FAUNA *of* AUSTRALIA

23. GENERAL DESCRIPTION AND DEFINITION OF THE SQUAMATA

Harold G. Cogger

The Squamata are members of the diapsid subclass Lepidosauromorpha, a group whose only living descendants are the lizards, amphisbaenians, snakes and tuataras. The lizards, amphisbaenians and snakes together constitute the Order Squamata (or Superorder Squamata, according to Estes 1983).

Because the Squamata include approximately 95% of living reptiles, the phylogenetic position of this group within the Lepidosauromorpha, its component taxa, and their diagnostic features, have been the subject of numerous reviews (Estes & Pregill 1988; Kluge 1989).

The three suborders of the Squamata include the Sauria (lizards) and the Serpentes (snakes), which are represented in Australia by diverse faunas of nearly 500 species, and 250 species, respectively. The third suborder, the Amphisbaenia, comprises a small group of worm lizards and related species which do not occur in Australia.

The earliest known squamate fossils date from the late Permian and early Triassic, approximately 230 million years ago. These early fossils were already clearly lizard-like in their preserved features. Carroll (1988a) points out that lizards (the first squamates) do not appear to have originated as a result of '...a significant shift in behavioral patterns or the evolution of major new structural elements, but rather may be seen as resulting from the gradual accumulation of improvements in feeding, locomotion, and sensory apparatus.' Carroll (1988b) includes among these changes the emargination of the lower temporal fenestra and the development of a joint between the upper end of the quadrate and the squamosal. This mobility of the quadrate is termed streptostyly, and provides the opportunity to increase the force of the *m. pterygoideus*, the largest of the jaw-closing muscles, by moving the effective jaw joint from the lower to the upper end of the quadrate. Improvements in the hearing apparatus involved an enlarged tympanum, and the development of epiphysial joint structures resulted in determinate growth of the affected long bones. Also unique to the squamates is the possession of paired intromittent or copulatory organs in the males, termed 'hemipenes'. The squamates lack abdominal ribs, or gastralia, and the vertebral centra are usually procoelous (concave anteriorly, convex posteriorly).

In Australia, squamates constitute about 97% of some 750 species of Australian reptiles. The Australian members of these two groups may be distinguished by the following key:

Key to the suborders of the order Squamata

1(a) Limbs usually present, but even if absent some remnants of pectoral and pelvic girdles remain; non-regenerated tail in limbless forms at least 50% of snout–vent length; maxilla united to, and forming an integral part of, the cranium; external ear-opening usually present; parietals not extending to ventral side of braincase; brain not enclosed by bone anteriorly . . . . . Sauria (sometimes Lacertilia)

(b) Limbs always absent; tail at most 35% of snout–vent length; maxilla free and attached to the cranium only by tendons and muscles; external ear-opening always absent; parietal bones extending to ventral surface of braincase; brain entirely enclosed by bone . . . . . Serpentes (sometimes Ophidia)

Though the first lizards appeared in the Triassic, forms which are clearly associated with what we think of as modern lizards did not appear until the Cretaceous, about 130 million years ago. These lizards, like modern forms, were generally small and probably preyed mostly on arthropods.

Modern lizards occupy most of the world's terrestrial environments. They are most abundant in the tropics, but extend to the Arctic Circle in the north and to the southernmost islands of Australia, New Zealand and South America. Except for the marine iguana of the Galapagos Islands, all other members of the group are restricted to terrestrial or freshwater habitats.

Most lizards have well-developed limbs; the head is normally held high off the ground, and they are agile predators. However, many have evolved adaptations which depart from the typical lizard body form and which allow them to exploit specialised habitats or lifestyles. Many burrowing forms have reduced limbs. The mandibles are fused anteriorly at the symphysis, and typically an external ear opening and some tympanic bones are present. The ear-opening and tympanum have been lost many times in lizard evolution.

Autotomy, a feature of many lizards, and one which is absent in snakes, is the ability to break off voluntarily all or part of the tail, to distract predators or during territorial fights. This is achieved at special fracture planes in some or all of the caudal vertebrae. When the tail is broken off, muscle spasms often make the lost section of tail wriggle violently for several minutes, distracting a predator from the escaping owner. Typically a tail lost by autotomy regrows from the point of fracture, usually within a few months, but lacks the bony caudal vertebrae of the original tail. Rather, the new section of tail is supported by a cartilaginous rod lacking fracture planes.

Lizards present a vast range of behaviours. As ectotherms, much of their daily cycle of behaviour is concerned with thermoregulation. This enables them to maintain body temperatures at a level which optimises metabolic processes while maintaining optimum locomotor ability, to feed, escape predators, or avoid potentially lethal environmental conditions. Both diurnal and nocturnal species thermoregulate, although their temperature requirements may differ greatly. Further, many species have evolved complex social and sexual behaviours, often associated with sexual differences in size and colour, and sometimes involving territoriality between males and/or females.

While most lizards lay eggs, various forms of livebearing (viviparity) have evolved in different groups. Parental care of nests, eggs or young is rare.

Snakes evolved from a lizard ancestor at some time during the Cretaceous, although animals that are unequivocally snakes are not known from the fossil record until relatively late in the Cretaceous, about 100–120 million years ago, and the characteristic cranial features of snakes were in place by this time. These features included even greater emargination of the lower temporal fenestra and increased mobility of the quadrate, while the lower and upper jaw elements were becoming highly mobile in the fashion of modern snakes. These features, together with limblessness, suggest that early snakes, like their modern descendants, were active predators which swallowed their prey whole.

It has long been accepted that snakes evolved from a fossorial (burrowing) lizard-like ancestor (Senn & Northcutt 1973), because snakes share a number of features with extant burrowing lizards. These include elongation of the body, limb girdle reduction, the loss of limbs, middle and outer ear structures, and movable eyelids, and the development of a fixed spectacle. This view has come under increasing challenge (Carroll 1988b).

Moreover, modern snakes appear to be most closely related to varanoid lizards, with which they share a highly mobile forked tongue, high mobility of the quadrate and jaw elements, and the highly developed role of the vomeronasal (Jacobson's) organ in sensory perception. However, this hypothesised relationship is also under challenge (Rieppel 1983).

Snakes are characterised, as mentioned above, by the loss of limbs and limb girdles (although vestiges of the pelvic girdle and rear limbs are found in some groups of primitive snakes) and the loss of outer and middle ear structures. There are no movable eyelids, the eye being covered by a fixed, transparent scale. The tongue is long, forked and highly mobile, collecting particles from its immediate environment which the tongue tip transfers to the vomero-nasal organ for sensory identification. The shape and position of the viscera reflect the elongate body form; the left lung is usually absent, or is much smaller than the right lung. In many species, but especially in aquatic, diving snakes, the trachea may also be highly vascularised to form a forward extension of the lung. The elongate body is also accompanied by a marked increase in the number of vertebrae and associated ribs. The vertebrae have additional bony projections (compared with lizards) to which the muscles of the back are attached, giving greater control and power in limbless locomotion. Like other squamates the male intromittent organs are paired.

The skull of snakes is generally highly kinetic in the mobile, loose attachment to each other of many of the bony elements. The great relative mobility, especially of the jaws and bones of the palate, including the two halves of the lower jaw, permits most snakes to swallow food items with diameter greater than the predator's head. In particular, the quadrate bone is more mobile than that of lizards, allowing the mouth to open very widely. All snakes swallow their prey whole, and the needle-like and backwardly-directed teeth constrain the prey while it is forced back into the throat by the alternate forward motion of the jaws on either side.

Unlike lizards, the parietal and frontal bones have grown downwards to fuse with the parabasisphenoid and so create a solid bony casing for the forebrain. This ensures that the brain is not damaged when the snake swallows large or struggling prey.

CLASSIFICATION OF THE SAURIA

Currently some 17 families of extant lizards are recognised (Savage 1992). These are believed to be derived from three major evolutionary lines. All date from about the end of the Mesozoic, and are usually treated as distinct infraorders: the Iguania, Gekkota, Scincomorpha, and Anguinomorpha. The last two are often placed together as a single assemblage. Estes (1983) and Greer (1989) provide further discussion of these and other groupings.

The Iguania includes one Australian family, the Agamidae (dragons) . Both families in the Gekkota, the Gekkonidae (geckos) and Pygopodidae) (snake-lizards), are found in Australia. The close relationship of the snake lizards with the Australian diplodactyline geckos has been recognised by Kluge (1987) by placing them together in the family Pygopodidae, and is discussed further in Chapter 28. The Scincomorpha is represented in Australia by the family Scincidae (skinks), of which we have the most diverse fauna in the world, while the Anguinomorpha is represented by the monitor lizards or goannas (family Varanidae). The five lizard families represented in the Australian fauna may be distinguished using the following key:

Key to the families of suborder Sauria

1(a) Limbs normally present, though often very small; if limbs are entirely absent, then the eyes are very small and lie within a slit-like opening and there is a single large frontonasal scale (Fig. 23.1A) 2

(b) No obvious or normal limbs, though a scaly flap or 'fin' may be present on each side of the vent in some species; all with round, snake-like, lidless eyes; one or two pairs of frontonasal scales (Fig. 23.1B) (Snake-lizards) (Pl. 4.9–4.12). . . . . .Pygopodidae

2(a) Eyes with or without movable lids; if eyelids are absent then the pupil in daylight is not a narrow, vertical slit and the scales on the dorsum are imbricate (overlapping) 3

(b) Eyes snake-like, without movable lids; pupil in daylight a narrow, vertical slit; scales on the dorsum small, juxtaposed (not overlapping) (geckos) (Pls. 4.1–4.8) . . . . . Gekkonidae

3(a) Top of head covered with very small, irregular scales, usually 10 or more between the eyes (Fig. 23.1C). 4

(b) Top of head covered with large, regular and usually symmetrical, shield-like scales, usually fewer than 8 between the eyes (Fig. 23.1D) (skinks) (Pl. 6). . . . . Scincidae

4(a) Tongue long, slender, sheathed at its base and deeply forked like that of a snake (Fig. 23.1E); tongue frequently flicked in and out when lizard is alert (goannas or monitor Lizards) (Pl. 5.10–5.13) . . . . . Varanidae[1]

(b) Tongue broad, flat, not sheathed at its base and with only a slight notch in front (Fig. 23.1F); tongue not normally protruded except for eating and drinking. (dragons) (Pl. 5.1–5.9). . . . . .Agamidae

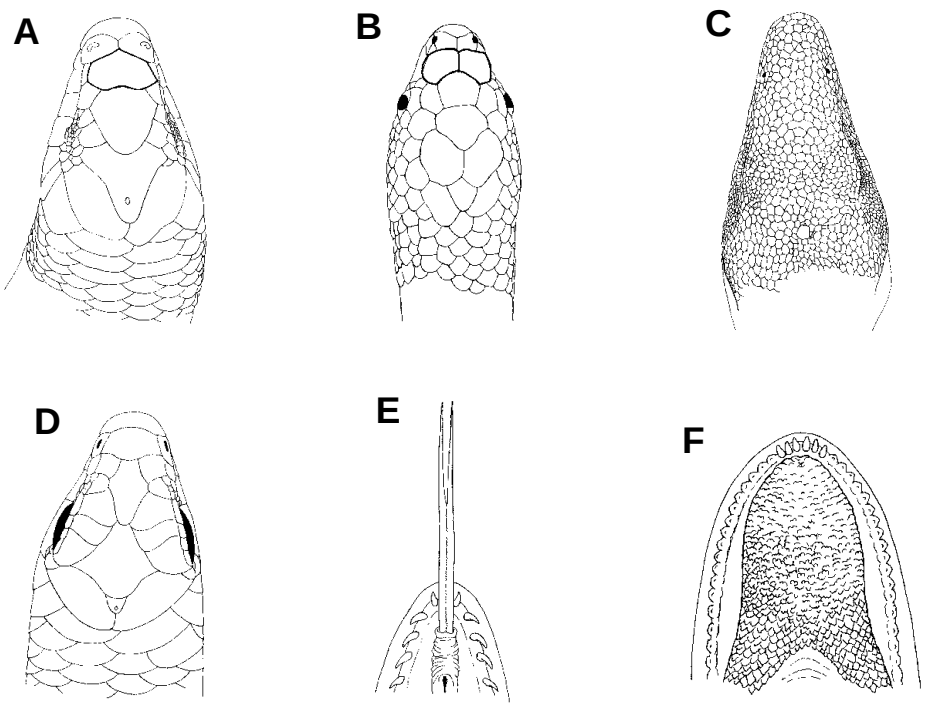

Figure 23.1 Key characters for families of the suborder Sauria. Pertinent features of elements **A–F** are noted in the adjacent key. [H.G. Cogger]

1 Single genus *Varanus*

Key to the genera of family Gekkonidae

1(a) Subdigital scales granular, without any enlarged terminal scales, tubercles or lamellae (Fig. 23.2A) 2

(b) Subdigital scales with at least enlarged terminal scales or one or more enlarged tubercles or transverse lamellae (Fig. 23.2B) 4

2(a) Rostral and mental shields rounded (Fig. 23.2C); labials much larger than adjacent scales, or, if subequal, tail not much longer than broad, strongly depressed 3

(b) Rostral and mental shields projecting, beak-like (Fig. 23.2D); labials and adjacent scales subequal; tail long and slender . . . . . *Rhynchoedura*

3(a) Tail ending in a globular knob (Fig. 23.2E); several scales between rostral and nostril (Fig. 23.2F) (Pl. 4.1). . *Nephrurus*

(b) Tail long and slender, not ending in a knob; rostral contacting nostril or separated from it by only one scale . . . . *Lucasium*[1]

4(a) Digits lying flat, entirely on the substrate when viewed laterally (Fig. 23.2G); terminal claws, if present, small and lying in a groove between distal lamellae (Fig. 23.2H) or arising from the upper surface of a large digital expansion (Fig. 23.2I). 5

(b) Digits angular when viewed laterally (Fig. 23.2J); feet bird-like, their terminal claws conspicuous and free (Fig. 23.2K) 12

5(a) At least some digits with claws 6

(b) All digits without claws. . . . . *Crenadactylus*

6(a) A distal pair of enlarged plates on the lower surface of each digit, quite distinct from and discontinuous with the remaining subdigital lamellae or tubercles (Fig. 23.2L) 7

(b) The enlarged subdigital lamellae in a continuous series (Fig. 23.2M). 9

7(a) Distal subdigital lamellae (excluding enlarged apical plates) single (Fig. 23.2L) 8

(b) At least some distal subdigital lamellae (excluding enlarged apical plates) paired (Fig. 23.2B) (Pl. 4.4) . . . . . *Oedura*

8(a) Scales above distal expansions of digits significantly larger than scales above basal parts of digits (Fig. 23.3A) . . . . . *Christinus*[2]

(b) Scales above distal expansions of digits more or less equal in size to those above basal parts of digits (Fig. 23.3B) (Pl. 4.5) . . . . . *Diplodactylus*[3]

1 sometimes regarded as a member of genus *Diplodactylus*

2 includes the Australian representatives of *Phyllodactylus*

3 sometimes divided into two or more distinct genera

9(a) Claws of digits free, arising from the upper surface of the digital expansion well within the border of the expansion (Fig. 23.2I) 10

(b) Claws of digits arising from the edge of the digital expansion (Fig. 23.3C) 11

10(a) Inner toe of each foot clawless (Pl. 4.6) . . . . . *Gehyra*

(b) Inner toe of each foot clawed. . . . . *Hemidactylus*

11(a) Claws of digits small, sessile and retractile in the distal median groove (Fig. 23.3C) (Pl. 4.3). . *Pseudothecadactylus*[1]

(b) Claws of digits large, not retractile in a distal median groove (Fig. 23.3D) . . . . . *Lepidodactylus*

12(a) Postmentals greatly enlarged (Fig. 23.3E); tail long and slender, without large spines 13

(b) Postmentals and adjacent gulars subequal (Fig. 23.3F); tail swollen, or broad and flattened, or covered in large spines. 15

13(a) Claw between three scales (Fig. 23.3G); two rows of lateral scales on digits (Fig. 23.3H) . . . . . *Heteronotia*

(b) Claw between two scales, the lower deeply notched (Fig. 23.3I); three rows of lateral scales on digits (Fig. 23.3J) 14

14(a) A lateral skin fold from axilla to groin . . . . . *Cyrtodactylus*

(b) No lateral skin fold from axilla to groin (Pl. 4.2) . . . . *Nactus*

15(a) Claw between two or three scales, body not laterally compressed 16

(b) Claw between five scales (Fig. 23.3K); body laterally compressed . . . . . *Carphodactylus*

16(a) Claw between two scales, the lower deeply notched; digits compressed with three or more rows of lateral scales; tail long, with large spines, or strongly depressed, leaf-shaped, and more than twice as broad as thick (Pl. 4.7, 4.8) . . . . . *Phyllurus*

(b) Claw typically between two scales, but lower scale may be deeply grooved or even divided; digits with two rows of lateral scales; tail without spines, less than twice as broad as thick . . . . . *Underwoodisaurus*[2]

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1 sometimes regarded as a synonym of the otherwise New Caledonian genus *Rhacodactylus*

2 sometimes treated as a synonym of *Nephrurus*

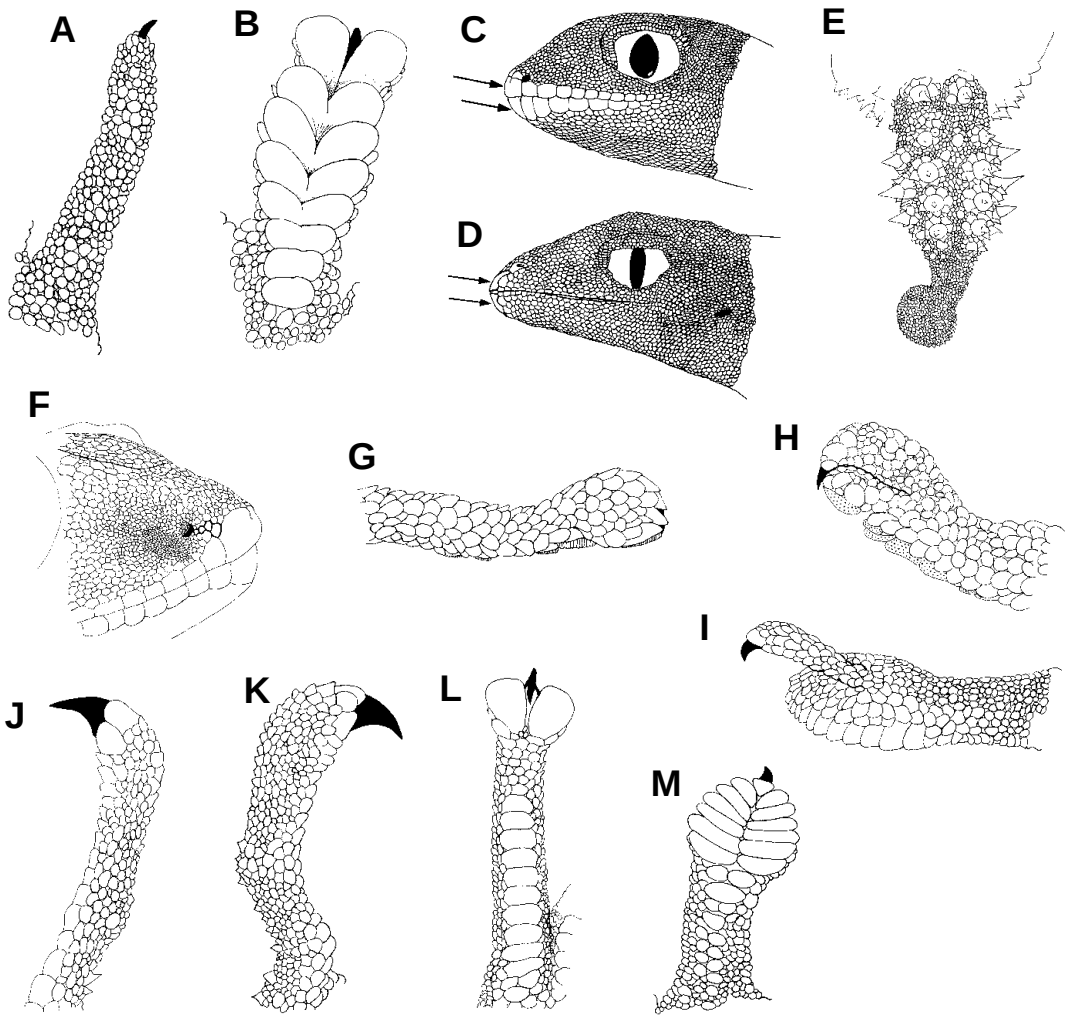

Figure 23.2 Key characters for genera of the family Gekkonidae. Pertinent features of elements **A–M** are noted in the key above. [H.G. Cogger]

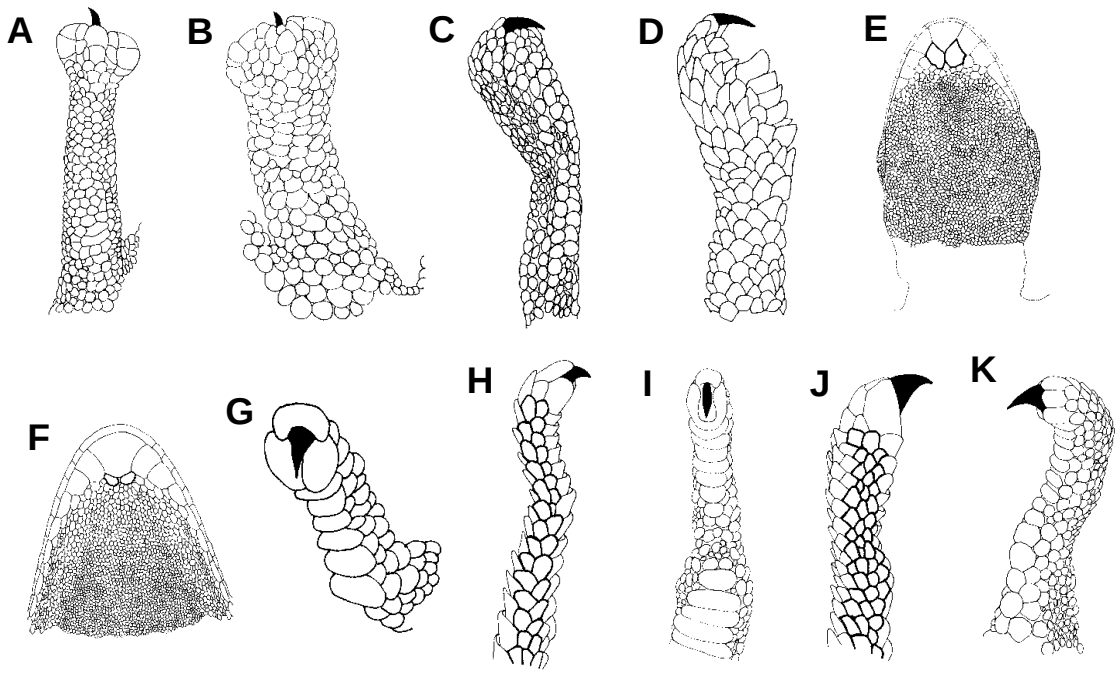

Figure 23.3 Key characters for genera of the family Gekkonidae. Pertinent features of elements **A–K** are noted in the key above. [H.G. Cogger]

Key to the genera of family Pygopodidae

1(a) Head covered with enlarged, symmetrical shields (Fig. 23.4A) 2

(b) Head covered with small, irregular shields (Fig. 23.4B) (Pl. 4.10) . . . . . *Lialis*

2(a) Ventral scales smooth 3

(b) Ventral scales keeled . . . . . *Pletholax*

3(a) Preanal pores present (Fig. 23.4C) 4

(b) Preanal pores absent 5

4(a) Eight or more preanal pores (Pl. 4.12). . . . . *Pygopus*

(b) Four preanal pores . . . . . *Paradelma*

5(a) Parietal scales present (Fig. 23.4D) 6

(b) Parietal scales absent (Fig. 23.4E) (Pl. 4.11) . . . . . *Aprasia*

6(a) Anterior nasals in contact (Fig. 23.4F), or fewer than 20 mid-body scale rows 7

(b) Anterior pair of nasals separated by rostral (Fig. 23.4G), and 20 mid-body scale rows . . . . . *Aclys*

7(a) External ear-opening present and obvious; more than eight scales along a line across the top of the head joining the angle of the mouth on each side (Fig. 23.4H) (Pl. 4.9) . . . . . *Delma*

(b) External ear-opening very small and hidden by overlying temporal scales; fewer than eight scales along a line across the top of the head joining the angle of the mouth on each side (Fig. 23.4I) . . . . . *Ophidiocephalus*

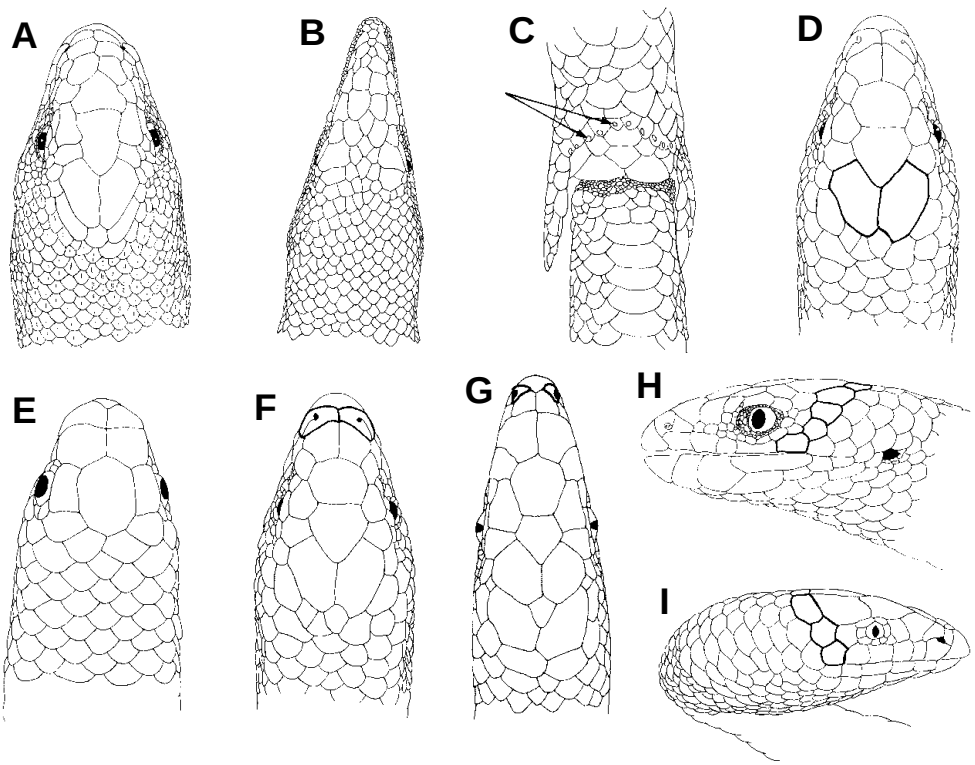

Figure 23.4 Key characters for genera of the family Pygopodidae. Pertinent features of elements **A–I** are noted in the key above. [H.G. Cogger]

Key to the genera of family Agamidae

1(a) Body without very large conical spines or a spiny nuchal hump 2

(b) Body covered above with large conical spines, each much larger than the eye; nape with a large spiny hump (Fig. 23.5A) (Pl. 5.6) . . . . . *Moloch*

2(a) No large, loose, erectile fold of skin around the neck 3

(b) A large, loose, erectile fold of skin, or 'frill', almost completely encircling the neck (Fig. 23.5B) (Pl. 5.9) . . . . . *Chlamydosaurus*

3(a) Tail shorter than head+body (snout–vent length) . . . . . *Cryptagama*

(b) Tail longer than head+body (snout–vent length) 4

4(a) Femoral and/or preanal pores absent 5

(b) Femoral and/or preanal pores present (Fig. 23.5C), at least in males 6

5(a) Transverse gular fold absent; tail about one and one quarter times as long as body; tip of tail rounded, not tapering to a point . . . . . *Chelosania*

(b) Transverse gular fold present (Fig. 23.5D); tail at least twice as long as head and body; tip of tail tapering to a point . . . . . *Hypsilurus*

6(a) Tail at most slightly laterally compressed, without a strongly differentiated dorsal keel 7

(b) Tail strongly compressed with a strongly differentiated dorsal keel (Pl. 5.3). . . . . *Physignathus*

7(a) Nil to two femoral pores present on either side 8

(b) Three or more femoral pores on either side 9

8(a) Femoral pores present or absent; keeled scales of snout irregularly aligned; tail tapers to a point (Pl. 5.5) *Diporiphora*

(b) Femoral pores absent; a median row of slightly enlarged keeled scales on the snout; tail ends abruptly, without a long taper . . . . . *Caimanops*

9(a) Nuchal crest and/or series of enlarged, keeled vertebral scales (Fig. 23.5E) present or absent; if latter, present along at least anterior two-thirds of body; enlarged, strongly keeled or spinose scales are present elsewhere on dorsum 10

(b) A distinct nuchal crest present (Fig. 23.5J), continuous with a series of enlarged, keeled scales forming a distinct vertebral series along at least the anterior two-thirds of the body; enlarged dorsal scales (excluding vertebrals) never strongly keeled or spinose (Fig. 23.5F) (Pl. 5.2) . . . . . *Lophognathus*

10(a) Spinose scales on sides of base of tail present or absent, but in a single linear row (Fig. 23.5H) if present. 11

(b) Sides of base of tail with a series of irregularly scattered spinose scales (Fig. 23.5I) (Pl. 5.8) . . . . . *Pogona*

11(a) No row of enlarged scales from below eye to above ear (Fig. 23.5K); dorsal scales of body heterogeneous, with distinctive vertebral and paravertebral rows of enlarged, keeled or spinose scales 12

(b) A row of enlarged scales from below the eye to above the ear (Fig. 23.5L); dorsal scales of body more or less homogeneous with at most a few slightly enlarged scattered tubercles . . . . . *Ctenophorus*

12(a) Tympanum exposed, the external ear-opening prominent (Fig. 23.5M); no enlarged spinose scales along each side of the base of the tail (Fig. 23.5H) . . . . . *Amphibolurus*

(b) External ear-opening either absent (Fig. 23.5N), with the tympanic region covered by skin, or, if present, a series of enlarged spinose scales along each side of the base of the tail (Fig. 23.5G) (Pl. 5.1) . . . . . *Tympanocryptis*

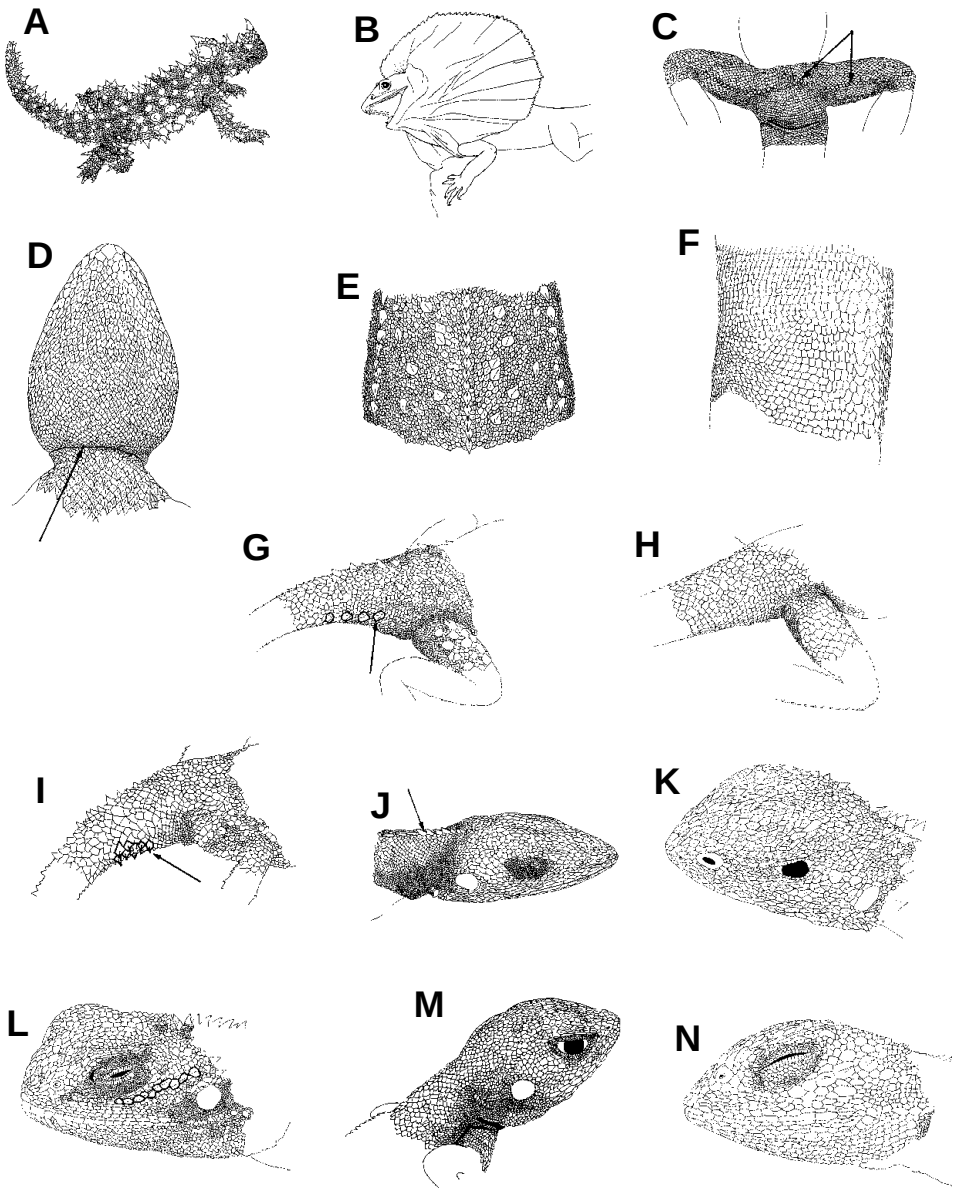

Figure 23.5 Key characters for genera of the family Agamidae. Pertinent features of elements **A–N** are noted in the adjacent key and above.
[H.G. Cogger]

Key to the genera of family Scincidae

1(a) Parietal shields (if unfragmented) nowhere in contact, being separated behind by the interparietal (Fig. 23.6A) 2

(b) Parietal shields in contact behind the interparietal (Fig. 23.6B) 5

2(a) Third and fourth toes subequal or the third slightly longer than the fourth (Fig. 23.6C) 3

(b) Fourth toe markedly longer than the third (Fig. 23.6D) (Pl. 6.5) . . . . . *Egernia*

3(a) Tail short, at most about 60% of snout–vent length 4

(b) Tail long, from nearly as long as to longer than snout–vent length . . . . . *Cyclodomorphus*

4(a) Tail moderate to long, tapering (Fig. 23.6E); dorsal scales moderate, smooth; head shields smooth, entire, symmetrical (Fig. 23.6F); subdigital lamellae undivided (Fig. 23.6G) (Pl. 6.3, 6.4) . . . . . *Tiliqua*

(b) Tail short, depressed, blunt-ended (Fig. 23.6H); dorsal scales grossly enlarged, strongly rugose; head shields broken up, only vaguely symmetrical (Fig. 23.6I); subdigital lamellae divided, at least basally (Fig. 23.6J) (Pl. 6.1, 6.2) . . . . . *Trachydosaurus*

5(a) Lower eyelid with a transparent disc and either movable (Fig. 23.7A) or fused (Fig. 23.7B) to form a permanent spectacle. 6

(b) Lower eyelid movable, scaly (Fig. 23.7C) or with an opaque disc. 21

6(a) Lower eyelid movable, or partly (open slit along upper edge) or totally fused to form a permanent spectacle; if the lower eyelid is fused the prefrontals are small and widely separated (Fig. 23.7D) or absent (Fig. 23.7E) 7

(b) Lower eyelid fused to form a permanent spectacle; prefrontals large (Fig. 23.7F), in contact or narrowly separated 17

7(a) Supranasals present, or nasals divided (Fig. 23.7G) 8

(b) Supranasals absent and nasals undivided (Fig. 23.7H) 9

8(a) Frontoparietals paired (Fig. 23.7I) or single (Fig. 23.7J); fewer than 30 lamellae under fourth toe; anterior auricular lobules present (Fig. 23.7K) . . . . . *Pseudemoia*

(b) Frontoparietals united to form a single shield (Fig. 23.7J); more than 30 lamellae under fourth toe; anterior auricular lobules absent (Fig. 23.7L) *Emoia*

9(a) Limbs well developed, meeting or overlapping when adpressed (Fig. 23.7M), or else separated by one or two scale lengths; ear-opening prominent 10

(b) Limbs short, separated by at least several scale lengths when adpressed (Fig. 23.7N); ear-opening small to minute, or hidden 14

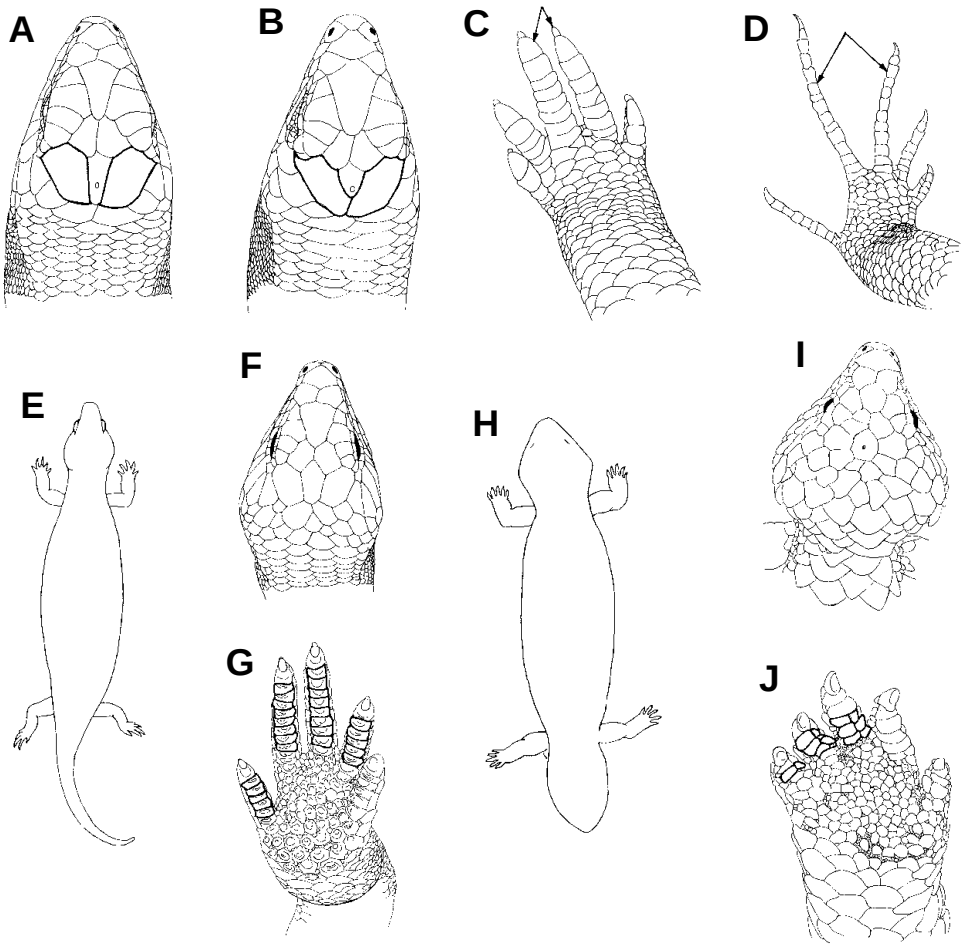

Figure 23.6 Key characters for genera of the family Scincidae. Pertinent features of elements **A–J** are noted in the keys above. [H.G. Cogger]

10(a) Fingers four; ear-opening with one or more obvious lobules (Fig. 23.7K) 11

(b) Fingers five, or if four, ear-opening without lobules 12

11(a) Ten or more scales along the top of the fourth toe (Fig. 23.7O) (Pl. 6.7) . . . . . *Carlia*

(b) Fewer than ten scales along the top of the fourth toe (Fig. 23.7P) . . . . . *Lygisaurus*

12(a) Nasals usually widely separated (Fig. 23.7Q) 13

(b) Nasals usually narrowly separated (Fig. 23.7R) . *Pseudemoia*

13(a) Frontoparietals fused (Fig. 23.7J) . . . . . *Lampropholis*

(b) Frontoparietals paired (Fig. 23.7I). . . . . *Saproscincus*

14(a) Nasals small to moderate, usually separated (Fig. 23.7Q) . 15

(b) Nasals enlarged, usually in contact medially (Fig. 23.7S) (Pl. 6.12) . . . . . *Lerista*

15(a) Forelimbs with two to five fingers, but if four fingers present then hindlimb with at most four toes 16

(b) Forelimbs with four fingers and hindlimbs with five toes. . . . . *Eroticoscincus*

16(a) Two to five fingers, two to five toes; ear-opening hidden in specimens with five fingers and five toes . . . . . *Hemiergis*

(b) Five fingers and five toes; ear-opening minute, punctiform, but distinct . . . . . *Nannoscincus*

17(a) Fingers and toes five 18

(b) Fingers four, toes five . . . . . *Menetia*

18(a) Frontoparietal single (Fig. 23.7J) or paired (Fig. 23.7I), but always distinct from the interparietal (Fig.23.7T); ear-opening absent, or smaller than eye if present. 19

(b) Frontoparietal and interparietal fused to form a single shield (Fig. 23.7U); ear-opening approximately same size as eye. 20

19(a) Frontoparietals paired (Fig.23.7I) . . . . . *Proablepharus*

(b) Frontoparietals fused to form a single shield (Fig. 23.7J). . . . . *Notoscincus*

20(a) Upper eyelid with three or four scales much larger than granules surrounding remainder of eye (Fig. 23.7V); frontal and prefrontals subequal (Fig. 23.7W) (Pl. 6.8) . . . . . *Cryptoblepharus*

(b) Eye more or less surrounded by a circle of uniformly small granules (Fig. 23.7X); frontal much larger than prefrontals (Fig. 23.8A) (Pl. 6.10) . . . . . *Morethia*

21(a) Supranasals absent and nasals undivided (Fig. 23.7H) 22

(b) Supranasals present (Fig.23.7G), although sometimes partially fused with nasals . . . . . *Eugongylus*

22(a) Dorsal scales moderate, smooth or with a faint median keel 23

(b) Dorsal scales very small, each with a sharp keel. . . . . *Gnypetoscincus*

23(a) Five fingers and toes five. 24

(b) Fewer than five fingers and toes 28

24(a) Ear lobules absent (Fig. 23.7L); pattern usually transversely aligned or of irregularly scattered spots and variegations . . 25

(b) Conspicuous ear lobules present (Fig 23.7K); pattern usually of dorsal and/or lateral longitudinal stripes (Pl. 6.11) *Ctenotus*

25(a) Dorsal and upper caudal scales smooth. 26

(b) Scales on the rump and the base of the tail, and sometimes on the remaining dorsals, with distinct median ‘humps’ or low keels forming a series of continuous longitudinal ridges . . . . *Eremiascincus*

26(a) Hindlimb short to moderate, its length contained at least 2.5 times in the snout–vent length. 27

(b) Hindlimb long, its length contained less than 2.5 times in the snout–vent length. . . . . *Eulamprus*

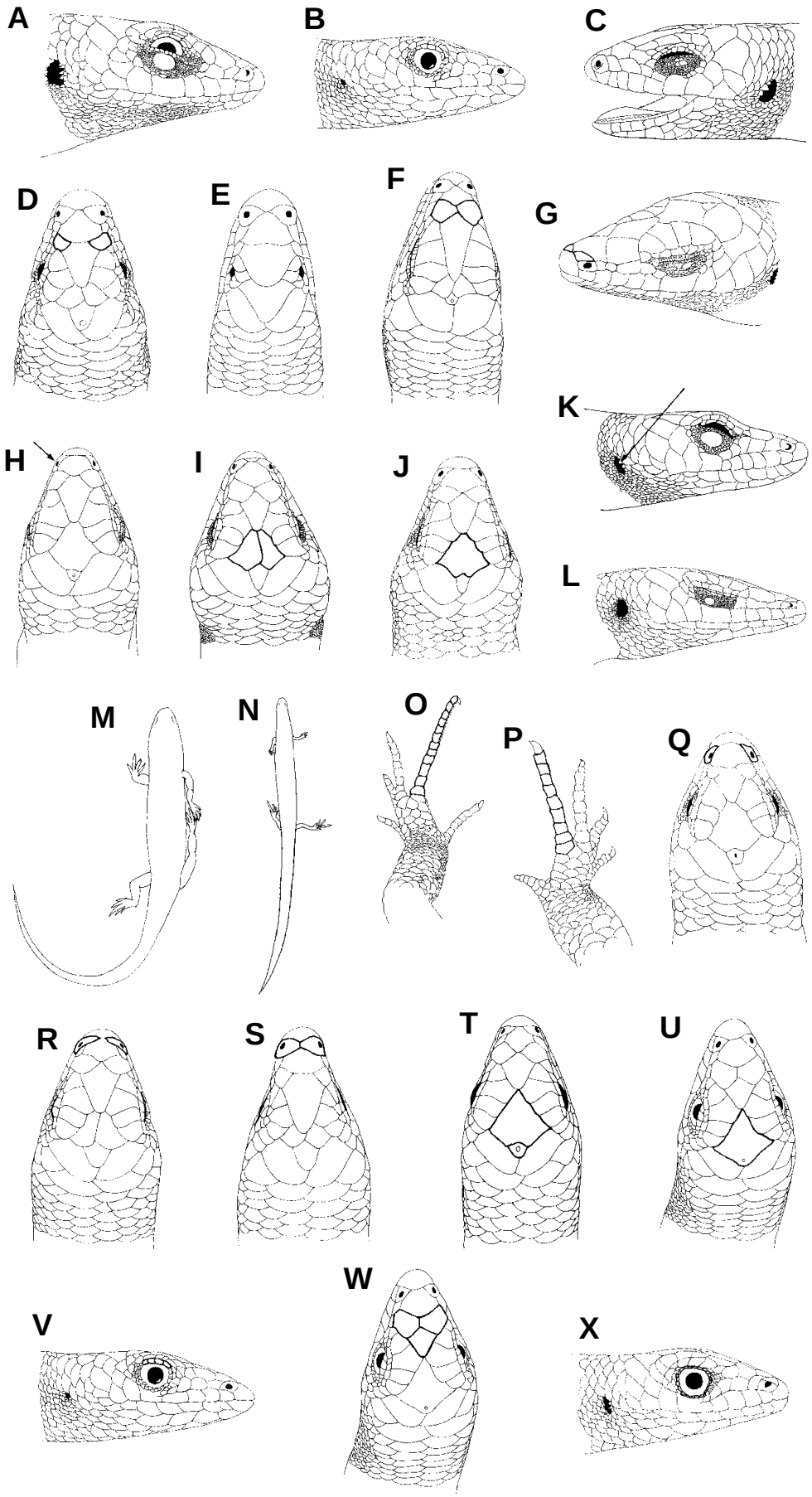

Figure 23.7 Key characters for genera of the family Scincidae. Pertinent features of elements **A–X** are noted in keys above and on the adjacent page. [H.G. Cogger]

27(a) Fourth toe lamellae fewer than 16; a single loreal scale (Fig. 23.8B) . . . . . *Calyptotis*

(b) Fourth toe lamellae usually more than 16 but, if fewer, then two or more loreal scales are present (Fig. 23.8C) (Pl. 6.8) . . . . . *Glaphyromorphus*

28(a) If limbs tridactyl, scales in 23 or more rows 29

(b) Limbs tridactyl; mid-body scales in fewer than 23 rows. . . . . *Saiphos*

29(a) With or without limbs; limbed forms with only one or two digits on each limb; limbless forms without prefrontals (Fig. 23.7E) or with prefrontals at most moderately developed and widely separated (Fig. 23.7D); five or six supralabials 30

(b) With or without limbs; limbed forms with three digits on each limb; limbless forms with large prefrontals, contacting (Fig. 23.7F) or only narrowly separated; 6 supralabials . . . . . *Coeranoscincus*

30(a) Either six supralabials and two to four supraoculars or five supralabials and two supraoculars (Pl. 6.13) . . . . *Anomalopus*

(b) Five supralabials and three supraoculars . . . . . *Ophioscincus*

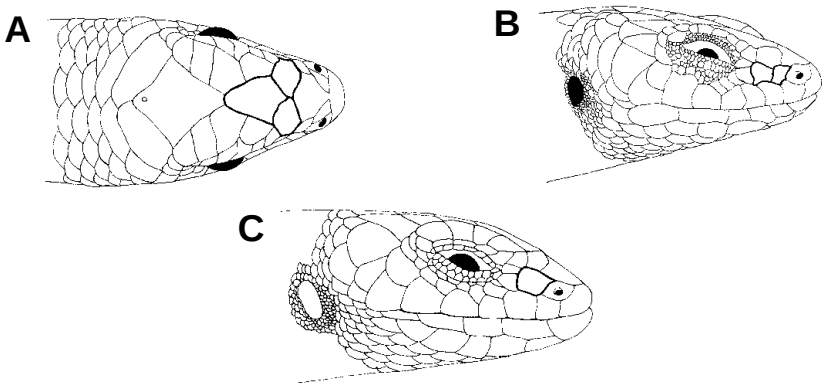

Figure 23.8 Key characters of the genera of the family Scincidae. Pertinent features of elements **A-C** are noted in the key above [H.G. Cogger]

CLASSIFICATION OF THE SERPENTES

Currently about 10 families of extant snakes are recognised (Savage 1992), and these are considered to be derived from three separate evolutionary stocks represented by the infraorders Scolecophidia, Henophidia and Caenophidia (Parker & Grandison 1977).

The Scolecophidia includes one Australian family, the blind or worm snakes (Typhlopidae). Only the pythons (Boidae) represent the Henophidia in Australian family. The remaining Australian snake families, the file snakes (Acrochordidae), colubrids (Colubridae) and front-fixed fang snakes, here grouped as ‘Elapidae’, are included in the Caenophidia. In this volume, the major groups within the ‘Elapidae’ are themselves given family status—the terrestrial elapids (Elapidae), the sea kraits (Laticaudidae) and sea snakes (Hydrophiidae). These changing classifications are discussed under each of these families. These seven Australian families may be distinguished using the following key.

Key to the families of suborder Serpentes

1(a) Tail more or less cylindrical, not flattened and paddle-shaped (Fig. 23.9A) 2

(b) Tail strongly vertically compressed and paddle-shaped (Fig. 23.9B) 6

2(b) No enlarged ventral scales, the scales on the belly more or less equal in size to those on the back and sides 3

(b) A single row of enlarged ventral scales which are at least three times as wide as those on the back and sides 4

3(a) More than 80 mid-body scale rows; body scales rough, strongly keeled; eyes well-developed (File Snakes) . . . . . Acrochordidae

(b) Fewer than 40 mid-body scale rows; body scales smooth; eyes vestigial, consisting of dark spots beneath scales of head (Blind Snakes) (Pl. 7.2) . . . . . Typhlopidae[1]

4(a) Fewer than 30 mid-body scale rows 5

(b) More than 30 mid-body scale rows (Pythons). . . . . Boidae

5(a) One or more loreal scales present (Fig. 23.9C), or, if absent, 23 or more mid-body scale rows and a divided anal shield (Colubrid Snakes) . . . . . Colubridae

(b) No loreal scales (Fig. 23.9D); anal single if mid-body scales are in 23 or more rows (Elapid Snakes). . . . . Elapidae

6(a) Ventral scales large, at least three times as wide as the adjacent body scales; nasals separated by internasals (Fig. 23.9F) (sea kraits) (Pl. 7.11, 7.12). . . . . Laticaudidae[2]

(b) Ventral scales small or large; if large (two to three times as wide as the adjacent body scales) then the nasals are in contact (Fig. 23.9G) (sea snakes) . . . . . Hydrophiidae

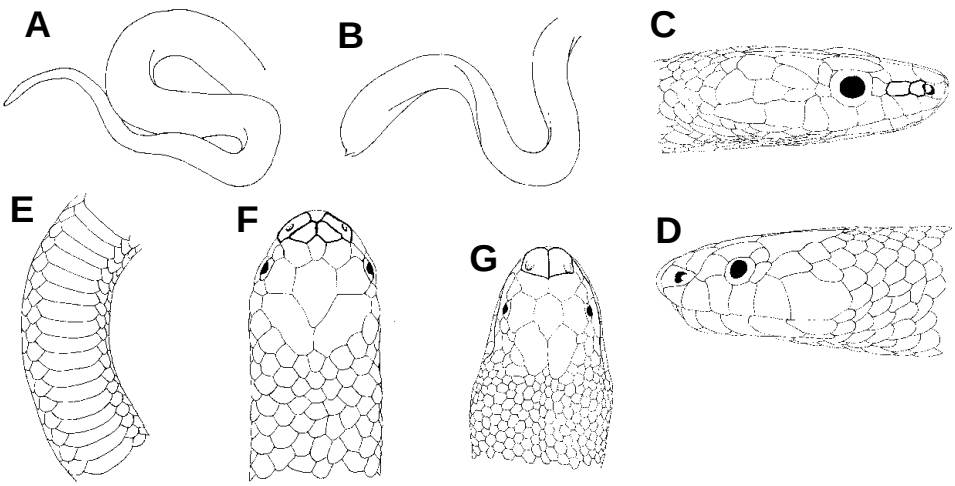

Figure 23.9 Key characters of the families of the suborder Serpentes. Pertinent features of elements **A**-**G** are noted in the key on the adjacent page and above. [H.G. Cogger]

1 Single genus *Rhamphotyphlops*

2 Single genus *Laticauda*

Key to the genera of family Boidae

1(a) Mental groove bordered by scales which are more or less equal in size to the other gular scales (Fig. 23.10A) 2

(b) Mental groove bordered by granular scales (Fig. 23.10B) (Pl. 7.3, 7.4) . . . . . *Chondropython*

2(a) Premaxilla with teeth (Fig. 23.10C) 3

(b) Premaxilla without teeth (Pl. 7.1) . . . . . *Aspidites*

3(a) Scales, at least on rear of body, with one or two apical pits (Pl. 7.5) . . . . . *Liasis*

(b) Most scales, including those on rear of body, without apical pits . . . . . *Morelia*

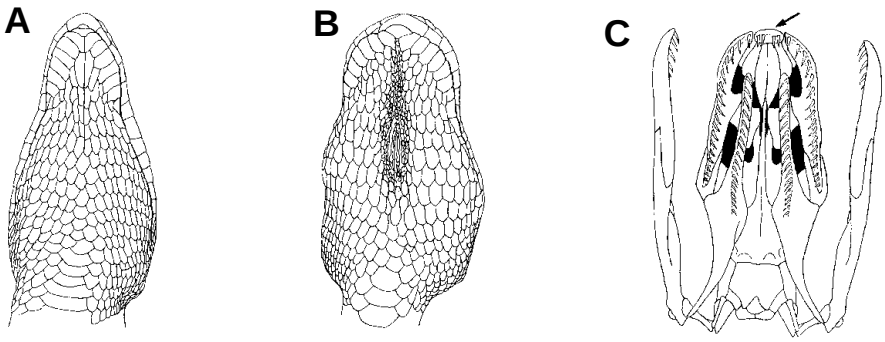

Figure 23.10 Key characters of the genera of the family Boidae. Pertinent features of elements **A**-**C** are noted in the key above. [H.G. Cogger]

Key to the genera of family Colubridae

1(a) Scales strongly keeled 2

(b) Scales smooth or feebly keeled 3

2(a) 23 or more mid-body scale rows . . . . . *Cerberus*

(b) 15 or 17 mid-body scale rows . . . . . *Tropidonophis*

3(a) More than 15 mid-body scale rows 4

(b) 13 (occasionally 15) mid-body scale rows . . . . *Dendrelaphis*

4(a) Anal scale single (Fig. 23.11A) 5

(b) Anal scale divided (Fig. 23.11B) 6

5(a) 17 mid-body scale rows . . . . . *Stegonotus*

(b) 19 or more mid-body scale rows (Pl. 8.1) . . . . . *Boiga*

6(a) Nasals not in contact (Fig. 23.11C) 7

(b) Nasals in contact (Fig. 23.11D) . . . . . *Enhydris*

7(a) Loreal scale (Fig. 23.11E) present; scales feebly keeled (Pl. 8.2) . . . . . *Myron*

(b) Loreal scale absent (Fig. 23.11F); scales smooth (Pl. 8.3) . . . . . *Fordonia*

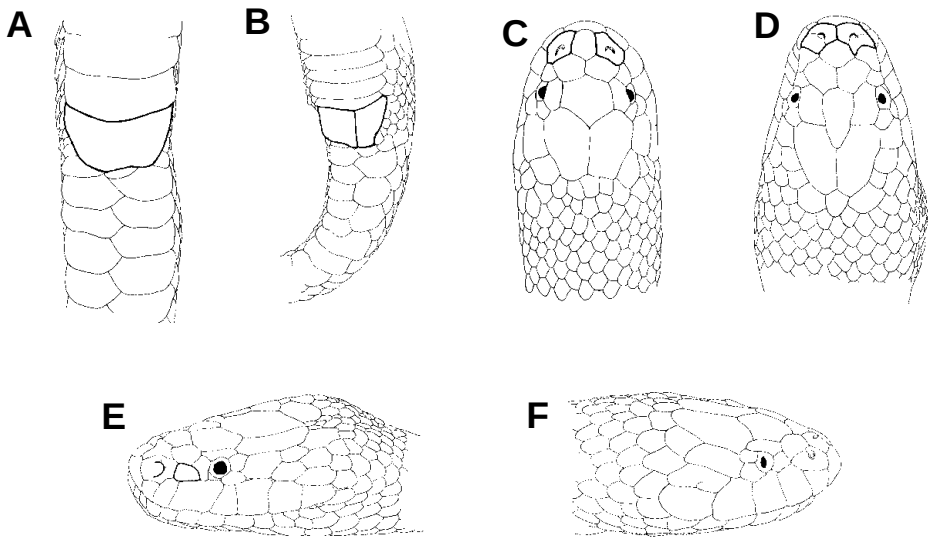

Figure 23.11 Key characters for genera of the family Colubridae. Pertinent features of elements **A–F** are noted in the key above and on the previous page. [H.G. Cogger]

Key to the genera of family Elapidae

1(a) No suboculars (Fig. 23.12A); no specialised curved soft spine on the tip of the tail (Fig. 23.12B) 2

(b) Suboculars (Fig. 23.12C); a curved soft spine on the tip of the tail (Fig. 23.12D) (Pl. 8.9) . . . . . *Acanthophis*

2(a) All subcaudals normally undivided 3

(b) At least some subcaudals divided 13

3(a) Dorsal scales smooth 4

(b) Dorsal scales strongly keeled . . . . . *Tropidechis*

4(a) Anal scale normally single (Fig. 23.12E) 5

(b) Anal scale normally divided (Fig. 23.12F) . . . . . *Hemiaspis*

5(a) Scales in 13–21 rows at mid-body; if in 19 or more rows, ventrals more than 140 or head not jet-black above contrasting with brown body colour 6

(b) Scales in 19 rows at mid-body; ventrals fewer than 140 or head jet-black above contrasting with paler brown body colouring . . . . . *Echiopsis*

6(a) Frontal shield longer than broad; where frontal is only slightly longer than broad, lower anterior temporal shield is shorter than frontal (Fig. 23.12G) 7

(b) Frontal shield not, or scarcely, longer than broad; lower anterior temporal about as long as or longer than the frontal (Fig. 23.12H) (Pl. 8.7) . . . . . *Notechis*

7(a) Scales in 15–21 rows at mid-body; ventrals not keeled or notched; if 19 or more, ventrals fewer than 190 8

(b) Scales in 19–21 rows at mid-body; ventrals keeled or notched; ventrals 190 or more . . . . . *Hoplocephalus*

8(a) Three or more solid maxillary teeth following the fang (Fig. 23.13A); belly without a series of crescent-shaped, transverse, black bars. 9

(b) No maxillary teeth following the fang (Fig. 23.13B); belly with a median series of crescent-shaped, transverse, black bars (Fig. 23.13C) . . . . . *Elapognathus*

9(a) Frontal less than one and a half times as broad as the supraocular (Fig. 23.13D) 10

(b) Frontal more than one and a half times as broad as the supraocular (Fig. 23.13E) 11

10(a) Lateral scales adjoining ventrals not noticeably enlarged (Fig. 23.13F) . . . . . *Drysdalia*

(b) Lateral scales adjoining ventrals noticeably enlarged (Fig. 23.13G) . . . . . *Austrelaps*

11(a) Scales in 15–21 rows at mid-body; upper labials uniformly pale, without darker bars 12

(b) Scales in 17 rows at mid-body; upper labials strongly barred. . . . . *Denisonia*

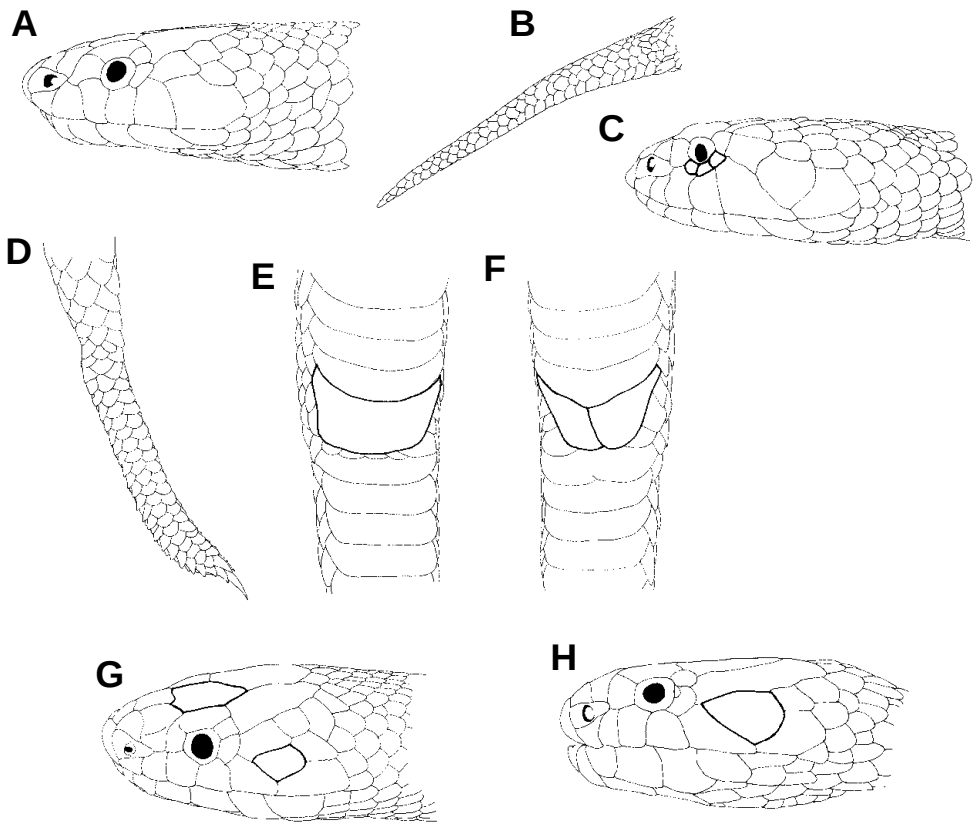

Figure 23.12 Key characters for genera of the family Elapidae. Pertinent features of elements **A–H** are noted in the key above and on the adjacent page. [H.G. Cogger]

12(a) Scales in 15 rows at mid-body; head and body usually uniformly coloured above, or sides of body and face a paler pink in one species (*R. nigrostriatus*) . . . . .*Rhinoplocephalus*

(b) Scales in 15–21 rows at mid-body; head with a dark, contrasting hood or with strongly contrasting darker spots and streaks . . . . . *Suta*

13(a) Anal scale normally divided; 21, or usually fewer, mid-body scale rows. 14

(b) Anal scale normally single; 21 or more mid-body scale rows. . . . . *Oxyuranus*

14(a) Subcaudals 35 or more. 15

(b) Subcaudals fewer than 35 19

15(a) Nasal and preocular scales in contact (Fig. 23.13H) 16

(b) Nasal and preocular scales widely separated (Fig. 23.13I) (Pl. 8.11) . . . . . *Furina*

16(a) Scales in 17 or more rows at mid-body 17

(b) Scales in 15 rows at mid-body. 18

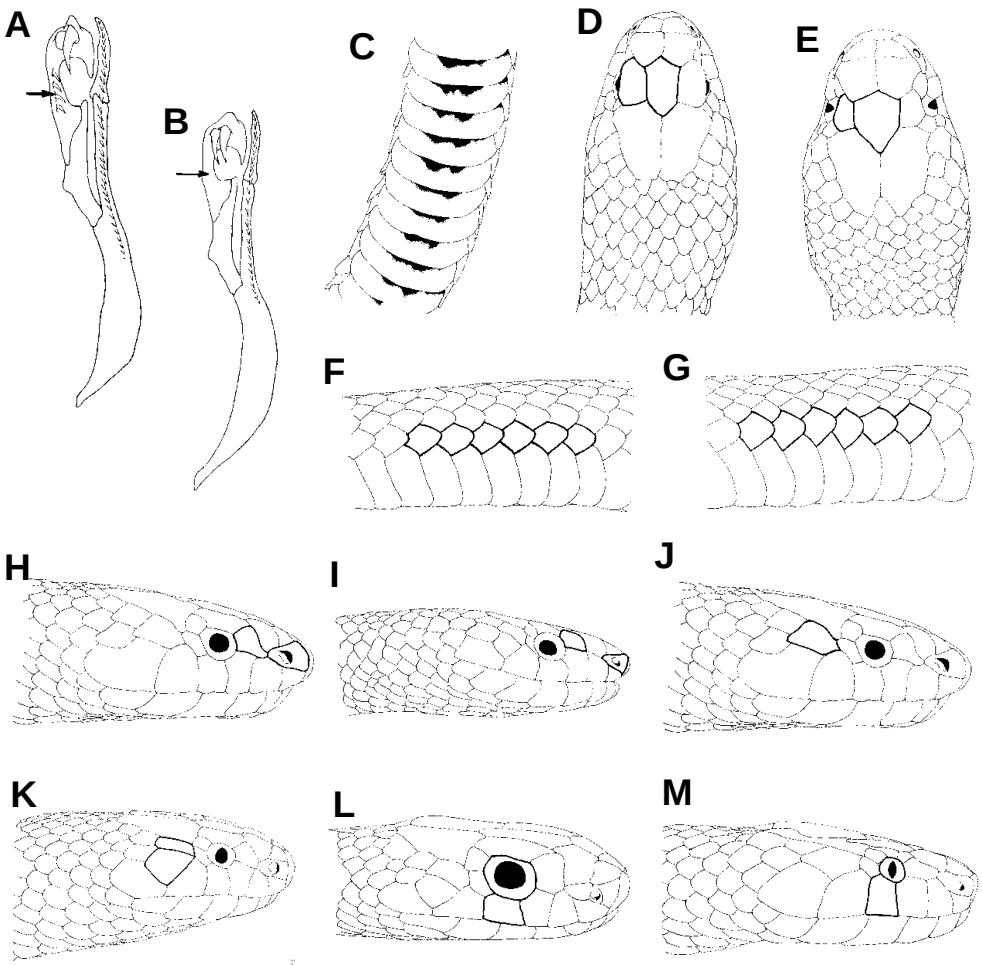

Figure 23.13 Key characters for genera of the family Elapidae. Pertinent features of elements **A–M** are noted in the key above and overleaf.
[H.G. Cogger]

17(a) Nearly always a single temporal scale between the fifth upper labial and the parietal scale (Fig. 23.13J); usually all subcaudals divided or at most a few anterior ones undivided (Pl. 8.8) . . . . . *Pseudonaja*

(b) Nearly always two temporal scales between the fifth upper labial and the parietal scale (Fig. 23.13K); usually at least anterior 20% of subcaudals undivided, remainder divided . . . . . *Pseudechis*

18(a) Diameter of eye markedly greater than its distance from the mouth (Fig. 23.13L) (Pl. 8.6, 8.12) . . . . . *Demansia*

(b) Diameter of eye about equal to or less than its distance from the mouth (Fig. 23.13M) . . . . . *Cacophis*

19(a) Colour pattern not consisting of alternate black and white bands 20

(b) Colour pattern consisting of black and white bands from head to tail (Pl. 8.4) . . . . . *Vermicella*

20(a) Body with or without cross-bands; if not banded, the ventral surface is immaculate white or cream (Pl. 8.5) . . . *Simoselaps*

(b) Body without cross-bands; ventral surface coloured and/or patterned . . . . . *Cacophis*

Key to the genera of family Hydrophiidae

1(a) Ventrals large, at least three times as wide as the adjacent body scales (Fig. 23.14A) 2

(b) Ventrals small, at most scarcely more than twice as wide as the adjacent body scales (Fig. 23.14B) 5

2(a) Six or more supralabials (Fig. 23.14C) 3

(b) Three supralabials (Fig. 23.14D). . . . . *Emydocephalus*

3(a) Posterior chin shields not reduced and separated by a mental groove (Fig. 23.14E); portion of rostral scale bearing median valve-like fold continuous with remainder of scale (Fig. 23.14F) 4

(b) Posterior chin shields usually reduced and separated by one or more scales (Fig. 23.14G) and/or portion of rostral scale bearing median valve-like fold sometimes separated from remainder of scale by a suture (Fig. 23.14H) (Pl. 7.7, 7.8) . . . . . *Aipysurus*

4(a) No preocular scale (Fig. 23.14I); rostral with a median lobe at its anterior-most end, this lobe fitting into a median notch in the mental and completely dividing the lingual fossa of the rostral into separate left and right grooves (Fig. 23.14F) . . . . . *Hydrelaps*

(b) Preocular scale present (Fig. 23.14J); rostral with a median sharp fold located within the mouth, behind the median and undivided lingual fossa, this fold formed from the posterior edge of the portion of the keratinised scale extending within the lining of the lip (Fig. 23.14K) 11

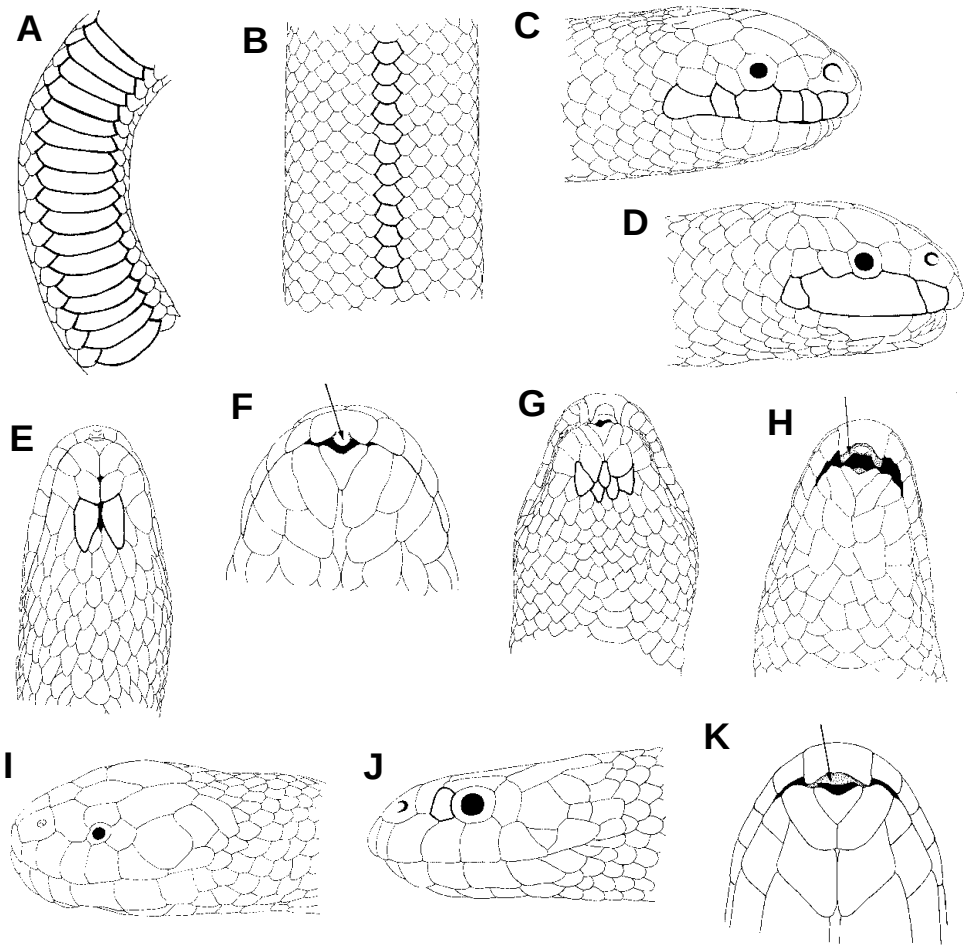

Figure 23.14 Key characters for genera of the family Hydrophiidae. Pertinent features of elements **A–K** are noted in the key above. [H.G. Cogger]

5(a) Head scales enlarged, regular, symmetrical, the supraoculars without projecting tubercles or spines (Fig. 23.15A) 6

(b) Head scales broken up into small, irregular and asymmetrical scales, the supraoculars with projecting tubercles or spines (Fig. 23.15B) . . . . . .*Acalyptophis*

6(a) A distinct mental groove (Fig. 23.15C). 7

(b) No distinct mental groove (Fig. 23.15D). . . . . .*Pelamis*

7(a) Mental normal, triangular, broader than long, and not partially hidden in the shallow mental groove (Fig. 23.15E) 8

(b) Mental narrow, splint- or dagger-shaped, much longer than broad, and partially hidden in the deep mental groove (Fig. 23.15F) . . . . . .*Enhydrina*

8(a) Either fewer than four solid maxillary teeth following the fang (Fig. 23.15G) or, if four or more, anterior chin shields reduced and not, or scarcely, contacting the mental groove, from which they are separated by the elongate first infralabials (Fig. 23.15H) 9

(b) Four or more solid maxillary teeth; anterior chin shield large and mostly bordering the mental groove (Fig. 23.15I) . . . . . .*Hydrophis*

9(a) Ventrals single or divided, but usually distinct posteriorly . 10

(b) Ventrals not distinct posteriorly. . . . . *Lapemis*

10(a) Ventrals, except on throat, divided into pairs of foliform scales which in most specimens form a mid-ventral keel (Fig. 23.15J) (Pl. 8.9, 8.10) . . . . . .*Astrotia*

(b) Ventrals mostly undivided, never foliform and never with a mid-ventral keel (Fig. 23.15K) . . . . . *Disteira*

11(a) Posterior dorsal scales smooth; scales in more than 30 rows at mid-body . . . . . *Parahydrophis*

(b) Posterior dorsal scales with spine-like keels; scales in fewer than 30 rows at mid-body . . . . . *Ephalophis*

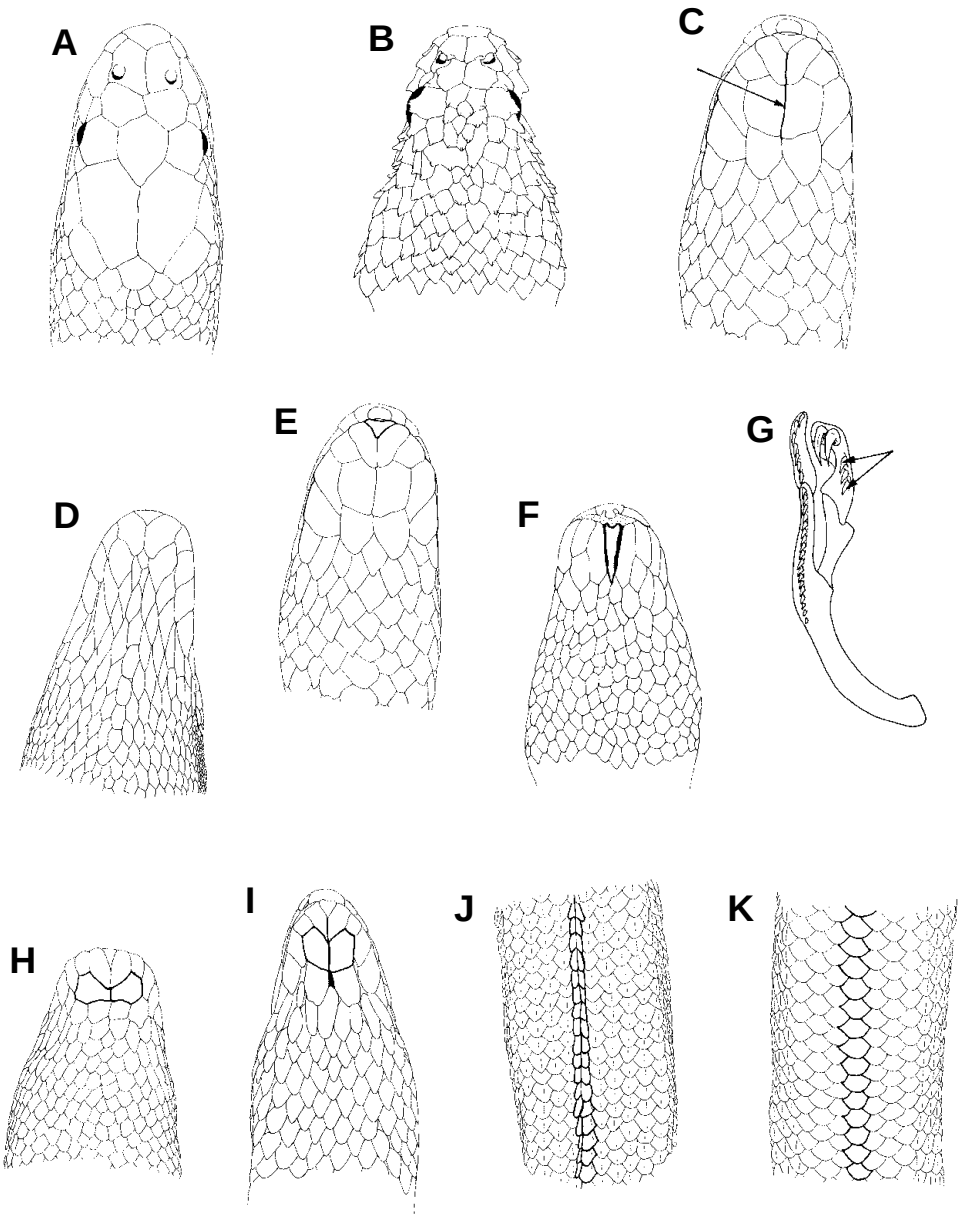

Figure 23.15 Key characters for genera of the family Hydrophiidae. Pertinent features of elements **A–K** are noted in the key below. [H.G. Cogger]