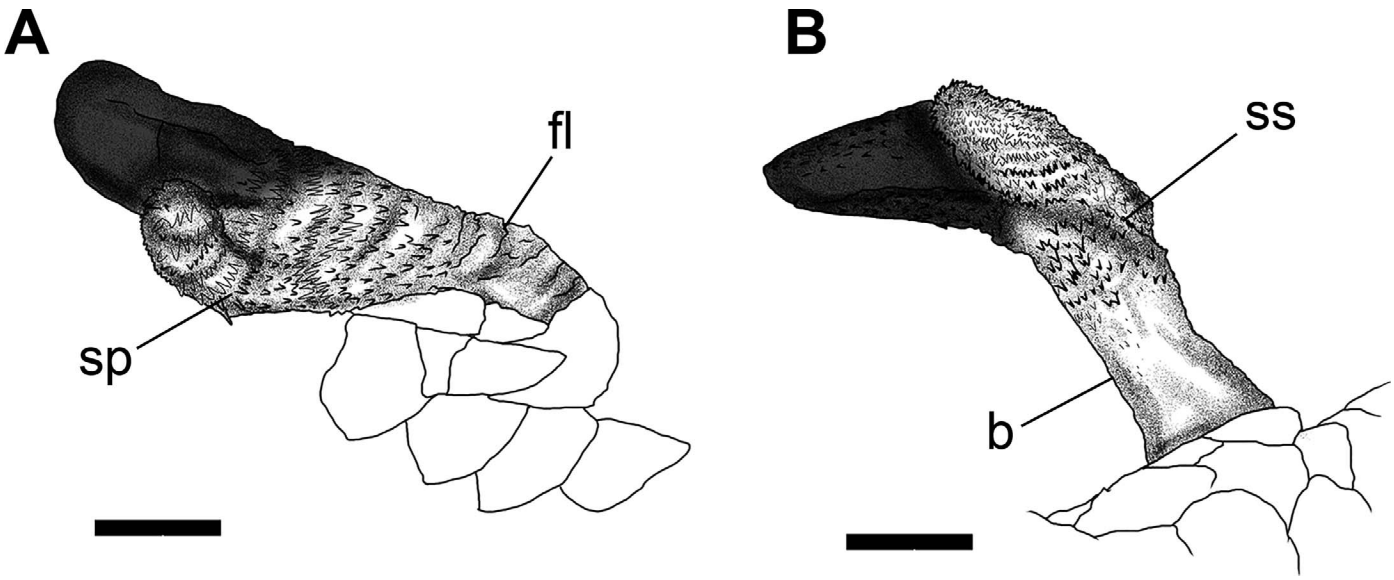

Fig. 11. Partially everted and damaged hemipenis of a roadkill *Uropeltis macrolepis* "*mahableshwarensis*" (U12; see Pyron et al., 2016) in asulcate (A) and sulcate (B) view. The damaged tissue is darkened; the remaining intact portion shows the typical "*Uropeltis*" morphology. Scale bars are 1 mm; organ length approximately 7.1 mm (~44% of 16.2 mm TL). Abbreviations: b, base; fl, folds or flounces; sp, lobular spines or hooks; ss, sulcus spermaticus.

similarity between uropeltid and typhlopoid hemipenes mirrors overall selective pressures for convergent similarity in body form and ecomorphology. Some authors have hypothesized, but failed to support, that calcified hemipenial spines may evolve in limb-reduced taxa to replace the function of limbs in couple anchoring (Nunes et al., 2014). However, this hypothesis was for terrestrial lizard species; the hemipenial simplicity observed in fossorial snakes may simply be related to an overall simplification in body form and ecomorphological complexity related to burrowing adaptations. In burrowing snakes, selective pressures for simplified hemipenes may arise from the physically constrained context of copulation; if individuals are mating underground in burrowed tunnels, little space may be available for cloacal contact.

In potential contradiction to this hypothesis of convergence, there are several other fossorial or semi-fossorial taxa that show very different and elaborate hemipenial morphol-

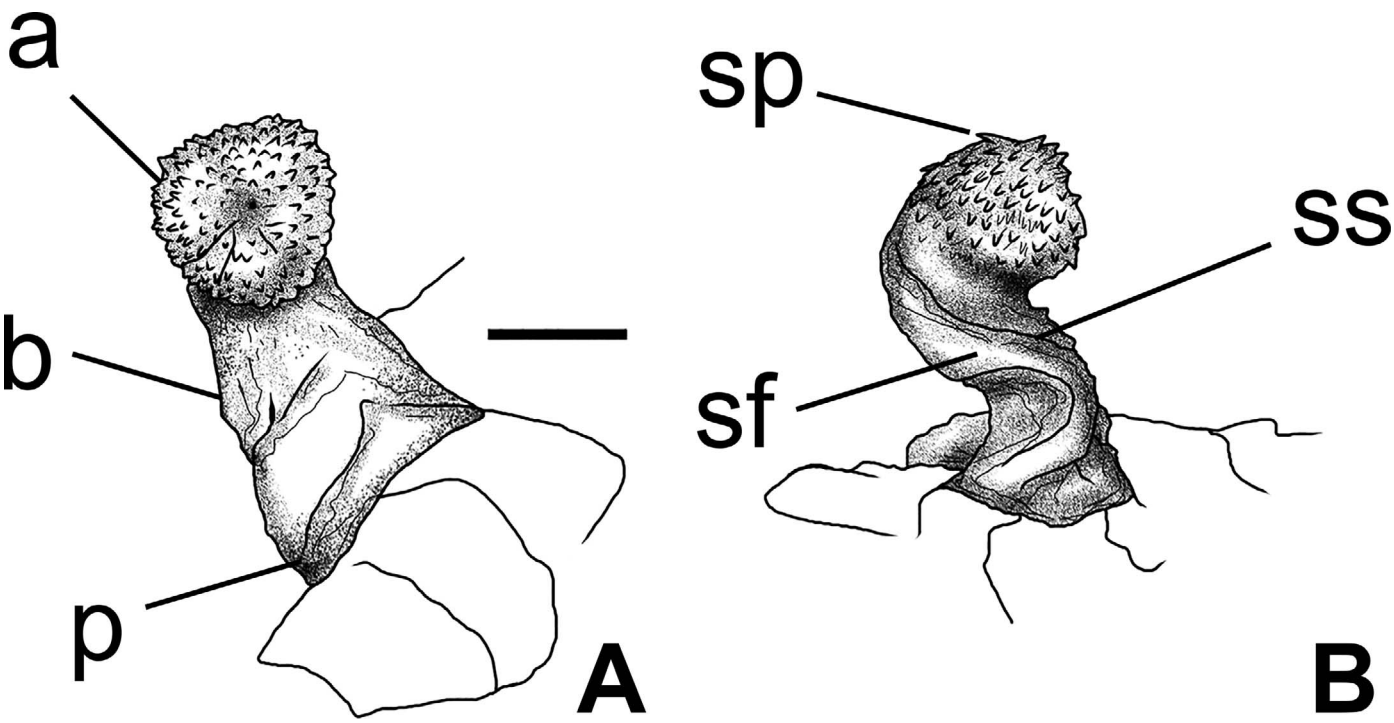

Fig. 12. Partially everted hemipenis of the holotype of *Uropeltis rajendrani* (BNHS 3359), previously photographed in Ganesh and Achyuthan (2020: img. 1H–I), illustrated here in asulcate (A) and sulcate (B) views. Scale bar is 1 mm; organ is ~3 mm, ~23% of TL. Abbreviations: a, apex; b, basal portion; p, pedicel; sf, sulcal folds; sp, lobular spines or hooks; ss, sulcus spermaticus.

ogies. These include *Apostolepis* (Santos et al., 2018), *Atractus* (Schargel and Castoe, 2003), *Geophis* (figured in Campell et al., 2018; Townsend, 2009), and *Eryx* (Andonov et al., 2017). Thus, the apparent convergence between typhlopoid and cylindrophiid + uropeltid hemipenes may not reflect selective pressures related to fossorial microhabitats or burrowing behaviors, but may instead stem from sexual selection during their recent radiation (Ganesh, 2015; Cyriac and Kodandaramaiah, 2017). Alternatively, the relatively simple hemipenes observed in typhlopoids, cylindrophiids, and uropeltids may represent symplesiomorphies from ancestral snakes, which have subsequently been heavily modified and derived in some advanced snakes. These provide alternate hypotheses that can be tested in a broader comparative context in snakes by future researchers.

Here, we provide a preliminary addition to our knowledge of hemipenial variation in uropeltids, one of the least-known snake families. Uropeltids possess at least four distinct hemipenis forms, with the simple, subcylindrical type apparently characterizing the largest number of species in *Rhinophis* and *Uropeltis*. The hemipenis is still unreported in the genera *Brachyophidium*, *Platyplectrurus*, and *Pseudoplectrurus*. Hemipenes appear to be useful in diagnosing uropeltids at least to the genus level, and in differentiating between Indian and Sri Lankan *Rhinophis*. Spinous ornamentation in some species of *Rhinophis* and *Uropeltis* may prove useful in delimiting species boundaries. Despite the overall reduced body form and ecomorphology of uropeltids compared to their henophidian relatives, uropeltid hemipenes are relatively labile and variable among genera, with some superficially resembling those of typhlopoid blindsnakes. This may be due to overall convergence toward a burrowing lifestyle, or due to other factors such as sexual selection. Uropeltids and their behavior and morphology continue to be understudied, and in need of further data in all aspects.

DATA ACCESSIBILITY

ACKNOWLEDGMENTS

This research was funded in part by US NSF grant DEB-1441719 to RAP. We thank the DBT-IISc Partnership Programme for support to KS. We thank T. Varghese of the CES Museum, and S. P. Vijayakumar, S. P. Pal, M. Prabhu, K. P. Dinesh, S. R. Chandramouli, and V. Torsekar for access to specimens. At SACON, SRG thanks P. Balsubramanian, R. Jayapal, and S. Babu for access to the museum specimens, and B. Rao and P. Karthik for curatorial help. VPC was partially funded by the Science & Engineering Research Board NPDF grant PDF/2020/000527 and thanks R. Koth and O. Adhikari for access to specimens at BNHS and photographs of the organs of paratypes of *R. melanoleucus* and *R. karinthandani*, A. Sayyed for specimens, and the Kerala Forest and Wildlife Department for permits issued to him (WL 10-7451/2013). In Sri Lanka, ADS and RAP thank the Department of Wildlife Conservation for issuing research permits.

LITERATURE CITED

Andonov, K., N. Natchev, Y. V. Kornilev, and N. Tzankov. 2017. Does sexual selection influence ornamentation of hemipenes in Old World snakes? The Anatomical Record 300:1680–1694.

Arnold, E. N. 1986. Why copulatory organs provide so many useful taxonomic characters: the origin and maintenance of hemipenial differences in lacertid lizards (Reptilia: Lacertidae). Biological Journal of the Linnean Society 29: 263–281.

Bossuyt, F., M. Meegaskumbura, N. Beenaerts, D. J. Gower, R. Pethiyagoda, K. Roelants, A. Mannaert, M. Wilkinson, M. M. Bahir, and K. Manamendra-Arachchi. 2004. Local endemism within the Western Ghats–Sri Lanka biodiversity hotspot. Science 306:479–481.

Branch, W. R. 1981. Hemipenes of the Madagascan boas *Acrantophis* and *Sanzinia*, with a review of hemipeneal morphology in the Boinae. Journal of Herpetology 15:91–99.

Branch, W. R. 1986. Hemipenial morphology of African snakes: a taxonomic review. Part 1. Scolecophidia and Boidae. Journal of Herpetology 20:285–299.

Campbell, J. A., E. N. Smith, and A. S. Hall. 2018. Caudals and calyces: the curious case of a consumed Chiapan colubroid. Journal of Herpetology 52:458–471.

Cope, E. D. 1893. Prodromus of a new system of the non-venomous snakes. The American Naturalist 27:477–483.

Cope, E. D. 1895. The classification of the Ophidia. Transactions of the American Philosophical Society 18: 186–219.

Cyriac, V. P., and U. Kodandaramaiah. 2017. Paleoclimate determines diversification patterns in the fossorial snake family Uropeltidae Cuvier, 1829. Molecular Phylogenetics and Evolution 116:97–107.

Cyriac, V. P., S. Narayanan, F. L. Sampaio, P. Umesh, and D. J. Gower. 2020. A new species of *Rhinophis* Hemprich, 1820 (Serpentes: Uropeltidae) from the Wayanad region of peninsular India. Zootaxa 4778:329–342.

Da Silva, F. O., A. C. Fabre, Y. Savriama, J. Ollonen, K. Mahlow, A. Herrel, J. Müller, and N. Di-Poï. 2018. The ecological origins of snakes as revealed by skull evolution. Nature Communications 9:376.

David, P., N. Vidal, and O. S. Pauwels. 2001. A morphological study of Stejneger's pitviper *Trimeresurus stejnegeri* (Serpentes, Viperidae, Crotalinae), with the description of a new species from Thailand. Russian Journal of Herpetology 8:205–222.

David, P., G. Vogel, O. S. Pauwels, and N. Vidal. 2002. Description of a new species of the genus *Trimeresurus* from Thailand, related to *Trimeresurus stejnegeri* Schmidt, 1925 (Serpentes, Crotalidae). Tropical Natural History 2:5–19.

de Silva, A., and K. Ukuwela. 2020. A Naturalist Guide to Reptiles of Sri Lanka. Second edition. John Beaufoy Publishing Ltd., Oxford, U.K.

Dowling, H. G. 2002. "Intraspecific variation of the hemipenis," a correction, with comments on other erroneous descriptions. Herpetological Review 33:12–14.

Dowling, H. G., and J. M. Savage. 1960. A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. Zoologica 45:17–28.

Dunn, E. R. 1928. A tentative key and arrangement of the American genera of Colubridae. Bulletin of the Antivenom Institute of America 2:18–24.

Ebel, R., J. Müller, T. Ramm, C. Hipsley, and E. Amson. 2020. First evidence of convergent lifestyle signal in reptile skull roof microanatomy. BMC Biology 18:185.

Ganesh, S. R. 2015. Shieldtail snakes (Reptilia: Uropeltidae)—the Darwin's finches of south Indian snake fauna?, p. 13–24. *In*: Manual on Identification and Preparation of Keys of Snakes with Special Reference to Their Venomous Nature in India. P. Kannan (ed.). Proceedings by Govt. Arts College, Udhagamandalam, Tamil Nadu, India.

Ganesh, S. R., and N. S. Achyuthan. 2020. A new species of shieldtail snake (Reptilia: Squamata: Uropeltidae) from Kolli Hill complex, southern Eastern Ghats, peninsular India. Journal of Threatened Taxa 12:15436–15442.

Gower, D. J., and J. D. Ablett. 2006. Counting ventral scales in Asian anilioid snakes. The Herpetological Journal 16: 259–263.

Gower, D. J., and K. Maduwage. 2011. Two new species of *Rhinophis* Hemprich (Serpentes: Uropeltidae) from Sri Lanka. Zootaxa 2881:51–68.

Gower, D. J., and L. M. Wickramasinghe. 2016. Recharacterization of *Rhinophis dorsimaculatus* Deraniyagala, 1941 (Serpentes: Uropeltidae), including description of new material. Zootaxa 4158:203–212.

Guo, P., and F. Zhang. 2001. Comparative studies on hemipenes of four species of *Trimeresurus* (sensu stricto) (Serpentes: Crotalinae). Amphibia Reptilia 22:113–118.

Jadin, R. C., and E. N. Smith. 2010. The hemipenis of *Trimorphodon quadruplex*. Herpetological Review 41:157.

Jins, V. J., F. L. Sampaio, and D. J. Gower. 2018. A new species of *Uropeltis* Cuvier, 1829 (Serpentes: Uropeltidae) from the Anaikatty Hills of the Western Ghats of India. Zootaxa 4415:401–422.

Köhler, J., M. Hahn, and G. Köhler. 2012. Divergent evolution of hemipenial morphology in two cryptic species of mainland anoles related to *Anolis polylepis*. Salamandra 48:1–11.

Lee, M. S. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. Biological Journal of the Linnean Society 65:369–453.

Maduwage, K., M. Meegaskumbura, A. de Silva, and R. Pethiyagoda. 2008. Phylogenetic implications of hemipenial morphology in Sri Lankan agamid lizards. Current Science 95:838–840.

McDiarmid, R. W., J. A. Campbell, and T. Touré. 1999. Snake Species of the World: A Taxonomic and Geographic Reference. Vol. 1. Herpetologists' League, Washington, D.C.

Myers, C. W. 1974. The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. Bulletin of the American Museum of Natural History 153:1–262.

Myers, C. W., and J. E. Cadle. 2003. On the snake hemipenis, with notes on *Psomophis* and techniques of eversion: a response to Dowling. Herpetological Review 34: 295–302.

Nunes, P. M. S., F. F. Curcio, J. G. Roscito, and M. T. Rodrigues. 2014. Are hemipenial spines related to limb reduction? A spiny discussion focused on gymnophthalmid lizards (Squamata: Gymnophthalmidae). The Anatomical Record 297:482–495.

Nunes, P. M. S., A. Fouquet, F. F. Curcio, P. J. Kok, and M. T. Rodrigues. 2012. Cryptic species in *Iphisa elegans* Gray, 1851 (Squamata: Gymnophthalmidae) revealed by hemipenial morphology and molecular data. Zoological Journal of the Linnean Society 166:361–376.

Pesantes, O. S. 1994. A method for preparing the hemipenis of preserved snakes. Journal of Herpetology 28:93–95.

Pyron, R. A., S. R. Ganesh, A. Sayyed, V. Sharma, V. Wallach, and R. Somaweera. 2016. A catalogue and systematic overview of the shield-tailed snakes (Serpentes: Uropeltidae). Zoosystema 38:453–506.

Pyron, R. A., H. D. Kandambi, C. R. Hendry, V. Pushpamal, F. T. Burbrink, and R. Somaweera. 2013. Genus-level phylogeny of snakes reveals the origins of species richness in Sri Lanka. Molecular Phylogenetics and Evolution 66: 969–978.

Rajendran, M. V. 1985. Studies in Uropeltid Snakes. Madurai Kamaraj University, Madurai, India.

Sampaio, F. L., S. Narayanan, V. P. Cyriac, G. Venu, and D. J. Gower. 2020. A new Indian species of *Rhinophis* Hemprich, 1820 closely related to *R. sanguineus* Beddome, 1863 (Serpentes: Uropeltidae). Zootaxa 4881:1–24.

Santos, F. M. D., O. M. Entiauspe-Neto, J. D. S. Araújo, M. B. D. Souza, T. D. Lema, C. Strüssmann, and N. R. D. Albuquerque. 2018. A new species of burrowing snake (Serpentes: Dipsadidae: *Apostolepis*) from the state of Mato Grosso, Central-West region of Brazil. Zoologia (Curitiba) 35:e26742.

Savage, J. M. 1997. On terminology for the description of the hemipenes of squamate reptiles. Herpetological Journal 7: 23–25.

Schargel, W. E., and T. A. Castoe. 2003. The hemipenes of some snakes of the semifossorial genus *Atractus*, with comments on variation in the genus. Journal of Herpetology 37:718–721.

Smith, M. A. 1943. The Fauna of British India Including Ceylon and Burma. Taylor and Francis, London.

Stuebing, R. 1994. A new species of *Cylindrophis* (Serpentes, Cylindrophiidae) from Sarawak, western Borneo. Raffles Bulletin of Zoology 42:967–973.

Thomas, R. 1966. A reassessment of the Virgin Islands *Typhlops* with the description of two new subspecies. Revista de Biología Tropical 13:187–201.

Torres-Carvajal, O., L. Y. Echevarría, P. J. Venegas, G. Chávez, and J. D. Camper. 2015. Description and phylogeny of three new species of *Synophis* (Colubridae, Dipsadinae) from the tropical Andes in Ecuador and Peru. ZooKeys 546:153–179.

Townsend, J. H. 2009. Morphological variation in *Geophis nephodrymus* (Squamata: Colubridae), with comments on conservation of *Geophis* in eastern nuclear Central America. Herpetologica 65:292–302.

Uetz, P., and J. Hošek. 2021. The Reptile Database. http://www.reptile-database.org/ (accessed 5 October 2021).

Underwood, G. 1967. A Contribution to the Classification of Snakes. Trustees of the British Museum (Natural History), London.

Wall, F. 1919. Notes on a collection of snakes made in the Nilgiri hills and the adjacent Wayanad. Journal of the Bombay Natural History Society 26:552–584.

Wall, F. 1923. Notes on a collection of snakes from Shenbaganur, Palni Hills. Journal of the Bombay Natural History Society 29:388–398.

Zaher, H. 1999. Hemipenial morphology of the South American xenodontine snakes: with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. Bulletin of the American Museum of Natural History 240:1–168.

Zaher, H., and A. L. C. Prudente. 2003. Hemipenes of *Siphlophis* (Serpentes, Xenodontinae) and techniques of hemipenial preparation in snakes: a response to Dowling. Herpetological Review 34:302.