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TAXONOMY, NATURAL HISTORY, AND ZOOGEOGRAPHY OF THE SOUTHERN AFRICAN SHIELD COBRAS, GENUS *ASPIDELAPS* (SERPENTES: ELAPIDAE)

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Abstract. The southern African elapid genus *Aspidelaps* remains poorly understood in most aspects of its biology. The available information is sparse and often only published via anecdotal notes in obscure journals or out-of-print books. The review presented here is not comprehensive in respect to many historical herpetological surveys of the southern African region, but we here provide a compilation of updated taxonomic, ecological, behavioral, zoogeographical, and toxicological information, including notes on captive husbandry.

Key Words. *Aspidelaps*; Behavioral ecology; Elapidae; Husbandry; Southern Africa; Taxonomy; Toxicology; Zoogeography.

The genus *Aspidelaps* currently comprises two species of relatively small stout-bodied elapids restricted to southern Africa. These are most easily recognized by an enlarged rostral scale, indicating fossorial habits, and a "hood" much smaller than those typically associated with the true cobras (*Naja*). *Aspidelaps lubricus* has come to be known by its common name Coral Snake, a reflection of the red to orange coloration with black cross-bands. The common name of *Aspidelaps scutatus* is Shield Snake, or Shield-Nosed Snake, after the most highly modified rostrum of any snake (Greene 1997). The genus remains poorly studied, and the available information is often rather difficult to obtain due to the obscurities of the journals in which it is typically published. We here present a review of the taxonomy, morphology, systematics, life history, zoogeography, toxicology, and captive husbandry for the genus *Aspidelaps*, with keys to the genera of southern African elapids including *Aspidelaps* species. The taxonomy of *A. lubricus* is revised based on material recently studied by DGB.

In Africa, *Aspidelaps scutatus* has always been called the Shield Snake or Shield-Nosed Snake, whereas *A. lubricus* is known as the Coral Snake (F.W. FitzSimons 1912; V. FitzSimons 1962; Spawls and Branch 1995; Visser and Chapman 1978). Frank and Ramus (1995) introduced the names Shieldnose Cobra and South African Coral Snake respectively, whereas Greene (1997) used Shield-Nosed Cobra and Coral Cobra. In a study of the phylogenetic relationships of elapid snakes, Slowinski and Keogh (2000) found significant bootstrap support for a core cobra group consisting of *Naja, Boulengerina, Paranaja, Aspidelaps, Hemachatus,* and *Walterinnesia*, but excluding *Elapsoidea* and *Dendroaspis.* Thus, in an attempt to stabilize common names for these snakes, we propose to use

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Shield Cobras for the genus, a direct translation of the scientific name. *Aspidelaps l. lubricus* then becomes the Coral Shield Cobra, *A. l. cowlesi* (including *A. l. infuscatus*) is the Namibian Shield Cobra, *A. s. scutatus* is the Kalahari Shield Cobra, *A. s. intermedius* is the Lowveld Shield Cobra, and *A. s. fulafula* is the Eastern Shield Cobra.

TAXONOMY, MORPHOLOGY, AND GEOGRAPHIC DISTRIBUTION

The genus *Aspidelaps* is a member of the Elapidae, a family of proteroglyphous snakes, usually with highly neurotoxic and fast-acting venom (or with cytotoxic venom in spitting cobras of the genus *Naja* and myotoxic venom in some Australian marine species). Members of this family usually lack a loreal shield, but otherwise head squamation is similar to that seen in the Colubridae. The *sulcus spermaticus* of the elapid hemipenis is forked; the mode of reproduction of southern African elapids is oviparity (Broadley 1983), with the exception of the ovoviparous *Hemachatus*. The family contains nearly 300 species in approximately 60 genera (Slowinski and Keogh 2000), distributed throughout tropical and subtropical regions of both the Old and New World, with a few species in temperate climates and none in Madagascar or Europe.

Key to the Families of Southern African Snakes

1a Body wormlike, covered above and below with small, smoothly polished, close-fitting, and more or less uniform-sized scales; eyes vestigial beneath head shields; mouth inferior and small 2

1b Body covered with small scales above, but usually with transversely enlarged ventral plates below (except in Hydrophiidae); eyes well developed, distinct and moveable beneath a transparent scale or brille...........3

2a Ocular shield not bordering the lip; teeth present only in the upper jaw; ≥ 20 midbody scale rows; tail as long as, or slightly longer than broad....**Typhlopidae**

2b Ocular shield bordering the lip; teeth present only in lower jaw; 14 midbody scale rows; tail at least three times as long as broad ....**Leptotyphlopidae**

3a Ventral plates distinctly narrower than body; supraocular broken up into small shields; upper labial shields with deep pits; vestigial hind limbs visible externally as a pair of claws bordering the vent ...... **Pythonidae**

3b Ventral plates almost as broad as the body (except in Hydrophiidae); supraocular, if present, not broken up; labials without pits; no vestiges of hind limbs.........4

4a No enlarged poison fangs present at the front of the upper jaw; if grooved fangs are present, they are situated far back below the eye; loreal shield usually present ....**Colubridae**

4b One or two pairs of enlarged caniculate or tubular poison fangs at the front of the upper jaw 5

5a Poison fangs large, moveable, folded back in a large membraneous sheath against the roof of the mouth when not in use; loreal shield(s) present; dorsal scales with apical pits ....**Viperidae**

5b Poison fangs more or less fixed, not or only partly concealed by a sheath; loreal shield absent; dorsal scale without apical pits 6

6a Fangs extending posterior to the eye; upper labials 5–6 (rarely four or seven); lower labials 5–6 (rarely four, seven, or eight) ....**Atractaspidae**

6b Fangs situated well forward of the eye; upper labials 6–10; lower labials 7–13 (rarely six)......................7

7a Tail cylindrical; dorsal scales imbricate; ventral shield nearly as broad as body ....**Elapidae**

7b Tail strongly compressed vertically and paddle shaped; dorsal scales juxtaposed; ventral scales much narrower than body or not differentiated from dorsals..**Hydrophiidae**

Key to the Genera of Southern African Elapids

1a Three preoculars, widely separated from nasal, prefrontals in contact with labials; > 90 subcaudals...... ....***Dendroaspis* (mambas)**

1b One or two preoculars, in contact with nasal and separating prefrontals from labials; < 75 subcaudals 2

2a Internasal not bordering nostril; dorsal scales in 13 or 15 rows at midbody 3

2b Internasal bordering nostril; dorsal scales in 17 (very rarely 15) or more rows at midbody 4

3a Nostril pierced in a single nasal shield; eye very small; scales in 15 rows at midbody ....***Homoroselaps* (harlequin snakes)**

3b Nostril pierced between two nasal shields; eye moderate; scales in 13 rows at midbody......................... ....***Elapsoidea* (African garter snakes)**

4a Rostral very large, detached laterally and shield-like ....***Aspidelaps* (shield cobras)**

4b Rostral not detached laterally or shield-like 5

5a Dorsal scales strongly keeled; ventrals 116–150; subcaudals 33–47 ....***Hemachatus* (rinkhals)**

5b Dorsal scales smooth; ventrals 175–228; subcaudals 50–78..***Naja* (cobras)**

Taxonomic History

The species now known as *Aspidelaps lubricus* was described as *Natrix lubrica* by Laurenti in 1768, based on a specimen from the "Cape of Good Hope" that was illustrated by Seba (1735, Thesaurus II, Pl. xliii, Fig. 3); it is not known if the original specimen still survives in a European museum. Early synonyms were *Coluber latonia* Daudin 1803 and *Naja somersetta* A. Smith 1826. Schlegel (1837) also considered this species to be a true cobra and included it in the genus *Naja* along with a variety of non-cobra elapids from South Africa (now considered different genera). Fitzinger (1843) erected the genus *Aspidelaps,* based on *Elaps lubricus* Merrem (1820) = *Natrix lubrica* Laurenti 1768, but Duméril and Bibron (1854) followed Merrem in calling the species *Elaps lubricus.* In 1849, Andrew Smith listed *Aspidelaps lubricus,* but also erected a new genus *Cyrtophis* for the type specimen of what is now known as *Aspidelaps scutatus*. Bianconi (1849) also described *Naja fula-fula* from Mozambique*,* but it was placed in the synonymy of *Aspidelaps scutatus* by Jan (1873), a move followed by Boulenger (1896), although Peters (1882) had still used *Cyrtophis scutatus*. Bogert (1940) described *A. lubricus cowlesi* from the only two Angolan specimens belonging to this genus. *Aspidelaps scutatus bachrani* Mertens 1954, a western race described from Namibia, was placed into the synonymy of *A. scutatus* by V. FitzSimons (1962). Broadley (1968) revived *fulafula* (Bianconi) as an eastern race of *A. scutatus* and described *A. s. intermedius* from the Transvaal lowveld.

During 1993–94 DGB undertook a revision of *Aspidelaps lubricus* and borrowed all the available material from southern African and U.S. museums. Unfortunately, the data file was lost before the data could be analyzed when his briefcase was stolen during a burglary. As most of the loan material had been returned, the project was abandoned. During a recent visit to Windhoek, it was confirmed that *A. l. infuscatus* Mertens 1954 is a synonym of *A. l. cowlesi* Bogert 1940, based on the external examination of 96 specimens. The types of *A. l. cowlesi* Bogert represent the northern end of a cline, the banded pattern gradually becomes less distinct and the head changes from black to pale brown. The variation in four specimens from Opuwo, Kaokoveld (NMWN 2464-5, 2471, 2668), shows this transition. Three have the head pale brown, the other is blackish; the dark bands are broad and very faint; two snakes have 21 midbody scale rows, the other two have 19. Institutional acronyms used in the text follow Leviton et al. (1985).

The Genus *Aspidelaps* Fitzinger 1843

Definition. The following is summarized from Boulenger (1896), Bogert (1943), and Broadley (1983). Maxillary extending forwards beyond the palatine, with a pair of large grooved poison fangs and no other maxillary teeth; palatine with five to six teeth, pterygoids with 8–13 and dentary with 11–14 teeth, with the anteriormost teeth longest. Head short and only slightly distinct from neck; eye moderate in size with round or vertically elliptical pupil; rostral shield very large, detatched on the sides; nostril between two or three nasals (the lower one very small or absent) and the internasal; loreal absent. Body cylindrical or somewhat depressed; scales oblique, smooth or keeled posteriorly, without apical pits, in 19–23 (very rarely 25) rows at midbody; ventrals rounded; cloacal shield entire. Tail short, obtuse; subcaudals in two rows. Oviparous. Two species.

Distribution. South Africa, Namibia, southwestern Angola, Botswana, Zimbabwe, southern Mozambique.

Aspidelaps lubricus lubricus (Laurenti 1768)
Coral Shield Cobra (Figs. 1A and 2A)

Type locality.—"Cape of Good Hope."

Description.—Rostral as broad or slightly broader than deep, one-third to two-fifths the width of the head (which is broader in males than in females) forming a right or acute angle above, but not completely separating the internasals, which are much longer than the prefrontals; frontal 1.3–1.6 times long as broad and broader than the supraoculars, shorter than its distance from the end of the snout and shorter than the parietals; internasal and posterior nasal in contact with the single preocular on either side; two or three postoculars; temporals 2 + 2, three or four, lower anterior very large and usually touching the labial margin between the fifth and sixth upper labials; six or seven upper labials, third and fourth entering the eye; eight lower labials, the fifth cuneate, the first three or four in contact with the anterior chin shields, which are as long as or longer than the posterior chin shields. Dorsal scales smooth, 19 (rarely 21) rows at midbody. Ventrals smooth, 139–179; cloacal shield entire; subcaudals 17–36.

Hemipenis in male extends backwards to the ninth subcaudal, bifurcating at the fifth; *sulcus spermaticus* divides at the fourth subcaudal and distal to its division there are well developed spines arranged in diagonal rows, while the ends of the lobes bear ill-defined calyces (Bogert 1940).

Color.—Orange to red in life with slightly angular conspicuous black annuli on the back, with the first often the widest, forming a nuchal collar and triangular in shape, subsequent cross-bands become progressively more narrow posteriorly and all bands are narrower on the ventral surface, 20–47 (15–39 on body and three to ten on tail) in number; head is more reddish, with a black bar below the eye; often a black cross-bar between the eyes and an oblique band on the temple. Venter is yellowish or infuscated with black medially, with at least the first two or three anterior dorsal bands extending ventrally, forming annuli. In juveniles, all black crossbands encircle the body but fade with age.

Size.—Lengths of largest recorded specimens (SVL + tail length in mm): male (NMZB 12177) 430 + 52; female (NMZB 12124) 630 + 68. Body to tail length ratio usually 9.2–10.8.

Distribution.—The Cape provinces of South Africa eastward to the Great Fish River and northward into the southern Free State Province and southwestern Namibia (Fig. 2). Buys and Buys (1983) illustrate a specimen allegedly from Windhoek, but no voucher specimens have been verified for this region.

Remarks.—Specimens from Little Namaqualand and southwestern Namibia, centered on Springbok, but extending south to Nuwerus and

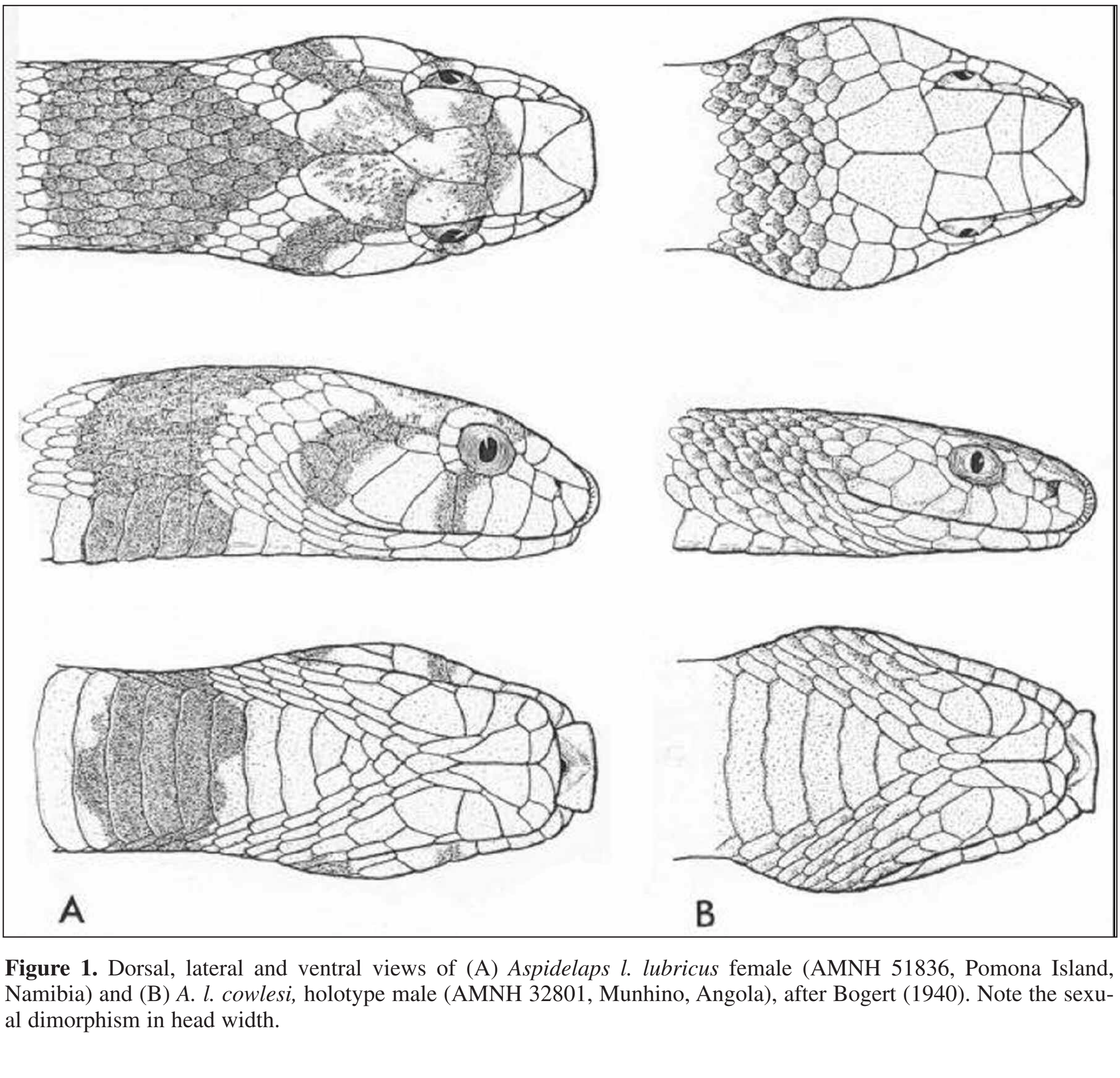

Figure 1. Dorsal, lateral and ventral views of (A) *Aspidelaps l. lubricus* female (AMNH 51836, Pomona Island, Namibia) and (B) *A. l. cowlesi,* holotype male (AMNH 32801, Munhino, Angola), after Bogert (1940). Note the sexual dimorphism in head width.

north to Aus and Pomona, may represent an undescribed taxon, characterized by high scale counts (ventrals 157–172 in males, 167–178 in females; subcaudals 28–37 in males, 21–32 in females) and a more tapering tail than the typical form, which it resembles in color pattern. More material, and preferably data from mtDNA sequencing, is needed to confirm the status of these populations.

Aspidelaps lubricus cowlesi Bogert 1940
Namibian Shield Cobra (Figs. 1B and 2B,C)

Type locality.—Munhino, southwest Angola.

Description.—Head scalation in general similar to typical *A. l. lubricus*, except that the lower anterior temporal is typically transformed into a large sixth labial (Fig. 1B); one preocular; three postoculars (rarely two or four); temporals usually 1 + 3; seven upper labials, with third and fourth entering orbit; eight (rarely nine) lower labials, the fifth cuneate, the first four (rarely three) in contact with anterior chin shields. Dorsal scales smooth in 19 or 21 rows at midbody; ventrals smooth, 142–170, cloacal shield entire; subcaudals 25–38.

Hemipenis extends to the eighth subcaudal, bifurcating at the fifth, the sulcus dividing at the third; stout spines arranged in diagonal rows are distal to the sulcus with a transition to coarsely reticulated calyces on the distal end of each lobe (Bogert 1940).

Color.—Dorsal coloration is dull dirty white to yellowish, pinkish to dark gray with scales usually dark-edged or with anterior half of each darkened to give a checkered effect; 24–66 black crossbands (18–52 on back, 5–14 on tail), which vary in distinctness in different parts of the taxon's range (northern specimens with markings indistinct to absent, southern specimens distinct); in juveniles and some adults broad and narrow crossbands alternate, but in most adults the narrow bands fade out. Head often uniformly black above or with black crossbands, the first between the eyes and continued down on either side below the eye to lip, the second over back of head, chevron-shaped, with apex on back of frontal and extending downwards on either side to angle of mouth, but head often uniformly pale in northern populations. The nuchal band and two or three following bands usually completely encircle body, while remaining bands seldom extend to the lower surface and, even when they do, are faint. Venter creamy to dirty white or yellowish with three to four conspicuous annuli on neck; remainder of venter uniformly pale or with faint continuations of dorsal crossbands and/or scattered dusky spots.

Size.—Lengths of largest recorded specimens (SVL + tail length in mm): Male (SMWN 9645) 655 + 85, Female (SMWN 2455) 690 + 80. Body to tail length ratio is 7.3 – 9.6.

Distribution.—Southwestern Angola and western Namibia south to Lüderitz (Fig. 3).

Remarks.—The 'diagnostic' characters for *A. l. cowlesi*, a uniformly pale head and 21 midbody scale rows, are occasionally seen in individuals throughout northern Namibia, though those seem to be unrelated occurrences. There is no justification at this time for the recognition of two subspecies (*cowlesi* and *infuscatus* [Fig. 2C]) and the name *cowlesi* has priority.

Aspidelaps scutatus scutatus (A. Smith 1848)
Kalahari Shield Cobra (Fig. 2D)

Type locality.—"Kaffirland and the country towards Natal", corrected to the Marico-Crocodile Confluence, South Africa, by Broadley (1968).

Description.—Head short and broad, rostral broader than deep, two fifths to half as broad as the head, forming an obtuse angle above, separating the internasals; frontal small, six-sided, breadth equal to or greater than length, as long as the prefrontals, shorter than the parietals; internasal and posterior nasal in contact with the preocular, which is single or rarely divided; a subocular present or absent; three postoculars (exceptionally two or four); temporals 2 + 4 (exceptionally 2 + 5, 2 + 6, or 3 + 5), lower anterior very large and nearly reaching the labial margin between the fifth and sixth upper labials (rarely actually separating latter [Broadley 1959]); six upper labials (exceptionally five, due to fusion of the fourth and fifth), fourth entering the orbit or excluded by a subocular; eight lower labials, the fifth cuneate, the first three or four in contact with the anterior chin-shields, which are longer than the posterior. Dorsal scales in 21 (exceptionally 23) rows at midbody, smooth to faintly keeled anteriorly but gradually becoming tubercularly keeled posteriorly and on the tail, distinctly larger and smoother on the sides than above. Ventrals 108–119 in males, 113–123 in females; cloacal shield entire; subcaudals 25–31 in males, 19–24 in females.

Hemipenis extends to the eleventh subcaudal, dividing at the sixth, the *sulcus spermaticus* dividing at the fifth; sulcus semi-revolute centripetal, asulcal surface surrounded by a short region of spinose calyces which merge into long, ossified, non-webbed spines that increase slightly in size proximately, carpeting the arms; the basal region is nude with a few scattered spinules, an unusual feature is two longitudinal flaps on the sides of the basal regions; terminating in a flat, nude region at the tips of the arms; sulcal folds unadorned and unraised.

Color.—Head and body pale gray-brown, reddish brown, orange or yellow, with a series of ill-defined light to dark brown transverse spots or blotches over middle of the back and tail; scales on body and tail usually dark-edged and often with a series of smaller dark spots on sides; a chevron-shaped black marking on the head followed by a pale interspace, and then by a black nuchal collar, nearly or completely encircling the neck, followed again by a large black blotch which may or may not extend downwards on the sides to form a band across the undersurface of the body; a black vertical streak below the eye and posterior temporal region also black; belly yellowish-white with the afore mentioned bands, which partly or completely encircle the body anteriorly. The degree of black on adults of this species increases westwards until the whole head and neck is more or less uniform shiny black, except for a pale patch below covering the first three to seven ventrals; the black below this white patch extends back as far as the 14th to 19th ventral; this latter color variety has been recognized as a race under the name of *bachrani* by Mertens (1954), but was later synonymized with typical *scutatus* by V. FitzSimons (1962) and Broadley (1968).

Size.—Lengths of largest recorded specimens (SVL + tail length in mm): male (NMZB 14306) 540 + 110+ (tail truncated); female (NMZB 6367) 530 + 65. Body to tail length ratio is 5–6.5 in males and 7–8+ in females.

Distribution.—Central and northeastern Namibia including the Caprivi Strip, Botswana, western Zimbabwe, and parts of the Northern, Gauteng, and Northwest Provinces of South Africa (Fig. 3). A number of southern range extensions have previously been rejected (V. FitzSimons 1962; Broadley 1968), but the records for Thabanchu (PEM specimen, now lost) and Rooipoort (Hewitt and Power 1913) both fall within the Kalahari Thornveld (Acocks 1975) with pockets of Kalahari sand in the vicinity, so these may represent former relict populations. Two specimens allegedly from Philippolis were illustrated by F.W. FitzSimons (1912: Fig. 71) and are now presumably PEM 1243 and USNM 63591. This locality has Karoo vegetation (Yeadon and Bates 2000) and if the record is valid, it would indicate sympatry between *A. s. scutatus* and *A. l. lubricus.* It is possible that a relict population of *A. scutatus* existed at Philippolis a century ago and subsequently died out. It is likely that the specimen allegedly from O'okiep in Little Namaqualand (DM) has erroneous locality data.

Aspidelaps scutatus intermedius Broadley 1968
Intermediate Shield Cobra (Fig. 2E)

Type locality.—Selati, Northern Province, South Africa.

Description.—One preocular (very rarely two or fused with supraocular); two or three postoculars; temporals 2 + 4; six (rarely seven) upper labials, the fourth (rarely third and fourth) entering the orbit; eight (very rarely nine) lower labials, the fifth cuneate, the first three or four (very rarely five) in contact with the anterior chin shields. Dorsal scales in 21–23 rows at midbody; ventrals 108–113 in males, 117–121 in females; cloacal shield entire; subcaudals 32–35 in males, 27–31 in females.

Hemipenis extends to the seventh or eighth subcaudal, sulcus and organ dividing at the fourth or fifth; ornamentation similar to *A. s. scutatus*, including the longitudinal basal flaps although the length of the retracted organ appears to be significantly shorter.

Color.—Dark markings are usually more poorly defined than those in the other subspecies, but overall color and pattern are similar to typical *A. scutatus*.

Size.—Total lengths for largest specimens (SVL + tail length in mm): male (TM 26753) 460 + 91, female (TM 26447) 510 + 80.

Distribution.—Restricted to the eastern lowveld portions of the Northern and Mpumalanga Provinces of South Africa, between the Drakensberg escarpment and the Lebombo range (Fig. 3). The record from Pongola, just south of Swaziland (FitzSimons 1962: DSP) probably had erroneous locality data.

Aspidelaps scutatus fulafula (Bianconi 1849)
Eastern Shield Cobra (Fig. 2F)

Type locality.—Inhambane, Mozambique.

Description.—One preocular; three (rarely one or two) postoculars; temporals 2 + 4 (rarely 2 + 5); six (very rarely seven) upper labials, the fourth entering the orbit; seven to nine lower labials; the

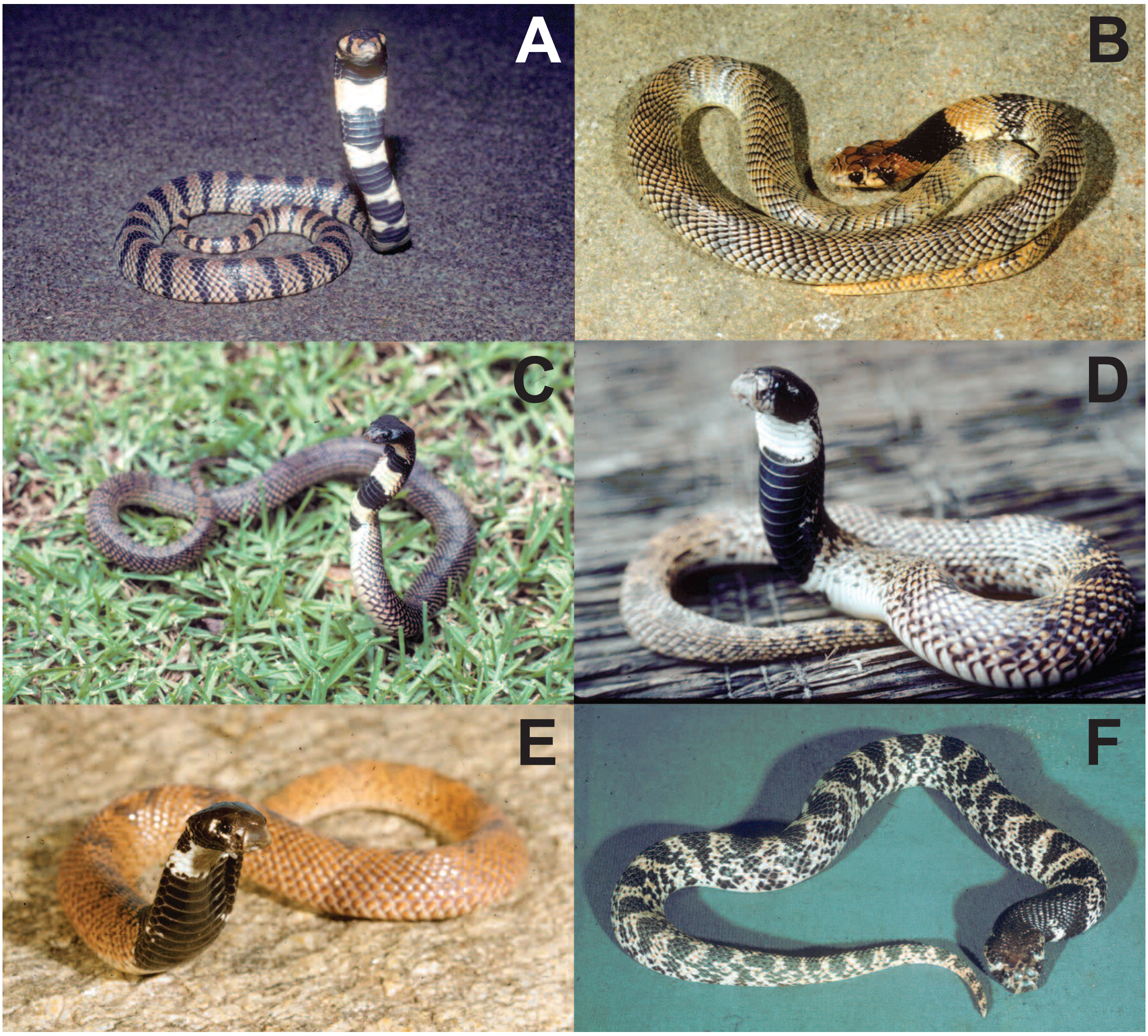

Figure 2. (A) *Aspidelaps l. lubricus* from South Africa. Photo by R.D. Auerbach. (B) *Aspidelaps l. cowlesi*, light phase, from Kamanjab, Namibia. Photo by J.D. Visser. (C) *Aspidelaps l. cowlesi*, dark (*infuscatus*) phase from Keetmanshoop, Namibia. Photo by J.D. Visser. (D) *Aspidelaps s. scutatus* from West Nicholson, Zimbabwe. Photo by R.D. Auerbach. (E) *Aspidelaps s. intermedius* from Limpopo Province, South Africa. Photo by J.D. Visser. (F) *Aspidelaps s. fulafula* from Gonareshou National Park, Zimbabwe. Photo by J.P. Coates-Palgrave.

fifth cuneate, the first three or four in contact with the anterior chin shields. Dorsal scales in 21–23 (rarely 25) rows at midbody; ventrals 111–123 in males, 117–125 in females; cloacal shield entire; subcaudals 33–39 in males, 30–33 in females.

Hemipenis does not differ from that of *A. s. scutatus*, despite the shorter tail of the typical form.

Color.—Ground color pale buff with a more prominent color pattern, consisting of a dorsal series of large blackish blotches and extensive lateral black blotches (Fig. 2), venter white.

Size.—Total lengths of largest specimens (SVL + tail length in mm): male (NMZB-UM 30694) 630 + 109, female (NMZB-UM 12379) 640 + 101.

Distribution.—Southern Mozambique (but not extending into KwaZulu) and the Gonarezhou National Park on the southeastern border of Zimbabwe (Fig. 3).

Remarks.—It is possible that *A. s. fulafula* and *A. s. intermedius* represent a good evolutionary species. Tissue samples for molecular analyses are required to settle the status of this form.

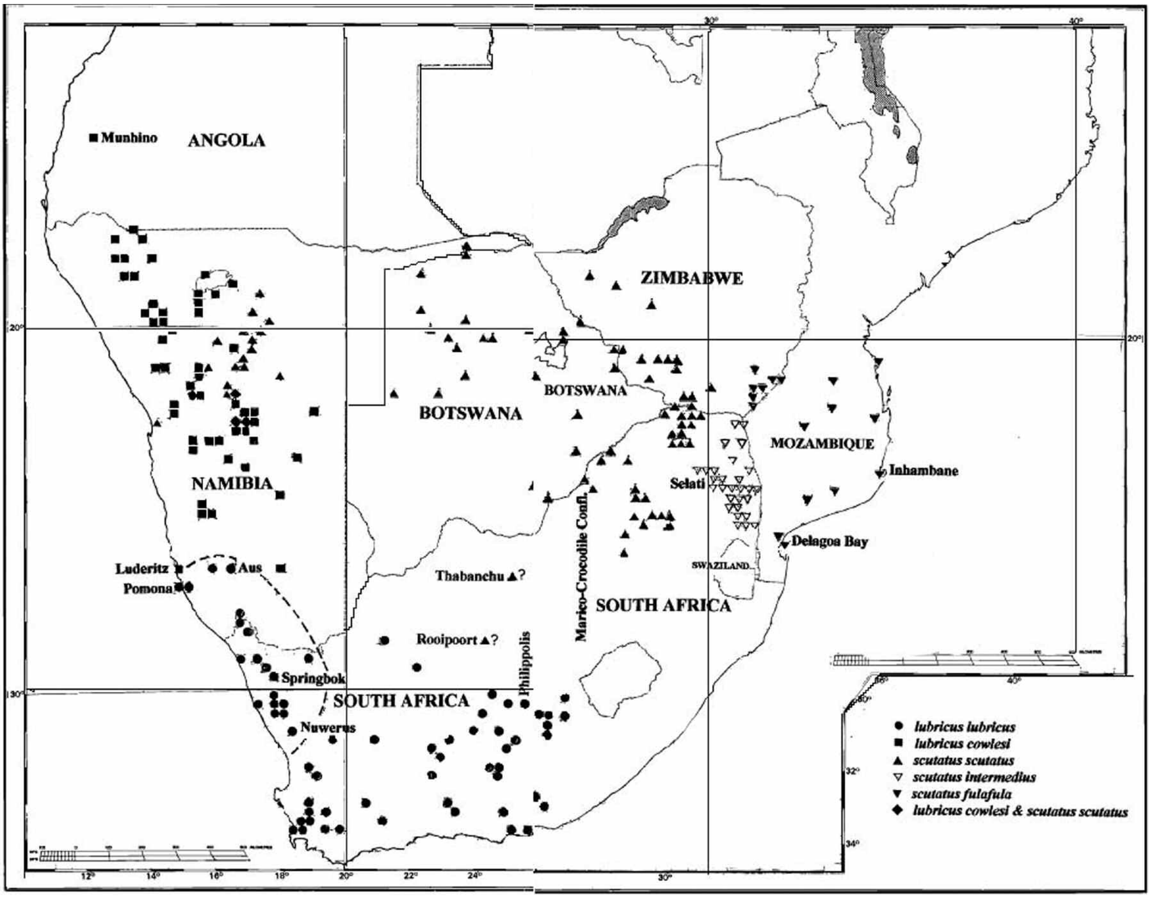

Figure 3. Distribution of *Aspidelaps* taxa in southern Africa by quarter degree cells. The broken line indicates the approximate range of the Namaqua form of *A. l. lubricus* with high ventral and subcaudal counts.

Key to the Species and Subspecies of *Aspidelaps*

1a Internasals completely separated by the very large rostral; usually only fourth upper labial entering the orbit (sometimes excluded by a subocular); dorsal scales on posterior half of body and tail keeled 2

1b Internasals in contact behind the rostral; third and fourth upper labials entering the orbit; dorsal scales smooth throughout 4

2a Subcaudals 25–31 in males, 19–24 in females ....*A. s. scutatus*

2b Subcaudals 32–39 in males, 27–33 in females 3

3a Dark markings usually poorly defined; snout-vent length rarely exceeds 500 mm, ventrals 108–113 in males, 117–121 in females; subcaudals 32–35 in males, 27–31 in females ....*A. s. intermedius*

3b Dark markings clear and extensive; snout-vent length often exceeds 500 mm; ventrals 111–123 in males, 117–125 in females; subcaudals 33–39 in males, 30–33 in females ....*A. s. fulafula*

4a Conspicuously banded in red and black ....*A. l. lubricus*

4b Pale gray to dark brown with or without black cross-bands...*A. l. cowlesi*

Systematics

Slowinski et al. (1997) and Slowinski and Keogh (2000) found rather substantial molecular support for the monophyly of the "cobras" (with the exception of *Ophiophagus*) including *Naja*, *Boulengerina*, *Paranaja*, *Aspidelaps*, *Hemachatus,* and *Walterinnesia*. However, maximum likelihood, parsimony analyses, and different sets of data offer different placements for most genera, which led Slowinski and Keogh (2000) to encourage more work to be done to resolve these relationships. In any case, Slowinski et al. (1997) determined that *Aspidelaps* is closely related to *Hemachatus* and *Naja,* to which it is either the sister taxon, or nested within that clade.

Life History and Ecological Characteristics

Habitat. These snakes are nocturnal and fossorial, spending the day underground in rodent burrows and similar retreats. They are not commonly encountered due to these habits. *Aspidelaps lubricus* is more common in rocky semi-desert areas and is most commonly collected on roads at night or turned up through the plowing of fields (Mavromichalis and Bloem 1997). Visser (1979) records the collection of 11 specimens of *A. l. lubricus* from rock crevices at Kharkams (Little Namaqualand) in midwinter, and reports (Visser, pers. comm. 2001) that specimens were always in vertical crevices of low (≤ 45 cm) rock ridges, two were found in abandoned termite mounds. Marais (pers. comm. 2001) found most Namaqualand specimens on roads at night, but twice found snakes near Spoegrivier in rock crevices close to the ground. Branch (pers. comm. 2001) reports collecting two *A. l. lubricus* under rocks in spring an summer, one on clayey soil in the Karoo National Park, the other on sand at Springbok, others have been on roads at night, usually on sandy flats with scattered rock outcrops. Visser (pers. comm. 2001) noted that in Windhoek *A. l. cowlesi* was frequently found trapped in open graves in cemeteries.

Aspidelaps scutatus inhabits sandy substrates centered on the Kalahari and probably takes refuge in rodent burrows during the day. Many specimens are found on roads at night (Broadley 1962; Haagner 1991). Jacobsen (1989) observed a specimen emerging from loose sand and leaf litter at the base of a tree at dusk. Pienaar et al. (1983) reported that a specimen of *A. s. intermedius* was caught alive in a trap set in a mole rat (*Cryptomys*) burrow.

Diet and Feeding. *Aspidelaps scutatus* is reported to feed mostly on amphibians (Spawls and Branch, 1995). Frogs have been found to comprise 58% of all food items from stomach content surveys (Shine et al. 1996) and male snakes ate all of these anurans. Anuran species identified in that study included *Breviceps adpersus*, *Bufo garmani*, *Hemisus* sp., *Pyxicephalus edulis*, *Tomopterna* sp., and *T. cryptotis*. Shine et al. (1996) suggest that there may be selection acting on the males, as the smaller sex, to have a wider gape, to better enable ingestion of wide prey (e.g., frogs). Even though male *A. scutatus* typically have larger heads, this sexual dimorphism is present in most elapids, many of which do not feed on frogs. Snakes eaten were *Crotaphopeltis hotamboeia* and *Lycophidion capense*, and there were four unidentified mammals. This species appears to be a generalist feeder (Broadley 1983) as it readily eats lizards, mammals, and even alate termites (Haagner 1991). Shine et al. (1996) found one squamate egg in the gut of a shield cobra, but determined that its presence was result of secondary ingestion after the reptile that contained it was fully digested. They also concluded that all of the prey species found in stomachs of these snakes were nocturnal, which thus predicts that shield cobras capture active prey (a technique atypical of most nocturnal elapids, which search for inactive diurnal prey in their retreat sites [Zinner 1971; Shine 1981]).

In the Gonarezhou National Park, after the first rain of the season, six *A. s. fulafula* were collected at night around clumps of *Hyphaene* palm scrub bordering Sazale Pan, where they were apparently lying in ambush for gerbils, another was lying on a dry stream bed early in the morning. These snakes ate mice and toads in captivity (Broadley 1968).

Contrary to the active hunting strategy of *A. scutatus*, Spawls and Branch (1995) report that *A. lubricus* specializes on sleeping diurnal lizards, for which little active hunting is required, but no stomach content data support this. Bogert (1940) found a small rodent and 19 soft-shelled reptile eggs in the stomach of the *A. l. lubricus* from Pomona Island, while Hewitt (1937) stated that this species eats other snakes. Hoffman (1988) recorded that a captive *A. l. cowlesi* at the Namib Desert Research Station fed readily on geckos (*Ptenopus garrulus, P. kochi, Pachydactylus laevigatus*) and lacertids (*Meroles suborbitalis*).

Behavior. Hoffman (1988) describes how a captive specimen of *A. l. cowlesi* at the Namib Desert Research Station, Gobabeb, excavated large quantities of sand from around and beneath rocks to create a shelter. This was accomplished by pushing the head forward and downwards into the sand and drawing it sideways, the sand being scooped out in the loop created by the neck. It was most active in the evenings.

Defensive behavior.—When disturbed both species of *Aspidelaps* rear up, flatten the neck and will assume the vertical defensive posture typical of cobras (Greene 1997), and *A. lubricus* forms a reduced 'hood' (they lack the elongate neck ribs of true cobras). When molested further, these snakes will produce abrupt loud hisses, often accompanied with rapid forward strikes. As a last resort, *A. scutatus* will occasionally feign death, similar to the closely related rinkhals (Broadley 1983; Haagner and Morgan 1992).

Documented predators of these snakes are rare, but remains of *Aspidelaps scutatus* have been found in stomachs of the small-spotted genet (*Genetta genetta*) and the white-tailed mongoose (*Ichneumia albicauda*) in Botswana (Broadley 1968) and there is a report of an *A. lubricus lubricus* being chewed by a domestic dog (Yeadon and Bates 2000), but it is not known what defensive behaviors the snakes offer towards these mammals.

Male-male combat behavior is common in African elapids (Greig and de Villiers 1983; Haagner 1986; Shine 1978) and has been recorded for *A. lubricus* (Mavromichalis and Bloem 1997), but not in *A. scutatus*.

Courtship behavior.—Haagner and Morgan (1992) provide the only published account of *Aspidelaps scutatus* courtship behavior that appears typical of many snakes in captivity: "The male was seen trailing the female around the cage, during which he moved slowly dorsally over the female, rapidly flickering his tongue, and nudging her with his snout several times and flicking his tail laterally. This behavior was observed for 24 minutes before the female ceased movement and the male moved his tail into a dorsolateral position and aligned it with that of the female. He then passed his tail under hers and attempted intromission with one hemipenis. The female responded by lifting her tail slightly permitting entry … Copulation lasted 32 minutes, after which the male moved off."

Oviposition and reproduction.—Mating takes place in the spring, eggs are laid in midsummer, and hatching occurs in the fall for *A. scutatus*, typical of snakes living in southern Africa (Shine et al. 1996). There are no records of eggs found in the wild, therefore information on oviposition site preferences pertain only to captive breeding (see below).

The following information was taken from three published accounts of captive breeding. Information for *A. lubricus* comes from Jaensch (1988) and Mavromichalis and Bloem (1997), and that for *A. scutatus* comes from Haagner and Morgan (1992), unless otherwise referenced and experimental data for both subspecies come from Reichling and Gutzke (1996). Supporting information regarding clutch, egg, and hatchling size is also provided by Spawls and Branch (1995).

Clutch size ranges from 4–11, means 8.3 (Haagner and Morgan 1992) and 7.9 (Shine et al. 1996) in *A. scutatus,* and three to 11 in *A. lubricus*. Captive *A. scutatus* females have been reported to produce two clutches per year and, for those kept in isolation after oviposition, this illustrates sperm retention in females. Egg length averaged 30.4 mm, width 17.7 mm, and mass 6.1 g for *A. scutatus* and were approximately 30 mm long and 20 mm wide for *A. lubricus*. Incubation ranged from 64–68 d for *A. scutatus* and 59–67 d for *A. lubricus*. Hatchling size averaged 15.9 cm for *A. scutatus* and ranged 15–20 cm for *A. lubricus*; their first slough occurred between 7–9 d (*A. lubricus*) and 11–14 d (*A. scutatus*). Clutch size, egg mass, and hatchling mass are similar for both species, but hatchling *A. lubricus* have significantly greater SVLs than hatchling *A. scutatus* (Reichling and Gutzke 1996).

The only experimental data on the influence of incubation conditions on the phenotypes of hatchling *Aspidelaps* was documented by Reichling and Gutzke (1996). They reported that whereas hatchling SVL was always greatest in mesic conditions, it was responsive to the incubation environment only in *A. lubricus* but not *A. scutatus*. Furthermore, a male-biased sex ratio observed under xeric conditions may have been attributable to the higher temperatures experienced by embryos rather than to moisture levels.

Egg guarding behavior.—One of the more unusual behaviors of female *Aspidelaps scutatus* is their egg guarding behavior after oviposition, and this behavior is independent of the number of eggs in the clutch (Shine et al. 1996). Females will nudge the eggs into a heap and remain coiled around them until they hatch, displaying an elevated level of aggression when disturbed (Haagner and Morgan 1992).

Zoogeography

The fossorial elapids of sub-Saharan Africa partition the savannas among them. The numerous species of *Elapsoidea* show tropical distribution patterns, with the exception of *E. sundevallii* on the southern periphery of the generic range, which could be considered to show a sub-tropical distribution (Broadley 1971). The two small species of *Homoroselaps* show a south temperate distribution, often living in termitaria and feeding on small fossorial reptiles, especially Typhlopidae, Leptotyphlopidae, and limbless skinks. *Aspidelaps lubricus* also shows a south temperate distribution, whereas *A. scutatus* has a sub-tropical distribution, the two species are only sympatric on the Namibian highlands around Windhoek (Fig. 3).

Aspidelaps scutatus is sympatric with *Elapsoidea boulengeri* and *E. sundevallii* throughout most of its range. Speculatively, competition may be reduced due to the greater body diameter of the shield cobra, which often preys upon amphibians and rodents and probably uses their burrows for refuges, whereas the *Elapsoidea* take more snakes and lizards and tend to hide under stones or in leaf litter. In the Gonarezhou National Park in southeast Zimbabwe, two adult *E. sundevallii longicauda* of the type series were dug out of the shallow runs of golden moles (*Calchochloris obtusirostris*) and one of these was recovered from the stomach of a Mozambique snake. In the same area, the more robust *Aspidelaps s. fulafula* was apparently preying upon gerbils (*Gerbillus paeba* and *Tatera leucogaster*) and probably using their burrows as daytime retreats.

Venom and Snakebite

Although bites from these snakes are infrequent due to their secretive fossorial behavior, the genus is medically important with respect to human envenomation as available antivenoms do not appear to neutralize *Aspidelaps* venom and their use is therefore contraindicated (Spawls and Branch 1995). Bites from these snakes have been considered potentially dangerous (Visser and Chapman 1978) and documented fatalities, although rare, have occurred from both *A. lubricus* (Branch 1979) and *A. scutatus* (van Egmond 1984). The fatal *A. scutatus* case report by van Egmond (1984) stated that approximately 3.5 h after the bite, the 4-yr-old female victim was "subcomatose and restless, hypersalivating and dyspnoeic with subnormal temperature and a pulse rate of 120/min, the only local signs were two tiny puncture wounds on the left hand." The report continues to relate that 30 min later breathing had stopped and, despite the injection of polyvalent antivenom, the child died 16 h after the bite.

Additional nonfatal bites have shown symptoms of neurotoxicity (e.g., impairment of respiratory muscles, facial muscle weakness, etc.), which further supports the claim that these snakes are not harmless (Zaltzman et al. 1984). However, Haagner and Carpenter (1990) recorded a bite from a Namibian *A. s. scutatus* that produced only cytotoxic symptoms, with swelling of the limb but no necrosis and Ulber (1998) described a series of insignificant *A. l. lubricus* bites suggesting serious symptoms occur in a minority of human envenomations.

Phospholipase A_2 (PLA_2) is a major component of *Aspidelaps scutatus* venom (Christensen 1968; Kini and Chan 1999), a common and highly variable enzyme found in many elapid species. All PLA_2 isoenzymes exhibit distinctly different pharmacological effects, which, among other functions, eventually result in the lysis of erythrocytes and other protein-bound phospholipid membranes such as plasma membranes. Joubert (1987) found CM-I and CM-II, and later S_2C_1 and S_2C_2 (Joubert 1988*a*) as active PLA_2s in which the amino acid sequences closely resembled those in *Naja* venoms. Joubert (1988*a*) reported additional peptides recovered from *Aspidelaps* venom: (1) four short (61–63 amino acids long) polypeptides that showed cytotoxic properties (two of which were later purified and named S_3C_3 and S_4C_8; Joubert 1988*b*) which showed a lethal dose in 50% of mice with a mass of 16–18 gm intravenously injected (LD_{50}) of 6.6–54 µg; (2) four very toxic proteins with LD_{50}s in mice ranging from 0.12–0.23 µg/g and whose amino acid sequence resembled long neurotoxins; and (3) a single protein, called S_4C_1 by Joubert (1988*a*), that was not very toxic (LD_{50} = 3.6 µg/g in mice) but could not be assigned to any specific toxin. The LD_{50} for *A. scutatus* venom was 13 µg (relative to 22 µg for *Hemachatus haemachatus*; 7 µg for *Naja nivea*; 26 µg for *Dendroaspis angusticeps*; 5 µg for *D. polylepis*; 7 µg for *Bitis arietans*; 185 µg for *Causus rhombeatus,* and 1.2 µg for *Dispholidus typus*), and functional antivenins were as follows: slight neutralization by SAIMR polyvalent antivenin (*Naja nivea*, *Hemachatus haemachatus*, *Bitis gabonica, B. arietans*), slight neutralization by trivalent (*Dendroaspis angusticeps-jamesoni-polylepis*) antivenin, and barely detectable neutralization by monovalent *Echis carinatus* antivenin (Christensen 1968). Branch (1979, 1981) recorded an average wet venom yield of 55 mg (25% solid) from a 720 mm male *A. l. cowlesi* from the Namib Desert Park and an intravenous LD_{50} of 6 µg (317 µg/kg), i.e. similar to that for the Cape cobra and black mamba. Christensen (1968) noted that large samples of *Aspidelaps* venom are difficult to obtain, and this explains the low number of laboratory tests on mice and antivenin serums. No recent analyses of venom composition from these snakes exist. Gold et al. (2002) provide a current summary of general snakebite treatment in the field and in the emergency departments.

Captive Husbandry

These snakes are not very common in the United States pet trade or zoological collections, but are increasing in popularity and, oddly, it seems that more females are available than males. Most of these snakes are most likely wild caught or captive-born, although captive-bred animals are available to a lesser extent. *Aspidelaps* is relatively easy to maintain, as they are kept as one would keep any other species of venomous snake without many special requirements.

Both species appear to prefer a substrate into which they can bury themselves (e.g., sand, wood-chip bedding, etc.) where they remain covered most of the day, emerging at night, when they are quite active. An adult trio of *A. scutatus scutatus* that the junior author has maintained for over a year is frequently observed drinking water and soaking. These snakes readily accept live or pre-killed mice (Broadley 1968; Haagner and Morgan 1992; ASB. pers. obs. 2000), although they seem more responsive to feeding when in the dark, indicative of their nocturnal habits. Although other authors (Haagner and Morgan 1992) do not offer weekly feedings during June-August, ASB. has found food to be readily accepted during this time and the animals seem to have a better outward appearance.

Daytime and nighttime temperatures between 28–32°C are maintained, water is always available, and regular misting of the cages during October–November (following Haagner and Morgan 1992) is done to simulate summer rains in their native Africa.

Pairs should be placed together in October (if housed separately) and courtship and copulation will likely occur (as described above). After copulation, a nest box (e.g., Tupperware shoebox) half filled with moist vermiculite should be placed in the cage (not unlike other snake species) and the females readily locate this box as a suitable oviposition site where she will both deposit and guard her eggs. After approximately 60 d, the young hatch by slitting the eggs, at which time they should be separated from the female and housed in smaller separate containers. Food should not be offered until after their first slough. Mavromichalis and Bloem (1997) described hatchling *A. lubricus* feeding on crickets, but Haagner and Morgan (1992) and personal experience of ASB. with *A. scutatus* has shown that newborn mice are accepted.

CONCLUSIONS

The genus *Aspidelaps* is poorly understood, in that the literature reviewed here, with the exceptions of locality records from historic surveys and taxonomic disagreements, is all that presently exists. Little is known about the ecology, venom, or abundance, and many of their behaviors are dangerously implied from observations of snakes in captivity. This is a unique taxon of snakes, quite different from other southern African elapids in numerous ways that offer ecological, toxicological, and evolutionary questions yet to be addressed. Hopefully this review will not only spark interest in this genus, but also offer a useful foundation for new research. DGB. continues collaborative work on the taxonomy of *Aspidelaps*.

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APPENDIX

Specimens Examined

Aspidelaps l. lubricus.—SOUTH AFRICA: 9 km S Springbok, Little Namaqualand, NMZB 12124; Klipheuwel, Western Cape Province, NMZB 12177.

Aspidelaps l. cowlesi.—NAMIBIA: Opuwo, Kaokoveld, NMWN 2464–65, 2471, 2668; Windhoek, SMWN 2455; Okaukuejo, SMWN 9645.

Aspidelaps s. scutatus.—SOUTH AFRICA: Philippolis, PEM 1243, USNM 63591. ZIMBABWE: Sentinel Ranch, Beitbridge, NMZB 14306; Beitbridge, NMZB 6367.

Aspidelaps scutatus intermedius.—SOUTH AFRICA: 120 km northeast of Tzaneen, TM 26447; Letaba, TM 26753.

Aspidelaps scutatus fulafula.—MOZAMBIQUE: Zinave, NMZB-UM 30694. ZIMBABWE: Malugwe Pan, Gonarezhou National Park, NMZB-UM 12379.

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