FAUNA
of
AUSTRALIA

28. FAMILY PYGOPODIDAE

Glenn M. Shea

Pl. 4.9. *Delma butleri* (Pygopodidae) is legless; it inhabits *Triodia* clumps in semi-arid and arid habitats in southern Australia; the pale yellow of the belly can brighten rapidly, perhaps in response to stress. [G. Shea]

Pl. 4.10. *Lialis burtonis* (Pygopodidae) is found throughout Australia except in the extreme south-west and south-east; highly variable in colour and pattern; inhabits low vegetation and ground litter; feeds mainly on small lizards.

[J. Wombey]

Pl. 4.11. *Aprasia parapulchella* (Pygopodidae): a little known species found near Canberra and parts of the Riverina, New South Wales.   [J. Wombey]

Pl. 4.12. *Pygopus nigriceps* (Pygopodidae): showing characteristic black head bands; a nocturnal insectivore found throughout Australia, except along the wetter south and south-east coasts and ranges.   [H. Cogger]
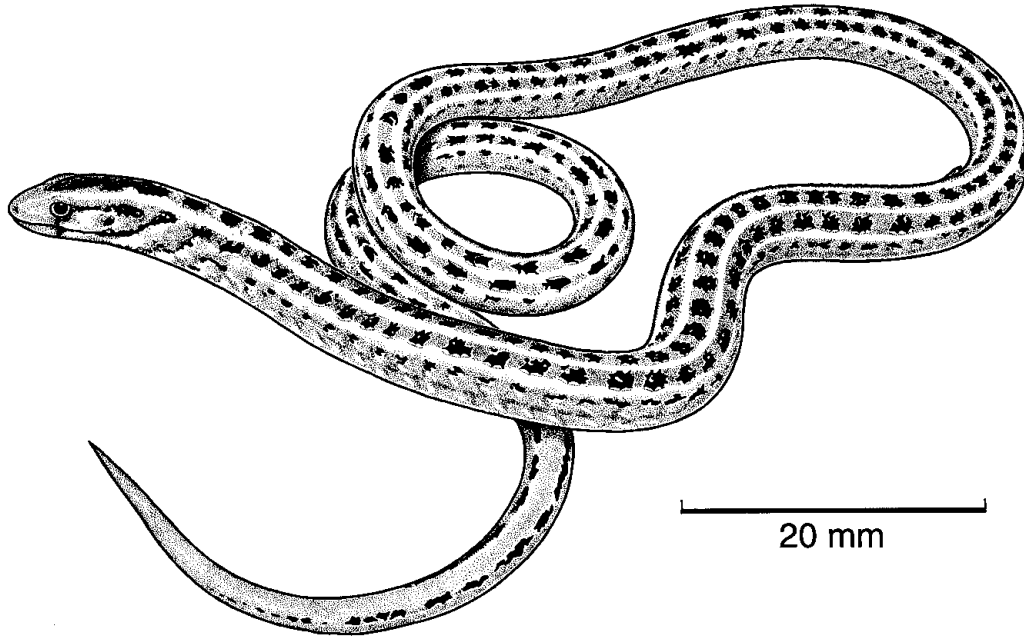
Figure 28.1 *Pygopus lepidopodus*, the most generally primitive pygopodid.
[B. Jantulik]

DEFINITION AND GENERAL DESCRIPTION

The Pygopodidae is a small family of 35 species, placed by most recent authors in eight genera. The family is endemic to Australia and New Guinea. All species are elongate, snake-like lizards (Fig. 28.1, Pls 4.9–4.12), with imbricate, or overlapping, body scales, hind limbs reduced to short scaly flaps without obvious toes (Fig. 28.2), and a tail which varies from slightly shorter to much longer than the body and is capable of being autotomised. There are no external traces of front limbs. The eyes have vertical pupils and are covered by a transparent spectacle.

The premaxilla is single in adults and lacks a median ventral process. The postorbital arch, temporal arch and parietal foramen are absent, and there are no palatine teeth. Osteoderms are also lacking. The vertebrae are procoelous, with a median constriction and prominent subcentral foramina. Post-cloacal bones are present.
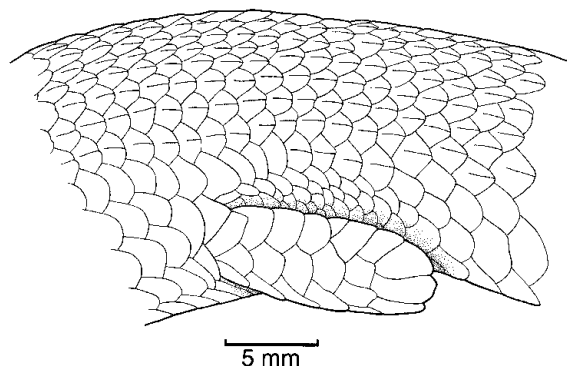

Figure 28.2 Hindlimb flap of *Pygopus lepidopodus*.   [B. Jantulik]

HISTORY OF DISCOVERY

The first pygopodid to be described was *Pygopus lepidopodus*, which Lacépède (1804) named *Bipes lepidopodus* from six specimens collected by the Baudin Expedition of 1800–1804. No precise locality data are given in the description, and only one of the types can now be identified in the Muséum d'Histoire Naturelle, Paris.

The first of three genera and species described by John Gray was *Delma fraseri*, in 1831, probably from a single specimen lacking precise locality data collected by James Hunter. The name was subsequently applied to a species found only in southern Western Australia and South Australia (Kluge 1974). In 1835, Gray described *Lialis burtonis* (Pl. 4.10) from a single specimen collected by Dr Mair from New South Wales (as Nova Cambria Australi). The holotype can no longer be identified in the collection of the Natural History Museum (formerly British Museum of Natural History). In 1839, Gray described *Aprasia pulchella*, again from a single specimen, later stated to be from Western Australia (Gray 1845).

Between 1842 and 1884, a total of 16 new species and subspecies of pygopodids were described, almost all by European workers. Included amongst these was a fifth genus, *Pletholax*, from a single specimen from south-west Australia, collected by J.A.L. Preiss, and now in the National Museum of Natural History, Leiden.

Working on the extensive British Museum material, Boulenger (1884, 1885) placed all of the genera into a single family Pygopodidae. However, he was unable to make sense of the wide variation in colouration within the genera, particularly in *Lialis*, and placed most of the described species into synonymy, leaving six genera and eight species.

Between 1885 and 1914, an additional 12 species and subspecies of pygopodids were described, including *Ophidiocephalus taeniatus*, another monotypic genus. This species was known only from the holotype until its rediscovery by Ehmann & Metcalfe (1978).

In a checklist, Werner (1912) recognised eight genera and 16 species. Kinghorn (1923b, 1924, 1926) revised the family, recognised eight genera and 14 species, and erected the genus *Paradelma* for *Delma orientalis* Günther, 1876.

With the exception of a revision of *Aprasia* by Parker (1956) and a checklist by Wermuth (1965), pygopodid systematics remained almost untouched until Kluge (1974, 1976a) revised the family in two monographs and provided a cladistic analysis of intrafamilial relationships. In the first monograph, he recognised eight genera and thirty species, describing one genus (*Aclys*) and twelve species as new.

Since Kluge's revision, two new species of *Aprasia*, one new subspecies each of *Aclys* and *Pletholax*, and four new species and one subspecies of *Delma* have been described, although one of the *Delma* species has since been synonymised (Storr 1978a, 1979a, 1987; Shea 1987, 1991).

It is important to recognise that with the recent subdivision of *Delma* (1 species: Boulenger 1887; 3 species: Kinghorn 1926; 16 species: Kluge 1974 and subsequent authors), much of the pre-1974 literature on *Delma fraseri* is based on material which was probably misidentified and can now only be identified to genus.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Adult pygopodids range from 63 mm (*Delma torquata*) to 314 mm (*Lialis jicari*) snout-to-vent length, although *Aprasia* species are the shortest in overall length, because their short tails are less than 92% of snout-vent length (Pl. 4.11). In other pygopodids, the tail is long, and may be up to 414% of snout-vent length in *Delma grayii*.

The head may be long and narrow, with snout pointed (*Aclys*, *Lialis*) to short and blunt (most *Aprasia*). Most species have a regular pattern of enlarged head shields (Fig. 28.3), although *Lialis* has small fragmented head shields.

Colour pattern, where present, typically involves stripes or longitudinal rows of spots on the body, which may continue onto the tail, or in a few species of *Delma* and *Pygopus*, be replaced by oblique bars converging distally on the tail dorsum. Several *Aprasia* species have a bright pink tail. Several *Delma* species and *Pygopus nigriceps* have a dark head which may or may not be interrupted by narrow pale bands. In these species, the side of the neck may also bear alternating light and dark bars. The undersurface in most species is white, grey or yellow. *Delma butleri* can change the intensity of the ventral colouration rapidly (Shea 1987b). *Lialis* is particularly variable in colouration, and several different colour patterns are often present at a single locality.

The dark heads of many *Delma* and *Pygopus* species tend to fade with age, while the prominent lateral markings of *Delma impar* develop with age (Greer 1989; Coulson 1990; Storr, Smith & Johnstone 1990; Shea 1991).
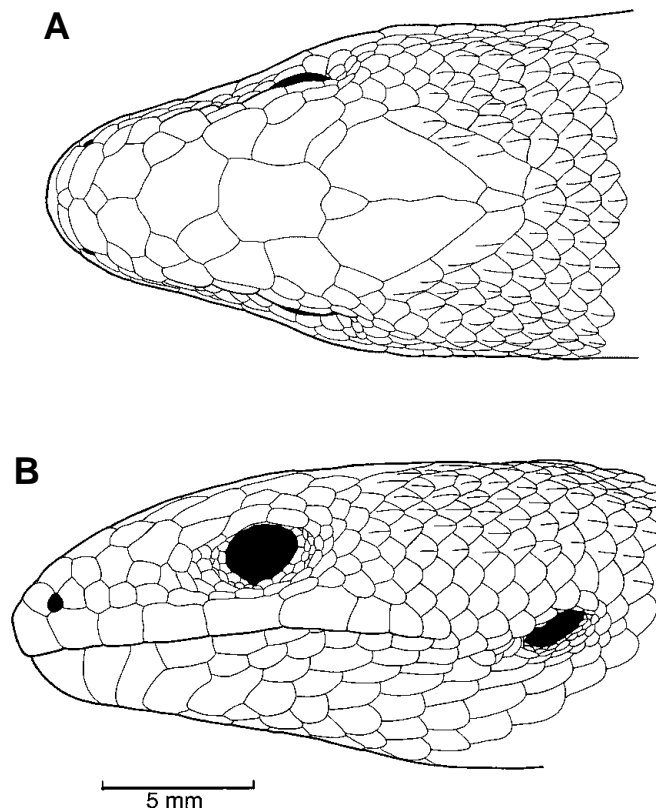

Figure 28.3 Head shields of *Pygopus lepidopodus*. **A**, dorsal view; **B**, lateral view.   [B. Jantulik]

Body Wall

The body bears overlapping scales in a regular pattern of longitudinal rows. The pair of scale rows along the belly are much wider than other adjacent body scales in many species. Scales may be keeled (*Pygopus*, *Pletholax*) or smooth. The outer keratin layers of the epidermis are sloughed regularly.

The skin is tightly bound to the superficial musculature by connective tissue, with little subcutaneous fat present.

Aspects of the epaxial, ventral abdominal and pectoral and pelvic girdle musculature are described by Fürbringer (1870), Kluge (1976b) and Gasc (1981).

Skeletal System

The skull is similar to that of geckos. Bony elements present in the most generally primitive genus (*Pygopus*) (Fig. 28.4) are: premaxilla, nasal, frontal, parietal, maxilla, prefrontal, postfrontal, squamosal, jugal, quadrate, vomer, septomaxilla, palatine, pterygoid, ectopterygoid, epipterygoid, supraoccipital, prootic, otoccipital, basioccipital, basisphenoid, stapes, dentary, splenial, coronoid, surangular, prearticular and articular. The frontals are fused into a single element, as are the premaxillae in adults. In the mandible, the articular, prearticular and surangular are fused into a single element (possibly also incorporating the absent angular), although the prearticular and surangular remain distinct anteriorly. In the adult neurocranium, the supraoccipital, prootic, otoccipital, basioccipital and basisphenoid are fused.

Both the postorbital and upper temporal arches are incomplete (Fig. 28.4). The forebrain is partially enclosed by ventral flanges of the frontal and parietals. The palate is formed mainly by the vomers. The palatines are narrow, widely separated, and form the caudal margin of the choanae (McDowell & Bogert 1954; Underwood 1957; Stephenson 1962; Rieppel 1984a; Kluge 1987).
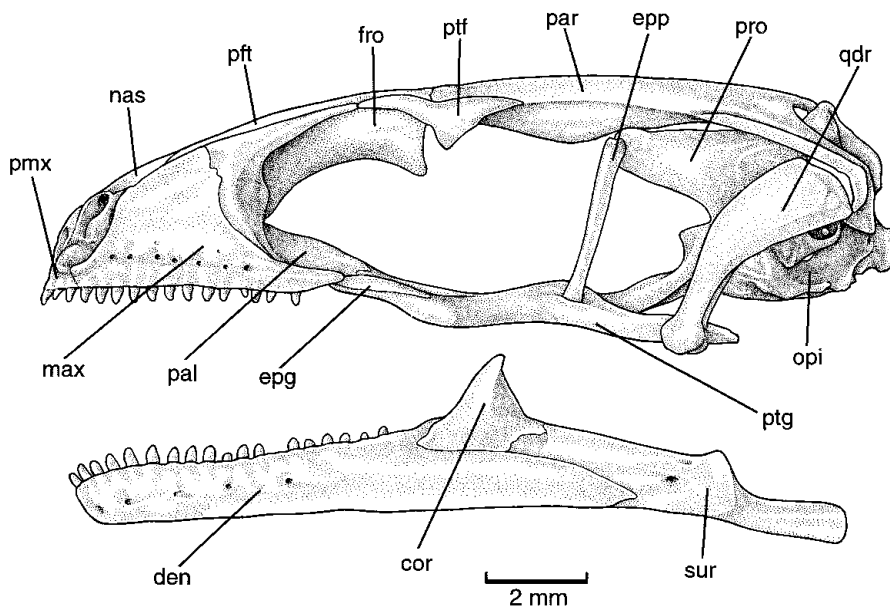

Figure 28.4 Skull of *Pygopus lepidopodus* in lateral view. **cor**, coronoid; **den**, dentary; **epg**, ectopterygoid; **epp**, epipterygoid; **fro**, frontal; **max**, maxilla; **nas**, nasal; **opi**, opisthotic; **pal**, palatine; **par**, parietal; **pft**, prefrontal; **pmx**, premaxilla; **pro**, prootic; **ptf**, postfrontal; **ptg**, pterygoid; **qdr**, quadrate; **sur**, surangular. [B. Jantulik]

In miniature burrowing genera (*Aprasia*, *Pletholax*), the postorbital regions of the skull are much elongated and the post-temporal fenestrae are either reduced or absent. The dentary of *Aprasia* is also very short (Stephenson 1962; Rieppel 1984a).

The skull of *Lialis* is elongate, particularly in the very narrow preocular region. The highly mobile fronto-parietal (mesokinetic) joint allows the snout to flex up to 40° from the horizontal. The parietals are fused, and the jugal is absent (Stephenson 1962; Patchell & Shine 1986a).

In all pygopodids, only the first ceratobranchial of the hyoid is osseous (Stephenson 1962).

The number of presacral vertebrae ranges from 44 to 110, and there are from 45 to 130 postsacral vertebrae (Greer 1989). The elements of the neural arch of the atlas are unfused in *Pygopus*, *Delma* and *Lialis*, but fused in *Aprasia* (Stokely 1947; Underwood 1957). The third vertebra in *Pygopus*, *Delma*, *Lialis*, or the fourth in *Aprasia*, bears the first ribs, and the number of cervical vertebrae is reduced to seven or fewer (Underwood 1957; Greer 1989). Postsacral vertebrae bear fracture planes immediately distal to the short transverse processes (Etheridge 1967). The ribs are unusual in possessing an antero-ventral process, but not a postero-dorsal process (Hoffstetter & Gasc 1969).

A pectoral girdle is present in all species, though there are no external vestiges of front limbs. The pectoral girdle of *Pygopus*, *Paradelma*, *Delma* and *Lialis* is represented by a sternum and paired clavicles, scapulocoracoids, epicoracoid cartilages and suprascapular cartilages. A humeral remnant is also present, though not in articulation with the scapula. A large interclavicle is present in *Pletholax* (Stephenson 1962). The pectoral girdle of *Aprasia* is modified and extremely reduced to a narrow, transverse rod composed of sternum, clavicles, scapulocoracoids and suprascapular cartilages (Stokely 1947; Stephenson 1962; Greer 1989).

The pelvic girdle consists of fused ilium, ischium and pubis (not fused in some *Aprasia*), and the ischium is often directed anteriorly rather than posteriorly. Ventrally, the two halves of the pelvis are widely separated. In *Pygopus*, *Delma* and *Lialis*, the pelvis is connected to the sacral vertebrae, but this connection has been lost in *Aprasia*. In the most complete state (*Pygopus*), the hindlimb consists of femur, tibia, fibula, tarsal elements and four digital elements (Fig. 28.5), while in the most reduced state (*Aprasia pulchella*), there is only a femoral remnant (Underwood 1957; Stephenson 1962; Greer 1989).

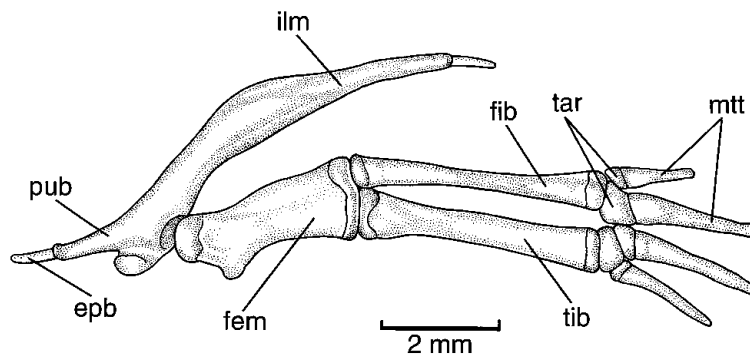Post-cloacal bones are present in males of all species (Kluge 1974, 1982).

Figure 28.5 Pelvic girdle and hindlimb skeleton of *Pygopus lepidopodus*. **epb**, epipubis; **fem**, femur; **fib**, fibula; **ilm**, ilium; **mtt**, metatarsals; **pub**, pubis; **tar**, tarsals; **tib**, tibia.   [B. Jantulik]

Locomotion

Pygopodids move by lateral undulations of body and tail. Surface-active species of the genera *Pygopus*, *Lialis* and *Delma* move through thick vegetation and litter, while the fossorial *Aprasia* and *Ophidiocephalus* use lateral undulations to burrow through loose soil, and crawl along narrow earth cracks and insect tunnels (Kluge 1974; Ehmann 1981; Greer 1989). Ehmann (1981) reported that *Ophidiocephalus* sometimes uses the head as a lever to pull the body through the substrate.

The hindlimb flaps are normally held tightly alongside the body when moving, although they may be extended when traversing rough terrain or climbing, or when stressed (Annable 1983; Greer 1989).

Feeding and Digestive System

The extensive cranial kinesis of *Lialis* allows it to grip firmly and subdue large prey. The tip of the snout bends down to contact the tip of the mandible in a pincer-like action, encircling the prey (Fig. 28.6; Greer 1989). *Pygopus* and *Delma* have been observed to disable large, potentially dangerous prey by rotating the body rapidly along the long axis (Kästle 1969; Philipp 1980).

Dentition is pleurodont, with the teeth of most taxa blunt and rounded, and firmly attached to bone. The teeth of *Lialis* species are narrow, recurved and hinged to bone, allowing them to fold posteriorly towards the jaws (Patchell & Shine 1986c). Apparently this is adaptive for feeding on skinks; it occurs convergently in several snake genera (Patchell & Shine 1986c). Teeth are present on the premaxilla, maxilla and dentary (except in *Aprasia*, where the maxilla is edentulous, as is the premaxilla in most juveniles and adult females; Parker 1956).

The gastrointestinal tract is simple, with few notable features. The oesophagus is straight and broad. The stomach lies dorso-sinistral to the liver, the cardia is at about mid snout-vent length, and the pylorus lies more posteriorly at about two-thirds of the snout-vent length, level with the gall bladder. The small intestine is divisible into an initial descending duodenum on the left, separated by a caudal flexure from an ascending duodenum. The latter is separated by a duodenojejunal flexure from a moderately convoluted jejunum on the right. The
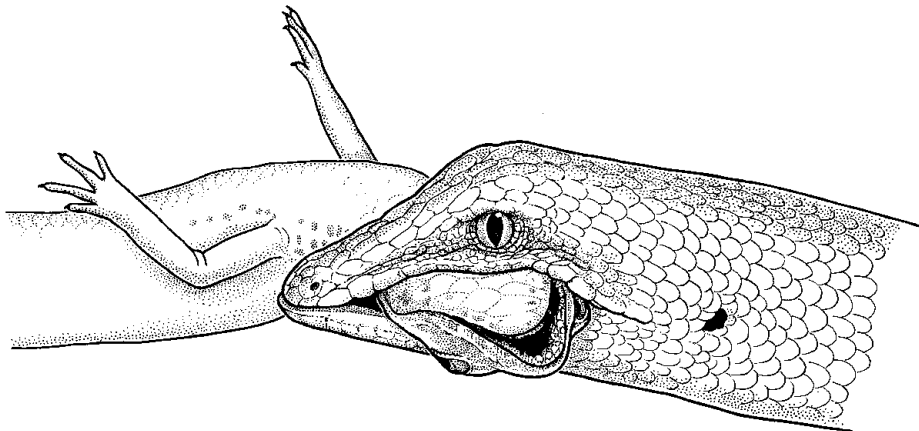

Figure 28.6 *Lialis burtonis* feeding on a skink. Note the flexion of the snout relative to the rest of the head. [B. Jantulik]

duodenal loop is short in *Pygopus* and long in *Lialis*. The small intestine opens eccentrically dextrally into the straight large intestine, the ileocolic ostium lying at about 80% of the body length in *Pygopus*.

The elongate liver is divided posteriorly into two lobes. The left lobe is the larger, and distally turns medially so that the interlobar fissure opens transversely and dextrally. This extension of the left lobe is least developed in *Lialis*. A gall bladder is present, lying between the lobes (Underwood 1957).

Circulatory System

The heart lies anteriorly within the body cavity, at about one quarter of the snout-vent length from the head. In *Lialis*, it is slightly elongate, and greatly so in *Aprasia* (Underwood 1957). Some aspects of the arteriovenous system have been described by Beddard (1904) and Underwood (1957). A ductus caroticus joins the carotid and systemic arches. In *Aprasia*, the common carotid bifurcates near the head, while in *Delma* and *Lialis*, the bifurcation is more posterior, near the carotid arch. Two (*Lialis*) or several (*Pygopus*) gastric arteries provide the gastric blood supply from the coeliac trunk, although they may arise independently from the aorta. More distal visceral branches of the aorta may arise from intercostal arteries.

The spleen is small and rounded, and is associated with the posterior end of the liver and the pancreas (Underwood 1957).

Respiration

The paired lungs are asymmetrical, the left lung being much shorter than the right. The ratio of lengths range from 34 to 68% in the larger, less attenuate species, to 9 to 15% in *Aprasia* (Butler 1895; Underwood 1957; Greer 1989). Respiration involves active expiration by constriction of the thoracic region, followed by passive inspiration (Greer 1989).

Excretion

The paired kidneys lie posteriorly in the body cavity, reaching to the level of the vent (*Lialis*) or extending slightly beyond the cloaca (*Delma*, *Pygopus*). In *Lialis*, the right kidney is slightly longer than the left (Underwood 1957). The ureters are short and open via a pair of urinary papillae into the urodaeum. A bladder may be absent (*Delma*) or weakly developed (*Lialis*) (Gabe & Saint Girons 1965).

Sense Organs

The eye is well developed, even in burrowing forms, and is similar to that of geckos. It is covered by a spectacle. The pupil is vertical, and the outer segments of the visual cells are enlarged. Oil droplets in these cells, and a fovea are lacking (Underwood 1957).

An external auditory meatus is present in all pygopodids except *Aprasia aurita* and *Pletholax gracilis edelensis*. The auditory meatus is narrow and the tympanum deeply sunk. The stapes is short, and lacks a stapedial foramen and an internal process. In some of the earless *Aprasia*, the stapes attaches to the skin rather than to a tympanum; in others it is very reduced (Underwood 1957; Greer 1989). The inner ear is similar in most respects to that of geckos (Shute & Bellairs 1953; Wever 1974).

Cutaneous sensilla are present on head and body scales (Fig. 28.7). They are particularly prominent around the margins of scales, and may bear one or more central bristles (Underwood 1957).
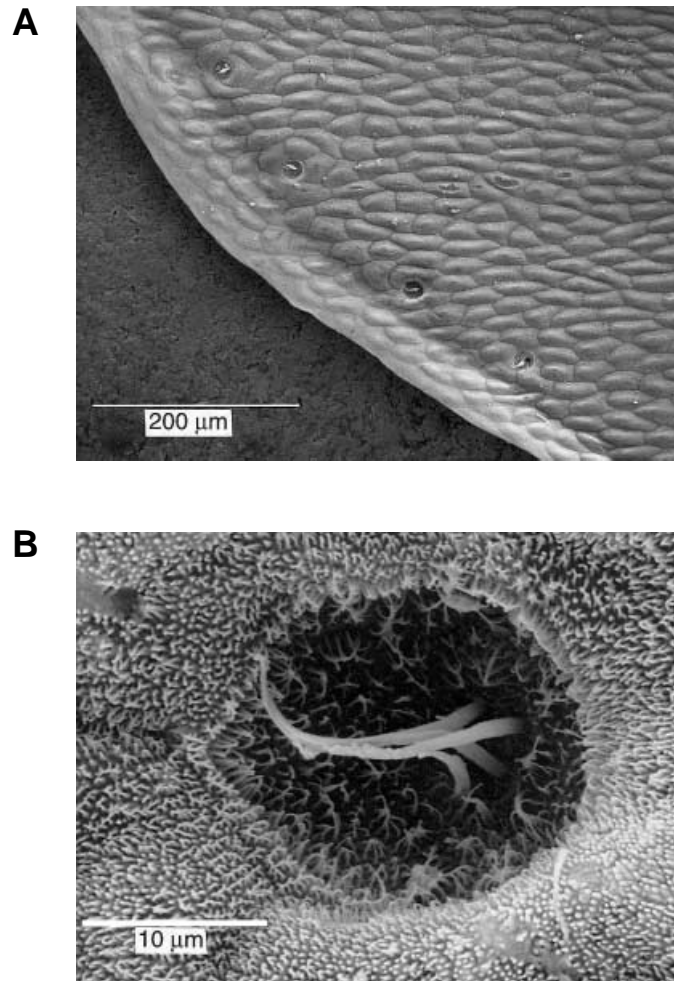
Figure 28.7 Scanning electron micrograph of cutaneous sensilla of a dorsal body scale of *Pygopus lepidopodus*. **A**, apical lateral quadrant of scale with several sensilla; **B**, detail of a single sensillum.   [Photos by G. Avern]

Endocrine and Exocrine Systems

The hypophysis of *Delma* is similar to that of geckos. In *Lialis*, the neural and intermediate lobe complex lies caudal to the distal lobe, on a similar horizontal plane, and the posterior part of the *pars nervosa* is flattened. The median eminence is narrowly connected to the diencephalon. The intermediate lobe is well developed, and its internal layer tends to form cellular cords (Saint Girons 1970a).

The thyroid is variable in shape. In *Delma*, it is a bilobed body associated with the fork of the brachiocephalic trunk, and embraces the trachea ventrally. In *Lialis* and *Pygopus*, it is a flattened, unlobed structure (Lynn & Komorowski 1957; Underwood 1957). The parathyroid lies lateral to the origin of the internal carotid artery (Underwood 1957).

The pancreas is V-shaped, its apex directed posteriorly, with a transverse or anteriorly directed hepatic lobe extending towards the gall bladder, and an intestinal lobe lying along the small intestine as far as the pylorus. In *Aprasia*, *Delma* and *Pygopus*, a posteriorly directed splenic lobe extends from the anterior end of the intestinal lobe (Underwood 1957).

The adrenals are small and narrow, lying immediately postero-medial to the testes, or antero-medial to the ovaries, the right adrenal more anterior than the left.

Several cephalic exocrine glands have been reported from *Delma* and *Lialis* by Saint Girons (1988). They are the inferior labial, palatine, anterior sublingual, lingual, Harderian and nasal glands.

In *Pygopus*, *Paradelma* and *Lialis*, preanal glands are present subcutaneously. Each drains via a separate duct to open posteriorly at a pore located in the free margin of a scale (Underwood 1957; Greer 1989).

Reproduction

The gonads lie dorso-medially within the body cavity, on either side of the dorsal mesentery. The right gonad lies more anteriorly than the left. In male *Pygopus*, the anterior pole of the right testis lies level with the gall bladder, that of the left gonad level with the posterior end of the liver. The ductus deferens is straight and passes over the ventral midline of the kidney before entering the urodaeum. Paired hemipenes lie within the base of the tail when inverted, and are everted from the proctodaeum for intromission. Hemipenial morphology was described by Böhme (1988).

In the female, the gonads are more posterior than those of the male. The right ovary is level with the ileocolic ostium. Each oviduct is initially narrow and thin-walled, and lies dorso-lateral to its ovary. Distally, the oviducts are broader and thicker walled. The left oviduct is much the shorter.

Pygopodids are oviparous, with a normal clutch size of two. Temperate climate species appear to mate in spring and lay in summer. Known incubation periods range from 66 to 77 days. *Pygopus* and *Lialis* species have been reported to lay communally (Patchell & Shine 1986b; Greer 1989).

Karyotypic data are available for sixteen species of pygopodid, including representatives of the genera *Aprasia*, *Delma*, *Lialis*, *Ophidiocephalus* and *Pygopus* (Gorman & Gress 1970; Gorman 1973; King 1990). Diploid number ranges from 34 to 42, most commonly 2n = 38 and chromosomes are predominantly biarmed. Many species have sex chromosome systems based on male heterogamety, some (*Lialis*) with complex multiple sex chromosome systems.

NATURAL HISTORY

Life History

Almost nothing is known of the life history of pygopodids. Captives have lived for up to seven years (Mertens 1966; Greer 1989).

Ecology

Most pygopodids feed on arthropods. *Lialis*, however, feeds exclusively on other squamates, mostly lizards, and both species of *Pygopus* have specialised diets. *Pygopus lepidopodus* feeds primarily on spiders (Patchell & Shine 1986b) and *P. nigriceps* is a scorpion specialist (Pianka 1986). *Aprasia* may be myrmecophagous (Jenkins & Bartell 1980; Robertson, Bennett, Lumsden, Silveira, Johnson *et al*. 1989). Most species appear to search actively for prey, although *Lialis* is a sit-and-wait predator (Greer 1989; Murray, Bradshaw & Edward 1991).

Pygopodids inhabit a wide range of habitats and microhabitats. In arid areas, *Triodia* tussocks are a major microhabitat. *Aprasia* is fossorial, inhabiting ant tunnels and burrowing in sandy soils, as is *Ophidiocephalus* which burrows in loose sandy loams. *Pygopus*, *Paradelma*, *Lialis* and *Delma* are terrestrial surface dwellers, although some *Delma* species burrow in loose soil. *Pygopus* has been found up to 1.5 m above the ground in vegetation. *Aclys* and *Pletholax* are both surface active in low vegetation and are partly fossorial (Greer 1989).

Although usually encountered singly, and hence presumably solitary, occasional aggregations of pygopodids have been reported, possibly related to breeding (Bush 1981, 1986).

Predators of pygopodids include the diurnal raptors *Falco cenchroides* and *Hieraaetus morphnoides*(Morrison in Sedgwick 1949; Storr 1965b), elapid snakes of the genera *Cacophis*, *Cryptophis*, *Demansia*, *Neelaps*, *Pseudechis*, *Pseudonaja*, *Simoselaps*, *Suta* and *Unechis* (Shine 1980a, 1980d, 1984a, 1984b, 1987e, 1988a, 1989), goannas (Pianka 1968; King & Green 1979; Losos & Greene 1988) and feral cats and foxes (Martensz 1971; Brooker 1978). *Lialis* will also eat other pygopodids (Smith 1976a). In all instances, pygopodids are a minor dietary component.

The few parasites recorded from pygopodids include the trematode *Paradistoma crucifer*, the cestode *Acanthotaenia striata*, nematodes (*Abbreviata* sp., as *Physaloptera*) and other unidentified nematodes and linguatulids (Brongersma 1953; Ehmann 1981).

Behaviour

Four defensive behaviour patterns have been described. Long-tailed species (*Delma*, *Pletholax*) attempt to escape by leaping into the air (Bauer 1986a; Greer 1989). When disturbed, fossorial species (*Aprasia*, *Ophidiocephalus*) writhe the tail, which is often brightly coloured (Rankin 1976a; Ehmann 1981). *Pygopus* and *Paradelma* raise the forepart of the body from the ground and flicker the tongue, the former genus also compressing the neck and striking, apparently in mimicry of elapid snakes (Shea 1987c; Greer 1989). If restrained, pygopodids attempt to break free by twisting the body and bracing with the tail (Greer 1989).

The ambush predator *Lialis* is known to writhe its tail to attract potential prey lizards (Bradshaw, Gans & Saint Giron 1980; Murray *et al*. 1991).

Like geckos, pygopodids have a voice. A distinct high-pitched squeak is produced under stress, and sometimes emitted in social interactions (Weber & Werner 1977; Annable 1983; Greer 1989). Also like geckos, pygopodids use the tongue to wipe the face and spectacle (Greer 1989).

Captive *Pygopus* have been observed to excavate tunnels in soft soil by removing soil with the mouth and rotating the body to widen the tunnel (Husband 1980). Such tunnelling behaviour may allow the animal access to the burrowing spiders on which it feeds.

Economic Significance

All pygopodids are legally protected in the Australian states in which they occur. Six species with small geographic distributions, often close to major human populations (*Aprasia aurita*, *A. parapulchella*, *A. pseudopulchella*, *Delma impar*, *Ophidiocephalus taeniatus*, *Paradelma orientalis*) may be threatened by habitat loss (Ehmann & Cogger 1985; Jenkins 1985; Robertson *et al*. 1989; Coulson 1990).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Pygopodids occur through most of Australia, with the exception of Tasmania, the extreme south-east of Australia, and the rainforests of the east coast. *Lialis* also occurs in the lowlands of New Guinea and New Britain. The most widespread species, *L. burtonis*, has an Australian distribution nearly covering that of all other pygopodids combined. *Pygopus*, with two species, and *Delma*, with 16 species, are similarly widespread. *Aprasia* (14 species) is predominantly southern Australian in distribution, extending north along the west coast. The monotypic *Aclys* and *Pletholax* are restricted to the lower west coast of Western Australia, while the monotypic *Ophidiocephalus* and *Paradelma* are restricted to deep-cracking sandy loams of northern South Australia and brigalow habitats of central eastern Queensland, respectively. The major centre of pygopodid diversity is the lower west coast of Western Australia, where up to ten species may occur together (Cogger & Heatwole 1981).

Affinities with other Groups

Pygopodids are closely related to geckos, sharing with them a large number of derived characters (Shute & Bellairs 1953; McDowell & Bogert 1954; Underwood 1957; Miller 1966; Wever 1974; Iordansky 1985; Kluge 1987). Of modern authors, only Camp (1923) has suggested an alternative relationship with anguinoids and helodermatids.

Most authors have assumed that the Pygopodidae and Gekkonidae are sister groups, derived independently from a common ancestor, and this traditional classification has been adopted here. However, Kluge (1987) examined the evidence critically for such a relationship and concluded that the pygopodids are the sister group of diplodactyline geckos, with the pygopodid-diplodactyline clade the sister group of gekkonine and sphaerodactyline geckos (Fig. 28.8). Hence he proposed the inclusion of diplodactyline geckos in an expanded family Pygopodidae. Kluge further suggested that pygopodids may be most closely related to certain genera of the tribe Diplodactylini. Kluge's classification has yet to be accepted by most Australian herpetologists, and has been criticised (King 1990; King & Mengden 1990) on karyotypic evidence. However, the karyotypic evidence supports Kluge's hypothesis of a cladistic relationship between the pygopodids and diplodactylines, merely introducing uncertainty as to which group of diplodactylines (the tribe Diplodactylini or Carphodactylini)
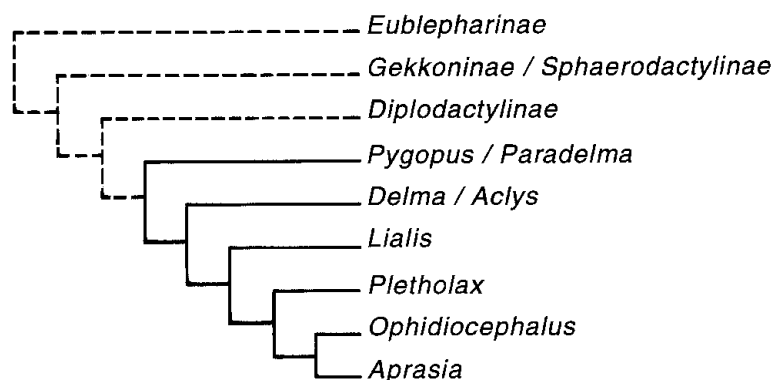

Eublepharinae
Gekkoninae / Sphaerodactylinae
Diplodactylinae
Pygopus / Paradelma
Delma / Aclys
Lialis
Pletholax
Ophidiocephalus
Aprasia

Figure 28.8 Hypothesised relationships between pygopodid genera, and with their nearest relatives. Solid lines indicate relationships within the family, broken lines with other gekkonid groups. (After Kluge 1976, 1987) [D. Wahl]

the pygopodids are most closely related. It is likely that the reluctance to accept Kluge's expanded Pygopodidae is because of the lack of any intermediary between the fully limbed diplodactylines and the nearly completely limbless pygopodids at such a low taxonomic level.

Affinities within the Pygopodidae

Of the eight genera of pygopodids recognised by Kluge (1974), four (*Aprasia*, *Ophidiocephalus*, *Pletholax* and *Lialis*) are well defined natural groups, successively more distantly related to each other (Fig. 28.8; Kluge 1976a). The relationships between the remaining, relatively primitive genera (*Delma*, *Aclys*, *Paradelma* and *Pygopus*) are less well defined. Although Kluge (1976a) recognised two groups among these genera (*Delma*/*Aclys* and *Pygopus*/*Paradelma*), his recognition of these two groups as genera (*Delma* and *Pygopus*) and his subfamilial classification have received little acceptance (Shea 1987a, 1987c; Böhme 1988; Greer 1989).

Fossil Record

No fossil material has yet been identified as being of pygopodid origin, probably due both to the fragile nature of the skeleton and the paucity of detailed data on pygopodid and gekkonid osteology.

COLLECTION AND PRESERVATION

Pygopodids are generally collected by hand from beneath ground debris, or in pitfall traps. *Pygopus nigriceps* (Pl. 4.12), *Lialis* and some *Delma* species are often found crossing roads on warm nights.

Pygopodids are best fixed in 10% formalin, injected into the body cavity and carefully into the tail, and stored in 70% ethanol. Due to the persistence of reflexes in the tail long after death, it may be necessary to delay injection of fixative into the tail for several hours post mortem if contortion and tail breakage are to be avoided. The keratin layer of the epidermis of preserved pygopodids is fragile and readily sloughs with handling.