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The Taxonomy of Australian Elapid Snakes: A Review

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ABSTRACT. Published data on Australian elapid snake taxonomy are reviewed. Both classical morphological studies and relevant ecological, chromosomal and biochemical data are summarized.

Attention is focused on two major areas:

(1) the phylogenetic relationships between Australian terrestrial elapids and other proteroglyphs; and

(2) the interrelationships among the Australian terrestrial elapids.

From this review four key questions are identified:

(1) Are the continentally endemic groups of terrestrial elapids confamilial?

(2) Do the Australian elapids represent a distinct familial group?

(3) Are the Australian elapids monophyletic or have the extant forms been derived from distinct lineages which may represent more than one invasion of the continent?

(4) What is the precise relationship between laticaudine and hydrophiine sea snakes and the Australian elapids?

There is considerable disagreement concerning generic allocations and suprageneric relationships within the Australian proteroglyphs. Ecological, cytological and biochemical studies currently under way may be useful adjuncts to morphological information in resolving these questions.

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The combined proteroglyphous or fixed-front-fanged snakes are represented world-wide by approximately 63 genera and 245 species (Elapidae, Laticaudidae and Hydrophiidae of some authors). Of these, 16 genera and 53 species are marine forms. This group contains a large percentage of those venomous snake species dangerous to man.

This report summarizes the published classifications on the Australian elapids, including those based on morphological criteria as well as the recent biochemical and cytological work that has obvious taxonomic implications. The aim of this review is to clarify the problems still to be resolved in elapid taxonomy and provide a taxonomic baseline for future contributions. This paper provides a summary of previous taxonomic studies, but does not suggest any new taxonomic designations. Nor do I wish to offer a reassessment of characters. Consequently, I have avoided weighting characters or biasing the presentation toward any one of the classifications that have been published. The paper deals first with the question of relationships among proteroglyphous snakes world-wide, and then focuses on relationships among the Australian terrestrial proteroglyphs.

I. A BACKGROUND TO "ELAPID" CLASSIFICATION

Table 1 lists all genera of proteroglyphs, their common names and some relevant taxonomic comments from the literature.

The sparse fossil record of elapids commences in the upper Miocene in France and Morocco (Hoffstetter, 1962). This rccord, however, has been of little help in determining precise categories of snake taxa owing to the lack of critical fossils (Dowling, 1959; Marx & Rabb, 1973), the incomplete nature of most of the fossil forms, and consequent difficulty of recognizing primitive and derived character states in them (Dowling & Duellman, 1978; see also Schwaner & Dessauer, 1982).

Storr (1964) pointed out that the Elapidae (presumably referring to all terrestrial proteroglyphs) give the appearance of an "old declining group". He also commented that, with the exception of *Naja* (true cobras), all the forty or so then recognized genera formed distinct geographic groups endemic to particular continents.

The terrestrial elapids are generally considered to have been derived from a colubrid ancestor. The marine proteroglyphs are assumed either to have been derived directly from terrestrial elapid snakes or else to share a common ancestral stock with them (see Cogger, 1975a for summary). Indeed their close affinities were indicated by Underwood (1967), who gave them confamilial status with a single division between all terrestrial (subfamily Elapinae) and marine (subfamily Hydrophiinae) forms (Table 1). This was subsequently supported by Hardaway & Williams (1976) following an analysis of the costal cartilages of the ribs and modified by Underwood (1979) to include subfamily Laticaudinae. Dowling (1967) also placed all proteroglyphs in the family Elapidae but divided the family into four subfamilies: Apisthocalaminae ("stem elapids"), Elapinae ("terrestrial elapids"), Laticaudinae ("recent sea snakes"), and Hydrophiinae ("advanced sea snakes").

1. The Origins and Affinities of the Terrestrial Proteroglyphs

1(a). The Morphological Data

Doubt was cast on the monophyletic origin of the proteroglyph condition by the work of Bourgeois (1965) on the African Mole Viper (*Atractaspis*) and that of McDowell (1968) on the African elapid snake *Elaps* (=

Homorelaps sensu Boulenger 1896 = *Homoroselaps* as per opinion 1201 of Int. Comm. Zool. Nomenclature, 1982). Both authors attempted to demonstrate that the closest affinities of their respective forms lay with the same group of rear-fanged (opisthoglyphous) African colubrids. This would mean that the two separate venom delivery systems of the Viperidae (solenoglyphous [movable-front-fanged] snakes), to which *Atractaspis* then belonged, and the Elapidae (proteroglyphous [fixed-front-fanged] snakes), to which *Elaps* then belonged, would have arisen in parallel from a somewhat similar ancestral stock. In the most recent summaries of snake classification (Smith *et al.*, 1977; Underwood, 1979; Harding & Welch, 1980), which relied heavily on the morphological work of McDowell, *Atractaspis* has been accorded the status of a separate subfamily (Atractaspinae) within the family Colubridae, though Branch (1981) suggested that tribal designation within the subfamily Aparallactinae may more accurately reflect its relationship. *Elaps*, the type genus for the family Elapidae, appears to be well differentiated from all other members of the Elapidae in dental and skull characters. In the light of this, McDowell (1968) adopted the generic name *Homorelaps* used by Boulenger (1896) and suggested the affinities of the genus lie with the Aparallactinae, family Colubridae, a transfer which has not been accepted by all workers (Kochva & Wollberg, 1970). A recent decision by the International Commission on Zoological Nomenclature (Opinion 1201, 1982) resulted in suppression of the name *Elaps* and validation of *Homoroselaps* for *'Elaps' lacteus* and *dorsalis*. Elapidae was retained as the family name.

McDowell (1970) regarded the fossorial African *Elapsoidea* as among the most primitive of existing elapids, together with *Bungarus, Boulengerina* and to a lesser extent *Paranaja*. Branch (1979) pointed out that the absence of both apical pits and a loreal scale, two characteristics common to all elapids, may indicate a fossorial ancestor. These characters are shared with the aparallactine colubrids of Africa, which also show a fossorial mode of life. This has led both McDowell (1970) and Branch (1979) to conclude that the aparallactines most resemble the presumed ancestral stock.

An alternative point of view regarding the origin of the proteroglyph condition was proposed by Savitsky (1978). He argued that the New World coral snakes, composed of the three genera *Micrurus* (50+ species), *Leptomicrurus* (3 species), and *Micruroides* (1 species), and making up approximately 30% of the world's terrestrial elapid fauna, represent an independent derivation of the proteroglyphous condition. He suggested that these three genera share an origin with the rear-fanged xenodontine colubrids of South America. Duellman (1979) has supported this idea by removing them to a separate family, the Micruridae. McDowell (1967, 1969a), on the other hand, had earlier placed the micrurines with a group of semifossorial Asian elapids including *Calliophis, Parapistacalamus, Maticora* and the sea kraits *Laticauda*. McDowell's classification was adopted by Smith *et al.* (1977) and three tribes within the subfamily Elapinae were erected: the Elapini (= American and North Asian coral snakes), the Maticorini (= South Asiatic coral snakes) and Laticaudini (= sea kraits).

1(b). The Biochemical Data (Terrestrial Proteroglyphs)

Turning to the chemotaxonomic data, the immunological study of Cadle & Sarich (1981) refuted the classification proposed by Savitsky (1978) and Duellman (1979). Using microcomplement fixation analysis (MC'F) Cadle and Sarich (1981) demonstrated a closer relationship between the micrurines, the Asian elapids *Ophiophagus* and *Bungarus*, the Australian elapid *Austrelaps* and the sea kraits *Laticauda*, on the one hand, than between the micrurines and any of the xenodontine colubrids or hydrophiine sea snakes on the other. They claimed that their data unequivocally placed the micrurines "on a common lineage with Asian and Australian terrestrial elapids and with the sea snakes". However, as it stands their data neither supported nor refuted the association of micrurines specifically with *Laticauda* as proposed by McDowell. In a further immunological study (Cadle & Gorman, 1981) no strong association was found between *Micrurus* and *Laticauda*. Instead, four major lineages of elapid genera were identified: (1) hydrophiine sea snakes, (2) *Laticauda*, (3) New World coral snakes and (4) one or more lineages including *Demansia* (Australian), *Bungarus* and *Ophiophagus* (Asian) which were close to none of the reference antisera they studied. Moreover, *Demansia* was clearly distinguishable from all other Australian elapids examined by these authors.

Cadle & Gorman (1981) pointed out that neither their study nor that of Cadle & Sarich (1981) included either Old World coral snakes or African elapids. Consequently many of the relationships suggested by McDowell could not be tested, nor could the relationships of the Australian elapids exclusive of *Demansia* be elucidated.

The recent MC'F work of Mao *et al.*(1983) is in concordance with the findings of Cadle & Gorman (1981) in that they too found no close affinity between *Micrurus* and *Laticauda*. The immunological distance units (IDU's) for *Micrurus* when tested along with other elapid genera against the four antisera (*Pseudonaja, Bungarus, Hydrophis* and *Laticauda*) were quite close to those obtained for *Bungarus* and *Elapsoidea* with the same four antisera, leading Mao *et al.* to agree with Cadle & Sarich's (1981) placement of *Micrurus* in Elapinae. Their report also confirmed the distinctiveness of *Demansia* from other Australian elapids. They supported the placement of the Australian elapids in the subfamily Acanthophinae by Dowling & Duellman (1978), emphasizing their distinctness from Asian and African elapids. Mao *et al.* (1983) reported an unusual character in the albumin of *Naja*. They suggested that the *Naja* albumin either is widely divergent from other elapids or has evolved at a much faster rate.

Cadle (in press) recently utilized the MC′F technique to test the hypothesis of independent origin of the proteroglyph condition from colubrid stock in micrurines and *Atractaspis*. His interpretation of these data refuted the hypothesis of affinity of either of these groups with colubrids and strongly supported the relationship of micrurines to elapids. He was unable to place *Atractaspis* unambiguously with either the elapids or viperids and suggested it may represent an independent lineage.

1(c). *Dendroaspis*—A Distinctive Elapid?

Among the African elapids the mambas (*Dendroaspis*) can be distinguished from all other forms on the basis of the morphology of the maxilla. In his classic work on reptilian osteology, Romer (1956) gave the genus separate subfamilial status (Dendroaspinae) on the basis of this character. Dowling (1959) found this to be an unacceptable criterion for subfamilial distinction. It is interesting to observe that Underwood (1967) described the skull of *Dendroaspis* as differing from all other African elapids in lacking both choanal and maxillary processes on the palatine bones. The Australasian elapids also lack the choanal process and, with the exception of *Ogmodon* (Fiji), lack the maxillary process as well (McDowell, 1970). McDowell further elaborated upon the distinctiveness of the dentition and palatine kinesis in *Dendroaspis* but did not remove them taxonomically from other African elapids.

More recently several authors have used a variety of biochemical characters to infer relationships. Saint Girons & Detrait (1980), for example, have analysed *Dendroaspis* venom in terms of per cent common antigens, immunodiffusion, and immunoelectrophoretic comparisons against African (*Naja* and *Hemachatus*), Australian (*Austrelaps* and *Pseudechis*) and Asian (*Naja* and *Bungarus*) elapids. They found only minor similarities between the venom of *Dendroaspis* and all the other genera examined. Saint Girons & Detrait argue that, when they exist, antigenic similarities reflect phylogenetic and not functional affinities.

2. The Origins and Affinities of the Marine Proteroglyphs

2(a). The Morphological Data

An affinity between the sea snakes and the terrestrial proteroglyphs has long been suspected. In a series of studies on proteroglyphs McDowell (1967, 1968, 1969a, 1969b, 1970, 1972, 1974) analysed a suite of morphological characters, including the osteology of the skull, dentition, venom gland musculature and hemipenial structure. Two important points emerged from his analysis. First, the sea kraits of the genus *Laticauda* were held to have originated quite separately from other sea snakes, which collectively form the hydrophiids. Second, the structure of the palatine bone and associated processes was held to imply a taxonomic dichotomy based on the functional kinesis of these structures among proteroglyphs. McDowell termed the two groups "palatine erectors" and "palatine draggers". Most terrestrial elapids fall into the category of "palatine erectors" with the notable exception of the Australian elapid snakes which, like the hydrophiine sea snakes, are "palatine draggers" (McDowell, 1970). This information led Smith *et al.* (1977) to propose a rather controversial classification in which the Australian elapids are transferred from the family Elapidae to a subfamily Oxyuraninae within the Hydrophiidae. The laticaudine sea snakes, formerly a subfamily of the Hydrophiidae, are placed in the tribe Laticaudini, subfamily Elapinae, together with North Asiatic and American coral snakes. The remaining elapid subfamily, the Bungarinae, then contains two tribes which include all Asiatic and African terrestrial elapids (see Tables 1 and 2).

McDowell considered the laticaudine sea snakes no more than a divergent line within the terrestrial elapids while Voris (1969) concluded, in agreement with Smith (1926), that *Laticauda* is the most primitive of extant sea snakes though sharing a common origin with the more specialized forms (see Cogger, 1975a). Voris (1977) subsequently reported on a multivariate analysis of 43 characters and concluded that: "*Laticauda* do not stand on a character-by-character basis between the terrestrial elapids and the other sea snakes . . . They (the *Laticauda*) are very distinct from all other sea snakes and either represent an independent evolutionary line or a very early separation from all other sea snakes. They are by far the most primitive sea snakes and possess many elapid character states". These later views of Voris appear to bring his assessment in closer line to McDowell's than earlier indicated.

Smith (1931) drew attention to the monotypic genus *Ephalophis* which he considered primitive and perhaps intermediate between the laticaudine and hydrophiine sea snakes. McDowell (1969b) placed *Hydrophis mertoni* in the genus *Ephalophis* and suggested that through it the hydrophiines were derived from the Australian elapids of the "*Demansia*" group and specifically *Drepanodontis* (= *Hemiaspis*) and *Rhinoplocephalus* (McDowell, 1967, 1972, 1974). McDowell also divided the hydrophiine sea snakes into three groups based on scalation, vertebral anatomy, venom gland musculature and skull morphology, namely:

(1) the *Hydrelaps* group including only the distinctive, and in many respects primitive, genus *Hydrelaps*;
(2) the *Aipysurus* group with *Ephalophis* being the most primitive genus in this group but also including *Aipysurus* and the very specialized *Emydocephalus* which feeds exclusively on fish eggs;
(3) the most advanced, *Hydrophis* group containing most of the remaining sea snake genera (see McDowell, 1967, 1970 for list of generic changes).

This differed radically from Smith's (1926) concept of the family Hydrophiidae, which he believed should contain subfamily Laticaudinae, including *Laticauda, Aipysurus* and *Emydocephalus,* and the subfamily

Hydrophiinae, including *Hydrophis* and all other genera.

Voris (1977) agreed with the classification of McDowell (1967, 1970), who pointed out the primitive status of *Hydrelaps*, though Voris placed *Ephalophis* with *Hydrelaps* in a separate group instead of including it among the *Aipysurus* group. Voris also points to *Hydrophis* (= *Disteira* of McDowell, 1972) *kingi, H.* (*D.*) *major, Kerilia jerdoni* and *Thalassophis* as "relatively primitive" and possibly divergent from the main and more recent *Hydrophis* stock.

Cogger (1975a) reduced McDowell's (1972) genus *Disteira* substantially by retaining the species *schistosa* and *stokesii* in the genera *Enhydrina* and *Astrotia* respectively, a move adopted by all subsequent authors.

In a brief review of the sea snakes, Burger & Natsuno (1974) reassessed the available data and analysed internal morphological features. They drew attention again to *Ephalophis* (*Hydrophis*) *mertoni* and, because of the location of the heart, lack of the vestigial left lung seen in *E. greyi*, and dorsal scale differences, *E. mertoni* was considered more advanced than *E. greyi* and a new genus *Parahydrophis* was erected to include only *P. mertoni*. A new subfamily Ephalophiinae was erected to include five genera which the authors divided into three groups: (1) "*Hydrelaps* group" for *Hydrelaps* only; (2) "*Ephalophis* group" for *Ephalophis* and *Parahydrophis*, with *Ephalophis* selected as the type genus of the subfamily; and (3) "*Aipysurus* group" for *Aipysurus* and *Emydocephalus*. This bears an obvious resemblance to the grouping of genera suggested by McDowell except for the splitting of the *Aipysurus* group of McDowell and the elevation of these three groups to form a subfamilial assemblage. The other genera remained in the Hydrophiinae, though *Disteira* (McDowell, 1972, and *sensu lato* Cogger, 1975a) has been put back into *Hydrophis*. Burger and Natsuno also reaffirmed the distinction between *Laticauda* and the hydrophiid sea snakes and emphasized it by placing them in separate families, resurrecting the Laticaudidae for the sea kraits and the Hydrophiidae for all other sea snakes.

2(b). The Biochemical Data (Marine Proteroglyphs)

Turning to the published biochemical data on this group, Mao *et al.* (1977) have examined the structural affinities of the transferrins of *Hydrophis, Lapemis, Pelamis* ("*Hydrophis* group" of McDowell), *Aipysurus, Emydocephalus* (the "*Aipysurus* group" of McDowell), *Laticauda, Naja* and *Bungarus* (the Elapidae of McDowell), using the MC′F technique. Their interpretation of the data agrees well with McDowell's (1972) classification with two exceptions: (1) the indices of dissimilarity suggest that the sea snakes, here including the *Laticauda*, have diverged from Asian terrestrial elapids at the familial level (Australian genera were not examined), and (2) the two-way reciprocal titrations between *Laticauda* and *Hydrophis* demonstrate closer affinities between the genera than the morphological criteria indicated, though this does not seem to be supported by Cadle and Gorman's MC′F work (1981).

The data of Mao *et al.* (1977) are broadly compatible with the immunoelectrophoretic data of Minton & da Costa (1975). The latter authors supported many of McDowell's associations with the exception that they found *Emydocephalus* to be more distinct from *Aipysurus* serologically than it is morphologically. Minton & da Costa also suggested that the sea snakes represent "a homogeneous group closely related to the Australian elapids". From their data *Laticauda* showed greater reactivity to the Australian elapid antisera of *Denisonia* (= *Austrelaps* in this instance) than did *Lapemis* and *Hydrophis*. The sample species, however, did not allow the authors to test McDowell's theory of an Asian rather than an Australian origin of *Laticauda* or to determine its relation to the family Elapidae. In a subsequent review of his own work Minton (1981; see also Minton, 1978) concluded that the elapid stocks have probably been distinct since the Miocene though the origin and affinities of the family remain unknown. Minton further describes the Hydrophiidae as containing two stocks, with *Laticauda* being distinct. The venom analysis of Coulter *et al.* (1981) found a close relationship between Australian elapids and sea snakes, in agreement with Minton & da Costa (1975), but did not find a close relationship between 'exotic' terrestrial elapid venom (here presumably referring to African and Asian elapids) and Australian venoms.

As mentioned above, the MC′F work of Cadle & Gorman (1981), included a comparison of sea snakes with both Asiatic and Australian elapids and indicated that sea snakes comprise three groups similar to McDowell's classification (i.e. hydrophiids, aipysurids and laticaudids). Though the question of a single versus a multiple origin of sea snakes could not be answered by the immunological data, it appeared that, with the exception of *Demansia psammophis,* the Australian forms are close to both *Hydrophis* and *Laticauda.*

The more recent MC′F work of Mao *et al.* (1983) utilized albumin and from these data the authors suggested *Laticauda* is closely related to hydrophiines, thus supporting their earlier transferrin data (Mao *et al.*, 1977). They also found the sea snakes to be closer to Australasian elapids than to the elapids on other continents.

2(c). The Chromosomal Data (Marine Proteroglyphs)

Gorman (1981) has reviewed published data on sea snake karyology. He reported gross karyotypic data for three species of laticaudine sea snakes and reviewed chromosomal data for 18 species of elapids (excluding those published by De Smet, 1978, and Gutiérrez & Bolaños, 1979). It is apparent from this study that a considerable amount of gross karyotypic data is available on sea snakes. This is due largely to the efforts of Singh (1972a,b, 1974). Sea snakes reported thus far vary in diploid number from 32 to 40 with some hydrophiids having undergone rearrangements of the W sex chromosome, giving rise to ZW_1W_2 females. It is also interesting to note that all hydrophiids karyotyped thus far display a secondary constriction on pair one while no such constriction has been mentioned in *Laticauda*. No karyotypic data have been published for any of the species making up the *Aipysurus* group of McDowell, which is thought to comprise the primitive and intermediate hydrophiids. Gorman (1981) concluded that most of the chromosomal variation observed in sea snakes can be attributed to centric fission and sex chromosome rearrangements with general conservation of macrochromosomes. On the basis of this and the similarity of gross karyotype (2n = 34; 14 M + 20 m) between one of the three *Laticauda* species he reported and *Notechis scutatus*, the only Australian terrestrial elapid for which chromosomal data are currently available (Shine & Bull, 1977), Gorman suggested that these two genera share a primitive karyotype. Indeed, Gorman (1981) proposed that this karyotype may represent the ancestral condition for the elapid radiation. Such an assumption would seem highly tenuous considering the lack of chromosome data on the remaining 24 genera of Australian terrestrial elapids.

3. A Summary of Proteroglyph Relationships

The one thing that should be apparent from the foregoing discussion is the inability of taxonomists to arrive at any unanimity. This stems directly from the difficulty of defining primitive and derived character states.

The affinities of proteroglyphs to their possible colubrid ancestors remain poorly understood. Three distinct colubrid groups have been suggested as showing ancestral relationship to various elapid stocks. On morphological criteria aparallactine colubrids are suggested to resemble some African elapids (McDowell, 1970; Branch, 1979) while other workers have suggested that xenodontine colubrids resemble the precursor of the micrurine elapids (Savitsky, 1978). Minton & da Costa (1975) have cautiously suggested an unexpected relationship between natricine colubrids and sea snakes on the basis of serological studies. Anthony & Guibé (1951, 1952) have even suggested a polyphyletic origin, with some elapids being derived from the boids *Bolyeria* and *Casarea*. Cadle, however, insisted that molecular data do not support a close affinity between these elapid and colubrid groups.

A greater consensus of opinion has prevailed on the groupings and relationships of sea snakes. Both morphological and biochemical data have suggested a close relationship between Australian terrestrial proteroglyphs and hydrophiid sea snakes. Likewise, most authors agreed on the general division of hydrophiid sea snakes into three groups, yet there is little agreement upon the precise relationship of *Laticauda*.

From the confused taxonomic picture three key questions remain to be resolved at the familial level, namely: (1) Are the continentally endemic groups of terrestrial elapids confamilial (as suggested by Underwood, 1967) or, if not, do the Australian elapids represent a distinct familial group? (This possibility was also referred to by Underwood, 1967, in reference to the work of Storr, 1964; Dowling & Duellman, 1978, placed them in a separate subfamily Acanthophinae.), (2) Are Australian elapids a monophyletic group?, and (3) What is the precise relationship between the laticaudid and hydrophiid sea snakes and the Australian elapids, and is there evidence to demonstrate an independent origin of hydrophiid and laticaudid sea snakes?

II. TAXONOMIC RELATIONSHIPS WITHIN THE AUSTRALIAN TERRESTRIAL ELAPID SNAKES

Two of the zoogeographic works which included reference to the Australian elapid fauna were those of Storr (1964) and Cogger & Heatwole (1980). Both studies pointed out the high degree of endemism in Australian elapids. Cogger & Heatwole (1980), for example, found that 94% of all Australian elapids (approx. 25 genera and 63 + species) are endemic, with the remainder being shared with New Guinea. Only one species of Death Adder (*Acanthophis*) extends to the islands beyond New Guinea. Such a high degree of generic endemism among reptiles in Australia is exceeded only by the pygopodid lizards.

Storr (1964) suggested that Australian elapids are derived from early colubrids, probably originating in Asia and invading the Australian continent at a time when more primitive colubrids were waning and before the modern colubrid radiation (see also Cogger & Heatwole, 1980). Storr interpreted the high degree of continental endemism to imply that the Elapidae are an old, declining group. The fossil record provides no information on the age of the elapid radiation in Australia, although Cogger & Heatwole (1980) suggest "the major adaptive radiations within Australia in such groups as the elapid snakes, diplodactyline geckoes, the endemic family Pygopodidae and major segments of the lizard families Agamidae, Varanidae and Scincidae are almost certainly derived from elements which arrived no later than the mid-Tertiary. These indigenous radiations, however, apparently proceeded with little or no modification by later migrations of the same families until well into the Quaternary, suggesting that Australia's reptile fauna evolved in virtual isolation between at least mid-Tertiary and the beginning of the Quaternary (a period of 30–35 million years) when a new series of migrations from Asia commenced".

1. The Classifications since Günther (1858)

The taxonomic interrelations of the Australian elapid snakes have long been a question for debate. Before attempting to outline the problems I would like to draw the reader's attention to the distinction between that portion of the literature that reflects a failure to apply the rules of zoological nomenclature and those problems which actually reflect a difference between authors' concepts of the relationships of organisms. It is cases of the latter type that will be discussed in detail here. To assist the reader with nomenclatural problems of the former type, Table 3 provides a list of all generic and specific names that have been applied to Australian terrestrial and marine proteroglyphs and their currently used synonyms. These data were derived largely from the checklist of Cogger *et al.* (1983); for a more detailed synonymy and justification of some of the taxonomic allocations listed I refer the reader to that work.

Table 2 provides an alphabetic list of currently recognized species cross-referenced to the classifications of the eight major workers since Günther (1858). This table demonstrates that many species have been assigned to four or more genera over the years. Likewise currently accepted generic divisions (Cogger, 1975b, 1979) may contain species that were at one time thought to be related to four different generic groups (see *Simoselaps* Table 2). The opinions of Cogger (1975b, 1979) have been used as a taxonomic guideline in these comparisons, because they represent the most recent and complete review of the Australian elapids and more fully adhere to the basic guidelines of the International Code for Zoological Nomenclature. Table 2 also includes recent synonymies and lists species described since Cogger's 1979 publication.

2. The Morphological Data

What is immediately apparent from Table 2 is the variety of classifications that can be derived from the same morphological data base. This lack of agreement among taxonomists again reflects an inability to distinguish between primitive and derived character states. Until McDowell's contribution on hemipenial morphology and venom gland musculature all workers relied essentially upon the same morphological data set, consisting largely of scale and skeletal characteristics.

A cursory examination of Table 2 indicates that many authors have used the work of Boulenger (1896) as a taxonomic guide to the Australian elapid fauna. Indeed, the subsequent studies of Worrell (1955, 1960, 1961, 1963), based largely on skull morphology, represented the first major shift since Boulenger's early work. Prior to Worrell over 50% of Australian elapid species were assigned to two large genera *Denisonia* and *Diemenia* (*Demansia*). A chronological treatment of the taxonomic changes to these and other major genera will serve to illustrate the alterations to elapid classification outlined in the table.

2(a). Taxonomic changes to Boulenger's *Denisonia*

As mentioned above, Worrell's work in the early 1960's was the first major deviation from the classification of Boulenger (1896). Worrell attempted to reassign Australian elapid species into groups more closely reflecting similarities in cranial and dental characteristics and to a lesser extent in external morphology. This resulted in his dividing the large genus *Denisonia* into a series of genera including: *Austrelaps* for *D. superba* and *D. signata; Cryptophis* for *D. pallidiceps* (type species), *D. nigrescens, D. flagellum* and *D. dwyeri*; *Drepanodontis* for *damelii; Drysdalia* for *coronata, coronoides* and *mastersi; Parasuta* for *gouldii* and *nigrostriatus; Suta* for *suta;* and *Unechis* for *carpentariae.* The genus *Denisonia* thus was left with only four species: *devisii, fasciata, maculata* and *punctata.*

As with any major change in taxonomic convention, Worrell's efforts elicited varied reactions. His dismemberment of *Denisonia* proved to be his most controversial taxonomic move. While most workers to date have accepted the use of *Austrelaps* (for *superba* but not *signata*) and *Drysdalia* they show differing attitudes toward the remaining genera. Brongersma and Knaap-Van Meeuwen (1964) for example, strongly opposed the splitting of *Denisonia* in their description of *D. boschmai* (later synonymized with *S.* (*Unechis*) *carpentariae* by Parker, 1972. It has been found that the holotype of *carpentariae* is conspecific with *Suta suta* and Cogger *et al.* (1983) have applied the next available name, *boschmai*, for *carpentariae* of authors). Based on a comparison with Worrell's figures and referring to the data of Kinghorn (1920), Brongersma and Knaap-Van Meeuven (1964) demonstrated variation in two of the characters Worrell had used to define *Cryptophis.* As the diagnostic characters did not hold up they thus rejected the generic proposals of Worrell's division of *Denisonia.* Coventry (1971) avoided any mention of the generic classification of Worrell in his treatment of the black-headed *Denisonia* of Victoria, but stated that this group was polyphyletic and that similarities were due to convergence.

The next investigator after Worrell to assess the relationships of Australian elapids was McDowell (1967). In a study of the New Guinea species of *Aspidomorphus* and their relatives he examined many Australian species and attempted to group them according to hemipenial morphology and the structure of the adductor externus superficialis muscle surrounding the venom gland. In the Australasian elapid snakes, with the exception of *Elapognathus, Laticauda* and *Parapistocalamus,* the hemipenis lacks the alveolar calyces which are seen in many African and Asian forms (e.g. *Naja* and *Bungarus*).

The absence can, however, be explained in two ways, which in terms of *Denisonia* resulted in the separation of *D. devisii* and *D. maculata* into one group while McDowell placed in another group the remainder of Boulenger's *Denisonia.*

McDowell's (1967) classification of species according to the morphology of the adductor externus superficialis muscle resulted in somewhat different groupings (see Section 2[f]). All of the four categories recognized by McDowell (1967) contained species formerly referred to *Denisonia* by Boulenger. Thus, the *"Glyphodon* group" contained *Cryptophis pallidiceps, C. nigrescens* and *Drysdalia coronoides* of Worrell. The *"Oxyuranus* group" contained *Denisonia maculata, D. devisii* and *Drysdalia coronata.* The *"Pseudechis* group" contained *Parasuta gouldii, P. nigrostriata, Unechis carpentariae, Denisonia boschmai, Austrelaps superbus, Cryptophis flagellum* and *Denisonia punctata* of Worrell. The fourth group, the *"Demansia* group" contained *Drepanodontis daemelii* and *Austrelaps signata.* This classification further divided every genus Worrell had erected from Boulenger's *Denisonia,* including the four species which he retained in *Denisonia.*

McDowell (1967), stated that, despite cases of parallelism and convergence, venom gland musculature "shows better correlation with other features than does any other single character". In Worrell's division of *Denisonia,* McDowell found fault in the placement of *flagellum* with *pallidiceps* and *nigrescens* in *Cryptophis* and suggested its association with *gouldii,* the type of Worrell's *Parasuta.* He indicated a further anomaly in the inclusion of *Denisonia punctata* with the remaining species of *Denisonia* as restricted by Worrell. The venom gland musculature of *D. punctata* is more like that of the genera *Suta, Parasuta* and *Unechis* of Worrell; and this is in agreement with data on hemipenial morphology. Shine (1983b) demonstrated that the feeding strategies and food preferences of *D. fasciata* and *D. punctata* differ from those of *D. maculata* and *D. devisii.* In a publication defining the *"Pseudechis* group" McDowell (1970: see below) moved to include all those species of Worrell in the genus *Suta,* thus resulting in *S. flagellum, S. punctata, S. fasciata, S. carpentariae* (= *boschmai*), *S. monachus* and *S. gouldii.* This move was adopted by Parker (1972) in his revision of *S. carpentariae* (= *boschmai*) and *S. nigrostriata* in Australia and New Guinea. Subsequent authors, however, have not accepted McDowell's use of *Suta.*

Cogger (1975b, 1979) attempted to provide a general consensus of the relationships of species in this large group by critically applying the rules of taxonomic nomenclature to the morphological studies of McDowell (1967, 1969, 1970). In this process some of the generic names of Worrell were retained while species formerly allocated to *Parasuta* and *Drepanodontis* were referred to other genera (see Table 3 and below). In his report McDowell (1967) pointed out that *signata,* placed in *Austrelaps* by Worrell (1963), could be identified as *Drepanodontis* using Worrell's (1961) key. In fact the venom gland musculature, dentition and skull morphology of *signata* were much like those of *Drepanodontis daemelii,* so McDowell placed the two species together in *Drepanodontis.* Cogger (1975b) followed this but adopted the earlier name *Hemiaspis* for the two species. Thus McDowell's groupings based on his new morphological data set were reflected in Cogger's (1975b) classification though *Unechis* was used for *carpentariae* (= *boschmai,* see Cogger *et al.*, 1983), *gouldii, nigrostriatus,* and *flagellum;* and *Cryptophis* was retained for *pallidiceps* and *nigrescens. Austrelaps* was restricted to *superbus* while *signata* was placed along with *damelii* (*daemeli*) in the genus *Hemiaspis.* Cogger recognized Worrell's *Drysdalia.*

In contrast to the classifications of McDowell and Cogger some authors (Storr, 1981b; Coventry, 1971) have preferred to treat the problematic *Denisonia* in terms of species groups within a large genus. Though the distinction between species groups and genera may simply be a matter of semantics the definition of these species groups has suffered from the practice of restricting reports to species and specimens whose ranges coincide with political or State boundaries. As a consequence, no complete treatment of the species groups involved has been produced. The reviews of the *"Denisonia* (*Unechis*) *gouldii"* species group in Victoria by Coventry (1971) and in Western Australia by Storr (1964, 1981b) resulted in redefining *gouldii* (restricted to W.A.) and *dwyeri* (distributed in Victoria, N.S.W. and Queensland) and in describing several new forms from Western Australia.

The most recent change to *Denisonia* (*sensu* Boulenger) was that of Storr (1982) who suggested the transfer of the species of *Drysdalia* and *Austrelaps* to the genus *Notechis* (see below).

2(b). Taxonomic Changes to Boulenger's *Diemenia* (*Demansia*)

Unlike his treatment of *Denisonia,* Worrell's division of Boulenger's *Diemenia* has stood the test of time. Using skull characteristics Worrell divided *Diemenia* into the whip snakes *Demansia* and the brown snakes *Pseudonaja.* Though a number of additional species are currently recognized in *Demansia* based largely on colour pattern differences, both genera appear well defined. On the basis of venom gland musculature McDowell (1967) fully supported Worrell's separation of the genus *Pseudonaja* from *Demansia.* This generic division was recognized by all subsequent workers.

2(c). Taxonomic Changes to *Pseudelaps, Furina* and *Glyphodon*

Affinities between the species Boulenger assigned to these three genera have long been recognized, but generic divisions within this complex continue to be debated. Worrell divided the genus *Pseudelaps* as used by Boulenger (1896) by reviving *Brachysoma* for *diadema,* erecting *Lunelaps* for *christianus* [sic], recognizing the genus *Aspidomorphus* in Australia for *squamulosus* alone, placing *harriettae* in the genus *Glyphodon* and resurrecting *Cacophis* for *krefftii.* Boulenger recognized in *Furina* only *F. occipitalis* and *F. calonotus,* whereas Worrell described the new genera *Narophis* for *bimaculata* and *Melwardia* for *calonotus* and *minima.* (*F. occipitalis* is now a synonym for *Vermicella annulata.*)

In his report McDowell demonstrated that *christianus* and *diadema* were congeneric. As *Brachysoma* was a junior homonym and therefore unavailable, McDowell placed the two species in *Furina.* This move eliminated *Lunelaps* of Worrell. McDowell states *"Furina* is related to *Glyphodon* rather than to *Aspidomorphus* (here presumably including *Cacophis*) or *Demansia*". *Furina christianus* [sic] was included in *F. diadema* by Cogger & Lindner (1974). In a recent review of the genus *Furina* in Western Australia, Storr (1981) considered specimens previously allocated to *F. christianus* to be distinct from *diadema,* and resurrected the name *F. ornata.* Storr (1981) also included in *Furina,* however, two species of the genus *Glyphodon* (*barnardi* and *tristis*) and one species of *Simoselaps* (*warro*) though no reassessment of these species was offered. It should be noted that Shine (1981) suggested that *Furina* and *Glyphodon* are ecologically similar.

McDowell (1967) also analysed the species *kreffti, harrietae* and *squamulosus,* which Worrell had placed in *Cacophis, Glyphodon* and *Aspidomorphus* respectively, and, on the basis of hemipenial morphology, dentition, head scutellation and colour, combined them all in *Cacophis.*

2(d). Taxonomic Changes to *Vermicella* and *Simoselaps*

One of the most prolific contributors to Australian elapid taxonomy has been Storr. In his 1967 work on *Vermicella* he combined species which Worrell (1960, 1961, 1963) and Kinghorn (1955, 1956), had earlier referred to the genera *Narophis, Melwardia, Brachyurophis, Rhynchoelaps, Rhinelaps* and *Vermicella.* He also described several new forms. In a subsequent revision of the genus Storr (1978) elevated to species status three taxa—*bertholdi, littoralis,* and *anomala*—previously considered as subspecies of *V. bertholdi,* and also reinstated *V. approximans* and *M. minima* as full species. Having thus disposed of all other *Simoselaps* species (*sensu* Cogger, 1975b), Storr (1979) left *warro* in its original combination, *Cacophis warro.* He subsequently chose to place it in the genus *Furina* (see above, Storr, 1981c).

In his detailed analysis of the New Guinean genus *Toxicocalamus* McDowell (1969a) showed that *Vermicella* was most closely related to the Australian genera *Brachyurophis, Melwardia, Narophis, Rhinelaps* and *Rhynchoelaps* of Worrell (1963). McDowell recognized and agreed with Storr's (1967) move to group these genera together but excluded *annulata.* Since *annulata* is the type species for *Vermicella,* McDowell restricted the genus to *annulata* and proposed *Rhynchoelaps* Jan, 1758 as the next available name (type *Elaps bertholdi* Jan) for Storr's remaining species. The *Rhynchoelaps* group of McDowell (1969a) therefore contained two genera: *Rhynchoelaps,* including the *Vermicella* of Storr (1967) (except for *V. annulata* and presumably *multifasciata*), and the genus *Toxicocalamus* as redefined. Cogger, (1975b, 1979) restricted *Vermicella* to *V. annulata* and *V. multifasciata* following McDowell (1969d), but divided the species assigned to *Rhynchoelaps* by McDowell between *Neelaps* (*bimaculata* and *calonota*) and *Simoselaps* (all other species; Cogger regarded *Rhynchoelaps* as a *nomen nudem* and used *Simoselaps* as the next available name).

In a recent ecological study Shine (in press) follows Cogger's (1975b, 1979) use of the genera *Simoselaps* and *Neelaps* but recognizes five species groups based on feeding habits, structure and scalation of the snout and dentition. The two latter characters Shine correlates with the first. Within the two genera Shine defines the following five distinct "species groups". (1) *Neelaps bimaculatus* and *N. calonotus,* both saurophagous; (2) the "*Simoselaps bertholdi* group", including *S. bertholdi, S. anomala, S. littoralis* and *S. minima.* All are saurophagous and lack the exaggerated shovel-like snout of some other species as well as the dentition adaptations; (3) the "*S. semifasciatus* group", of *S. semifasciatus, S. s. roperi, S. approximans* and *S. incinctus.* These species have a sharply upturned angular snout and are exclusively oophagous. *S. semifasciatus* possesses a single enlarged triangular tooth at the back of the maxilla; (4) *Simoselaps australis* and *S. fasciolatus,* which Shine states may not be closely related, but resemble *S. semifasciatus;* only *S. australis* shares the angular snout. Both are saurophagous and oophagous; (5) *S. warro,* which Shine, following Storr (1979), regards as being so aberrant that it is only doubtfully included in this genus (see above for Storr's assignments of this species). Shine also notes that *S. warro* resembles the "*S. bertholdi* group" in being saurophagous and lacking the modifications of the other species.

2(e). Additional Taxonomic Changes to Australian Elapids

The genera of larger Australian elapid snakes have remained relatively stable since the "dissection" by Glauert (1948), Worrell (1963) and Kinghorn (1921) of the tiger snakes (*Notechis*) into a variety of subspecies, and the recognition of *Austrelaps* and *Pseudonaja.* Most workers recognize that some species of *Pseudonaja* may be composite (Cogger, 1979; Gillam, 1979). The review of the "black snakes" of the genus *Pseudechis* by Mackay (1955) resulted in synonymizing the species into the forms recognized today. In a recent comprehensive study of the Taipan, *Oxyuranus scutellatus,* and the Small-scaled Snake, *Parademansia microlepidota,* Covacevich *et al.* (1981) analysed scalation, skull morphology, dentition, hemipenial anatomy and karyotypes, concluding that these two species are congeneric and referable to *Oxyuranus.*

Apart from these few assessments of species, however, the intra- and intergeneric relationships remain poorly understood. McDowell (1970) associated *Pseudechis* and *Austrelaps.* The genus *Pseudechis* in Western Australia has recently been reviewed by Smith (1982), with the description of a new species, *P. butleri.* Rawlinson (1969) reexamined the monotypic genus *Austrelaps* and several species are likely to be recognized. White (1981) recognized the Adelaide Hills form as distinct, but refrained from naming it. McDowell (1967) reported an unexpected resemblance between *Drysdalia coronata* and the genera *Notechis, Tropidechis* and *Oxyuranus.* Indeed, he could find no internal character separating *D. coronata* and *Notechis*. McDowell (1967) indicated *D. coronata* may merit generic distinction. Shine (1981) pointed out that *coronata* is more similar to *Notechis* in its dietary preferences than are the other *Drysdalia* species. Shine and Charles (1983) suggested a close relationship between *Notechis* and *Tropidechis,* based on a review of the morphological, ecological, behavioural and cytological data. Storr (1982) has recently discussed similarities between *D. coronata* and *Notechis* and subsequently placed all *Drysdalia, Austrelaps, Elapognathus* and *Echiopsis* in *Notechis*. He did not consider *Tropidechis*. The review of *Drysdalia* by Coventry and Rawlinson (1980) resulted in the separation of *D. rhodogaster* from *D. mastersi*. Storr (1981a) reviewed the death adders (*Acanthophis*) of Western Australia and resurrected a third species, *A. praelongus*.

2(f). The Intergeneric Relationships Proposed by McDowell

While all the preceding taxonomic changes deal with the definition and allocation of species to genera, the only worker who has attempted to group related genera is McDowell. Because McDowell provided a new data set and examined a wide variety of elapid species his findings influenced both the species groupings discussed above, and intergeneric relationships. His groupings, therefore, bear repeating here.

The hemipenial morphology reported by McDowell (1967) yielded the following two groups:

—**Group 1,** consisting of Boulenger's *Denisonia* (*Austrelaps, Drysdalia, Cryptophis, Hemiaspis, Suta* and *Unechis* of Cogger, 1975b) and *Demansia, Pseudechis, Pseudonaja* (except *P. guttata*), *Brachyaspis* (= *Echiopsis* of Cogger, 1975b), *Oxyuranus, Ogmodon, Hydrelaps* (sea snake), and *Aspidomorphus* sensu stricto; and

—**Group 2,** the *"Glyphodon* Series", showing odd resemblance to *Ophiophagus* and including *Denisonia maculata* and *devisii, Acanthophis, Hoplocephalus, Glyphodon,* and Australian snakes then assigned to *Aspidomorphus* (= *Cacophis* and *Furina* of Cogger).

The groupings based on venom gland musculature were as follows: (names with asterisks have been changed to accord with Cogger, 1975b; for original names see Table 2):

—In Group 1, the *"Glyphodon* type" of adductor externus superficialis, considered primitive, is found. It contains most American elapids (*Micrurus*), *Calliophis,* African elapid genera (except *Dendroaspis*), *Naja* and most sea snakes and the following Australasian forms: *Glyphodon, Furina, Cacophis, Vermicella**, Neelaps*, Simoselaps*, Apistocalamus, Toxicocalamus, Ultrocalamus, Ogmodon, Loveridgelaps, Elapognathus, Drysdalia*, Cryptophis**, and *Pseudonaja**.

—In Group 2, with the *"Oxyuranus* type" of adductor externus superficialis, the following are included: *Denisonia maculata, D. devisii, Acanthophis, Hoplocephalus, Salomonelaps, Drysdalia coronata, Notechis, Tropidechis, Oxyuranus,* and *Echiopsis**.

—In Group 3, the *"Pseudechis* type" of adductor externus superficialis occurs. The group is almost confined to Australasian terrestrial elapids but includes also *Astrotia, Laticauda* and *Parapistocalamus*. Others are *Pseudechis, Micropechis, Unechis gouldi**, *U. nigrostriatus, U. carpentariae, U. flagellum, Suta, Austrelaps* and *Denisonia punctata*.

—Group 4 has the *"Demansia* type" of adductor externus superficialis, most easily derived from the *"Pseudechis* type". This group contains the sea snakes *Laticauda schistorhynchus* and *Hydrophis* (*Parahydrophis*) *mertoni* as well as *Rhinoplocephalus, Hemiaspis**, *Demansia* and *Aspidomorphus*.

In a subsequent analysis of Australasian elapids, McDowell (1970) defined two groups of genera: (1) the *"Vermicella* group" consisting of *Vermicella* (*sensu* McDowell 1967, see above, Section 2[d]) within Australia, *Salomonelaps,* and *Loveridgelaps* within the Solomon Islands and *Ogmodon* in Fiji; and (2) the *"Pseudechis* group" including *Micropechis* in New Guinea, *Pseudechis, Austrelaps* (for *A. superbus* only), *Suta* (for *Suta, Parasuta and Unechis* of Worrell, 1963) as well as *Denisonia fasciata, D. punctata* and *"Cryptophis"* (*Unechis*) *flagellum*. These species groups and the ones described above (McDowell, 1967) were apparently elevated to tribal status in the classification of Smith *et al.* (1977). These generic relationships or tribal affinities based on the morphological data represent the first groupings tested by biochemical means.

3. The Biochemical Data

In addition to the classifications based on morphological criteria, the possible relationships indicated by venom characterization and immunological studies are of interest. Unfortunately, data are generally available only for the species of larger Australian elapids owing to the difficulty in obtaining venom and blood samples from the smaller varieties. Minton & da Costa (1975) indicated close affinities between sea snakes and the two Australian terrestrial elapids *Denisonia* (= *Austrelaps*) *superba* and *Notechis* when their venoms were cross-reacted to other venoms. They also pointed out that *Notechis* venom did not react with *Denisonia* (*Austrelaps*) antiserum though these gross measures were intended to determine the relationship of these terrestrial elapids to sea snakes and not the intergeneric relationships of the Australian forms. In a more recent study, Minton (1981) analysed serological data from 11 genera native to eastern New South Wales and found *Pseudechis, Pseudonaja* and *Tropidechis* to be closely related while *Acanthophis, Demansia, Hemiaspis* and *Vermicella* were somewhat remote from this group. No comment was made on the interrelationships of the latter three genera. Coulter *et al.* (1981) examined the venoms of *Pseudechis, Pseudonaja, Austrelaps, Acanthophis, Oxyuranus* and *Notechis,* as well as Asian terrestrial elapids and the sea snake *Enhydrina*, by enzyme immunoassay (EIA) and agreed with Minton & da Costa (1975) that the venoms of sea snakes were closely related to those of Australian elapids but not to those of the Asiatic species. The venoms of several Australian species differed greatly in respect to each other and it is interesting to note that in the reaction of species to anti-Notexin (from *Notechis*), as assayed by EIA, *Austrelaps* gave a reaction most similar to *Notechis* itself. Morrison (pers. comm.) has found great similarities in the venom characteristics of *Tropidechis* and *Notechis* with an immunological cross-reactivity of greater than 50%. The venom studies of both Saint Girons & Detrait (1980) and Fohlman (1979) point to a close similarity of the venoms of *Oxyuranus* and "*Parademansia*" (now = *Oxyuranus*) and their distinctness from *Pseudonaja*. Saint Girons & Detrait (1980) went on to demonstrate that the venoms of *Austrelaps* and *Pseudechis* possess many common antigens and they suggested that, along with *Bungarus*, *Austrelaps* and *Pseudechis* occupy "a central position among elapines of the Old World". They concluded that Australian genera do not form a homogeneous group, since the venoms of many species share antigens with *Bungarus*, whereas *Oxyuranus*, "*Parademansia*" (= *Oxyuranus*) and *Pseudonaja* have very weak cross-reactivity with other elapids.

It should be recalled from the previous section that the MC′F work of Cadle & Gorman demonstrated that *Demansia* was distinctive among Australian elapids in displaying the greatest immunological distance from all the elapid reference species they used and thus may be phylogenetically distinct.

From the limited chemotaxonomic data several inadequacies are evident. First, with the exception of the preliminary report of Minton (1981), none of the phylogenetic studies utilizing MC′F and immunodiffusion were initiated within Australia. The sample species studied were consequently very limited. As for the venom analysis, only one study, that of Saint Girons & Detrait (1980), appears to have been initiated to elucidate phylogenetic relationships and it, like those studies within Australia, was limited to species containing large specimens from which adequate venom samples are more commonly available.

4. A Summary of the Taxonomic Relationships of Australian Terrestrial Elapids

This review of morphological and chemotaxonomic characters, and the classifications derived from them, demonstrates that only two (*Rhinoplocephalus* and *Hoplocephalus*) of the 25 genera of Australian elapid snakes have not been altered taxonomically in the past two and a half decades. This reflects the small measure of agreement on intergeneric relationships, and indeed on the definition of suprageneric or tribal affinities.

Looking at the generic allocation of species, genera *Acanthophis, Demansia, Hoplocephalus, Oxyuranus, Pseudechis* and *Pseudonaja* appear clearly defined though there are species within most of these that are obviously composite. However, many species that made up Boulenger's *Denisonia* continue to be problematic. In practice there remain two schools of thought. That following Storr (1964, 1981b) would treat *Denisonia* as a large genus in similar fashion to Boulenger (1896), though recognizing species group relationships within the genus. It should be recalled, however, that Storr (1982) has transferred the species of Worrell's *Drysdalia* from *Denisonia* to *Notechis* along with *Elapognathus, Austrelaps* and *Brachyaspis* (= *Echiopsis*).

An alternative school of thought has been expressed through the works of Cogger (1975b, 1979), where the generic groupings of the species formerly allocated to *Denisonia* and other complexes generally rely on the morphological data of McDowell, though the generic designations do not (see Cogger *et al.*, 1983). These efforts to express species relationships highlight the lack of agreement on the definition of generic and tribal categories. Though this may be a matter of semantics it is surely essential that an understanding precede efforts to express intergeneric relationships.

These areas of nomenclatural controversy point out those groups for which additional analyses must be performed before relationships are understood and a consensus met. Both ecological and morphological data have suggested a dichotomy between *D. devisii* and *D. maculata* on the one hand and *D. fasciata* and *D. punctata* on the other. Additionally, the genus *Unechis* (*sensu* Cogger, 1975) may be composite with some species showing affinities to *Suta* and *D. punctata* while others resemble *Cryptophis pallidiceps*. The ecological data of Shine have divided *Simoselaps* and *Neelaps* into distinct groupings while demonstrating similarities between *Tropidechis* and *Notechis*. These associations along with the relationships of the species making up *Furina* and *Glyphodon* are clearly the areas of most fruitful investigation.

5. Concluding Remarks

The data reviewed here and the resulting variety of classifications demonstrate that the morphological data reported thus far have failed to resolve the taxonomic questions. The biochemical data offer new hope in that they provide a novel data base that in some vertebrate groups has been found to be a powerful taxonomic tool. Such studies are, however, lacking in that they have been limited to small sample sizes of species of the larger elapids. To be effective there must be a cooperative effort to provide workers with live material from a broad representation of species. Only through a synthesis of more complete morphological, biochemical and cytological data sets will a meaningful and stable taxonomy be derived.

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Table 1. Genera of Proteroglyphs

This table lists all genera of proteroglyph snakes and where available their common names and relevant comments from the literature. An attempt has been made to list genera according to current tribal designations (see Smith *et al.,* 1977, and Harding & Welch, 1980). Unfortunately, none of the published classifications derived from the morphological studies of McDowell have specified the genera included in these tribes.

Family ELAPIDAE (Palatine Erectors)

Subfamily BUNGARINAE		
Tribe Bungarini		
Bungarus Daudin, 1803 (12 spp.)	Kraits; India, SE Asia, Malaysia, Indonesia	Primitive among proteroglyphs (McDowell, 1970)
Tribe Najini		
Aspidelaps Fitzinger, 1843 (2 spp.)	Shield-nosed cobras; Africa	
Boulengerina Dollo, 1886 (2 spp.)	Water cobras; Africa	Primitive among proteroglyphs (McDowell, 1970)
Dendroaspis Schlegel, 1848 (4 spp.)	Mambas; Africa	Subfamily Dendroaspinae (Romer, 1956)
Elapsoidea Bacage, 1866 (6 spp.)	African garter snakes	Primitive among proteroglyphs (McDowell, 1970)
Hemachatus Fleming, 1822 (1 sp.)	Ringhals Cobra, Africa	
Naja Laurenti, 1768 (6 spp.)	Cobras; Africa, Asia, India, Philippines, etc.	
Ophiophagus Günther, 1864 (1 sp.)	King Cobra; India, Asia, Indonesia, etc.	
Paranaja Loveridge, 1944 (1 sp.)	Burrowing Cobra; Africa	Primitive among proteroglyphs (McDowell, 1970)
Pseudohaje Günther, 1858 (2 spp.)	Tree cobras; Africa	
Walterinnesia Lataste, 1887 (1 sp.)	Desert Cobra	
Subfamily ELAPINAE		
Tribe Elapini		
Calliophis Gray, 1834 (includes former *Hemibungarus* (10 spp.)	Asian coral snakes	
Leptomicrurus Schmidt, 1937 (= *Micrurus*) (3 spp.)	Coral snakes	Micruridae of Duellman, 1979
Micruroides Schmidt, 1928 (1 sp.)	Arizona Coral Snake; U.S.A.	Micruridae of Duellman, 1979
Micrurus Wagler, 1824 (43 spp.)	Coral snakes; the Americas	Micruridae of Duellman, 1979
Tribe Maticorini		
Maticora Gray, 1834 (2 spp.)	Coral snakes	
Parapistocalamus Roux, 1934 (1 sp.)	Hediger's Snake; Bougainville I.	
Tribe Laticaudini		Family Laticaudidae Burger and Natsumo, 1974
Laticauda Laurenti, 1768 (5 spp.)	Sea kraits	

Family HYDROPHIIDAE (Palatine Draggers)

Subfamily OXYURANINAE (Terrestrial palatine draggers)		Subfamily Acanthophinae Dowling & Duellman, 1978
Acanthophis Daudin, 1803 (2 spp.)	Death adders; Australia, Papua New Guinea and islands.	Presumed tribe Acanthophini
Aspidomorphus Fitzinger, 1803 (2 spp.)		"*Demansia* Group", related to *Demansia, Hemiaspis, Rhinoplocephalus* (McDowell, 1967)
Austrelaps Worrell, 1963 (1 sp.)	Copperhead; Australia	"*Pseudechis*" group of McDowell, 1970
Cacophis Günther, 1863 (3 spp.)	Crowned snakes; Australia	Presumed tribe Glyphodontini, related (very close) to *Aspidomorphis* (McDowell, 1967)
Cryptophis Worrell, 1961 (2 spp.)	Small-eyed snakes; Australia	
Demansia Gray, 1842 (5 spp.)	Whip snakes; Australia, Papua New Guinea	"*Demansia* Group", related to *Aspidomorphus, Rhinoplocephalus* and *Hemiaspis*
Denisonia Krefft, 1869 (4 spp.)	Australia	"*Pseudechis* Group" (*D. fasciata* and *D. punctata*)
Drysdalia Worrell, 1961 (4 spp.)	White-lipped snakes; Australia	*D. coronata, Oxyuranus* type of adductor externus superficialis
Echiopsis Fitzinger, 1843 (2 spp.)	Desert Snake; Australia	
Elapognathus Boulenger, 1869 (1 sp.)	Little Brown Snake; Australia	
Furina Duméril, Bibron and Duméril, 1854 (1 sp.?)	Red-naped Snake; Australia	Presumed tribe Glyphodontini (Smith, 1977; McDowell, 1967)
Glyphodon Günther, 1858 (3 spp.)	Australia, Papua New Guinea	Presumed tribe Glyphodontini (Smith, 1977; McDowell, 1967)
Hemiaspis Fitzinger, 1861 (2 spp.)	(*Drepanodontis*) Marsh Snake; Australia	"*Demansia* Group", related to *Demansia, Rhinoplocephalus, Aspidomorphus* (McDowell, 1967)
Hoplocephalus Cuvier, 1832 (3 spp.)	Broad-headed snakes; Australia	Maybe Oxyuranini; *Oxyuranus* type of adductor externus superficialis
Loveridgelaps McDowell, 1970 (1 sp.)	Banded Small-eyed Snake; Solomon Is.	"*Vermicella* Group"
Micropechis Boulenger, 1896 (1 sp.)	New Guinea Small-eyed Snake; Papua New Guinea	"*Pseudechis* Group"
Neelaps Günther, 1863 (2 spp.)	Australia	Presumed tribe Apistocalamini (Smith *et al.*, 1977; McDowell, 1969)
Notechis Boulenger, 1896 (2 spp.)	Tiger snakes; Australia	*Oxyuranus* type of adductor externus superficialis
Ogmodon Peters, 1864 (1 sp.)	Fiji	"*Vermicella* Group": most primitive palatine dragger (McDowell, 1970)
Oxyuranus Kinghorn, 1923 (2 spp.)	Taipans; Australia, Papua New Guinea	Presumed tribe Oxyuranini
Pseudechis Wagler, 1830 (5 spp.)	Black snakes and King Brown; Australia, Papua New Guinea	"*Pseudechis* Group" of McDowell, 1970
Pseudonaja Günther, 1858 (6 spp.)	Brown snakes; Australia, Papua New Guinea	Presumed tribe Pseudonajini
Rhinoplocephalus Muller, 1885 (1 sp.)	Muller's Snake, Australia	"*Demansia* Group", related to *Demansia, Aspidomorphus, Hemiaspis* (McDowell, 1967)
Salomonelaps McDowell, 1970 (1 sp.)	Solomon Islands	"*Vermicella* Group" of McDowell, 1970)

Simoselaps Jan, 1859 (6+ spp.)	Desert banded snakes; Australia	Presumed tribe Apistocalamini (Smith, 1977; McDowell, 1969)
Suta Worrell, 1961 (1 sp.)	Curl snakes; Australia	"*Pseudechis* Group" of McDowell, 1970
Toxicocalamus Boulenger, 1896 (9 spp.) (includes *Apistocalamus* and *Ultracalamus)*	Papua New Guinea	Presumed tribe Apistocalamini (Smith, 1977; McDowell, 1969)
Tropidechis Günther, 1863 (1 sp.)	Rough-scaled snake; Australia	Maybe Oxyuranini; "*Oxyuranus* type" of adductor externus superficialis
Unechis Worrell, 1961 (7+ spp.)	Blackheaded snakes; Australia	"*Pseudechis* Group" of McDowell, 1970
Vermicella Günther, 1858 (2 spp.)	Bandy-bandy, Australia	"*Vermicella* Group" of McDowell, 1970
Subfamily HYDROPHIINAE	True sea snakes	Family Hydrophiidae of Burger and Natsuno, 1974
Tribe Ephalophiini		Subfamily Ephalophiinae of Burger and Natsuno, 1974
Ephalophis Smith, 1931 (1 sp.) (for *E. greyi* only)		Primitive in many respects, shows relationship to terrestrial elapids *Rhinoplocephalus, Hemiaspis* (McDowell, 1969, 1974)
Parahydrophis Burger and Natsuno, 1974 (1 sp.)		Related to *Ephalophis* but stands at the base of linages leading to both Aipysurini and Hydrophiini (McDowell, 1969)
Tribe Hydrelapini		"*Hydrelaps* Group" of McDowell, 1969
Hydrelaps Boulenger, 1896 (1 sp.)		In subfamily Ephalophinae of Burger and Natsuno, 1974
Tribe Aipysurini		In subfamily Ephalophinae of Burger and Natsuno, 1974
Aipysurus Lacépède, 1804 (7 spp.)		"*Aipysurus* Group" of McDowell, 1969
Emydocephalus Krefft, 1869 (2 spp.)		"*Aipysurus* Group" of McDowell, 1969
Tribe Hydrophiini		All below in subfamily Hydrophiinae of Burger and Natsuno, 1974
Acalyptophis Boulenger, 1896 (1 sp.)		
Astrotia Fisher, 1856 (1 sp.)		
Disteira Lacépède, 1804 (2 spp.) (contains some *Hydrophis* and *Hydrus*)		Considered a subgenus by Burger and Natsuno (1974); McDowell (1972) recognizes 5 species.
Enhydrina Gray, 1849 (1 sp.)		
Hydrophis Latreille, 1802 (24 spp.) (contains *Aturia*)		
Kerilia Gray, 1849 (1 sp.)		
Kolpophis Smith, 1926 (1 sp.)		
Lapemis Gray, 1835 (2 spp.)		Includes *Kolpophis* and *praescutata*—McDowell, 1972
Thalassophis Schmidt, 1852 (2 spp.)		Included in *Lapemis* by Burger and Natsuno, 1974
Pelamis Daudin, 1803 (1 sp.)	Pelagic sea snake	

Table 2. Nomenclatural History

This table provides a comparison of all major classifications of Australian terrestrial elapids from Günther (1858) to the present. Accompanying the table is an alphabetical list of currently recognized species cross-referenced to the classification of Cogger (1975b, 1979) in the far left hand column. Species recognized since Cogger (1979) are marked with an asterisk (*). Blank spaces in the table indicate that the particular worker

Cogger 1975b, 1979	**Storr** 1982, 1981a,b,c, 1979, 1967	**McDowell** 1967,1970, 1969	**Worrell** 1961, 1963,a,b 1950, 1960
1.1 *Acanthophis antarcticus*	*Acanthophis*	*Acanthophis*	*Acanthophis*
1.2 *A. pyrrhus*	*Acanthophis*		*Acanthophis*
	1.3 * *A. praelongus*		
2. *Austrelaps superbus*	*Notechis*	*Austrelaps*	*Austrelaps*
3.1 *Cacophis harriettae*		*Cacophis*	*Glyphodon*
3.2 *C. krefftii*		*Cacophis*	*Cacophis*
3.3 *C. squamulosus*		*Cacophis*	*Aspidomorphus*
4.1 *Cryptophis nigrescens*	*Denisonia*	*"Denisonia"*	*Cryptophis*
4.2 *C. pallidiceps*	*Denisonia*	*"Denisonia"*	*Cryptophis*
5.1 *Demansia atra*	*Demansia*		
5.2 *D. olivacea*	*Demansia*	*Demansia*	*Demansia*
5.3 *D. psammophis*	*Demansia*	*Demansia*	*Demansia*
5.4 *D. torquata*		*Demansia*	*Demansia*
	5.6 * *D. simplex*		
	5.7 * *D. reticulata*		
	5.8 * *D. papuensis*		
6.1 *Denisonia devisii*	*Denisonia*	*Denisonia*	*Denisonia*
6.2 *D. fasciata*	*Denisonia*	*Suta*	*Denisonia*
6.3 *D. maculata*	*Denisonia*	*Denisonia*	*Denisonia*
6.4 *D. punctata*	*Denisonia*	*Suta*	*Denisonia*
7.1 *Drysdalia coronata*	*Notechis*	*"Denisonia"*	*Drysdalia*
7.2 *D. coronoides*	*Notechis*		*Drysdalia*
7.3 *D. mastersi*	*Notechis*		*Drysdalia*
7.4 *D. rhodogaster*	*Notechis*		
8.1 *Echiopsis curta*	*Brachyaspis*	*Brachyaspis*	*Brachyaspis*
8.2**E. atriceps*	*Brachyaspis*		
9. *Elapognathus minor*	*Notechis*	*Elapognathus*	*Elapognathus*
10. *Furina diadema*	*Furina*	*Furina*	*Brachysoma*
	10.2 * *F. ornata* (= *christieanus)*		*Lunelaps*
11.1 *Glyphodon barnardi*	*Furina*		*Lunelaps*
11.2 *G. dunmalli*			*Glyphodon*
11.3 *G. tristis*	*Furina*	*Glyphodon*	*Glyphodon*
12.1 *Hemiaspis damelii*	*Denisonia*	*Drepanodontis*	*Drepanodontis*
12.2 *H. signata*	*Denisonia*	*Drepanodontis*	*Austrelaps*
13.1 *Hoplocephalus bitorquatus*		*Hoplocephalus*	*Hoplocephalus*
13.2 *H. bungaroides*		*Hoplocephalus*	*Hoplocephalus*
13.3 *H. stephensi*		*Hoplocephalus*	*Hoplocephalus*
14.1 *Neelaps bimaculatus*	*Vermicella*	*Rhynchoelaps*	*Narophis*
14.2 *N. calonotus*	*Vermicella*	*Rhynchoelaps*	*Melwardia*
15.1 *Notechis ater*	*Notechis*		*Notechis*
15.2 *N. scutatus*	*Notechis*	*Notechis*	*Notechis*
16. *Oxyuranus scutellatus*		*Oxyuranus*	*Oxyuranus*
17. *Parademansia (O.) microlepidota*			*Oxyuranus*
18.1 *Pseudechis australis*	*Pseudechis*	*Pseudechis*	*Pseudechis*
18.2 *P. colletti*	*Pseudechis*	*Pseudechis*	*Pseudechis*
18.3 *P. guttatus*	*Pseudechis*		*Pseudechis*
18.4 *P. porphyriacus*	*Pseudechis*	*Pseudechis*	*Pseudechis*
	18.5 * *P. butleri* (Smith)		

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made no reference to the species. By utilizing the list of synonyms in Table 3 coupled with this table the reader can determine the currently recognized species name as well as examine its taxonomic stability through time and that of its congeners. It should be realized that the classifications of both Cogger and Storr are currently in use.

Kinghorn 1956	**Loveridge** 1934	**Krefft** 1869	**Boulenger** 1896	**Günther** 1858
Acanthophis	*Acanthophis*	*Acanthophis*	*Acanthophis*	
Acanthophis	*Acanthophis*			
Denisonia	*Denisonia*	*Hoplocephalus*	*Denisonia*	*Hoplocephalus*
Aspidomorphus	*Pseudelaps*	*Cacophis*	*Pseudelaps*	
Aspidomorphus		*Cacophis*	*Pseudelaps*	
Aspidomorphus	*Pseudelaps*	*Petrodymon*	*Pseudelaps*	
Denisonia	*Denisonia*	*Hoplocephalus*	*Denisonia*	
Denisonia	*Denisonia*		*Denisonia*	*Hoplocephalus*
			Diemenia	
Demansia	*Demansia*	*Diemenia*	*Diemenia*	
Demansia	*Demansia*	*Diemenia*	*Diemenia*	*Demansia*
Demansia		*Diemenia*	*Diemenia*	*Demansia*
Demansia	*Demansia*	*Diemenia*		*Demansia*
Denisonia				
Denisonia	*Denisonia*			
Denisonia	*Denisonia*	*Denisonia*	*Denisonia*	
Denisonia			*Denisonia*	
Denisonia	*Denisonia*	*Hoplocephalus*	*Denisonia*	*Hoplocephalus*
Denisonia	*Denisonia*	*Hoplocephalus*	*Denisonia*	*Hoplocephalus*
Denisonia		*Hoplocephalus*	*Pseudelaps*	
			Denisonia	
Denisonia		*Hoplocephalus*	*Brachyaspis*	*Hoplocephalus*
Elapognathus		*Hoplocephalus*	*Elapognathus*	*Hoplocephalus*
Aspidomorphus	*Pseudelaps*	*Cacophis*	*Pseudelaps*	*Brachysoma*
Aspidomorphus	*Pseudelaps*		*Pseudelaps*	*Glyphodon*
Glyphodon				
Glyphodon		*Brachysoma*	*Glyphodon*	*Glyphodon*
Denisonia			*Denisonia*	*Hoplocephalus*
Denisonia	*Denisonia*	*Hoplocephalus*	*Denisonia*	
Hoplocephalus	*Hoplocephalus*		*Hoplocephalus*	
Hoplocephalus	*Hoplocephalus*	*Hoplocephalus*	*Hoplocephalus*	*Hoplocephalus*
Hoplocephalus		*Hoplocephalus*	*Hoplocephalus*	
Vermicella	*Furina*	*Furina*	*Furina*	*Brachysoma*
Vermicella		*Brachysoma*	*Furina*	*Brachysoma*
Notechis		*Hoplocephalus*	*Notechis*	
Notechis	*Notechis*	*Hoplocephalus*	*Notechis*	
Oxyuranus		*Pseudechis*	*Pseudechis*	
Parademansia			*Pseudechis*	
Pseudechis		*Pseudechis*	*Pseudechis*	
Pseudechis				
Pseudechis				
Pseudechis		*Pseudechis*	*Pseudechis*	*Pseudechis*

Cogger 1975b, 1979	**Storr** 1982, 1981a,b,c, 1979, 1967	**McDowell** 1967,1970, 1969	**Worrell** 1961, 1963,a,b 1950, 1960
19.1 *Pseudonaja affinis*	*Pseudonaja*		*Pseudonaja*
19.2 *P. guttata*	*Pseudonaja*	*"Demansia"*	*Pseudonaja*
19.3 *P. ingrami*	*Pseudonaja*		*Pseudonaja*
19.4 *P. modesta*	*Pseudonaja*	*"Demansia"*	*Pseudonaja*
19.5 *P. nuchalis*	*Pseudonaja*	*"Demansia"*	*Pseudonaja*
19.6 *P. textilis*	*Pseudonaja*	*"Demansia"*	*Pseudonaja*
20. *Rhinoplocephalus bicolor*	*Rhinoplocephalus*	*Rhinoplocephalus*	*Rhinoplocephalu*
21.1 *Simoselaps australis*	*Vermicella*	*Rhynchoelaps*	*Brachyurophis*
	21.2 * *V. anomalus*		
	21.3 * *V. approximans*		*Rhinelaps*
21.4 *S. bertholdi*	*Vermicella*	*Rhynchoelaps*	*Rhynchoelaps*
21.5 *S. fasciolatus*	*Vermicella*	*Rhynchoelaps*	*Rhinelaps*
21.6 *S. incinctus*	*Vermicella*	*Rhynchoelaps*	*Rhynchoelaps*
21.7 *S. semifasciatus*	*Vermicella*	*Rhynchoelaps*	*Brachyurophis*
	21.8 * *V. littoralis*		
21.9 *S. warro*	*Furina*	*Rhynchoelaps*	*Rhinelaps*
21.10 *S. minimus*	*Vermicella*		*Melwardia*
22. *Suta suta*	*Denisonia*	*Suta*	*Suta*
23. *Tropidechis carinatus*		*Tropidechis*	*Tropidechis*
24.1 *Unechis brevicaudus*	= * *D. nigriceps*	*Suta*	*Parasuta*
24.2 *U. carpentariae* (= *boschmai)*	*Denisonia*	*Suta*	*Unechis*
24.3 *U. flagellum*	*Denisonia*	*Suta*	*Cryptophis*
24.4 *U. gouldii*	*Denisonia*	*Suta*	*Parasuta*
	Denisonia	*Suta*	24.4.1 *Denisonia dwyer*
24.5 *U. monachus*	*Denisonia*		
24.6 *U. nigrostriatus*		*Suta*	*Parasuta*
	24.7 * *D. spectabilis*		
25.1 *Vermicella annulata*	*Vermicella*	*Vermicella*	*Vermicella*
25.2 *V. multifasciata*			

Currently Recognized Species of Australian Elapids (derived largely from the checklist currently in press by Cogger *et al.*, 1983)

affinis, P., Günther, 1872	19.1
annulata, V., (Gray, 1841)	25.1
anomalus, S., (Sternfield, 1919)	21.2
antarcticus, A., (Shaw & Nodder, 1802)	1.1
approximans, S., (Glauert, 1954)	21.3
ater, N., (Krefft, 1856)	15.1
atra, D., (Macleay, 1884)	5.1
atriceps, E., (Storr, 1980)	8.0
australis, P., (Gray, 1842)	18.0
australis, S., (Krefft, 1864)	21.1
barnardi, G., Kinghorn, 1939	11.0
bertholdi, S., (Jan, 1859)	21.4
bicolor, R., Müller, 1885	20.0
bimaculatus, N., (Duméril, Bibron & Duméril, 1854)	14.0
bitorquatus, H., (Jan, 1859)	13.0
boschmai, U., (Brongersma & Knapp-Van Meeuwen, 1961)	24.2
bungaroides, H., (Schlegel, 1837)	13.2
butleri, P., Smith, 1981	18.5
calonotus, N., (Duméril, Bibron & Duméril, 1854)	14.2
carinatus, T., (Krefft, 1863)	23.0
carpentariae, U., (= *boschmai*)	24.2
colletti, P., Boulenger, 1902	18.2
coronata, D., (Schlegel, 1837)	7.1
coronoides, D., (Günther, 1858)	7.2
curta, E., (Schlegel, 1837)	8.0
damelii, H., (Günther, 1876)	12.0
devisii, D., Waite & Longman, 1920	6.1
diadema, F., (Schlegel, 1837)	10.0
dunmalli, G., Worrell, 1955	11.2
dwyeri, U., (Worrell, 1963)	24.4.1
fasciata, D., Rosén, 1905	6.2
fasciolatus, S., (Günther, 1872)	21.5
flagellum, U., (McCoy, 1878)	24.3
gouldii, U., (Gray, 1841)	24.4.2
guttata, P., (Parker, 1926)	19.2
guttatus, P., DeVis, 1905	18.3

Kinghorn 1956	Loveridge 1934	Krefft 1869	Boulenger 1896	Günther 1858
Demansia	*Demansia*			
Demansia				
Demansia				
Demansia	*Demansia*		*Diemenia*	*Cacophis*
Demansia	*Demansia*	*Pseudonaja*	*Diemenia*	*Pseudonaja*
Demansia	*Demansia*	*Diemenia*	*Diemenia*	
Rhinoplocephalus			*Rhinoplocephalus*	
Brachyurophis	*Rhynchoelaps*	*Brachyurophis*	*Rhynchoelaps*	
Rhinelaps				
Rhynchoelaps	*Rhynchoelaps*		*Rhynchoelaps*	
Rhinelaps			*Rhynchoelaps*	
Brachyurophis			*Rhynchoelaps*	
Rhinelaps				
Denisonia	*Denisonia*		*Denisonia*	
Tropidechis		*Tropidechis*	*Tropidechis*	
Denisonia	*Denisonia*		*Denisonia*	
Denisonia	*Denisonia*		*Denisonia*	
Denisonia	*Denisonia*		*Denisonia*	*Hoplocephalus*
Denisonia			*Denisonia*	
Vermicella	*Furina*	*Vermicella*	*Furina*	*Vermicella*

harriettae, C., Krefft, 1869	3.1
incinctus, S., (Storr 1968)	21.6
ingrami, P., (Boulenger 1908)	19.3
krefftii, C., Günther, 1863	3.2
littoralis, S., (Storr, 1968)	21.8
maculata, D., (Steindachner, 1867)	6.3
mastersi, D., (Krefft, 1866)	7.3
microlepidota, O., (McCoy, 1879)	17.0
minor, E., (Günther, 1863)	9.0
minimus, E., (Worrell, 1960)	21.10
modesta, P., (Günther, 1872)	19.4
monachus, U., (Storr, 1964)	24.5
multifasciata, V., (Longman, 1915)	25.2
nigrescens, C., (Günther, 1862)	4.1
nigriceps, U., (Günther, 1863)	24.0
nigrostriatus, U., (Krefft, 1864)	24.6
nuchalis, P., Günther, 1858	19.5
olivacea, D., (Gray, 1842)	5.2
ornata, F., (Gray, 1842)	10.2
pallidiceps, C., (Günther, 1858)	4.2
papuensis, D., (Macleay, 1877)	5.8
porphyriacus, P., (Shaw, 1794)	18.4
praelongus, A., Ramsay, 1877	1.3
psammophis, D., (Schlegel, 1837)	5.3
punctata, D., Boulenger, 1896	6.4
pyrrhus, A., Boulenger, 1898	1.2
rhodogaster, D., (Jan & Sordelli, 1873)	7.4
scutatus, N., (Peters, 1861)	15.2
scutellatus, O., (Peters, 1867)	16.0
semifasciatus, S., (Günther, 1863)	21.7
signata, H., (Jan, 1859)	12.2
simplex, D., Storr, 1978	5.6
spectabilis, U., (Krefft, 1869)	24.7
squamulosus, C., (Duméril, Bibron & Duméril, 1859)	3.3
stephensi, H., Krefft, 1869	13.3
superbus, A., (Günther, 1858)	2.0
suta, S., (Peters, 1854)	22.0
textilis, P., (Duméril, Bibron & Duméril, 1863)	19.6
torquata, D., (Günther, 1862)	5.4
tristis, G., Günther, 1858	11.3
warro, S., (DeVis, 1884)	21.9

Table 3. Names applied to Australian snakes.

This table is a complete alphabetical list of all junior synonyms under which Australian proteroglyphs have been described and their authors. This information has been derived largely from the checklist currently in press by Cogger *et al.*, but differs from it in a few instances. The terrestrial and marine forms have been separated for the reader's convenience.

Terrestrial Proteroglyphs

acantophis, Ophryas, Merrem, 1820	= *Acanthophis antarcticus*
Acanthophis Daudin, 1803	= *Acanthophis*
Acantophis Berthold, 1827	= *Acanthophis*
aculeata, Boa, Boulenger, 1896	= *Acanthophis antarcticus*
acutirostris, Demansia, Mitchell, 1951	= *Pseudonaja nuchalis*
affinis, Pseudonaja, Günther, 1872	= *Pseudonaja affinis*
albiceps, Pseudelaps, Boulenger, 1898	= *Simoselaps warro*
Alecto Wagler, 1830	= *Pseudechis*
ambigua, Boa, Leach, 1814	= *Acanthophis antarcticus*
angulata, Denisonia, DeVis, 1905	= *Hoploceplalus bitorquatus*
angusticeps, Diemenia, Macleay, 1888	= *Demansia olivacea*
annulata, Calamaria, Gray, 1841	= *Vermicella annulata*
annulata, Demansia, Günther, 1858	= *Pseudonaja textilis*
anomalus, Rhynchelaps, Sternfield, 1919	= *Simoselaps anomalus*
antarctica, Boa, Shaw & Nodder, 1802	= *Acanthophis antarcticus*
approximans, Rhyncho-elaps, Glauert, 1954	= *Simoselaps approximans*
aspidorhyncha, Diemenia, McCoy, 1879	= *Pseudonaja nuchalis*
assimilis, Hoplocephalus, Macleay, 1885	= *Cryptophis nigrescens*
ater, Hoplocephalus, Krefft, 1866	= *Notechis ater*
atra, Diemenia, Macleay, 1884	= *Demansia atra*
atriceps, Brachyaspis, Storr, 1980	= *Echiopsis atriceps*
atropolios, Pseudoelaps, Jan & Sordelli, 1873	= *Cacophis squamulosus*
australis, Naja, Gray, 1842	= *Pseudechis australis*
australis, Simotes, Krefft, 1864	= *Simoselaps australis*
australis, Tortrix	= incertae sedis
Austrelaps Worrell, 1963	= *Austrelaps*
bancrofti, Denisonia, DeVis, 1911	= *Furina diadema*
bancrofti, Pseudelaps, DeVis, 1911	= *Pseudonaja nuchalis*
barnardi, Glyphodon, Kinghorn, 1939	= *Glyphodon barnardi*
beckeri, Pseudoelaps, Jan & Sordelli, 1873	= *Pseudonaja textilis*
bertholdi, Elaps, Jan, 1858	= *Simoselaps bertholdi*
bicolor, Rhinoplocephalus, Müller, 1885	= *Rhinoplocephalus bicolor*
bicucullata, Furina, McCoy, 1879	= *Pseudonaja textilis*
bilineata, Furina	= incertae sedis
bimaculata, Furina, Duméril, Bibron & Duméril, 1854	= *Neelaps bimaculatus*
bitorquata, Alecto, Jan, 1859	= *Hoplocephalus bitorquatus*
blackmanii, Cacophis, Krefft, 1869	= *Furina diadema*
boschmai, Denisonia, Brongersma & Knaap-van Meeuwen, 1961	= *Unechis boschmai*
Brachyaspis Boulenger, 1896	= *Echiopsis*
Brachysoma Fitzinger, 1843	= *Furina*
Brachyurophis Günther, 1863	= *Simoselaps*
brankysi, Hoplocephalus, Goldman, Hill & Stanbury, 1969	= *Austrelaps superbus*
bransbyi, Hoplocephalus, Macleay, 1878	= *Austrelaps superbus*
brevicauda, Denisonia nigrostriata, Mitchell, 1951	= *Unechis nigriceps*
brownii, Acanthophis, Leach, 1814	= *Acanthophis antarcticus*
brunnea, Denisonia, Mitchell, 1951	= *Pseudechis australis*
bungaroides, Naja, Schlegel, 1837	= *Hoplocephalus bungaroides*
butleri, Pseudechis, Smith, 1981	= *Pseudechis butleri*
Cacophis Günther, 1863	= *Cacophis*
caledonicus, Neelaps, Hoffman, 1890	= *Neelaps calonotus*
calodera, Demansia olivacea, Storr, 1978	= *Demansia olivacea*
calonotos, Furina, Duméril, 1853	= *Neelaps calonotus*
cambelli, Rhynchoelaps, Kinghorn, 1929	= *Simoselaps semifasciatus*
canni, Oxyuranus scutellatus, Slater, 1956	= *Oxyuranus scutellatus canni*
carinata, Diemenia, Longman, 1915	= *Pseudonaja nuchalis*
carinatus, Hoplocephalus Krefft, 1863	= *Tropidechis carinatus*
carpentariae, Hoploceph-alus, Macleay, 1887	= *Suta suta*

carpentariae, Unechis, Worrell, 1961 = *Unechis boschmai*
cerastinus, Acanthophis, Daudin, 1803 = *Acanthophis antarcticus*
christieanus, Lunelaps, Worrell, 1963 = *Furina ornata*
christieanus, Pseudelaps, Fry, 1915 = *Furina ornata*
collaris, Hoplocephalus, Macleay, 1887 = *Drysdalia mastersii*
colletti, Pseudechis, Boulenger, 1902 = *Pseudechis colletti*
coronatus, Elaps, Schlegel, 1837 = *Drysdalia coronata*
coronoides, Hoplocephalus, Günther, 1858 = *Drysdalia coronoides*
Cryptophis Worrell, 1961 = *Cryptophis*
cucullata, Diemansia, Günther, 1862 = *Cacophis squamulosus*
cucullata, Furina, Boulenger, 1896 = *Pseudonaja textilis*
cupreiceps, Demansia reticulata, Storr, 1978 = *Demansia reticulata*
cupreus, Pseudechis, Boulenger, 1896 = *Pseudechis australis*
cupreus, Pseudechis, Boulenger, 1896 = *Pseudonaja textilis*
curta, Naja, Schlegel, 1837 = *Echiopsis curta*
cuvieri, Oploceph[alus], Gray, 1831 = *Notechis scutatus*
daemelii, Denisonia, Boulenger, 1896 = *Hemiaspis damelii*
damelii, Hoplocephalus, Günther, 1876 = *Hemiaspis damelii*
darwiniensis, Pseudechis, Macleay, 1878 = *Pseudechis australis*
Demansia Günther, 1858 = *Demansia*
Denisonia Krefft, 1869 = *Denisonia*
denisonioides, Pseudechis, Werner, 1909 = *Pseudechis australis*
devisi, Denisonia maculata, Waite & Longman, 1920 = *Denisonia devisii*
diadema, Brachysoma, = *Neelaps bimaculata*
diadema, Calamaria, Schlegel, 1837 = *Furina diadema*
Diemansia Günther, 1858 = *Demansia*
Diemenia Günther, 1863 = *Demansia*
Diemennia Günther, 1863 = *Demansia*
dorsalis, Alecto, Jan, 1863 = *Unechis nigrostriatus*
Drepanodontis Worrell, 1961 = *Hemiaspis*
Drysdalia Worrell, 1961 = *Drysdalia*
dunmalli, Glyphodon, Worrell, 1955 = *Glyphodon dunmalli*
dwyeri, Denisonia, Worrell, 1956 = *Unechis dwyeri*
Echiopsis Fitzinger, 1843 = *Echiopsis*
Elapidocephalus Macleay, 1884 = *Demansia*
Elapocephalus Macleay, 1878 = *Demansia*
Elapocormus Fitzinger, 1843 = *Hoplocephalus*
Elapocranium Macleay, 1878 = *Demansia*
Elapognathus Boulenger, 1896 = *Elapognathus*
Euprepiosoma Fitzinger, 1860 = *Pseudonaja*
fasciata, Denisonia, Rosen, 1905 = *Denisonia fasciata*
fasciata, Vermicella, Stirling & Zietz, 1893 = *Simoselaps fasciolatus*
fasciolata, Alecto, Jan, 1863 = *Notechis scutatus*
fasciolatus, Rhinelaps, Günther, 1872 = *Simoselaps fasciolatus*
fenestrata, Denisonia, DeVis, 1905 = *Glyphodon tristis*
ferox, Diemenia, Macleay, 1882 = *Oxyuranus (Parademansia) microlepidota*
flagellum, Hoplocephalus, McCoy, 1867 = *Unechis flagellum*
flavicollis, Cacophis harriettae, McDowell, 1967 = *Cacophis harriettae*
fordei, Cacophis, Krefft, 1869 = *Cacophis krefftii*
forresti, Denisonia, Boulenger, 1906 = *Suta suta*
frenatus, Hoplocephalus, Peters, 1870 = *Suta suta*
frontalis, Hoplocephalus, Ogilby, 1890 = *Suta suta*
Furina Duméril, 1853 = *Furina*
fuscicollis, Rhynchelaps, Lönnberg & Andersson, 1915 = *Simoselaps warro*
fuscus, Hoplocephalus, Steindachner, 1867 = *Notechis scutatus*
Glyphodon Günther, 1858 = *Furina*
Glyphodon Günther, 1858 = *Glyphodon*
gouldii, Elaps, Gray, 1841 = *Unechis gouldii*
guntheri, Cacophis, Steindachner, 1867 = *Pseudonaja textilis*
guttata, Demansia, Parker, 1926 = *Pseudonaja guttata*
guttata, Pseudechis, DeVis 1905 = *Pseudechis guttatus*
harriettae, Cacophis, Krefft, 1869 = *Cacophis harriettae*
Hemiaspis Fitzinger, 1860 = *Hemiaspis*
Homaloselaps Jan, 1858 = *Vermicella*
Hoplocephalus Wagler, 1830 = *Hoplocephalus*
Hornea Lucas & Frost, 1896 = *Simoselaps*
humphreysi, Notechis ater, Worrell, 1963 = *Notechis ater humphreysi*
incincta, Vermicella semifasciata, Storr, 1968 = *Simoselaps incinctus*
inframacula, Demansia textilis, Waite, 1925 = *Pseudonaja textilis*
ingrami, Diemenia, Boulenger, 1908 = *Pseudonaja nuchalis*
kubingii, Pseudoelaps, Jan, 1859 = *Pseudonaja textilis*
kubinyi, Pseudoelaps, Jan, 1863 = *Pseudonaja textilis*
labialis, Alecto, Jan, 1859 = *Austrelaps superbus*

labialis, Alecto, Jan & Sordelli, 1873	= *Drysdalia coronoides*
laevis, Acanthophis, Macleay, 1878	= *Acanthophis antarcticus*
laevis, Boa	= incertae sedis
latizonatus, Rhynchelaps, DeVis, 1905	= *Vermicella annulata*
leptocephalus, Trimeresurus, Lacépède, 1804	= *Pseudechis porphyriacus*
littoralis, Vermicella bertholdi, Storr, 1968	= *Simoselaps littoralis*
Lunelaps Worrell, 1961	= *Furina*
lunulata, Vermicella, Krefft, 1869	= *Vermicella annulata*
maclennani, Oxyuranus, Kinghorn, 1923	= *Oxyuranus scutellatus*
maculatus, Hoplocephalus, Steindachner, 1867	= *Denisonia maculata*
maculiceps, Diemenia, Boettger, 1898	= *Demansia atra*
Mainophis Macleay, 1877	= *Glyphodon*
mastersii, Hoplocephalus, Krefft, 1866	= *Drysdalia mastersii*
mattozoi, Elaps, Ferreira, 1891	= *Simoselaps bertholdi*
melaena, Demansia papuensis, Storr, 1978	= *Demansia papuensis*
melanocephalus, Elaps, Gray & Neill, 1845	= *Drysdalia coronata*
melanotus, Alecto, Jan, 1863	= *Cryptophis nigrescens*
Melwardia Worrell, 1960	= *Simoselaps*
microlepidota, Diemenia, McCoy, 1879	= *Oxyuranus (Parademansia) microlepidota*
minima, Melwardia, Worrell, 1960	= *Simoselaps minimus*
minor, Hoplocephalus, Günther, 1863	= *Elapognathus minor*
minutus, Pseudelaps, Fry, 1915	= *Drysdalia rhodogaster*
modesta, Cacophis, Günther, 1875	= *Pseudonaja modesta*
monachus, Denisonia, Storr, 1964	= *Unechis monachus*
mortonensis, Pseudechis, DeVis, 1911	= *Pseudechis guttatus*
muelleri, Hoplocephalus, Fischer, 1885	= *Denisonia maculata*
multifasciata, Furina, Longman, 1915	= *Vermicella multifasciata*
Narophis Worrell, 1961	= *Neelaps*
Neelaps Günther, 1863	= *Neelaps*
neocaledonicus, Neelaps, Palacky, 1898	= *Neelaps calonotus*
niger, Notechis scutatus, Kinghorn, 1921	= *Notechis ater*
nigra, Denisonia, DeVis, 1905	= *Drysdalia coronoides*
nigrescens, Hoplocephalus, Günther, 1862	= *Cryptophis nigrescens*
nigriceps, Hoplocephalus, Günther, 1863	= *Unechis nigriceps*
nigrostriatus, Hoplocephalus, Krefft, 1864	= *Unechis nigrostriatus*
Notechis Boulenger, 1896	= *Notechis*
nuchalis, Pseudonaja, Günther, 1858	= *Pseudonaja nuchalis*
nullarbor, Denisonia spectabilis, Storr, 1981	= *Unechis spectabilis*
occidentalis, Notechis scutatus, Glauert, 1948	= *Notechis scutatus*
occipitale, Rabdion, Girard, 1858	= *Furina diadema*
occipitalis, Elaps, Duméril, Bibron & Duméril, 1854	= *Vermicella annulata*
olivaceus, Lycodon, Gray, 1842	= *Demansia olivacea*
olivaceus, Trimeresurus, Gray, 1841	= *Drysdalia coronata*
Ophrias Cuvier, 1829	= *Acanthophis*
Ophryas Merrem, 1820	= *Acanthophis*
Oplocephalus Gray, 1831	= *Hoplocephalus*
ornata, Denisonia, Krefft, 1869	= *Denisonia maculata*
ornaticeps, Elapocephalus, Macleay, 1878	= *Demansia olivacea*
ornatus, Elaps, Gray, 1842	= *Furina diadema*
ornatus, Hoplocephalus, DeVis, 1884	= *Denisonia devisii*
Oxyuranus Kinghorn, 1923	= *Oxyuranus*
pallidiceps, Hoplocephalus, Günther, 1858	= *Cryptophis pallidiceps*
palpebrosa, Boa, Shaw, 1802	= *Acanthophis antarcticus*
papuensis, Diemenia, Macleay, 1877	= *Demansia papuensis*
Parasuta Worrell, 1961	= *Unechis*
Parademansia Kinghorn, 1955	= *Oxyuranus*
permixta, Alecto, Jan, 1863	= *Cryptophis nigrescens*
Petrodymon Krefft, 1866	= *Cacophis*
platycephalus, Pseudechis, Thomson, 1933	= *Pseudechis australis*
porphyraicus, Pseudechis, McCoy, 1867	= *Pseudechis porphyriacus*
porphyriacus, Coluber, Shaw, 1794	= *Pseudechis porphyriacus*
prophyrica, Naja, Schlegel, 1837	= *Pseudechis porphyriacus*
praelongus, Acanthophis, Ramsay, 1877	= *Acanthophis praelongus*
propinqua, Denisonia frontalis, DeVis, 1905	= *Suta suta*
psammophidius, Pseudelaps, Duméril, Bibron & Duméril, 1854	= *Demansia psammophis*
psammophis, Elaps, Schlegel, 1837	= *Demansia psammophis*
Pseudechis Wagler, 1830	= *Pseudechis*
Pseudechys Stirling & Zietz, 1893	= *Pseudechis*
Pseudonaja Günther, 1858	= *Pseudonaja*
pulchella, Hornea, Lucas & Frost, 1896	= *Simoselaps fasciolatus*
punctata, Denisonia, Boulenger, 1896	= *Denisonia punctata*
pyrrhus, Acanthophis, Boulenger, 1898	= *Acanthophis pyrrhus*

ramsayi, Furina, Macleay, 1885 = *Pseudonaja modesta*
ramsayi, Hoplocephalus, Krefft, 1864 = *Austrelaps superbus*
reticulatus, Lycodon, Gray, 1842 = *Demansia psammophis*
revelata, Denisonia, DeVis, 1911 = *Hoplocephalus bitorquatus*
Rhinelaps Günther, 1872 = *Simoselaps*
Rhinhoplocephalus Boulenger, 1896 = *Rhinoplocephalus*
Rhinoplocephalus Müller, 1885 = *Rhinoplocephalus*
rhinostomus, Pseudelaps, Jan & Sordelli, 1873 = *Simoselaps semifasciatus*
rhodogaster, Alecto, Jan, 1863 = *Drysdalia rhodogaster*
Rhynchelaps Boulenger, 1896 = *Simoselaps*
Rhynchoelaps Jan, 1858 = *Simoselaps*
robusta, Furina, DeVis, 1905 = *Simoselaps bertholdi*
robusta, Mainophis, Macleay, 1877 = *Glyphodon tristis*
roperi, Rhynchoelaps, Kinghorn, 1931 = *Simoselaps semifasciatus*
rostralis, Denisonia, DeVis, 1911 = *Simoselaps warro*
rufescens, Demansia olivacea, Storr, 1978 = *Demansia olivacea*
rugosus, Acanthophis antarcticus, Loveridge, 1948 = *Acanthophis praelongus*
schmidti, Alecto, Jan & Sordelli, 1873 = *Austrelaps superbus*
scutata, Naja (Hemadryas), Peters, 1861 = *Notechis scutatus*
scutellatus, Pseudechis, Peters, 1867 = *Oxyuranus scutellatus*
semifasciata, Brachyurophis, Günther, 1863 = *Simoselaps semifasciatus*
serventyi, Notechis ater, Worrell, 1963 = *Notechis ater serventyi*
signata, Alecto, Jan, 1859 = *Hemiaspis signata*
simile, Brachysoma, Macleay, 1878 = *Furina diadema*
Simoselaps, Jan, 1859 = *Simoselaps*
simplex, Demansia, Storr, 1978 = *Demansia simplex*
smithii, Rhynchoelaps, Kinghorn, 1931 = *Simoselaps semifasciatus*
snelli, Vermicella annulata, Storr, 1968 = *Vermicella annulata*
sorda, Viper, Salvado, 1851 = *Acanthophis antarcticus*
sordellii, Pseudelaps, Jan, 1859 = *Pseudonaja textilis*
sp., Glyphodon, Worrell, 1963 = *Cacophis harriettae*
spectabilis, Hoplocephalus, Krefft, 1869 = *Unechis spectabilis*
squamulosus, Pseudelaps, Duméril, 1853 = *Cacophis squamulosus*
stephensii, Hoplocephalus, Krefft, 1869 = *Hoplocephalus stephensii*
stirlingi, Hoplocephalus, Lucas & Frost, 1896 = *Suta suta*
suboccipitalis, Hoplocephalus, Ogilby, 1892 = *Hemiaspis damelii*
sulcans, Hoplocephalus, DeVis, 1884 = *Hoplocephalus bitorquatus*
Superbus, Hoplocephalus, Günther, 1858 = *Austrelaps superbus*
superbus, Hoplocephalus, Günther, 1858 = *Elapognathus minor*
superciliaris, Diemenia, McCoy, 1867 = *Pseudonaja textilis*
superciliosus, Pseudoelaps, Fischer, 1856 = *Pseudonaja textilis*
Suta Worrell, 1961 = *Suta*
sutherlandi, Brachysoma, DeVis, 1884 = *Pseudonaja nuchalis*
sutus, Hoplocephalus, Peters, 1863 = *Suta suta*
tanneri, Demansia nuchalis, Worrell, 1961 = *Pseudonaja affinis*
temporalis, Hoplocephalus, Günther, 1862 = *Echiopsis curta*
textilis, Furina, Duméril, Bibron & Duméril, 1854 = *Pseudonaja textilis*
torquata, Diemansia, Günther, 1862 = *Demansia torquata*
tortor, Acanthophis, Lesson, 1829–1831 = *Pseudechis porphyriacus*
tristis, Glyphodon, Günther, 1858 = *Glyphodon tristis*
Tropidechis Günther, 1863 = *Tropidechis*
Unechis Worrell, 1961 = *Unechis*
vagrans, Denisonia, Garman, 1901 = *Hemiaspis signata*
variegata, Alecto, Duméril, Bibron & Duméril, 1854 = *Hoplocephalus bungaroides*
Vermicalla Günther, 1858 = *Vermicella*
Vermicella Günther, 1858 = *Vermicella*
vestigiatus, Hoplocephalus, DeVis, 1884 = *Demansia atra*
waitii, Hoplocephalus, Ogilby, 1894 = *Hoplocephalus bitorquatus*
warro, Cacophis, DeVis, 1884 = *Simoselaps warro*
wilesmithii, Pseudechis, DeVis, 1911 = *Oxyuranus scutellatus*
woodjonesii, Rhynchelaps, Thomson, 1934 = *Simoselaps semifasciatus*

Marine Proteroglyphs

abbreviatus, Hydrophis, Jan, 1863 = *Lapemis hardwickii*
Acalyptophis Boulenger, 1896 = *Acalyptophis*
Acalyptus Duméril, 1853 = *Acalyptophis*
Aepyrus Agassiz, 1846 = *Aipysurus*
affinis, Platurus, Anderson, 1871 = *Laticauda laticaudata*
Aipysurus Lacépède, 1804 = *Aipysurus*
alcocki, Hydrophis, Wall, 1906 = *Hydrophis atriceps*

alternans, Hydrophis (Pelamis) bicolor, Fischer, 1856	= *Pelamis platurus*
andamanica, Distira, Annandale, 1905	= *Hydrophis ornatus*
anguillaeformis, Thalassophis, Schmidt, 1852	= *Aipysurus eydouxii*
annulata, Hydrophis (Pelamis) pelamidoides, Fischer, 1856	= *Lapemis hardwickii*
annulatus, Emydocephalus Krefft, 1869	= *Emydocephalus annulatus*
annulatus, Hydrus, Gray, 1849	= *Astrotia stokesii*
annulatus, Polyodontes, Lesson, 1834	= *Hydrophis caerulescens*
apraefrontalis, Aipysurus, M.A. Smith, 1926	= *Aipysurus apraefrontalis*
Aspisurus Gray, 1841	= *Aipysurus*
Aturia Gray, 1842	= *Hydrophis*
Astrotia Fischer, 1856	= *Astrotia*
Asturia Gray, 1842	= *Hydrophis*
atriceps, Hydrophis, Günther, 1864	= *Hydrophis atriceps*
australis, Aipysurus, Sauvage, 1877	= *Aipysurus duboisii*
belcheri, Aturia, Gray, 1849	= *Hydrophis belcheri*
bengalensis, Hydrophis, Gray, 1842	= *Enhydrina schistosa*
bicolor, Hydrus, Schneider, 1799	= *Pelamis platurus*
brevis, Hydrophis, Jan, 1863	= *Lapemis hardwickii*
caerulescens, Hydrus, Shaw, 1802	= *Hydrophis caerulescens*
chelonicephalus, Aipysurus, Bavay, 1869	= *Emydocephalus annulatus*
Chitulia Gray, 1849	= *Hydrophis*
cincinnatii, Disteira, Van Denburgh & Thompson, 1908	= *Hydrophis atriceps*
cloris, Hydrophis, Daudin, 1803	= *Hydrophis obscurus*
colubrinus, Hydrus, Schneider, 1799	= *Laticauda colubrina*
coronata, Hydrophis, Günther, 1864	= *Hydrophis obscurus*
cyanosoma, Distira, Wall, 1913	= *Hydrophis inornatus*
darwiniensis, Hydrelaps, Boulenger, 1896	= *Hydrelaps darwiniensis*
Disteira Lacépède, 1804	= *Disteira*
Distira Boulenger, 1896	= *Disteira*
doliata, Disteira, Lacépède, 1804	= *Disteira major*
Dolichodira Wall, 1921	= *Hydrophis*
duboisii, Aipysurus, Bavay, 1869	= *Aipysurus duboisii*
dumerilii, Disteira, Jan, 1859	= *Disteira major*
elegans, Aturia, Gray, 1842	= *Hydrophis elegans*
ellioti, Hydrophis, Günther, 1864	= *Hydrophis ornatus*
Emydocephalus Krefft, 1869	= *Emydocephalus*
Enhydrina Gray, 1849	= *Enhydrina*
Ephalophis M.A. Smith, 1931	= *Ephalophis*
eydouxii, Tomogaster, Gray, 1849	= *Aipysurus eydouxii*
fasciata, Chitulia, Gray, 1849	= *Hydrophis inornatus*
fischeri, Platurus, Jan, 1859	= *Laticauda laticaudata*
floweri, Hydrophis, Boulenger, 1898	= *Hydrophis melanosoma*
foliosquama, Aipysurus, M.A. Smith, 1926	= *Aipysurus foliosquama*
frontalis, Hydrophis, Jan, 1863	= *Hydrophis caerulescens*
frontalis, Platurus, DeVis, 1905	= *Laticauda colubrina*
fuliginosus, Aipysurus, Duméril, Bibron & Duméril, 1854	= *Aipysurus laevis*
fusca, Stephanohydra, Tschudi, 1837	= *Aipysurus fuscus*
godeffroyi, Hydrophis, Peters, 1872	= *Hydrophis ornatus*
gracilis, Hydrus, Shaw, 1802	= *Hydrophis gracilis*
grandis, Distira, Boulenger, 1896	= *Hydrophis elegans*
granosa, Hydrophis, Anderson, 1871	= *Astrotia stokesii*
greyi, Ephalophis, M.A. Smith, 1931	= *Ephalophis greyi*
guentheri, Hydrophis, Theobald, 1868	= *Astrotia stokesii*
guntheri, Hydrophis, Murray, 1884	= *Hydrophis gracilis*
guttata, Hydrophis, Murray, 1887	= *Astrotia stokesii*
hardwickii, Lapemis, Gray, 1835	= *Lapemis hardwickii*
horrida, Pseudodistira, Kinghorn, 1926	= *Acalyptophis peronii*
hybrida, Hydrophis, Schlegel, 1844	= *Hydrophis caerulescens*
Hydrelaps Boulenger, 1896	= *Hydrelaps*
Hydrophis Sonnini de Manoncourt & Latreille, 1802	= *Hydrophis*
Hypotropis Gray, 1846	= *Aipysurus*
inornata, Chitulia, Gray, 1849	= *Hydrophis inornatus*
jukesii, Hypotropis, Gray, 1846	= *Aipysurus laevis*
kadellnagam, Hydrophis, Boie, 1827	= *Hydrophis gracilis*
kingii, Hydrophis, Boulenger, 1896	= *Disteira kingii*
Kolpophis M.A. Smith, 1926	= *Lapemis*
lacepedei, Hydrophis, Jan, 1859	= *Disteira major*
laevis, Aipysurus, Lacépède, 1804	= *Aipysurus laevis*

laevis, Hydrophis, Lütken, 1863 = *Hydrophis ornatus*
Lapemis Gray, 1835 = *Lapemis*
Laticauda Laurenti, 1768 = *Laticauda*
laticaudatus, Coluber, Linnaeus, 1758 = *Laticauda laticaudata*
laticaudatus, Coluber, Linnaeus, 1758 = *Laticauda colubrina*
latifasciata, Hydrophis, Günther, 1864 = *Hydrophis obscurus*
laurenti, Platurus, Rafinesque, 1817 = *Laticauda laticaudata*
Leioselasma Lacépède, 1804 = *Hydrophis*
leprogaster, Hydrophis, Duméril & Bibron, 1856 = *Hydrophis gracilis*
Liopala Gray, 1842 = *Hydrophis*
Liopola Gray, 1842 = *Hydrophis*
longiceps, Hydrophis, Günther, 1864 = *Hydrophis inornatus*
loreatus, Lapemis, Gray, 1843 = *Lapemis hardwickii*
lubricus, Pelagophis, Peters & Doria, 1878 = *Aipysurus duboisii*
macfarlani, Distira, Boulenger, 1896 = *Hydrophis cyanocinctus*
maculata, Hydrophis bicolor, Jan, 1863 = *Pelamis platurus*
major, Hydrus, Shaw, 1802 = *Disteira major*
major, Hydrus, Shaw, 1802 = *Astrotia stokesii*
manillae, Hydrophis, Owen, 1859 = *Hydrophis inornatus*
margaritophorus, Aipysurus, Bleeker, 1858 = *Aipysurus eydouxii*
melanocephala, Hydrophis sublaevis, Gray, 1849 = *Hydrophis melanocephalus*
Melanomystax Wall, 1921 = *Disteira*
melanosoma, Hydrophis, Günther, 1864 = *Hydrophis melanosoma*
mentalis, Hydrophis, Gray, 1842 = *Disteira major*
mertoni, Distira, Roux, 1910 = *Parahydrophis mertoni*
microcephalus, Hydrophis, Lesson, 1834 = *Hydrophis gracilis*
microcephala, Thalassophis, Schmidt, 1852 = *Hydrophis gracilis*
Micromastophis Wall, 1921 = *Hydrophis*
mjobergi, Distira, Lönnberg & Andersson, 1913 = *Hydrophis ornatus*
muelleri, Platurus, Boulenger, 1896 = *Laticauda laticaudata*
muraeneformis, Thalassophis, Schmidt, 1852 = *Aipysurus eydouxii*
nasalis, Distira, DeVis, 1905 = *Disteira major*
obscura, Hydrophis, Daudin, 1803 = *Hydrophis obscurus*
ocellata, Hydrophis, Gray, 1849 = *Hydrophis ornatus*
orientalis, Disteira, Stejneger, 1901 = *Hydrophis melanocephalus*
ornata, Aturia, Gray, 1842 = *Hydrophis ornatus*
ornata, Pelamis, Gray, 1842 = *Pelamis platurus*
pachycercos, Hydrophis, Fischer, 1856 = *Hydrophis belcheri*
pachycerios, Hydrophis, Jan, 1859 = *Hydrophis belcheri*
pacificus, Hydrophis, Boulenger, 1896 = *Hydrophis pacificus*
Parahydrophis Burger & Natsuno, 1974 = *Parahydrophis*
pelamidoides, Hydrophis, Schlegel, 1837 = *Lapemis hardwickii*
Pelamis Daudin, 1803 = *Pelamis*
pelamis, Hydrophis, Schlegel, 1837 = *Pelamis platurus*
pelamoides, Hydrophis, Hilgendorf, 1876 = *Lapemis hardwickii*
Pelamydrus Stejneger, 1910 = *Pelamis*
peronii, Acalyptus, Duméril, 1853 = *Acalyptophis peronii*
platura, Anguis, Linnaeus, 1766 = *Pelamis platurus*
Platurus Sonnini de Manoncourt & Latreille, 1802 = *Laticauda*
platycaudatus, Coluber, Oken, 1836 = *Laticauda colubrina*
Platyurus Agassiz, 1846 = *Laticauda*
Polydontognathus Wall, 1921 = *Hydrophis*
polydonta, Hydrophis, Jan, 1863 = *Hydrophis caerulescens*
Polypholophis Wall, 1921 = *Hydrophis*
pooleorum, Aipysurus laevis, L.A. Smith, 1974 = *Aipysurus laevis*
Porrecticollis Wall, 1921 = *Hydrophis*
Praescutata Wall, 1921 = *Lapemis*
problematicus, Hydrophis, Jan, 1859 = *Lapemis hardwickii*
protervus, Hydrophis, Jan, 1859 = *Hydrophis caerulescens*
Pseudodistira Kinghorn, 1926 = *Acalyptophis*

rostralis, Hydrophis, M.A. Smith, 1917 = *Hydrophis gracilis*
russellii, Disteira, Fitzinger, 1827 = *Enhydrina schistosa*

schneideri, Pelamis, Rafinesque, 1817 = *Pelamis platurus*
schistosus, Hydrophis, Daudin, 1803 = *Enhydrina schistosa*
schistotus, Hydrophis, Jan, 1859 = *Enhydrina schistosa*
schizopholis, Hydrophis, Schmidt, 1846 = *Astrotia stokesii*
schlegelii, Thalassophis, Schmidt, 1852 = *Hydrophis inornatus*
scutata, Laticauda, Laurenti, 1768 = *Laticauda laticaudata*
shavii, Pelamis, Merrem, 1820 = *Disteira major*
sinuata, Pelamis bicolor, Duméril, Bibron & Duméril, 1854 = *Pelamis platurus*
Stephanohydra Tschudi, 1837 = *Aipysurus*
stokesii, Hydrus, Gray, 1846 = *Astrotia stokesii*

subcinctus, Hydrophis, Gray, 1842	= *Hydrophis obscurus*
subfasciata, Hydrophis, Gray, 1842	= *Enhydrina schistosa*
superciliosus, Acalyptus, Duméril, Bibron & Duméril, 1854	= *Acalyptophis peronii*
tenuis, Aipysurus, Lönnberg & Andersson, 1913	= *Aipysurus tenuis*
thai, Hydrophis caerulescens, M.A. Smith, 1920	= *Hydrophis caerulescens*
Thalassophina, M.A. Smith, 1926	= *Lapemis*
Tomogaster Gray, 1849	= *Aipysurus*
trachyceps, Hydrophis	= *Hydrophis cyanocinctus*
tuberculatus, Emydocephalus, Krefft, 1869	= *Emydocephalus annulatus*
valakadyn, Disteira, Boie, 1827	= *Enhydrina schistosa*
variegata, Pelamis, Duméril, Bibron & Duméril, 1854	= *Pelamis platurus*
werneri, Thalassophis, Schmidt, 1852	= *Enhydrina schistosa*

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