THE AUSTRALIAN ELAPID GENUS *CACOPHIS*: MORPHOLOGY AND PHYLOGENY OF RAINFOREST CROWNED SNAKES

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The genus *Cacophis*, comprising four species endemic to eastern Australia, is uniquely derived among terrestrial Australasian elapid snakes in the temporal scale pattern, presence of a relatively high and narrow dorsal crest ('choanal process') on the palatine bone, and presence of keeled supra-anal scales in adult males. Recent analyses based on morphology and genetics do not completely resolve relationships among Australasian elapids, but support relationships of *Cacophis* with the (*Furina, Glyphodon*) and (*Aspidomorphus, Demansia*) clades, which are adopted here as outgroups for intrageneric analysis. Within *Cacophis*, morphoclines in size, head scalation, tooth numbers and colour patterns indicate that *C. squamulosus* is the sister-group to the remaining three species; among the latter, there is conflicting evidence for both (*harriettae, krefftii*) and (*churchilli, krefftii*) clades, but the latter alternative has greater support. Revised diagnoses are given for the genus and included clades, and a simple phylogeographic model proposed.

Key words: Hydrophiinae, morphology, skull, head scales, colour patterns, behaviour, phylogeography

INTRODUCTION

Numerous studies have contributed to understanding the phylogeny of Australian elapid snakes, providing evidence for monophyly of a number of genera and of several suprageneric units (e.g. Schwaner *et al.*, 1985; Mengden, 1985; Shine, 1985; Hutchinson, 1990; Greer, 1997; Keogh, 1998, 1999; Keogh *et al.*, 1998, 2000). These probable clades include: the 'subfamily' Hydrophiinae comprising all terrestrial Australasian elapids as well as marine forms (in either the sense of McDowell, 1987, or that of Slowinski & Keogh, 2000, which differ in whether *Laticauda* is included); the viviparous radiation (Shine, 1985); the true sea snakes (here regarded as a monophyletic 'tribe' Hydrophiini, despite a recent analysis suggesting diphyly; Rasmussen, 2002); and a '*Notechis* lineage' comprising chromosome groups 4, 5 and 10 of Mengden (1985). However, resolution remains poor because characters have often been inadequately defined or polarized, or insufficiently numerous to resolve the large number of species (e.g. McDowell, 1967; Storr, 1985; Wallach, 1985; Greer, 1997; Lee, 1997). I have studied external and skeletal morphology in the terrestrial Australasian elapid snakes, attempting to define and test additional characters in order to improve phylogenetic resolution (e.g. Scanlon, 1985) and as a basis for interpretation of Miocene fossils (Scanlon, 1996). An important intermediate goal is to establish the monophyly and internal relationships of groups of species (e.g. genera) which can conveniently be used as discrete units in a higher-level analysis (cf. Hutchinson, 1990). Such a 'global' analysis will not be presented here, as I concentrate on a particular genus and its putative close relatives.

Hutchinson (1990) considered diagnosis of the genus *Cacophis* problematic, and recognized it only 'tentatively' as distinct from *Furina*. *Cacophis* consists of four species of small nocturnal saurophagous (lizard-eating) snakes, all restricted to rainforest or wet sclerophyll habitats in coastal regions of eastern Australia (Queensland and New South Wales). Three of the species have long been recognized, although they were previously referred to as many as three separate genera (*Cacophis*, *Aspidomorphus* and *Glyphodon* in Worrell, 1963). McDowell (1967) suggested that these three species (*krefftii*, Dwarf crowned snake; *harriettae*, White-crowned snake; and *squamulosus*, Golden-crowned snake) formed a single natural group distinct from other genera; Cogger (1975) brought them together in *Cacophis*, and full synonymies are given in Cogger, Cameron & Cogger (1983).

The fourth species, found in the Wet Tropics of northern Queensland, was first recognized informally as '*Glyphodon* sp.' by Worrell (1963: 125 and plate 56), and subsequently as *Cacophis h.* [*harriettae*] *flavicollis* [nomen nudum] (McDowell, 1967: 536) and *Cacophis* sp. (Wilson & Knowles, 1988: 332; Gow, 1989: 84; Ehmann, 1992: 392). Cogger (in Cogger *et al.*, 1983: 219) includes the mentions by Worrell (1963) and McDowell (1967) in the synonymy of *C. harriettae*, but notes that both refer to what is probably a distinct species. The name *Cacophis churchilli* Wells & Wellington, 1985 is available for this form, though it has only recently come into wider use (Greer, 1997: 160, 178; Shea & Sadlier, 1999; Queensland Museum, 2000: 239; Cogger 2000: 771). Ehmann (1992) calls it the

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'Northern Dwarf Crowned Snake', but 'dwarf' is not especially appropriate since it attains body sizes similar to *C. harriettae* (see below).

While detailed studies of geographic and genetic variation remain to be done (J. Sumner in prep.), I regard the the identity and boundaries of these species as now being stable, and a formal revision is not given here. Rather, this paper reviews evidence for relationships between *Cacophis* and other genera, reports observations of some unusual morphological features contributing to the diagnosis of the genus, and uses readily available data to derive an explicit phylogenetic hypothesis for the four included species.

One motive for investigation of this genus is the discovery of fossil material of small elapid snakes from the Miocene of northern Australia, including a maxilla with features resembling those of *Cacophis* species (Scanlon, 1995, 1996). However, as variation in skeletal features (apart from tooth counts) within the genus is dominated by ontogenetic change in proportions (pers. obs.), the emphasis here is on external morphology.

METHODS

All data are drawn either from published sources or examination of specimens – including those in the collections of the Australian Museum, Sydney (AMS); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAM); and Western Australian Museum, Perth (WAM). Some additional specimens at the American Museum of Natural History, New York (AMNH) and Museum of Comparative Zoology, Harvard (MCZ) were examined on my behalf by M. Lee.

A large number of external and skeletal morphological features have been investigated for their potential to contribute phylogenetic information for Australian elapids, and many of them show overlapping variation of continuous or discrete characters across species or more inclusive groups (Wallach, 1985; Scanlon, 1985; Lee, 1997). This is consistent with the uncontroversial hypotheses that novel characters (genetic, morphological, or behavioural) must pass through a stage of polymorphic coexistence with their alternative, plesiomorphic states before being fixed in one or more descendant populations, and that such polymorphisms may be retained for evolutionarily significant periods. In many cases, I recognize polymorphic coexistence of alternate conditions as a single, separate, intermediate state, and such characters are treated as ordered morphoclines. In other instances, polymorphic taxa are assigned to several states on the basis of relative frequency of alternate conditions observed in samples. This approach to definition and ordering of character states corresponds to a simplified version of the 'frequency bins' method, and has been shown to perform well in simulations (Wiens, 1998).

Data matrices and constraint trees were edited using MacClade version 4.0 for Power PC (Maddison & Maddison, 2000) and phylogenetic analyses carried out on a Macintosh G4 using PAUP* version 4.0b10 (Swofford, 2002), in some cases using batch commands generated using TreeRot version 2 (Sorenson, 1999).

OUTGROUP RELATIONSHIPS OF *CACOPHIS*

In order to assess the polarity of morphological characters contributing to the diagnosis of *Cacophis* and resolution of relationships among the included species, relevant outgroups must be identified. Ideally, these should include the two clades most closely related to the ingroup to allow the outgroup comparison procedure of Maddison *et al.* (1984). Previous analyses of Australasian elapid relationships support the basal position of *Laticauda* and the Solomon Island genera (McDowell, 1970; Keogh *et al.*, 1998), and the monophyly of a large viviparous lineage which includes mainly Australian terrestrial elapids and hydrophiine sea snakes (Shine, 1985; Keogh *et al.*, 1998, 2000). These results imply that the remaining Australo-Papuan oviparous genera form either one or several clades along the stem lineage of the viviparous group. This intervening part of the tree (including *Cacophis*) has been poorly resolved by prior work, which is attributable mainly to insufficient sampling of characters and (especially Melanesian) taxa, but perhaps also to the rapidity of the adaptive radiation (cf. Schwaner *et al.*, 1985; Wallach, 1985; Mengden, 1985; Lee, 1997; Greer, 1997). The selection of outgroups must therefore be provisional at this stage.

Classifications up to that of Worrell (1963, 1970) referred at least some *Cacophis* species to *Aspidomorphus* (see Mengden, 1983, for review), but it has since been considered that *Aspidomorphus* is closest to *Demansia* (McDowell, 1967; Keogh *et al.*, 1998). Also, a consensus has developed that *Cacophis* is closely related to *Furina* and *Glyphodon* (McDowell, 1967; Wallach, 1985; Hutchinson, 1990; Greer, 1997; Keogh *et al.*, 1998; Keogh, 1999). A recent analysis of DNA sequence data (Keogh *et al.*, 1998) has found support for a clade comprising *Cacophis*, *Demansia*, *Aspidomorphus*, *Furina* and *Glyphodon*. While the detailed results varied with different methods of data analysis, they 'consistently grouped these four genera in various combinations' (p. 77), with *Demansia* and *Aspidomorphus* most strongly linked. As shown in Fig.

FIG. 1. Relationships assumed between *Cacophis* and other genera used in outgroup comparisons. The two outgroups *Aspidomorphus* + *Demansia*, and *Glyphodon* + *Furina*, contribute equally to the estimation of plesiomorphic characte states for *Cacophis*.

1, the two outgroups to *Cacophis* adopted in this paper are (*Furina, Glyphodon*) and (*Aspidomorphus, Demansia*), which is thus consistent with Keogh *et al.* (1998) and most previous classifications and analyses.

FURINA AND *GLYPHODON*

McDowell (1967) and Wallach (1985) concluded from morphological analyses that *Cacophis* was most closely related to *Furina* and *Glyphodon*. The latter genera were synonymized as *Furina* by Hutchinson (1990) and, as noted above, regarded only tentatively as distinct from *Cacophis*. Keogh (1999) found strong similarities among the hemipenes of *Cacophis* and *Furina* (*sensu lato*), including both in his 'Group 4' which he regards as a monophyletic group.

Synonymy of *Glyphodon* and *Furina* has been adopted by Hutchinson (1990) and others, in part to deal with the apparent problem of classifying *Glyphodon barnardi* Kinghorn, 1939. Cogger's (1975) key to genera purports to distinguish the genera on the criterion of 'nasal undivided' (*Furina*) vs. 'nasal divided' (*Glyphodon*), but in fact *G. barnardi* has the nasal undivided and would be assigned to *Furina* by this criterion. Polarity of this character is ambiguous since both states occur in related genera (see below), but other cranial and external morphological evidence suggests that *G. tristis* and *G. dunmalli* are sister taxa (e.g. in both species the parasphenoid is excluded from the optic fenestra, an uncommon derived character not observed in *G. barnardi* or other *Furina* spp.; pers. obs.), while *G. barnardi*, *Furina diadema* and *F. ornata* are more closely related to the fossorial radiation of *Neelaps* and *Simoselaps* (Scanlon, 1985, 1988, unpublished data). I therefore retain *Glyphodon* as a distinct genus for *G. tristis* and *G. dunmalli*, and refer *G. barnardi* to *Furina*.

I provisionally recognize a (*Glyphodon* (*Furina* (*Neelaps*, *Simoselaps*))) clade which can be diagnosed as follows: nasal and second supralabial separated from the preocular (reversing twice in fossorial lineages); ventral surface white; dorsal scales highly glossed; eyes dark (Scanlon, 1985; Hutchinson, 1990; characters discussed below). *Glyphodon* spp. lack additional derived states shared by *Furina* with *Simoselaps* and *Neelaps* spp.: postorbital bones with kinetic attachment to parietal (involved in mechanism for maxillary erection and retraction; McDowell, 1969a; Scanlon, 1985); frontal may contact preocular scales (rare to common variant, [Storr, 1968, 1981], never observed in *Glyphodon* or any other elapid genera, pers. obs.); black head and nape blotches contrasting with the dorsal ground colour and separated by a distinct pale spot or bar; and a reticulate dorsal pattern where each scale may have a black edge, yellow basal spot and red intermediate zone (three distinct pigments; [Storr, 1968]). *Cacophis* spp. lack most of these derived features and retain the alternate states common to most other Australasian taxa (preocular contacts second labial and frequently nasal; ventrals

strongly pigmented; scales less glossy; eyes pale; postorbital lacks anteroposterior kinesis; no contact of preocular and frontal scales; occipital and dorsal ground colour similar; pale spots on dorsal scales single-coloured), and can thus be excluded from the (*Glyphodon* (*Furina* (*Neelaps*, *Simoselaps*))) clade.

Thus *Glyphodon* and *Furina*, either alone or together with *Simoselaps* and *Neelaps* (Scanlon, 1985, 1988: Fig. 1), form a close outgroup to *Cacophis* (Hutchinson, 1990; Keogh, 1999). Either way, the species of *Glyphodon* and *Furina* are the most appropriate taxa to estimate the ancestral states of this outgroup clade.

DEMANSIA AND *ASPIDOMORPHUS*

These two genera, suggested by McDowell (1967) to be closely related, share several probable synapomorphies, including uniquely derived features of the maxilla: tooth numbers are the highest of any elapids (Bogert, 1943; McDowell, 1967), the medial (ectopterygoid) process is elongate, and in most species the suborbital region is dorsoventrally extremely thin and (in fresh or wet-preserved specimens) flexible (pers. obs.). Mengden (1985) found that *Demansia* 'possesses a unique karyomorph not easily associated with any other Australian elapid', while the karyotype of *Aspidomorphus* has not been reported. The relatively high genetic distances found by Cadle & Gorman (1981) and Schwaner *et al.* (1985) between *Demansia* and all other genera – including *Aspidomorphus* – conflict with evidence from morphology (the skeletal characters just given, and others in McDowell, 1967) and DNA sequences (Keogh *et al.*, 1998), but can be explained by, for example, accelerated genetic change (autapomorphy) in *Demansia*, as already suggested by Cadle & Gorman (1981).

Demansia and *Aspidomorphus*, provisionally accepted as sister taxa forming a single clade, are used as one outgroup in comparisons below. Skulls of all three species of *Aspidomorphus* have been examined (see also McDowell, 1967), and a preliminary analysis suggests that *A. schlegelii* is basally related to the other two species, although *A. muelleri* is the least derived in morphology (unpublished data). The larger number of species (approximately 15 [Shea & Scanlon, unpublished data]) and morphological diversity within *Demansia* present a greater problem, but it seems likely from external characters (e.g. number of ventral scales, occurrence of posterior scale-row reduction) that *D. simplex* is basally related to all the other, larger and more elongate species (see Table 1 and characters discussed below). While cranial data have been obtained for only a few species of *Demansia*, *D. simplex* is also plesiomorphic relative to the others examined (*D. psammophis*, *D. vestigiata* and *D.* sp. cf. *olivacea*) in having a relatively broader frontal, less constricted parietal, and less developed 'interorbital septum' (Underwood, 1967) of the parasphenoid.

DISTINCTIVE FEATURES OF *CACOPHIS*

A revised diagnosis of *Cacophis* is given in a later section, in which several classes of characters are included: unambiguous autapomorphies, characterizing *Cacophis* but absent or uncommon in the outgroups and other Australasian elapids; possible apomorphies, conditions with a more restricted distribution including one or more of the outgroup genera; and likely plesiomorphies, conditions which are shared widely among Australasian elapids but lost or modified in various lineages from which *Cacophis* can thereby be excluded. Contrary to Hutchinson (1990), *Cacophis* can readily be diagnosed on the basis of autapomorphic states of external as well as cranial characters.

AUTAPOMORPHIES

A1. Parietal foramina. Most Australasian elapids, like many other colubroids, have a pair of small foramina (or sometimes closed pits, not piercing the bone) near the centre of the dorsal surface of the parietal. These are presumably not equivalent to the median pineal foramen which was lost in an ancestor of all snakes, but there do not seem to have been any descriptions of the detailed anatomy, function or phylogenetic value of the paired openings. Greer (1997: 178) noted their ab-

sence in *Cacophis* but did not discuss their occurrence in any other taxa. The foramina are present in nearly all outgroup skulls examined (but not in *D. simplex*, NTM R18625; one specimen of *F. diadema*, SAM R 6703), and absent in nearly all *Cacophis* (Figs 2, 3c; present unilaterally in one specimen of *C. krefftii*, SAM R26974, Fig. 3a). In some other taxa (e.g. *Pseudechis* spp.), the foramina may be obliterated during adult life by forward extension of median contact between the mandibular adductor muscles forming a sagittal crest, but in *Cacophis* they are typically absent even when the muscles are still widely separated.

A2. Choanal process of palatine bone. McDowell (1970, 1987) diagnosed the subfamily Hydrophiinae of 'palatine draggers' on the basis of the palatine's clasping articulation with the pterygoid, and lack of choanal and perforate lateral processes. The dorsomedial edge of the palatine is smooth and nearly parallel to the tooth row (i.e. choanal process totally absent) in most hydrophiine taxa and their probable sister group *Laticauda* (McDowell, 1970; pers. obs.; State 0). However, a number of species in the Australian radiation have a low to moderate laminar dorsal process similar to the choanal process of such forms as *Bungarus*, but it is usually nearly vertical rather than arching medially over the choana. Greer (1997) recognized this as diagnostic

TABLE 1. Comparative morphological data for species of *Cacophis* and outgroup genera: maximum known snout-vent length (max. SVL); and observed ranges of the number of ventral and subcaudal scales; and number of alveoli for tooth attachment on the maxilla (excluding the two enlarged anterior fangs), palatine, pterygoid and dentary. Scalation and size data from Brongersma (1934), Cogger (1992, 2000), Greer (1997), McDowell (1967), Scanlon (1985, unpublished data), Shea and Scanlon (unpublished data), Shine (1980a,b, 1981), Shine and Keogh (1996), Storr (1978), Storr *et al.* (1986). Tooth counts from skeletal material listed in Appendix, with additional data from Boulenger (1896) for *Glyphodon tristis*, and McDowell (1967) for *Cacophis harriettae*, *C. krefftii* and *Aspidomorphus* spp.

Genus	species	Max. SVL	Ventrals	Subcaudals	Maxilla	Palatine	Pterygoid	Dentary
Cacophis								
	churchilli	53.8	154-176	25-38	6	9-12	17-18	21-23
	harriettae	48.8	168-200	25-45	3-5	9-12	12-18	16-19
	krefftii	34.5	140-160	25-40	2-5	9-11	11-16	14-16
	squamulosus	71.5	165-185	30-50	6-8	11-17	19-24	21-28
Aspidomorphus								
	lineaticollis	48.0	139-174	24-40	11-18	13-16	31-34	31-32
	muelleri	62.0	160-177	29-40	10-18	16-19	36-40	31-36
	schlegeli	50.8	137-160	19-29	11-13	14	24	30
Demansia								
	psammophis	83.5	172-205	63-91	8-13	12-15	26-38	19-25
	simplex	43.6	140-158	49-66	9	12	33-34	30
	other species	47.6-154.5	160-230	63-113	8-13	10-18	22-38	19-25
Glyphodon								
	dunmalli	56.2	166-189	37-46	8-9	13	20-23	24
	tristis	77.8	171-181	44-51	6-8	9-15	16-23	16-20
Furina								
	barnardi	54.8	157-221	35-58	6-7	10-12	15-23	19-21
	diadema	34.3	156-203	35-54	4-5	8-12	15-18	14-17
	ornata	58.1	164-217	37-63	5	12	19-20	18-19
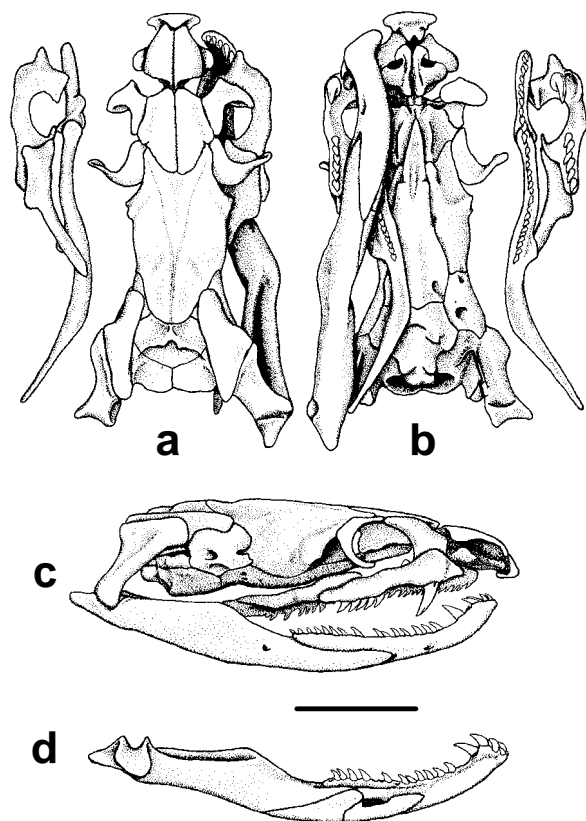
FIG. 2. Skull of *Cacophis churchilli* (QM J53282). Dorsal (a) and ventral (b) views of skull, right mandible, and displaced left palatal elements; (c) right lateral view of skull and right mandible, and (d) medial view of left mandible. While smaller than some of the *C. squamulosus* skulls examined, this relatively large adult specimen (SVL 421 mm) exceeds them in the development of bony crests for muscle attachment and other features associated with large size. Scale bar = 5.0 mm.

FIG. 3. Skulls of *Cacophis krefftii* and *C. squamulosus*. *C. krefftii* (SAM R26974) in (a) dorsal view, and (b) left lateral view of the anterior part of the skull; the left prefrontal and palatomaxillary arch, postorbitals, quadrates and mandibles are not shown. Braincase of *Cacophis squamulosus* (SAM R2263A) in (c) dorsal view, and (d) anterior view of the frontals and parasphenoid rostrum; the snout unit, prefrontals, palatomaxillary arches, postorbitals, quadrates and mandibles are not shown. Scale bar = 5.0 mm (for a and c only).

of *Cacophis*, but a crest-like process is also present in *Glyphodon*, *Demansia*, and *Aspidomorphus* spp. (but not in any *Furina* spp. examined) as well as a number of other Australasian taxa. The crest may be either angular or rounded dorsally, and is never as high as long in the outgroups or other hydrophiines. The 'short' choanal process is therefore considered plesiomorphic for *Cacophis* (State 1). In all *Cacophis* palatines examined there is a well-developed choanal process which is higher than long (i.e. 'tall'), and directed dorsally or slightly anteromedially (Figs 2, 3; also figured by Greer, 1997). This condition (State 2), while structurally approaching that of *Naja* and more distant outgroups, is considered derived within Hydrophiinae, and diagnostic of *Cacophis*.

Loss or reduction of the choanal process in hydrophiine elapids appears to be related to increased longitudinal mobility of the palatines relative to the vomer and snout complex, in contrast to the rotation of the palatine about its contact with the vomer in many other snakes (McDowell, 1970; cf. Cundall, 1995; Cundall & Shardo, 1995). In incompletely cleaned skulls the palatine dorsal process is seen to lie within a sheet of connective tissue connecting to the parasphenoid, prefrontal and palatine shaft, forming the medioventral wall of the orbit, but even in *Cacophis* the process remains completely free of other bones and does not appear to form a functional articulation with the snout.

A3. Anterior extent of the ectopterygoid. The anterior extremity of the ectopterygoid, nearly always its anteromedial tip, lies close to the same horizontal plane as the palatine-pterygoid joint, and slightly lateral to it, so these landmarks are readily comparable. The common and primitive condition appears to be a longitudinal overlap with the palatine, i.e. the ectopterygoid extends anteriorly somewhat past the joint (State 0). This occurs in some *Furina*, some *Aspidomorphus*, and all *Demansia* examined apart from *D. simplex*. An intermediate state can be recognized where the ectopterygoid extends to approximately level with the joint (or within the region of overlap), which characterizes the remaining outgroup taxa (State 1). The most derived state, where the ectopterygoid fails to reach the palatine (State 2), is not found in the outgroups and is hence considered apomorphic in *Cacophis*, where it is the only state observed.

A4. Supra-anal keels. A patch of keeled lateral scales is present in the cloacal region in males of all four *Cacophis* species (a series of each examined at the AMS). This secondary sexual character is sporadic but quite widespread among colubroids (e.g. Blanchard, 1931; Mertens, 1936; Gyi, 1970; Roze, 1996), but has

not been seen in the outgroups or any other Australasian elapids examined. Extent of the keeling is variable when present, ranging from barely detectible (one or two keeled midlateral scales on each side in *C. krefftii* AMS R77370, SVL 237 mm) to extensive (from 12th-last ventral to 20th subcaudal, and extending from lowest laterals to the paravertebral scale rows in *C. squamulosus* AMS R37187, SVL 410 mm). Two individuals with weak keeling (*churchilli*, AMS R11512, R12480) appear to be female based on tail shape, and some are unlikely to be mature based on size (*churchilli* AMS R11340, SVL 145 mm; *squamulosus* R28232, SVL 187 mm). Conversely, no keeling was detected in some likely adult males of *krefftii* (e.g. AMS R81158, SVL 235 mm), but generally this seems to be a useful indicator of sex and maturity in each species. Similar variability of supra-anal keels is reported within *Micrurus* by Roze (1996; see her Fig. 7).

A5. Parietal and postocular scales: occurrence of contact. In most elapids with two (or sometimes three) postoculars, the uppermost contacts a temporal (or sometimes labial) scale below the parietal (State 0). In some of each species of *Cacophis*, the parietal contacts

a

b   **c**

d
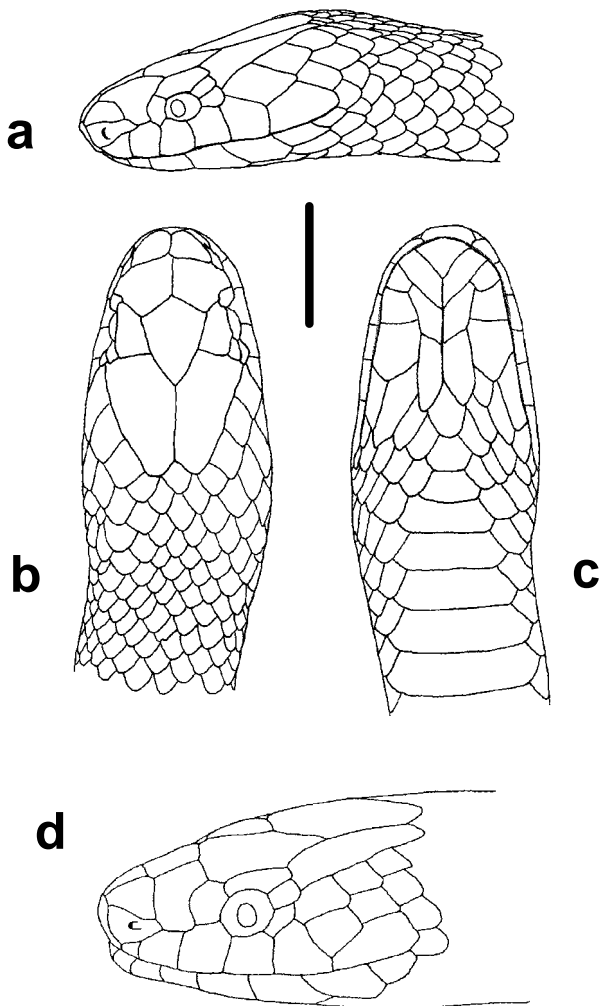
FIG. 4. Head of *Cacophis churchilli* (SAM R22392) in (a) lateral, (b) dorsal, and (c) ventral views, and (d) *Furina ornata* (AMS R110357) for comparison of head scales. Scale bar = 5.0 mm (for a-c only).

the lower postocular, separating the upper postocular from the temporals (State 1). Among the outgroups, this state characterizes only *Aspidomorphus* spp. (it also occurs as a variant in some derived *Simoselaps*, e.g. *S. morrisi* Horner, 1998). Hence, it is parsimoniously interpreted as an apomorphy of *Cacophis*, convergent in *Aspidomorphus* (and again in *Pseudonaja* and *Oxyuranus*, which form a more distantly related clade). Variation in frequency of contact within *Cacophis* is treated as a further binary character (C7).

A6. Temporal scales. The practice of writers on Australian elapids has generally been to recognize two series of temporal scales, anterior and posterior, and give a formula such as '2+2' or '3+4'. McDowell (1967: 500) described the widespread 2+2 condition in Australasian elapids, and introduced the term 'temporolabial' for the lower anterior temporal "which appears to be the homologue of the penultimate supralabial of elapids with seven supralabials, but which has been squeezed out of contact with the oral border". Describing the temporolabial as present or absent (e.g. Wallach, 1985) is an oversimplification, but a number of distinct characters can be defined using a more detailed notation. Storr (1968) used a three-term formula (e.g. '1+1+2'; see also Aplin & Donnellan, 1999), but without adequate explanation. The following definition gives counts consistent with Storr's on the same specimens (Scanlon, 1985), and is applicable to most Australasian elapids.

The postsupralabial is the scale at the corner of the mouth, overlapped by the most posterior supralabial and infralabial but not counted in either series (this follows the usage of Greer & Cogger, 1985, for skinks, and is consistent with supra- and infralabial counts given by most authors). The anterior (or primary) temporal row includes the temporolabial, when distinct – regardless of whether it reaches the lip or contacts a postocular – and any other scales between supralabials and parietal which do contact the postoculars. The oblique row of scales connecting the parietal to the postsupralabial, but excluding the latter, is considered to be the last row of temporals (2nd, 3rd or 4th in Australian elapids), and the formula is given to a corresponding number of terms. Individual scales can be identified by row and position as 1°1, 2°1, 3°2 etc.; thus, the temporolabial (TL) is 1°2 in typical Australian elapids.

Using this definition, all of the outgroup species (and most other Australian elapids) normally have 2+2+3 (Fig. 4d), while the condition in *Cacophis* spp. can be written as 1+3 or 1+2 (Fig. 4a). McDowell (1967: 535) suggests the temporolabial is fused to the sixth labial in *Cacophis*, but this does not explain the reduction from three to two rows of temporals. Rather, it seems simplest to assume that the single large anterior temporal of *Cacophis* represents the four scales of the ancestral primary and secondary temporal rows (as suggested by Greer, 1997). If fusion of adjacent scales (failure of a suture to develop; Resetar & Marx, 1981) represents a single evolutionary 'step', the inferred transformation

from four scales to one could have involved two or more steps, but these are not counted as separate characters here because ingroup variation is so limited. Variants in *C. churchilli* and *C. krefftii* do corroborate the suggestion of fusion among temporals (loss of sutures rather than loss of scales). For example, AMS R75961 (*krefftii*) has '2+2' on each side, but on the right side of the head the anterior temporals are both elongate and contact the postorbitals (interpreted as 1°1=2°1 and TL=2°2, where '=' indicates fusion), while on the left there is a large L-shaped scale (representing TL=1°1=2°1) with a smaller adjacent scale (2°2) widely separated from the postoculars. Similar conditions occur asymmetrically in R81158, R90609, and R114956 (*krefftii*), and in R11512 and R11362 (*churchilli*). Accepting this evidence for fusion of the two anterior temporal rows, we may write the formula for the common *Cacophis* conditions as 1=1+3 or 1=1+2. The variation in the posterior row is used below as evidence for relationships within the genus (C6).

Many specimens of *Simoselaps* and *Vermicella* spp. also have 1=1+2, but the most common condition in these genera is 1+1+2 (Storr, 1968; Greer, 1997: 169; Horner, 1998: Fig. 2), and when fusion occurs between primary and secondary the resulting scale is either trapezoidal (deep anteriorly and tapering posteriorly) or long and shallow, in either case quite different from that in *Cacophis*. Moreover, contrary to McDowell (1969*a*), the temporolabial does occur as a separate element in this group (*Simoselaps warro* normally retains the ancestral 2+2+3, while 2+1+2 is a common variant in the *S. semifasciatus* group), which has not been observed in *Cacophis*.

Some specimens of *Demansia* spp. (like all species of *Pseudonaja,* and some *Oxyuranus microlepidotus*; Storr *et al.*, 1986; pers. obs.) have a temporal condition even more similar to *Cacophis* superficially ('1+2'). However, the complete formula in these cases is 1+2+3 or 1+2+4, indicating retention of three distinct rows. This results from a single fusion between the temporolabial and 6th supralabial, as shown by the concave upper edge and frequent partial suture of the labial scale, and comparison with normal (or in *Pseudonaja*, occasional atavistic) individuals with 2+2+3.

Conditions precisely equivalent to those of *Cacophis* (1+3 or 1+2, with a deep single anterior temporal) are found in the primitive marine hydrophiines *Ephalophis*, *Parahydrophis*, *Hydrelaps* and *Disteira*, and a further fusion to 1+1 occurs in some *Parahydrophis* (McDowell, 1969*b*, 1972, 1974; Burger & Natsuno, 1974; figures in Storr *et al.*, 1986; Cogger, 1992, 2000). Most other sea snakes have an increased number of temporals, often quite irregular and presumably secondarily fragmented.

The state seen in *Cacophis* is here considered functionally analogous to those of other lineages with a reduced number of temporal sutures, but to have been derived independently from the common ancestral condition 2+2+3. Head-scale fusions in snakes have been interpreted as adaptations to fossoriality, related to reduction in head width and the minimization of soil accumulation along sutures (e.g. Resetar & Marx, 1981; Savitzky, 1983). While *Cacophis* spp. are not strictly fossorial in habit, they utilize crevices and cavities in moist soil as refugia and in foraging nocturnally for inactive prey, mainly skinks (Wells, 1980; Shine, 1980a; Ehmann, 1992). Similar selective pressures would apply to the primitive sea snakes, which capture gobiid fish within burrows on intertidal mud flats (Storr *et al.*, 1986; accounts cited by Greer, 1997).

A7. Pale iris. Non-melanin pigmentation of the iris is rapidly affected by preservatives or freezing, and observations should be based on live specimens or clear photographs (cf. Gillam, 1979). On the other hand, 'dark' and 'pale' eyes can usually be distinguished in well-preserved material, so two characters are used here (see also C17 below). *Glyphodon* and *Furina* have very dark brown or black eyes (Hutchinson, 1990), while most other elapids, including the other outgroup taxa, have the dark pigment varied by a lighter ring, spot or variegations (combined as State 0). A specimen of *Demansia flagellatio* Wells & Wellington, 1985 (a valid species – Shea & Scanlon, unpublished data) at Riversleigh, north-west Queensland, had bright red eyes in life (pers. obs.), so apparently, like *Cacophis*, has little or no melanin in the iris. Hence *Demansia* is scored as polymorphic, although most species – including *D. simplex* – have only a narrow pale ring. The almost uniformly 'pale' iris of *Cacophis* (State 1) appears to be diagnostic of this genus (Hutchinson, 1990); further comparison might justify defining an intermediate state for *squamulosus*, which appears to have more speckling or variegation than its congeners.

POSSIBLE APOMORPHIES SHARED WITH OUTGROUP TAXA

A number of characters of *Cacophis* spp., despite being possibly or actually derived within the Australasian radiation, also occur in both outgroup clades and are likely to be locally plesiomorphic (Table 2, B1-10; see also generic diagnosis below, and Appendix 2). These characters will not be discussed further here.

CHARACTERS VARIABLE WITHIN *CACOPHIS*

Characters which vary among the four species of *Cacophis* (referred to here by their species names alone) provide the basis of a phylogenetic analysis carried out below. I include several autapomorphies of terminal taxa, one of which is behavioural rather than strictly morphological, in order to provide adequate diagnoses for species as well as higher groups. The distribution of character states in outgroup genera and ingroup species is given in Table 3.

C1. Maxillary tooth number. Observed ranges of tooth (alveolus) counts for the maxilla, palatine, pterygoid and dentary of ingroup and outgroup taxa are given in Table 1. The number of maxillary teeth behind the fangs is often relatively high among Australasian and

TABLE 2. Distribution of character states (characters labelled 'A' and 'B' in main text and Appendix 2) in outgroup genera and *Cacophis*. Abreviations for character types: b, binary; u, unordered; 012 (etc.), ordered multistate. Characters marked * are cladistically uninformative for analyses performed here.

Character	**A**	1	2	3	4	5	6	7	**B**	1*	2*	3*	4*	5*	6*	7*	8*	9*	10
type		b	012	012	b	b	b	b		b	b	b	b	b	b	b	b	0123	012
Aspidomorphus		0	1	01	0	1	0	0		1	1	1	1	1	01	1	01	3	2
Demansia		01	1	01	0	0	0	01		0	01	0	1	1	01	01	01	3	01
Glyphodon		0	1	1	0	0	0	0		1	1	1	1	1	0	1	1	01	12
Furina		0	0	01	0	0	0	0		1	0	01	1	1	01	1	01	23	1
Cacophis		1	2	2	1	1	1	1		1	1	1	1	1	1	1	1	3	2

TABLE 3. Distribution of character states (characters labelled 'C' in main text and Appendix 2) in outgroup genera and *Cacophis* spp. Abreviations for character types: b, binary; u, unordered; 012 (etc.), ordered multistate. Characters marked * are cladistically uninformative for analyses performed here.

Character (**C**)	1	2	3	4	5	6	7	8	9*	10	11	12	13	14	15*	16*	17	18	19*
type	b	b	b	b	012	b	b	b	012	0123	0123	b	b	b	b	b	012	b	b
Aspidomorphus	0	0	0	0	0	0	1	0	1	123	23	0	0	0	01	01	0	0	?
Demansia	0	0	0	0	0	0	0	01	01	013	0	0	01	01	01	0	0	1	0
Glyphodon	0	0	0	01	2	0	0	0	01	01	0	0	-	0	0	01	-	0	?
Furina	01	1	01	1	2	0	0	1	12	012	0	0	-	0	0	0	-	0	0
C. churchilli	0	1	1	0	1	1	1	0	1	2	3	0	1	1	0	0	2	1	0
C. harriettae	1	1	1	1	1	1	0	1	1	0	1	0	1	0	0	1	2	0	0
C. krefftii	1	1	1	1	0	1	0	1	2	3	2	1	1	1	0	0	0	1	0
C. squamulosus	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	1

marine elapids (Hydrophiinae), whereas no African, Asian or American elapids are reported to have more than four (Bogert, 1943). Some counts in the literature are probably unreliable, and dentigerous elements other than the maxilla have been mostly neglected by previous workers, but tooth counts on all bones of many elapids have recently been tabulated by Greer (1997).

Nine skulls of *squamulosus* examined show a range of 6-8 maxillary alveoli behind the fangs (Worrell, 1963 reported 7-10); *harriettae* usually has 5 (seven of eight specimens examined), but only 3 in one specimen; *churchilli* has 6 in both skulls examined; and *krefftii* 3-5 in three skulls (but Worrell, 1963; McDowell, 1967 and Greer, 1997, all report 2 in this species, so the range can be given as 2-5). Based on these figures, two non-overlapping ranges can be recognized: 6-8 (State 0) and 2-5 (State 1). State 0 is regarded as plesiomorphic, being similar to counts in *Glyphodon*, overlapping with *Demansia* and *Furina*, but lower than any in *Aspidomorphus*. The higher counts in *Demansia* and *Aspidomorphus* are a likely synapomorphy of these genera, while reduction has probably occurred independently in *Furina*, as in several other Australian lineages.

C2. Palatine tooth number. Despite overlapping ranges, *C. squamulosus* clearly tends to have a higher number of palatine teeth than the other species, and thus two states are recognized: usually more than 11 (State 0), usually 11 or fewer (State 1). The mostly high counts in *Aspidomorphus*, *Demansia* and *Glyphodon* imply that State 0 is plesiomorphic, while *Furina* tends to haver lower tooth numbers (as on the maxilla).

C3. Pterygoid tooth number. Two states can be recognized on the basis of non-overlapping ranges: 19-24 (State 0) and 11-18 (State 1). The outgroup species all have 19 or more except for *F. diadema* and *F. barnardi*, which overlap both ranges, so State 0 is considered plesiomorphic.

C4. Dentary tooth number. Again, two non-overlapping states can be defined for *Cacophis*: more than 20 (State 0) and fewer than 20 (State 1). Most of the outgroup species exhibit State 0, but *Glyphodon tristis* and *Furina* spp. fall mainly in the range of State 1, so polarity is equivocal.

C5. Nasal and preocular: frequency of contact. These scales are either in contact or narrowly separated (by contact between the prefrontal and a supralabial) in *Cacophis*, but variable within each species so that states can be defined based on frequencies. State 0 (usually contacting) occurs in *krefftii* (15 bilateral and 1 unilateral of 16 specimens; on the remaining side, nasal and preocular separated by a distinct 'loreal') and *squamulosus* (11 and 3 of 14; again one with a loreal on one side), and can be identified with the state in *Aspidomorphus* and *Demansia* (separation rare or absent). State 1 (usually narrowly separated) characterizes *churchilli* (0 bilateral contact, 1 unilateral of 15) and *harriettae* (1 bilateral of 15; indeterminate unilaterally in another where the preocular and prefrontal are fused). In *Glyphodon* and *Furina* the scales are widely separated (State 2). While State 0 is the only ingroup state shared with outgroup taxa, polarity cannot be inferred if the character is interpreted as an ordered morphocline (0-1-2).

C6. Posterior temporal scales. As noted above (character A6), variation is observed in the number of scales in the last row of temporals. Three posterior temporals is the usual condition in all outgroups and most other elapids (State 0); in a sample of *C. squamulosus* examined, three posterior temporals occur in 13 of 14 specimens, so this species is assigned the primitive state. The frequent occurrence of only two posterior temporals is recognized as an apomorphy (State 1) shared by the remaining species: *churchilli* has two in 12 of 15 (and unilaterally in another), *harriettae* in 14 of 15, and *krefftii* in every one of 16 specimens. The relative sizes of the scales indicate that it is the upper two of the three scales which fuse ($3°1=3°2$).

C7. Parietal and postocular scales: frequency of contact. Contact of parietal and lower postocular scales is a shared derived condition of all *Cacophis* species (see A5), but two distinct levels of frequency are apparent in samples examined for this trait. Relatively low frequency is coded as plesiomorphic (State 0), present in *harriettae* (contact bilateral in 1, and unilateral in 5 of 15 specimens) and *krefftii* (1 and 3 of 16). High frequency (State 1) characterizes *churchilli* (11 and 3 of 15) and *squamulosus* (12 and 1 of 14).

C8. Division of nasal scale: frequency. The nasal scale may be either single (pierced by the nostril) or divided (separated into anterior and posterior scales by grooves or sutures above and below the nostril). Complete separation of the nasal by the nostril extending its full depth, from supralabial to internasal, occurs in some other elapids (including some outgroup species), but is not observed in *Cacophis*. Division of the nasal is intraspecifically variable within *Cacophis*, so two states are recognized on the basis of frequency of division: high (State 0) in *churchilli* (bilateral in 10 and unilateral in 3 of 15 specimens) and *squamulosus* (13 and 0 of 14); and low (State 1) in *harriettae* (2 and 0 of 15) and *krefftii* (0 and 0 of 16). Because of the pattern of variation in the outgroups, polarity can not be assigned to this character.

C9. Body size (maximum snout-vent length [SVL]). The species of *Cacophis* vary considerably in size (Table 1; means might be preferable as the basis for this character, but good samples are not available for all species). A linear size increment close to the cube root of two (1.26 approx.) has been reported for sympatric species-pairs in numerous animal lineages by Hutchinson (1959) and others (see Sweet, 1980). In the three southern (sympatric) species of *Cacophis*, maximum SVL differs by ratios greater than 1.4 (implying ratios of 2.75 or more in mass), so that three distinct character states can be recognized. Most *churchilli* are relatively small, but the largest examined (QM J67837; SVL 538 mm, tail 58 mm) is slightly longer than the maximum recorded for *harriettae* (Shine, 1980*a*), so these two species are assigned the same intermediate state (1). Among the outgroups only *Glyphodon tristis* and some species of *Demansia* reach greater lengths than *squamulosus*, so large size (State 0, SVL > 70 cm) is probably apomor-

phic for this character. *C. krefftii* is one of the smallest of elapids (the largest specimen examined, AMS R13000, has SVL 345 mm, tail 39 mm), and all outgroup species except *Furina diadema* have a greater maximum SVL, so that it also represents an apomorphic extreme of the genus (State 2, SVL <35 cm). As each of the apomorphic states occurs in a single species, this character contributes no cladistic information within *Cacophis*. However, this 'uninformativeness' depends on the particular outgroup arrangement adopted here, and could possibly change if *Cacophis* were later determined to have a different pattern of relationships with other taxa.

C10. Ventral scale number. Ventral and subcaudal ranges of *Cacophis* species and outgroups are shown in Table 1; detailed frequency distributions would be preferable (cf. Wiens, 1998) but are not currently available for most species. All outgroup genera, and nearly all outgroup species, have ranges overlapping from 170 to 175 (all lower in *Aspidomorphus schlegelii* and *Demansia simplex*, all higher in some other *Demansia* species). Three species of *Cacophis* also overlap in this 'core' range, so the exception (*krefftii*) is regarded as an apomorphic extreme. The high ventral counts characterizing some *harriettae* may also be apomorphic, as they are outside the ranges of *Glyphodon* and *Aspidomorphus*. In order to utilize the maximum possible cladistic information from the data on ranges, each ingroup species is assigned a distinct state, and the four states are assumed to form a morphocline in the same order as the maximum and minimum observed ventral counts (State 0, *harriettae*; 1, *squamulosus*; 2, *churchilli*; 3, *krefftii*). Outgroup species are assigned the same state(s) as that of the ingroup species with which it most strongly overlaps; polarity remains indeterminate.

C11. Subcaudal scale number. As long-bodied snakes may have short tails (and *vice versa*), the ventral and subcaudal scale counts are considered independent characters. This character can be defined in the same way as the previous one – the four states ordered as the maxima for the ingroup species (State 0, *squamulosus*; 1, *harriettae*; 2, *krefftii*; 3, *churchilli*) since three of the minima are equal. Among the outgroups, counts below 35 occur only in *Aspidomorphus*; State 0 is parsimoniously considered plesiomorphic for *Cacophis*.

C12. Ventral melanin pattern. This character concerns only the distribution of dark brown or black, alcohol-insoluble pigment on the ventral surface; variation in dorsal colour is more continuous, and attributable to the combination of melanin and carotenoid patterns with schemochromes or structural colours (the latter responsible for whites as well as the bluish colour common in *krefftii*, and as a component of greens in some outgroup species; cf. Fox, 1953; Bechtel, 1978).

The outgroups vary considerably in ventral colour; *Demansia* spp. range from dark grey to immaculate white or yellowish, often with a median dark line or zone. The venter is usually white in *Furina* and *Glyphodon*; 'smoky' grey, peppered more or less

densely with melanin granules, in *Aspidomorphus* spp. and some individuals of *Glyphodon* spp. The dark slate-grey or black venter of *harriettae* and *churchilli* is similar to the conditions in some *Demansia* (*vestigiata*, some *torquata*) and *Aspidomorphus muelleri*, and approached by some *Glyphodon*, so uniformly distributed dark pigment is here presumed plesiomorphic (State 0). Southern (NSW) *C. squamulosus* have irregular black spots and blotches across the base of each ventral, and under the tail the black blotches form a continuous zig-zag line, while in many Queensland specimens (and at least as far south as Liston, northern NSW; pers. obs.) the black blotches on the ventrals are narrow and also form either a midventral line, or three distinct longitudinal rows. I have also seen a uniformly 'peppered' condition (precisely as in some *Aspidomorphus*) in a Sydney specimen of *squamulosus*, but this is rare. The state in *krefftii* is also contrasting, usually with a median line under the tail, but more regular on the body than *squamulosus*; the ventrals have a yellowish base and black posterolateral corners, typically forming a double saw-tooth pattern, but often joined as a continuous dark border across the free edge of some or most scales (as in the holotype of *C. fordei* Krefft, 1869). Despite the differences in detail, *squamulosus* and *krefftii* are coded with the same apomorphy (State 1).

C13, C14. Facial pattern and collar shape. The colour pattern on the face and nape is very similar in the four species of *Cacophis*; the dark upper surface of the head is bordered by a more or less continuous pale band extending from the rostrum, through and over the eyes and onto the nape; the pale stripe is broken up by dark markings at scale boundaries in the labial and temporal regions. Similar patterns are found in *Aspidomorphus* and *Demansia* (most complete in some *A. lineaticollis* and *D. torquata*), but patterns in *Glyphodon* and *Furina* are unlike these, with more discrete light and dark areas. A dark comma-shaped or 'bridle' marking from the eye to the lip is present in all *Cacophis* and some *Aspidomorphus* and *Demansia* (also some *Pseudonaja*).

In *squamulosus* the pale facial band is continuous with longitudinal stripes on the neck, somewhat expanded towards the midline but separated from each other by dark-pigmented vertebral and paravertebral scale rows (sometimes greatly elongated as shown by Gow, 1989: 95 and Greer, 1997: 178, rarely connecting to form a complete collar). This is quite similar to the 'upper light line' present in some *Aspidomorphus* populations (McDowell, 1967) which are most similar to *Cacophis* in pigmentation, and possibly also comparable to the pale or reddish dorsolateral streaks in some *Demansia* spp. (common in *D. psammophis*). The 'broken' collar is thus regarded as the plesiomorphic condition for *Cacophis*. One species of *Demansia* (*D. torquata*) has a complete, narrow pale collar continuous with a pale facial stripe; pale or dark collars in other outgroups are less similar (involving contrast between head and dorsal ground colour, or not continuous with facial markings). The collar is complete across the mid-

line in the other species of *Cacophis*, but varies in width: about four scales wide in *harriettae*, i.e. similar in extent to that of *squamulosus* but without a dark median zone, and one or two scales wide in *krefftii* and *churchill*. Two binary characters are used, for separation vs. contact of the lateral pale markings, and width of the collar. *Furina* and *Glyphodon* are coded as not comparable for the first character, because of the very different distribution of dark pigment.

C15. Carotenoid pigment on body. Carotenoid pigments are highly soluble in alcohol, so best studied in live animals; I have not examined living *Aspidomorphus*, but O'Shea (1996) has photographs of two species in life. In *Glyphodon*, *Furina* and *krefftii* (in between dark markings) the venter is white or very pale yellow (carotenoid very faint or absent); white or yellow also occurs in some *Demansia* spp. including *D. simplex*. *Aspidomorphus lineaticollis* and some other *Demansia* have pink or orange ventral colours, and in *squamulosus* the venter varies among individuals from orange or pink to deep red, the same colour also suffusing the light centres on the dorsal scales and sometimes the collar. In one specimen from a variable population at Greenwich, NSW, the venter was a very deep red posteriorly, and there were dark orange to red centres on all of the dorsal scales of the body and tail (pers. obs.). The dark-bellied species of *Cacophis* and *A. muelleri*, appear to lack red pigments since none are visible on the sides or dorsum. Since red is present in only one ingroup species, this character is cladistically uninformative.

C16. Carotenoid pigment on face and collar. The facial stripe and collar are normally yellow in three of the species (State 0), but usually white (sometimes faintly yellow) in *harriettae* (State 1); in this species the pale centres of the dorsal scales are also whitish (an extreme condition is shown by a specimen illustrated in Wilson & Knowles, 1988: pl. 723). Yellow markings on the face and nape are considered plesiomorphic as they are usually present in nearly all outgroup species. In *Glyphodon*, yellow pigment is nearly or completely absent except for the nape patch of *G. tristis*, while in *Aspidomorphus lineaticollis* the face stripe is white in the specimen shown by O'Shea (1996: 149).

C17. Iris colour. This character concerns variation not due to melanin (see A7 above). Because of the density of melanin in the irides of *Furina* and *Glyphodon*, the presence or colour of other pigments in these taxa has not been observed; their relatives *Simoselaps bertholdi* and *S. littoralis* have white eyes, but may have apomorphically reduced carotenoid as well as melanin. Iris colour in life is not known for all *Demansia* and *Aspidomorphus* species, but in most of them, reddish pigments combine with the melanin to produce orange-brown eyes (e.g. *A. lineaticollis*, O'Shea, 1996; *Demansia* spp. illustrated in Storr *et al.*, 1986; Wilson & Knowles, 1988; Gow, 1989; Ehmann, 1992; Cogger, 1992, 2000). Red eyes, which also occur in *kreffti*, are therefore assumed to be plesiomorphic for *Cacophis* (State 0). The iris is predominantly yellow in

squamulosus (State 1), and at least partly white in *harriettae* and *churchilli* (State 2). Because the states can be ranked in order of intensity of colour, they are provisionally treated as ordered (0-1-2).

C18. Pupil shape. Pupils are strongly vertically elliptical in *squamulosus* and *harriettae*, as in *Glyphodon*, *Furina* and most *Aspidomorphus* (only weakly so in *A. muelleri*; McDowell, 1967) (State 0), but weakly oval or quite round in the other species of *Cacophis*, and round in all *Demansia* (State 1).

C19. Defensive threat display. In the threat displays of all *Cacophis* spp. the head is raised and angled downward (displaying the pale collar); from this position they may strike forward and downward, but almost never actually bite. In three of the species the neck is held straight and the jaws not or only slightly expanded during the display, while *squamulosus* is distinctive in two ways: the neck is formed into S-shaped lateral curves and the quadrates and rear of the mandibles are spread laterally, making the head much wider than the neck (e.g. Grigg, Shine & Ehmann, 1985: pl. 5; the narrow dark zone interrupting the pale collar, and longitudinal pattern on the lateral neck scales, tend to exaggerate this visual effect). All three *Furina* spp. have stiff-necked displays most like the smaller *Cacophis* spp. (e.g. Greer, 1997: 161), and *Demansia* spp., although relying on speed and venom in defence and thus apparently lacking a comparable 'bluff' display, have a similar raised-head 'alert' posture while foraging (e.g. Scanlon, 1998). *Glyphodon tristis* has a different defensive display (thrashing wildly in a horizontal coil, head- and tail-hiding), while *G. dunmalli* is described as inoffensive (Wilson & Knowles, 1988; Ehmann, 1992; Greer, 1997: 162). I know of no published descriptions of defensive or foraging behaviour in *Aspidomorphus*; *A. muelleri* strikes (and bites) from a more-or-less upright defensive posture when prevented from escaping (S. Richards, *pers. comm.* 2001), but on present evidence this cannot be identified with either of the states in *Cacophis*. Although a number of other (mostly large) Australian elapids have high lateral S-bends in the defensive display (e.g. some *Pseudonaja* spp., *Oxyuranus microlepidotus* and *Hoplocephalus* spp.), the behaviour in *squamulosus* is considered unequivocally derived since it is not paralleled in the outgroups; however, this apomorphy is not cladistically informative.

PHYLOGENETIC ANALYSIS

PARSIMONY WITH ORDERED CHARACTERS

Because of the small number of taxa, it is not considered useful to construct a 'hypothetical ancestor': the outgroup genera can be included explicitly along with ingroup species, and still allow exhaustive search of tree topologies.

Characters A1-7 and B1-10 are invariant within *Cacophis*, hence uninformative for intrageneric relationships. However, A1-7 (five binary, and two three-state ordered characters) and B10 (three-state or-

dered) are parsimony-informative for more inclusive analyses and hence retained. Of characters C1-19 which vary among *Cacophis* spp., 14 characters are binary; characters C9 and C17 are assumed to form ordered three-state morphoclines, and C5, C10 and C11 have four ordered states (Table 2). However, characters C9, C15, C16 and C19 are cladistically uninformative (derived states, or combinations of states for those coded as polymorphism, occur in single terminal taxa). When uninformative characters are excluded, the effective size of the data set is therefore 16 binary, 5 three-state ordered, and 2 four-state ordered characters.

There are two equally most parsimonious trees, one with the topology (*Aspidomorphus* ((*Demansia* (*Glyphodon*, *Furina*)), (*C. squamulosus* (*harriettae* (*churchilli*, *krefftii*)))))), and the other differing only in the interchange of *harriettae* and *churchilli*. For both, tree length = 46 steps, consistency index (CI) = 0.652, homoplasy index (HI) = 0.348, retention index (RI) = 0.686, rescaled consistency index (RC) = 0.448. However, these trees conflict with the outgroup assumptions (Fig. 1), and because the characters analysed are chosen for informativeness relative to *Cacophis* rather than the outgroups, their basal nodes are considered unreliable.

Therefore, a constraint tree was used to enforce the (*Furina*, *Glyphodon*) and (*Aspidomorphus*, *Demansia*) clades. These topological constraints reduce the space of unrooted trees for eight taxa from 10 395 to 105 distinct alternatives. With the constraints, the single most parsimonious tree has total length 48 steps (Fig. 5); CI = 0.625, HI = 0.375, RI = 0.647, RC = 0.404. Cladistic relationships among the four ingroup species are identical to one of those found in the unconstrained analysis, where *Cacophis* also emerged as monophyletic.

The degree of support for each grouping was measured by the support index (Bremer, 1988), calculated in PAUP using a command file generated by TreeRot (Sorenson, 1999). These commands were modified to use branch-and-bound rather than a heuristic search algorithm. Nonparametric bootstrapping (10 000 replicates, employing branch-and-bound search) was also used to assess the robustness of each clade (apart from the outgroup clades where monophyly was enforced). Support for monophyly of *Cacophis* with respect to the outgroups (support index 4, boostrap frequency 94%) and of the (*churchilli, harriettae, krefftii*) clade (5, 94%) are strong, but that for a clade comprising *churchilli* and *krefftii* is weak (1, 58%). The alternative grouping of *harriettae* with *krefftii* was found in 30% of bootstrap replicates, but was less parsimonious (by one step) under the assumed constraints on outgroup relationships.

On the preferred phylogenetic hypothesis (Fig. 5), characters **C1**, C2, **C4**, **C5**, **C7**, **C8**, C11, **C12**, C17, C18, A5, and B10 are homoplasious (CI = 0.5 in each case except C4, C7, C8 [0.33], and C11 [0.60]). Of these, six are convergences between ingroup and outgroup taxa (not discussed further here), while those
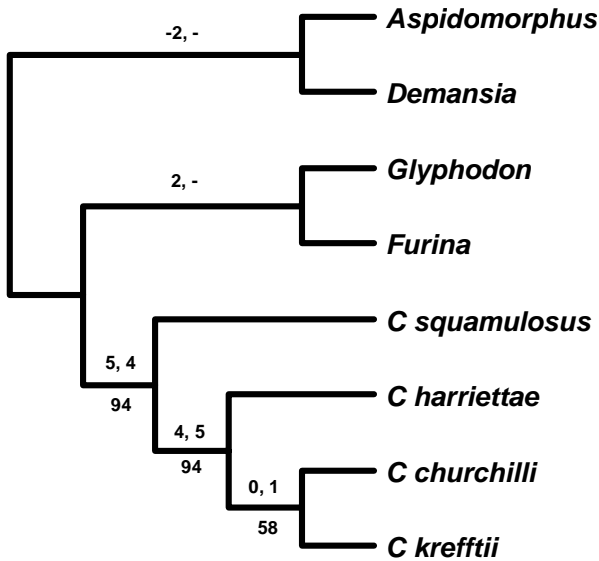
FIG. 5. Cladogram showing most parsimonious hypothesis of phylogenetic relationships among *Cacophis* spp., with multistate characters treated as ordered where applicable (analyses described in text). Numbers above branches show Bremer support for unconstrained analysis and when monophyly of both outgroups is enforced; numbers below branches bootstrap frequency (percent) in constrained analysis. Bootstrap values not applicable for the two outgroup clades (i.e. fixed at 100% by constraint tree).

shown in bold involve convergence or reversal within *Cacophis*. Characters C1 and C4 (tooth numbers on the maxilla and dentary) appear as putative synapomorphies of *harriettae* and *krefftii*, but they could easily have undergone convergence or reversal together due to common genetic basis (pleiotropy) or selective factors (i.e. they are probably not independent, cf. Lee, 1998). The frequency-based head-scale characters C5, C7 and C8 conflict with each other as well as the optimum topology, implying their independence but also the lability of such variables, consistent with 'neutral drift' or fluctuating selection on the equilibrium frequencies in each species. C12 (contrasting 'barred' ventral pattern), linking *squamulosus* and *krefftii*, is likely to be convergent as the patterns in these species differ in detail and may thus be considered to fail the similarity test of homology.

ALL CHARACTERS UNORDERED

The definitions of multi-state characters used above rely on the ordering implicit in topological and numerical relationships, i.e. on abstract properties of number rather than independent assumptions about evolutionary processes. It is nevertheless possible to analyse the 'same' matrix while disregarding this trivially available information about order, but character C10 (based entirely on rank order of meristic values) then becomes parsimony-uninformative, in addition to those excluded above. The shortest tree overall then has the topology (*Aspidomorphus* ((*Demansia* (*Glyphodon*, *Furina*)), (*squamulosus* (*churchilli* (*harriettae*, *krefftii*)))))), one of the two found in the previous analysis; tree length = 38

steps, CI = 0.711, HI = 0.290, RI = 0.732, RC = 0.520. As before, this tree conflicts with the outgroup assumptions (Fig. 1).

When the unordered data are reanalysed with the two outgroups constrained to be monophyletic, there is a single most parsimonious tree with total length 41 steps; CI = 0.659, HI = 0.342, RI = 0.659, RC = 0.434. This tree differs from that found in the 'ordered' analysis (Fig. 5) in the interchange of *churchilli* and *harriettae*, i.e. the sister group of *krefftii* is found to be *harriettae*. In a bootstrap analysis under the same constraints, monophyly of *Cacophis* is found in 98% of replicates, and a clade comprising *churchilli*, *harriettae* and *krefftii* in 90% (cf. values in Fig. 5). The sister taxon to *krefftii* is found to be *harriettae* in 52% and *churchilli* in 22.4% of bootstrap replicates.

REVISED DIAGNOSES

The previous diagnosis of *Cacophis* is that of Cogger (2000; little modified from Cogger, 1975; see also Hutchinson, 1990; Greer, 1997). The revised diagnoses below list autapomorphies of *Cacophis*, included clades, and species, and to facilitate comparison with other taxa, I also list many plesiomorphic conditions for the genus, including both widespread characters and those shared with only a few outgroup taxa. Character states discussed in the text are identified by their labels (A1(0) etc.). Some of the characters listed but not mentioned elsewhere in the text, including features of the skull, dentition and vertebrae, will be discussed elsewhere (in prep.). Diagnoses of clades and species within *Cacophis*, based on the most parsimonious cladogram discovered in this work, list apomorphies according to the delayed transformation (deltran) optimization assumption; those invariant under acctran and deltran assumptions (unambiguous synapomorphies) are marked with an asterisk.

CACOPHIS GÜNTHER, 1863

Autapomorphies. Loss of paired dorsal foramina of parietal bone (A1(1)*; one member of pair may occur); palatine choanal process relatively tall, i.e. higher than long (A2(2)*); ectopterygoid does not extend forward past pterygoid-palatine joint (A3(2)*); supra-anal keels frequently present (A4(1)*; often extensive in adult males, occasionally developed in females and juveniles); parietal scale may contact lower postocular (A5(1); see also C7); temporal formula reduced from 2+2+3 to 1+3 by fusion of two anterior rows (1=1+3; A6(1)*, see also C6); iris pale (A7(1)*, melanin pigmentation reduced to faint speckling; C17(1), carotenoid yellow rather than reddish).

Features shared with outgroups. Small (C9(0/1); less than 75 cm snout-vent, 1 m total length), terrestrial, oviparous hydrophiine elapid snakes, dark brown or greyish above with pale centres on many of the dorsal scales tending to form a longitudinal pattern on the flanks and neck; no trace of transverse bands on the

body or tail. A yellowish band, including dark spots and variegations, across the snout (including most or all of the internasal scales), over and through the eyes and temporal region, and expanding towards the midline at the rear of the head, beginning one to several scale-rows behind the parietals (C13(0), not forming a continuous transverse band; C14(0), extending four or more scale rows back on the neck); dark variegations absent or faint in the nuchal portion. Pale facial band broken by a distinct dark 'bridle' marking joining the eye to the lip. Eyes equal or smaller in diameter than their distance from the lip, pupil vertically elliptical (C18(0)). Venter with diffuse dark melanin pigment (C12(0)); yellowish carotenoid pigment also present ventrally (C15(0)). Snout short and rounded, no canthus rostralis; nasal usually divided (C8(0)), usually in contact with preocular (C5(0)); preocular contacts second supralabial; six supralabials, third and fourth entering eye; seven infralabials. Internasal and prefrontal scales usually overlapping left over right (*krefftii*, Greer, 1993; remaining species, pers. obs.). 17 to 23 longitudinal rows of dorsal scales at the first ventral (pers. obs.), reducing to 15 on neck and rarely reducing again before vent (B9(3), B10(1/2)). Anal and usually all subcaudals divided (sometimes a few anterior or scattered subcaudals single). Dorsal scales matt to slightly glossy, lacking keels (except in the cloacal region, see A4). Skin between dorsal scales pale (light brown or grey). Tongue with dark pigment only on middle portion, so base reddish and tips pale pink or white in life. Superficial venom-gland constrictor muscle (m. adductor externus superficialis) without separate quadrate head from rear of gland, and m. adductor externus medialis exposed posterior to superficialis (i.e. '*Glyphodon* type' of venom-gland musculature; McDowell, 1967). Hemipenis forked, apical lobes with terminal awns; basal portion nude, bounded distally by a row of weakly enlarged spines (Keogh, 1999).

Frontal bones together oval or diamond-shaped, prefrontal articulated to anterolateral border but not usually reaching parietal or postorbital (so frontal nearly always narrowly enters orbital margin) (B1(1)); interolfactory pillars of frontals as wide as the frontal-septomaxilla contact (B2(1)). Postorbitals in edge-to-edge contact with parietal (allowing mediolateral but not anteroposterior kinesis), not or barely reaching frontals, so parietal may enter orbital margin. Parietal relatively long, narrow and slightly bulbous (not constricted), with triangular supraorbital processes clasping frontals, distinct and elongate but narrow postorbital processes, and weak adductor crests either separated or just meeting posteriorly (not forming a sagittal crest except in the largest individuals). Parasphenoid in ventral view triangular, not narrow and awl-like. Fenestra ovalis in opisthotic-exoccipital open laterally for its full width (from border of prootic), so shaft of stapes not enclosed laterally by bony crista circumfenestralis. Maxilla extends to or beyond posterior limit of orbit (B4(1)); suborbital portion smoothly concave dorsally and con-

vex laterally; two anterior canaliculate fangs with ridged or striated surfaces, followed after a diastema by 6-8 small solid or grooved teeth (C1(0)) extending onto a rod-like posterior process defined by concavities laterally and medially. Palatine with 11-17 teeth (C2(0)), extends approximately as far anteriorly as maxilla; posterior end with lateral and medial processes clasping anterior end of pterygoid; without lateral (maxillary) process or sphenopalatine foramen, but with distinct dorsomedial 'choanal' process on the posterior part of the shaft (A2(1/2)). Ectopterygoid not extending anteriorly beyond pterygoid-palatine joint (A3(1/2)); lateral edges of ectopterygoid parallel anteriorly, angling posteromedially at a slight knob-like prominence level with the rear of the maxilla. Pterygoid with 19-24 teeth (C3(0)); lateral edge with an angular inflection or triangular process for ectopterygoid attachment; posteromedial edge usually convex, posterior tip blunt. Dentary with 14-28 teeth (C4(0/1)), increasing steeply in size from inflected anterior tip to two subequally large, robust teeth (B7(1)) with anterolateral grooves; large 6th, 7th or 8th tooth usually followed by a gap (diastema; B8(1)) and shorter, more recumbent, posterior teeth.

Zygosphenes of vertebrae in dorsal view trilobate, with rounded median lobe; prezygapophyseal processes prominent, acuminate (terms of Auffenberg, 1963) and angled anterolaterally; hypapophyses of posterior trunk vertebrae in lateral view with angle separating oblique from horizontal portions of ventral edge (B6).

Habitat is wet sclerophyll or rainforest; nocturnal, sheltering by day under rocks, logs, leaf litter, or in cavities associated with ant or termite nests; diet mainly of diurnal skinks captured at night under cover, also frogs, small snakes, and reptile eggs (Shine, 1980*a*). In defensive threat display, the anterior part of the body is raised stiffly and the head turned downward but not markedly flattened (C19(0)).

CACOPHIS SQUAMULOSUS (DUMÉRIL, BIBRON & DUMÉRIL, 1854)

Parietal contacts lower postocular in majority of specimens (C7(1)*); snout-vent length may exceed 70 cm (C9(0)*); dark ventral pigment usually forming distinct blotches or bars across base of each ventral scale, and a zig-zag median line on the subcaudals (C12(1)*); carotenoid pigment suffusing ventral and lateral scales reddish (pink or orange to deep red; C15(1)*); in defensive threat display, neck held in lateral S-shaped coils, and rear end of jaws spread laterally to widen and flatten the head (C19(1)*).

(*CACOPHIS HARRIETTAE*, *C. CHURCHILLI*, *C. KREFFTII*)

Palatine with 11 or fewer teeth (C2(1)*); pterygoid with fewer than 19 teeth (C3(1)*); usually only two scales in posterior temporal row (C6(1)*); subcaudal count may be lower than 30 (C11(1)*); pale band continuous across dorsal midline at back of head (C13(1)*).

CACOPHIS HARRIETTAE KREFFT, 1869

Maxilla with fewer than six teeth behind diastema (C1(1)); dentary with fewer than 20 teeth (C4(1)); nasal and preocular usually separated (C5(1)); nasal usually undivided (C8(1)); ventral count not less than 170 and may exceed 175 (C10(0)*); collar (and longitudinal pale stripes on body) usually white, not yellowish (C16(1)*); iris mainly white (C17(2)).

(CACOPHIS CHURCHILLI, C. KREFFTII)

Ventral count less than 176 and may be less than 165 (C10(2)*); subcaudal count not exceeding 40 (C11(2)*); pale collar only one or two scales wide (C14(1)*); pupil round or only slightly elliptical (C18(1)*).

CACOPHIS CHURCHILLI WELLS & WELLINGTON, 1985

Nasal and preocular usually separated (C5(1)); parietal usually contacts lower postocular (C7(1)*, see also A5); subcaudal counts less than 40 (C11(3)*); iris partly white (C17(2)).

CACOPHIS KREFFTII GÜNTHER, 1863

Maxilla with fewer than six teeth behind diastema (C1(1)); dentary with fewer than 20 teeth (C4(1)); nasal scale undivided (C8(1)); snout-vent length less than 35 cm (C9(2)*); ventral count does not exceed 160 (C10(3)); melanin pigment on ventral scales concentrated at posterolateral corners forming double saw-tooth pattern, or also extending medially as a continuous dark border on each ventral (leaving base of each scale white or pale yellow), and usually forming a median zig-zag stripe under tail (C12(1)*); iris red (C17(0)*).

DISCUSSION

The evidence for a sister-group relationship between *Cacophis squamulosus* and the remaining members of the genus allows us the option of resurrecting *Petrodymon* Krefft, 1866 (cf. Wallach, 1985). However, this would result in a monotypic (i.e. redundant) genus unless populations currently assigned to *C. squamulosus* prove to belong to more than one species. Variation in ventral colour patterns within this species has been noted above, and northern specimens tend to be slightly larger (Shine, 1980*a*), but no detailed investigation of geographic variation has been made. The autapomorphic modifications of defensive display and ventral pigmentation in *C. squamulosus* could be regarded as adaptive mimicry of the sympatric *Pseudechis porphyriacus*. The difference in relative height of the display, and flattening of the head rather than the neck, do not contradict this hypothesis, since *C. squamulosus* thereby both displays its black-barred red belly to advantage, and reaches the height and head-width of a 'Red-bellied Black' larger than itself.

Within the (*churchilli, harriettae, krefftii*) clade, the characters used here indicate that the sister taxon to the most derived species, *krefftii*, is either *churchilli* or *harriettae*, and less likely to be a clade comprising both. The alternative preferred here is the tree obtained in the 'ordered' analysis with outgroup constraints (Fig. 5). This hypothesis is also the only one in which the two most recently separated species have disjunct geographic distributions, consistent with a vicariance process: *krefftii* occurs from Gosford, NSW, to Mackay (e.g. QM J14287) on the Queensland coast, while *churchilli* is found further north, from Townsville (J3640) to Mossman (J5193). The greater divergence of *krefftii* (autapomorphy in features such as head shape, eye colour, and small body size) could be interpreted as character displacement due to selection, since it is broadly sympatric with both *harriettae* and *squamulosus*, whereas the distribution of *churchilli* overlaps little, if at all, with either species (see distribution maps in Wilson & Knowles, 1988, and Ehmann, 1992; those in Cogger, 1992, 2000 are less accurate, and in Longmore, 1986 the maps for *harriettae*, *krefftii*, and *squamulosus* include misidentified records of *churchilli*).

Interpretation of the cladogram in terms of species-level historical biogeography (phylogeography) is complicated by the broad sympatry between species; vicariance alone is not a sufficient explanation for their present distribution. However, even non-vicariance hypotheses are testable in terms of congruence with phylogenetic and distributional patterns in other lineages, and in this case we are favoured by the strong habitat-fidelity of *Cacophis* spp. We may assume several cycles of interruption and reconnection of the eastern wet forest corridor, which have been frequent during Plio-Pleistocene times (e.g. Bowler, 1982). One possibility would involve a persistent northern population expanding southward during three successive periods of forest continuity (cool or moist periods, perhaps the three major glaciations), and the southern populations then differentiating after interruption of the forest corridor, giving rise to the three more divergent, sympatric, southern species (*squamulosus, harriettae* and *krefftii* sequentially; Fig. 6).

This model is simple in several senses: it invokes only passive allopatric speciation (the preferred null hypothesis in, e.g., Brooks & McLennan, 1991), no extinctions, and a known process of historical environmental change in (at this scale) an essentially one-dimensional geographic space. The spatial asymmetry in the model (only southward range expansions) provides a uniform explanation for the observed distributions based on the most parsimonious cladogram.

Some other Australian elapids (*Hemiaspis signata, Cryptophis nigrescens, Hoplocephalus bitorquatus* and *Tropidechis carinatus*) have distributions comparable to that of *Cacophis* as a whole, interrupted by drier belts along the Queensland coast, but without evidence of speciation. In *H. signata*, a northern form *vagrans* Garman, 1901 is sometimes recognized as a subspecies or species, but no such distinction has been demon-
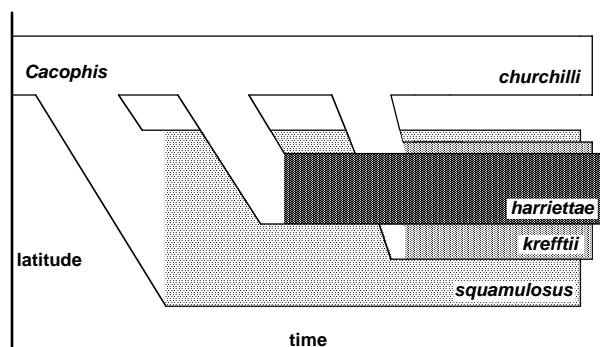
FIG. 6. Schematic distribution of *Cacophis* in space and time, according to phylogenetic hypothesis in Fig. 5 and speciation model proposed in text. Vertical axis represents latitude; present distribution of the genus is between 15° and 35°S, with *C. churchilli* north of 20° and other species mainly or entirely further south. Horizontal axis represents time, from before beginning of Pleistocene climatic fluctuations (left) to the present day (right). Connectivity of 'overlapped' regions of branches is indicated by shading.

strated. The genera *Hypsilurus* (Agamidae) and *Coeranoscincus* (Scincidae) each have two well-differentiated allopatric species with similar distributions to *Cacophis churchilli* and *krefftii* respectively; *Litoria xanthomera* and *L. chloris* (Anura, Hylidae) form a similar vicariant pair, while patterns which may be comparable to *Cacophis* as a whole are seen in *Calyptotis*, *Lampropholis*, *Saproscincus* (Scincidae) and *Mixophyes* (Myobatrachidae), each with five or more species (Cogger, 1992, 2000; Barker, Grigg & Tyler, 1995). Among small, terrestrial forest mammals, *Dasyurus maculatus*, *Antechinus flavipes* and *A. stuartii* (Marsupialia, Dasyuridae), *Rattus fuscipes* and *R. lutreolus* (Rodentia, Muridae) also have breaks between southern and north-Queensland populations (subspecies; Strahan, 1983). As relevant sequence data become available, the estimation of divergence dates using molecular 'clocks' may indicate whether *Cacophis* and other such lineages have been affected by the same sequence of environmental changes (undergoing evolution as a community), or have followed independent timetables. Based on differences in the DNA sequences of two genes, Keogh *et al.* (1998) infer a split between *Cacophis squamulosus* and *krefftii* 'of considerable antiquity', but do not give a quantitative age estimate, and comparable sequences have not yet been reported for the other species.

The monophyly of *Cacophis* is now well supported, and the results of this analysis will allow it to be treated as a unit in future work. For example, the evidence presented here may help to determine the relationships of *Demansia* with other lineages, which seems to be one of the central problems of elapid phylogeny. Morphological analyses have associated *Demansia* with *Aspidomorphus* and members of the viviparous lineage (McDowell, 1967, 1969*b*, 1985), or with *Pseudechis* (Wallach, 1985), while most genetic studies have failed to show close relationships with any Australian lineages

(Cadle & Gorman, 1981; Mao, Chen, Yin & Guo, 1983; Schwaner *et al.*, 1985; Mengden, 1985). A view has developed that *Demansia* is only distantly related to other Australian taxa (Mengden, 1985; Shine, 1991; Greer, 1997), although this does not necessarily follow from large genetic distances (phenetic data). Keogh *et al.* (1998) report DNA sequence evidence for a clade comprising *Cacophis*, *Aspidomorphus*, *Demansia*, *Furina* and *Glyphodon*, and some of the skeletal characters referred to above may also support such a group. These results suggest that the earlier genetic studies were affected by accelerated genetic change in the whipsnake lineage (as first suggested by Cadle & Gorman, 1981), and that other methods may have more success.

Further studies will continue to improve understanding of the adaptive radiation of Australasian elapids, and external morphology, internal soft anatomy, cranial and axial skeletal morphology (including the fossil record), genetic and molecular methods, and behavioural and ecological data can all contribute to this end.

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APPENDIX 1

Sources of data for ingroup and outgroup species. Skeletal material examined marked with asterisk (*); specimens examined only for external characters omitted for taxa other than *Cacophis* spp. and *Demansia simplex* (available from author on request). Useful sources of further data and illustrations for Australian species include Cogger (1975, 1992, 2000), Storr *et al.* (1986), Wilson & Knowles (1988), Gow (1989), Hoser (1989), Ehmann (1992), and Greer (1997).

Aspidomorphus lineaticollis: AMS R125021*, AMNH 42376*; *A. muelleri*: AMS R16614*, R19013*; *A. schlegelii* : MCZ 7311* (AMNH and MCZ specimens examined by M. Lee); Brongersma (1934), McDowell (1967), Shine and Keogh (1996), O'Shea (1996).

Cacophis churchilli: AMS R6489, R10732, R11340, R11362, R11506, R11512, R12480, R12482, R12914, R17035, R20207, R53726, R63163, R63836, QMJ3640, J4295, J5193, J5292, J5296, J5720, J5722, J5723, J5724, J5725, J5954, J7339, J13674, J21206, J24539, J53282*; SAM R22392, JS63*.

Cacophis harriettae: AMS R648, R5844, R6182, R8507, R9399, R11687, R12734, R12854, R13027, R13701, R13716, R18277, R47545, R86763, R88468, QM J4443*, J20278*, J26544*, J46288*, J47658*, J47982*, J50600*, SAM R26989*; McDowell (1967), Shine (1980a).

Cacophis krefftii: AMS R877 (x2), R1502, R2303, R2411, R4118, R6545, R7492, R8026, R8768, R9198, R10013, R11812, R12356, R12738, R12919, R12995, R13000, R13001, R13064, R13662 (x2), R13743, R13799, R13823, R13824, R13869, R13982, R14344, R14359 (x2), R14422, R14815, R15690, R17917, R18482, R47474, R58486, R75961, R74466, R77370, R81158, R81159, R81160, R81161, R86762, R86797, R90609, R97275, R106956, R110341, R114956, R125410, AMS unreg.*, QM J966, J14287, J32725, J34031, J46583*, SAM R26974*; McDowell (1967), Shine (1980a), Wells (1980).

Cacophis squamulosus: AMS R28232, R29733, R30336, R37187, R41801, R47471, R47544, R47546, R47779, R48108, R50220, R52964, R62710, R64975, AMS unreg. (x4)*, QMJ47659*, J47976*, J47983*, SAM R2263A*, JS3*, JS14*; Shine (1980a).

Demansia psammophis: QMJ7134*, J26907*, J46291*, J47978*, AMS R-13-672*, JS 44*; *D. vestigiata* : AMS R-13-667*; *D.* sp. cf. *olivacea* : JS169*; *D.* sp. cf. *torquata* : QMJ46289*, SAM R20483*; *D. simplex* : AMS R13045, R13046, R13702, R14030, R14029, R 128403, R128404, NTM R18625*; Storr (1978), Shine (1980b), Shea and Scanlon (unpublished data).

Furina barnardi: SAM R27022*, AMS unreg.*; *F. diadema* : AMS R98165*, SAM R6075*, R6703*, JS32*; *F. ornata* : WAM R15088*; Shine (1981), Storr (1981), Scanlon (1985, unpublished data).

Glyphodon dunmalli: QM J23178*; *G. tristis* : SAM R13998*, MV unreg.*; Boulenger (1896), Worrell (1955), Shine (1981) , Scanlon (unpublished data).

APPENDIX 2

List of characters used in the phylogenetic analysis.

A. Autapomorphies of *Cacophis*. See Table 2 for distribution of states in outgroup genera.

1. Paired parietal foramina: present, at least in small specimens (0); normally absent (1).
2. Palatine choanal process: absent (0); present but low, i.e. 'short' (1); higher than long, i.e. 'tall' (2).
3. Ectopterygoid anterior extent: anterior to palatine-pterygoid joint (0); approximately level with (lateral to) joint (1); entirely posterior to palatine (2).
4. Supra-anal keels: lateral scales of cloacal region similar in gross morphology to those of rest of body (0); patch of keeled lateral scales present in adult males (1).
5. Parietal and lower postocular: separated by contact of upper postocular with anterior temporal (0); sometimes in contact, separating upper postocular from temporal (1).
6. Temporals: 2+2+3, three distinct rows (0); 1=1+3 (or 1=1+2), single large anterior temporal incorporating temporolabial (1).
7. Iris colour in preservative (melanin): entirely or mainly dark (0); pale, with at most dark flecks or faint variegation (1).

B. Characters possibly derived within Australasian elapids but shared by *Cacophis* with both outgroup clades. See Table 2 for distribution of states in outgroup genera.

1. Prefrontal and postorbital bones: widely separated and frontal broadly entering orbital margin (0); prefrontal and postorbital approach or meet, effectively excluding frontal from margin (1).
2. Interolfactory pillars of frontals: distinctly constricted (0); as wide as the septomaxillary-frontal contact, widely separating olfactory openings of frontal (1).
3. Maxilla anterior process: short and blunt (0); prominent or acute in ventral view (1).
4. Maxilla posterior extent, relative to postorbital in lateral view: short, not beyond orbit (0); long, beyond posterior margin of orbit as defined by the postorbital (1).
5. Coronoid eminence of mandible: absent, dorsal margin of compound smoothly curved (0); eminence present as slight to strong convex angulation of dorsal edge of surangular (1).
6. Hypapophysis shape in posterior trunk vertebrae: smoothly sigmoid in lateral view (0); some vertebrae with a distinct horizontal portion defined by an anteroventral angle (1).

7. Dentary teeth: uniform or with smooth gradient of size (0); distinctly larger anteriorly (1).

8. Dentary tooth row: lacks a diastema (0); diastema commonly present behind enlarged teeth (1).

9. Number of midbody scale rows: 19 or more (0); 17 (1); 15-17, intraspecifically variable (2); 15 (3). Polarity follows Wallach (1985), but state 0 is almost certainly derived within *Glyphodon* (21 rows in *G. dunmalli*).

10. Posterior scale-row reduction: one or more reductions always present (0); variable, reduction sometimes present (1); reduction rare or absent (2).

C. Characters varying within *Cacophis*. See Table 3 for distribution of states in *Cacophis* species and outgroup genera.

1. Maxillary teeth posterior to fangs: 6-8 alveoli (0); 2-5 (1).

2. Palatine teeth: usually more than 11 alveoli (0); 11 or fewer (1).

3. Pterygoid teeth: 19-24 alveoli (0): 11-18 (1).

4. Dentary teeth: 21 or more (0); less than 20 (1).

5. Nasal and preocular: usually in contact (0); usually separated, contact rare (1); normally widely separated, contact not observed (2). Ordered 0-1-2.

6. Posterior temporals: nearly always three in final row (2+2+3 or 1=1+3) (0); reduced to two in most individuals (1=1+2) (1).

7. Parietal-postocular contact, frequency: minority (0); majority (1).

8. Nasal scale: divided in majority (0); single in majority (1).

9. Maximum snout-vent length: greater than 70 cm (0); 40-65 cm (1); less than 35 cm (2). Ordered 0-1-2.

10. Ventral scale number (range): 176-200 (0); 170-175 (1); 165-169 (2); 161-164 (3); 140-160 (4). Ordered.

11. Subcaudal scale number: 41-50 (0); 38-40 (1); 30-37 (2); 25-29 (3). Ordered 0-1-2-3.

12. Ventral melanin pigment: uniformly distributed, 'peppered' or generally dark grey (0); strongly contrasting pattern, usually transverse dark and light bands on each ventral scale (1).

13. Upper light line or nape band: pale lines on neck longitudinal, separated across midline (0); transverse and connected across midline, forming a complete collar (1).

14. Upper light line or nape band: occupies at least 4 transverse scale rows (0), or 1-2 only (1).

15. Carotenoid on body: pale yellow or absent (0); orange to red (1).

16. Carotenoid on face and nape: yellow (0); very pale yellow or white (1).

17. Iris colour in life (non-melanin): red (0); yellow (1); partly or mainly white (2). Ordered 0-1-2.

18. Pupil shape: vertically elliptical (0); weakly oval or round (1).

19. Forebody in high defensive display: held straight (0); lateral curves (1).