

Figure 13.8 Family Idiosepiidae. Idiosepiids mature sexually at less than 20 mm total length. A, *Idiosepius notoides*, a southern Australian endemic, dorsal view. B–D, hectocotyliised arms of three Australian species: B, *Idiosepius notoides*; C, *Idiosepius paradoxus*; D, *Idiosepius notoides*. E, egg laying in *Idiosepius pygmaeus*. F, portion of radula of *Idiosepius notoides*, showing several transverse tooth rows. (D, after Voss, G.L. 1963; E, after Natsukari 1970) [A–E, K. Hollis; F, C.C. Lu]

Order TEUTHOIDEA

Teuthoids have four pairs of arms and one pair of tentacles. These are always present in 'larvae', but may be absent in adults. Such specimens have a typical squid form. The tentacular stalks are not retractile. Arms are usually not connected by webs, or when present, the webs are generally shallow. The suckers are stalked, and have a chitinous ring, usually with a denticulate edge. In some species, sucker rings on the arms and/or the tentacular club may be modified into hooks. Fins are located at the posterior part of the body or along the entire mantle and, generally, merge along the midline or near the posterior end. Nuchal, mantle, and funnel

cartilages are usually present. In some species, the mantle is fused with the head and, less frequently, with the funnel. If so, the mantle cavity communicates with the exterior by three openings, one on ventral side of body and two on sides of head. The non-calcified shell is represented by a thin, horny, pen-like or sagittate gladius. Small projections or 'angles' are located on the anterior edge of the mantle near the mantle locking cartilages. Between these the ventral mantle edge is slightly excavated. The central radular tooth is tricuspidate, or very rarely unicuspidate. The following key for the teuthoid families follows Roper, Young & Voss 1969. The family Walvisteuthidae (Nesis & Nikitina 1986) is not included.

Key to the families of the order Teuthoidea

- 1 (a) Eye covered by a transparent cornea. Suborder Myopsida 2
- (b) Eye without cornea and in open contact with seawater. Suborder Oegopsida 3
- 2 (a) Four rows of suckers on manus of tentacular clubs. Fins rhombic in outline. Medial posterior border of fins concave (Fig. 13.9; Pls 18.6, 18.9) Loliginidae
- (b) Two rows of suckers on manus of tentacular clubs. Fins rounded, ear-like. Medial posterior border of fins convex Pickfordioteuthidae
- 3 (b) Funnel free from mantle, a funnel-mantle locking apparatus present 4
- (b) Funnel fused to mantle on each side, no funnel-mantle locking apparatus present 24
- 4 (a) Funnel-mantle locking apparatus a simple, straight groove and ridge 5
- (b) Funnel-mantle locking apparatus not a simple, straight groove and ridge 18
- 5 (a) Arms with hooks, or with suckers in four rows on the proximal half of the ventral arms 6
- (b) Arms without hooks, or with suckers in two rows on the proximal half of the ventral arms 8
- 6 (a) Armature of arms in two rows 7
- (b) Armature of arms in four rows Gonatidae
- 7 (a) Tentacles present; fully developed clubs present (Fig. 13.11; Pl. 18.12) Enoploteuthidae
- (b) Tentacles and clubs absent in adults (Fig. 13.13); clubs always rudimentary when present in 'larvae' or occasionally juveniles (*Taningia*) Octopoteuthidae
- 8 (a) Buccal membrane connectives attach to the ventral side of ventral arms 9
- (b) Buccal membrane connectives attach to the dorsal side of ventral arms 13
- 9 (a) Hooks present on tentacular clubs (Fig. 13.14A, B; tentacles and clubs not described for *Chaunoteuthis*) Onychoteuthidae
- (b) Hooks lacking on tentacular clubs 10
- 10 (a) Cartilaginous scales present on mantle (Fig. 13.16; may be minute). Tentacular clubs with four longitudinal rows of suckers Lepidoteuthidae
- (b) Cartilaginous scales lacking. Tentacular clubs with more than four longitudinal rows of suckers on some areas 11
- 11 (a) Fins comb-like and nearly as long as the mantle, supported by strong, transverse, muscular ribs (Fig. 13.20A). Minute suckers on oral surface of buccal lappets Ctenopterygidae
- (b) Fins not comb-like, less than half the body length, without supporting ribs. No suckers on buccal lappets 12
- 12 (a) Tentacular clubs with six rows of suckers. Tail present, long and spike-like (greater than the fin length) Batoteuthidae
- (b) Tentacular clubs with four rows of suckers on distal portion, numerous rows on proximal portion. Tail absent. (Fig. 13.21) Brachioteuthidae
- 13 (a) Eye with row of photophores on ventral surface. Buccal membrane with eight lappets. (Fig. 13.10A, B) Lycoteuthidae
- (b) Eye without photophores. Buccal membrane with seven lappets or less 4
- 14 (a) Surface of mantle, head and arms covered with numerous photophores (usually large and distinct). (Fig. 13.18A, B) Histiototeuthidae
- (b) Surface of mantle and head without photophores; arms may have a few photophores 15
- 15 (a) Oral surface of buccal lappets with minute suckers. (Fig. 13.19A) Bathyteuthidae
- (b) Oral surface of buccal lappets without suckers 16
- 16 (a) Many small to minute suckers (or suckers and knobs) at the proximal end of the manus 17
- (b) No cluster of small suckers at proximal end of the manus Psychroteuthidae
- 17 (a) Medial posterior borders of fins slightly convex. Carpal knobs in a single dorsal row or absent. Small size Neoteuthidae
- (b) Medial posterior borders of fins concave (Fig. 13.17). Carpal knobs in a cluster alternating with carpal suckers. Attains gigantic size. Architeuthidae
- 18 (a) Funnel locking cartilage with a longitudinal and a transverse groove, \perp -shaped or \neg -shaped 19
- (b) Funnel locking cartilage oval, triangular or oval with inward projecting knobs 20

- 19 (a) Funnel locking cartilage with a longitudinal groove crossed by a transverse groove at its posterior end: L-shaped. Fins less than 60% of mantle length (Fig. 13.22A–U; Pl. 18.11) Ommastrephidae
- (b) Funnel locking cartilage with a longitudinal groove from which a shorter groove branches medially: –I-shaped. Fins more than 80% of mantle length (Fig. 13.23A, B) Thysanoteuthidae
- 20 (a) Funnel locking cartilage oval with one or two knobs directed toward the centre of the concavity 21
- (b) Funnel locking cartilage oval or subtriangular, without knobs 22
- 21 (a) Club with four rows of suckers (Fig. 13.24A) Chiroteuthidae
- (b) Club with more than 15 rows of minute suckers (Fig. 13.25A) Mastigoteuthidae
- 22 (a) Suckers on arms in four to six rows. Tail longer than mantle length (Fig. 13.27A) Joubiniteuthidae
- (b) Suckers on arms in two rows. Tail less than 50% of mantle length, or absent 23
- 23 (a) Suckers on the tentacular clubs in four longitudinal rows. Mantle free dorsally. (Fig. 13.15A, B) Cycloteuthidae
- (b) Suckers on the tentacular clubs in eight or more longitudinal rows. Mantle fused dorsally to head Promachoteuthidae
- 24 (a) Mantle free dorsally, articulates with head by ridge and groove. (Fig. 13.26) Grimalditeuthidae
- (b) Mantle fused dorsally with head. (Fig. 13.28) Cranchiidae

Suborder MYOPSIDA

The eyes of myopsids are covered by a transparent membrane (cornea), except for a tiny hole, the 'lacrimal pore'. The mantle is muscular. The buccal connectives are seven-pointed and connect to the ventral arms on the ventral border. The funnel locking cartilage is simple and straight. Only the left oviduct is developed. Paired nidamental glands and accessory nidamental glands are present. One or both ventral arms are hectocotylised in males.

Family Loliginidae

Loliginids are characterised by a transparent cornea covering the eyes. The mantle locking apparatus is straight and simple. There are seven buccal lappets each with a few small suckers, and the buccal connectives attach to the ventral borders of the ventral arms.

The mantle is elongate, and tapered posteriorly. The fins are oval, elongate rhomboidal or heart-shaped, either terminal on the posterior end, or marginal. The fins range in length from about half to nearly the entire length of the mantle. The arms bear two rows of suckers. The tentacles are not retractile and suckers occur in four rows on the tentacular club. In the mature males (Fig. 13.9), the left ventral arm is hectocotylised, except in the genus *Loliopsis*, in which both ventral arms are hectocotylised.

Eleven genera are recognised at present: *Loligo*, *Nipponololigo*, *Photololigo*, *Heterololigo*, *Sepioteuthis*, *Loliolus*, *Lolliguncula*, *Loliopsis*, *Doryteuthis*, *Alloteuthis* and *Uroteuthis*. *Photololigo*, *Sepioteuthis* and *Loliolus* are found in Australian waters (Fig. 13.9).

The name Loliginidae was introduced by Orbigny in 1839 (Férussac & Orbigny 1835–1848) to include the extant squid genera *Sepioteuthis* and *Loligo* and the fossil genera *Teudopsis*, *Leptoteuthis* and *Beloteuthis*. The currently recognised genera appear to be stable, with the exception of *Loligo* and *Doryteuthis* for which definition and composition remain to be settled. Natsukari (1983, 1984) separated three new genera, *Nipponololigo*, *Photololigo* and *Heterololigo*, from the genus *Loligo*, thus restricting *Loligo sensu stricto* to those species distributed in the eastern Atlantic.

Quoy & Gaimard (1832) provided the first report of loliginids from Australian waters, when they described *Sepioteuthis australis* and *S. bilineata* from Westernport Bay, Victoria. Gray's (1849) description of *Loligo australis* from Newcastle, New South Wales, is brief and the type specimen has deteriorated to the point that the name cannot be applied with certainty to any loliginid in the area. *Loligo etheridgei*, described by Berry (1918) from an unknown Australian locality, has been regarded as a junior synonym of *Loligo chinensis* (now *Photololigo chinensis*; Fig. 13.9A) (Natsukari & Okutani 1975).

Lu & Tait (1983) concluded that two species of the genus *Sepioteuthis*, *S. lessoniana* and *S. australis* (Fig. 13.9H, K) occur in Australian inshore waters. Lu, Roper & Tait (1985) described the new species, *Loliolus noctiluca* (Fig. 13.9C) from Australia and reviewed the taxonomy of the genus. The taxonomic problems with the remaining Australian loliginids are currently under study (for example, Yeatman & Benzie 1993).

The loliginid shell or gladius is quill-shaped (*Loligo*, *Photololigo*, *Nipponololigo*, *Heterololigo*, *Doryteuthis*, *Sepioteuthis*), leaf-shaped (*Loliolus*) or long and slender with a long conus (*Alloteuthis*, *Uroteuthis* males). Some sexual dimorphism occurs in the gladius of some species. Cohen (1976) noted that the vane (the posterior portion of the gladius) is wider in females of *Loligo pealei*, *L. plei* and *L. roperi*, and suggested that the wider gladius in the female may support or protect the large mass of eggs in a ripe female. In males of *Alloteuthis subulata* and *A. africana*, the posterior end of the mantle develops into a longer tail than in females (20 mm in females, 60 mm in males in *A. subulata*). The gladii reflect this sexual dimorphism.

Jet propulsion is the most important method of locomotion in loliginids. Contraction of circular muscles in the mantle produces high hydrostatic pressure in the mantle cavity, resulting in a jet of water from the funnel and the movement of the animal in the opposite direction. Trueman & Packard (1968) measured the momentum produced by the efflux of jet water from the mantle cavity in *L. vulgaris*, and concluded that the swimming tensions derived from the maximum jet pressures were, in general, equivalent to the body weight. Cole & Gilbert (1970) calculated the velocity in *L. pealei* to be about 4 knots for an animal of about 250 mm body length, comparable to that of *L. vulgaris* (Packard 1969).

Loliginids, in particular *L. pealei* and *L. forbesi*, are widely used in neurophysiological research, their giant axons providing systems for experimentation. Giant axons are the large diameter nerve fibres which serve the rapid coordination of large groups of muscle in quick escape or withdrawal responses. In squids, the jet propulsion depends on the rapid contraction of the mantle muscles which is initiated through giant axon innervation of these muscles. Much of our knowledge on neurophysiology stems from research performed on the giant axon of squids, particularly of loliginids. Adelman & Gilbert (1990) reviewed the techniques in this research and listed the squid species having useful giant axons. No Australian loliginids have been used for neurophysiological investigations.

Mating behaviour and other aspects of reproduction of have been studied in many non-Australian loliginids. Arnold (1962, 1965) reported that male and female *L. pealei* and *Sepioteuthis sepioidea* form pairs, in which the male pursues and protects the female

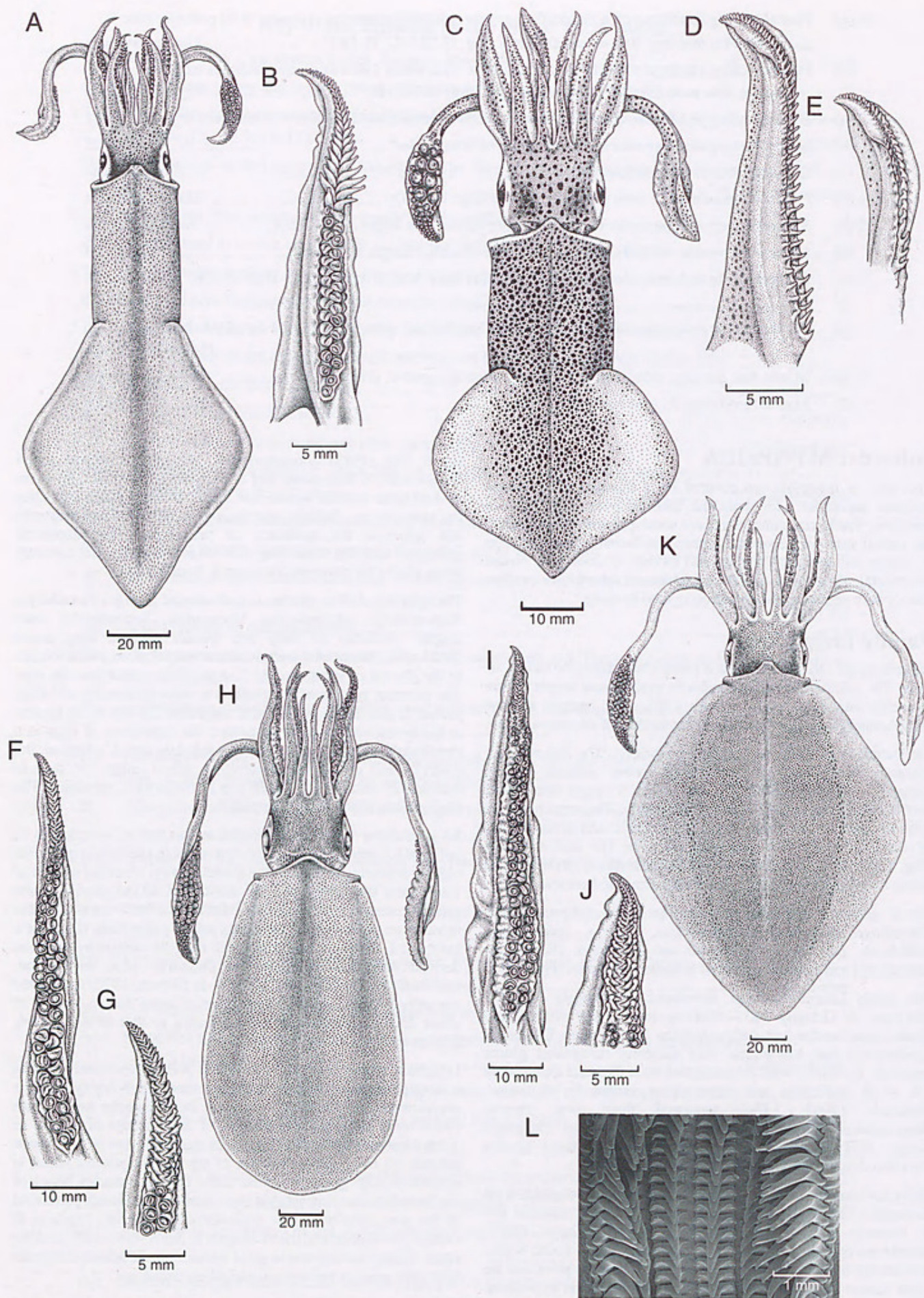


Figure 13.9 Family Loliginidae. Australian loliginids, members of a speciose group of common inshore squids. A, B, *Photololigo chinensis*: A, dorsal view; B, hectocotylied arm. C–E, *Loliolus noctiluca*: C, dorsal view; D, hectocotylied arm; E, detail of arm tip. F–H, *Sepioteuthis lessoniana*: F, hectocotylied arm; G, detail of arm tip; H, dorsal view. I–K, *Sepioteuthis australis*: I, hectocotylied arm; J, detail of arm tip; K, dorsal view. L, portion of radula of *Sepioteuthis lessoniana*, showing several transverse tooth rows. [A–K, K. Hollis; L, C.C. Lu]

from other males. Courting is initiated by an aggressive male who selects a female and swims parallel to her while displaying his courtship colour pattern. Typically, the females show little initial response. Later, the female responds by swimming parallel to the male and displaying her own courtship pattern. Similar courting behaviour has been observed in *S. lessoniana* in Japan (Segawa 1987) and *Loligo opalescens* in California (Hurley 1977).

Mating behaviour of *L. pealei*, *L. opalescens* and *S. lessoniana* has been described. Two postures were observed in *L. pealei*. A head-to-head posture preceded transfer of spermatophores to the buccal seminal receptacle of the female (Drew 1911; Arnold 1962). In the second pose, the mating squids are parallel to each other when the male grasps the female around the mantle behind the head, dips his hectocotylised arm into his own mantle cavity and picks up the spermatophores. He transfers them to the female via her funnel and cements them to the inside of the mantle near the oviduct (Arnold 1962).

A male *Loligo opalescens* copulates with a female by grasping her from below and inserting his right ventral arm into her mantle. The right arm is withdrawn just before the hectocotylised left ventral arm carrying spermatophores is inserted in its place (Hurley 1977). The head-to-head mating position also occurs in *L. opalescens* (Fields 1965). Mating in *S. lessoniana* is similar to that described above except the head-to-head posture was not observed (Segawa 1987).

At spawning, the eggs pass from the oviduct out through the funnel. The eggs are enveloped in secretions from the oviductal and nidamental glands (Pls 18.6, 18.7). The number of eggs in each egg capsule varies between species. The egg capsule of *L. opalescens* is 60–90 mm long, and contains an average of 156 eggs (Yang, Hixon, Turk, Krejci, Hulet & Hanlon 1986). Those of *S. sepioidea* contain only two to four eggs (LaRoe 1971). Similarly, *S. lessoniana* has only two to nine eggs in each capsule (Pls 18.7, 18.8) (Choe & Ohshima 1961) and *S. australis* (as *S. bilineata*) of New Zealand has two to six eggs (Larcombe & Russell 1971). In southern Australia, this last species also produces capsules containing up to six eggs each (Smith, B.J., Black & Shepherd 1989). The egg mass comprises many egg capsules.

Egg laying in *L. pealei* is initiated by visual stimuli. Arnold (1962) found that the presence of a naturally laid egg mass or an artificial egg mass made of water-filled polyethylene tubing induced animals to lay egg capsules; several females often contributed to the same egg mass. Several *S. australis* have also been observed to lay eggs on the same egg mass (Larcombe & Russell 1971).

Females of *Loligo opalescens* and *L. bleekeri* die after spawning, resulting in a mass mortality in the spawning area (Fields 1965; Hamabe 1973a). This phenomenon has not been observed in other species.

From commercial catch data, Fields (1965) estimated that *L. opalescens* spawns and dies at three years of age. He inferred also that the life span is one to four years, and that most live about three years. Spratt (1978) estimated the life span to be about one to two years, from the growth rings in the statoliths. Laboratory rearing indicates that *Loligo opalescens* is capable of spawning at one year of age (Hixon 1983).

Studies of growth rings in the statoliths led Jackson (1990a) to conclude that *S. lessoniana* reaches sexual maturity in less than 100 days in the tropical waters of northern Queensland. All the specimens studied (75–213 mm mantle length and 75–184 mm mantle length for males and females, respectively) were less than six months old. Using tetracycline staining techniques, Jackson (1990a, 1990b) established that daily growth rings are formed in *S. lessoniana*, *Photololigo chinensis* and *Loliolus noctiluca* under laboratory conditions. *Loliolus noctiluca* and *Photololigo chinensis* reach adult size in less than 200 days (Jackson & Choat 1992).

A wide range of food is eaten by loliginid squids. Crustaceans, polychaetes, fishes and cephalopods have all been found in the stomach contents of loliginids. *Loligo opalescens* of California

prey on euphausiids, calanoid copepods, cumaceans, mysids, shrimps, anchovies and squids (Fields 1965; Karpov & Cailliet 1978). Fields (1965) and Karpov & Cailliet (1978) described the food preference differences of *L. opalescens* that are associated with growth, habitat, sex and reproductive maturity. Vovk (1972) reported that euphausiid and decapod crustaceans are eaten by smaller *L. pealei* and that larger squids eat fishes and other squids.

Many loliginid species have been reared successfully in captivity. Boletzky & Hanlon (1983) reviewed the extensive literature on rearing of loliginids including *S. lessoniana*, *S. sepioidea*, *L. vulgaris*, *L. opalescens*, *L. pealei*, *Doryteuthis bleekeri*, *Lolliguncula brevis* and *L. panamensis*. All have been reared on diets of crustaceans and fishes. Among the species occurring in Australian waters, *Loliolus noctiluca*, *Photololigo chinensis* and *S. lessoniana* have been reared in captivity on live sergestid shrimps (*Acetes sibogae australis*), juvenile penaeid prawns, and fishes of the families Ambassidae, Mugilidae, and Sillaginidae (Jackson 1990a, 1990b). The radular arrangement in *Sepioteuthis lessoniana* is illustrated in Figure 13.9L.

Prey detection and capture in loliginids is visual. Kier (1982, 1985) divided the attack into three phases: attention, positioning and strike. In the attention phase, the head of the squid turns rapidly so that the arms and tentacles are pointed towards the prey and the eyes are directed forward. During the positioning phase the squid swims towards the prey with the arms held together in a tight cone-shaped arrangement with the tips of the tentacles protruding just beyond the arms. During the strike phase the arms flare out from the previous tight cone and the tentacular stalks extend rapidly in a straight trajectory, with the tentacular clubs reaching the prey in approximately 15–35 milliseconds. The clubs strike the prey and attach to it with the suckers. The tentacles then contract, pulling the prey within the reach of the arms. The arms then converge around the prey and subdue and orientate the prey for ingestion.

Loliginids are preyed on by many vertebrates, among them fishes, seabirds and marine mammals. *Loligo opalescens* was preyed on by 19 fish species, 13 seabird species and eight marine mammal species in Monterey Bay (Morejohn, Harvey & Krasnow 1978). *Loligo vulgaris* was also eaten by cetaceans, sharks, tunas and seabirds (Worms 1983). In Australian waters, *S. australis* has been found among the stomach contents of pilot whales *Globicephala melas*, bottlenose dolphins *Tursiops truncatus* (Gales, Pemberton, Clarke & Lu 1992), hammerhead sharks (Dunning *et al.* 1993), as well as the Australian fur seal, *Arctocephalus pusillus doriferus* (Gales *et al.* 1994). Beaks of *Loliolus noctiluca* have been identified from the stomach of an Australian fur seal found in Port Phillip Bay (Lu unpublished data).

The distributions of loliginids are influenced by temperature and salinity, like those of other cephalopods. Some loliginids have been reported to tolerate salinity far below the normal salinity of sea water. *Lolliguncula brevis* is known to inhabit water with a salinity of 20–30‰, and is recorded from salinities as low as 17‰ (Gunter 1950; Laughlin & Livingston 1982). *Loliolus noctiluca* has been captured from waters with bottom salinity of 24‰ and surface salinity of 17.5‰ at a temperature of 11°C (Lu *et al.* 1985).

Loliginid squids are important in fisheries, and account for approximately 9% of the world cephalopod catches (Roper *et al.* 1984). According to FAO data, the world catch of loliginids in 1990 was 103 609 tonnes. In Australia, about 300 tonnes of *S. australis* are sold on the domestic market annually (Dunning 1982). In northern Australian waters, where several loliginid species occur, 2000–3000 tonnes of squids were captured annually by Taiwanese trawlers prior to the declaration of Australia's 200 mile fishing zone (Dunning 1982; Dunning *et al.* 1994). Liu & Yeh (1984) estimated the standing stock of loliginids in the southern part of the Arafura Sea, the northern Timor Sea, the southern Timor Sea and the North West Shelf to be 39 400, 19 300, 700, and 4500 tonnes respectively.

13. SUBCLASS COLEOIDEA

Various loliginid species inhabit the shelf and upper slope of the world's oceans, except the Arctic and Antarctic regions. *Loliolus noctiluca* (Fig. 13.9C) is known only from the inshore waters of eastern Australia including Tasmania, the Gulf of Carpentaria, and the Gulf of Papua (Lu *et al.* 1985). *Sepioteuthis australis*, an endemic, is known only from southern Australia and northern New Zealand (Lu & Tait 1983). *Sepioteuthis lessoniana* (Fig. 13.9H) is a widely distributed Indo-West Pacific species known from northern Australia. Several species of *Photololigo* occur in northern Australian waters (Yeatman & Benzie 1993; Dunning *et al.* 1994). The south-eastern limit of the distribution of this genus is around Newcastle, New South Wales, on the east coast. The southern limit on the west coast has yet to be determined. The taxonomy of *Photololigo* requires clarification before discussion of the biogeography of the group is useful.

Suborder OEGOPSIDA

In members of this order, the eyes lack a cornea and the lens is in direct contact with seawater. The mantle may be muscular or semi-gelatinous. The buccal connectives are six-, seven- or eight-pointed and connect to the ventral arms on either the dorsal or the ventral border. The funnel locking cartilage may be simple or complex and modified, or may be fused with the mantle. Both oviducts are developed. Paired nidamental glands are present, except in *Enoploteuthinae*; accessory nidamental glands are absent. If the hectocotylus is present, one or both ventral arms are modified.

Family Lycoteuthidae

This family of small to medium-sized squids, less than 200 mm mantle length, is characterised by a simple, straight funnel locking cartilage, biserial sharp-toothed suckers on the arms and tetraseriate suckers on the tentacular clubs (Fig. 13.10). The buccal connectives attach to the dorsal border of the ventral arms and light organs are present on the viscera, at the apex of the mantle and on the ventral surface of the eyes in some genera. Sexual dimorphism is pronounced in some genera, in which males have brachial photophores and larger, more numerous, mantle photophores. The posterior mantle and the dorso-lateral arms are elongate in males. The four genera are divided into two subfamilies. The *Lampadioteuthinae* include only the genus *Lampadioteuthis*, and the *Lycoteuthinae* contain *Lycoteuthis*, *Selenoteuthis* and *Nematolampas*. These subfamilies are distinguished by the number of light organs on the eyes, four compared with five, respectively (Roper *et al.* 1969; Toll 1983).

Pfeffer (1912) described a specimen of *Lycoteuthis diadema* from south of Western Australia. *Lycoteuthis diadema* and *L. lorigera* were recorded for the first time from south-eastern Australian waters by Lu & Phillips (1985). No lampadioteuthine species have been recorded from Australian waters.

The considerable sexual dimorphism apparent in this relatively rare family (Fig. 13.10) resulted in taxonomic confusion until additional specimens of both sexes were examined recently (Toll 1983). Male *L. diadema* diverge from the typical oegopsid pattern in having paired genital ducts (Voss, G.L. 1962), although whether this is characteristic of all lycoteuthids awaits the examination of further specimens. No information regarding the life history of any lycoteuthid is available from Australian waters or elsewhere.

Recent studies of the feeding biology of a continental slope fish, *Macruronus novaezelandiae* (blue grenadier), around Tasmania have shown that lycoteuthids are a significant part of the diet of this species (Bulman & Blaber 1986). Around New Zealand, petrels commonly feed on lycoteuthids (Imber 1975) and these squids are also preyed upon by sperm whales and dolphins elsewhere (Clarke 1966). Lycoteuthids elsewhere are known to feed on pelagic crustaceans and fishes, including myctophids (Voss, G.L. 1962). The radular arrangement in *Lycoteuthis lorigera* is illustrated in Figure 13.10C.

G.L. Voss (1962) considered that *L. diadema* in the Gulf of Mexico occurs predominantly at depths of 300–600 m, with larvae in the upper 50 m. Its recent occurrence in demersal trawl catches off eastern Tasmania suggests that this species may be on or close to the seabed during part of the day. Extensive diel vertical migration is characteristic of the genus *Selenoteuthis* elsewhere and is suspected by Roper & Young (1975) to be typical of the family. Of the four recognised genera, only *Lycoteuthis* occurs in Australian waters; this genus has a worldwide distribution in subtropical oceanic waters. *Lycoteuthis diadema* and *L. lorigera* are known from off southern New South Wales and eastern Tasmania. Further clarification of their Australian distribution awaits the collection of additional specimens.

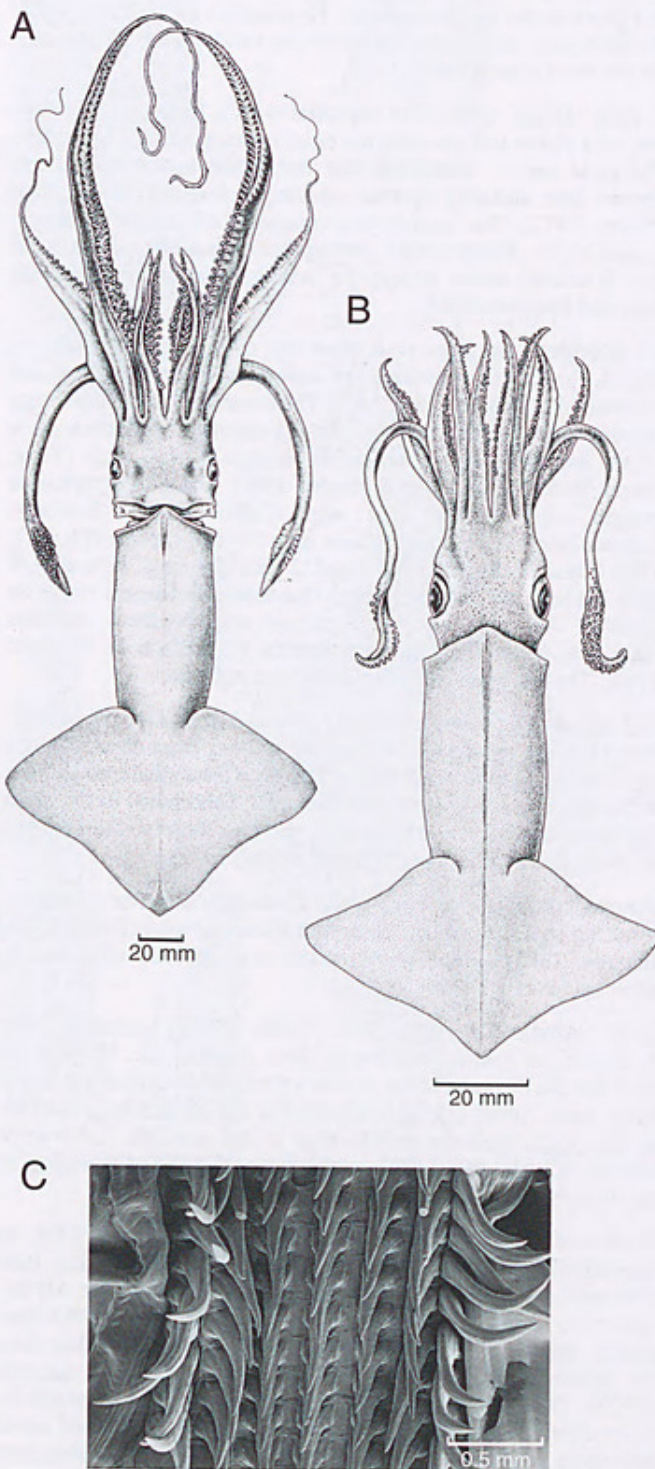


Figure 13.10 Family Lycoteuthidae. *Lycoteuthis lorigera*, a benthopelagic species common on the continental slope waters: A, male, dorsal view; B, female, dorsal view; C, portion of radula, showing several transverse tooth rows.

[A, B, K. Hollis; C, C.C. Lu]

Family Enoploteuthidae

The family Enoploteuthidae is represented in Australian waters mainly by an abundance of small to medium-sized mesopelagic species, all generally of less than 150 mm mantle length (Fig. 13.11A–E). Enoploteuthids are characterised by a simple, straight funnel locking apparatus, sharp-toothed suckers or suckers and hooks arranged in biserial rows on the arms and four rows on the tentacular clubs. Buccal connectives attach to the dorsal border of the ventral arms and light organs are present in adults of all genera. One or both of the ventral arms are hectocotylised in males. Three well-defined subfamilies designated by Pfeffer (1912) have become widely accepted (Roper *et al.* 1969; Riddell 1985), and are used in this treatment; these subfamilies were elevated to family level by Clarke & Trueman (1988).

The Enoploteuthinae have many small photophores on the ventral surface of the mantle, head and arms and large photophores on the eyeballs. Adults are not more than 150 mm mantle length.

In the Pyroteuthinae, photophores are present on the viscera and eyeballs, and embedded in the tentacles. Adults are not more than 60 mm mantle length.

The Ancistrocheirinae lack photophores on the eyeballs but have regularly spaced large bead-like photophores on the ventral and lateral surfaces of the mantle, head and tentacles. Adults are not more than 500 mm mantle length.

Berry (1918) described the first enoploteuthid recorded in Australian waters, *Enoploteuthis galaxias*, from material collected during the trawling investigations of the F.I.S. *Endeavour* in Bass Strait (Fig. 13.11A, F; Pl. 18.12). Paralavvae of three additional species were described from the New South Wales coast by Allan (1945), and Nesis (1979a) provided an overview of the zoogeography of the common oceanic representatives of this family from the Australian region. Clarke (1980) and Clarke & MacLeod (1982) recognised ancistrocheirine squids in the diets of sperm whales from south-western Australia and the Tasman Sea respectively. At least eight species were recorded by Brandt (1983) from an East Australian Current warm-core eddy. Lu & Phillips (1985) provided the most recent Australian checklist.

Hooks are strongly developed on the arms of all Australian enoploteuthids and on the tentacular clubs of all genera, except *Pterygioteuthis*, in which sucker rings only are present with slender pointed teeth on their distal margins. Fin shape varies among the subfamilies. In the Enoploteuthinae, the lanceolate subterminal fins have slightly concave posterior borders (Fig. 13.11A). In the Ancistrocheirinae, the large fins with slightly convex posterior margins extend almost the entire length of the mantle. The semi-gelatinous posterior tip of the mantle in these subfamilies is extended posteriorly in several species. The fins of pyroteuthine squids are nearly circular in outline with the sharp conus of the gladius obvious at the posterior tip of the mantle (Fig. 13.11D, E). The lateral arms are keeled in many enoploteuthine and pyroteuthine species. The arrangement, size and number of light organs in enoploteuthids are genus and species specific characteristics and their structure and function have been studied intensively in the same and closely related species elsewhere. These structures may provide concealment from potential predators through counter-illumination, the obliteration of the animal's silhouette through bioluminescence from below (Young, R.E. 1977, 1983). Radulae from species in each subfamily are illustrated in Figure 13.12.

Reproductive organs are typically oegopsid, except in the Enoploteuthinae which lack nidamental glands, and have the oviducal glands strongly developed. Hectocotylisation in males shows considerable variation between species. In the Enoploteuthinae (Fig. 13.11F), Ancistrocheirinae and in the genus *Pyroteuthis*, enlarged protective membranes are evident distally on the edges of the hook-bearing surface of the ventral arms of mature males. Hooks are modified in *Pyroteuthis* with the

development of a secondary cusp. All hooks are replaced in *Pterygioteuthis* by a single chitinous plate housed in a fleshy pocket midway along the oral surface of the ventral arm. Spermatophores are transferred to the nuchal crest region of females in some species, but no structures for their storage have been described (Roper *et al.* 1969; Riddell 1985).

No comprehensive life history data are available for enoploteuthids from Australian waters. Most squids deposit their eggs in masses. However, some female enoploteuthids release individual eggs into the plankton. Around Hawaii, eggs and larvae of enoploteuthine species closely related to those in Australian waters are common in near surface waters, although spawning locations are unknown (Young, R.E. & Harman 1986). Preliminary studies provide some indication of reproductive patterns in Australasian waters. Brandt (1983) found multimodal size distributions for *Abraliopsis gilchristi* and *Pterygioteuthis gemmata* from an eddy off the New South Wales coast. However, in this same study only a unimodal distribution was evident for *P. giardi*, perhaps indicating that congeners do not necessarily display similar reproductive patterns. In slope waters off New South Wales in the summer months, mature female *Ancistrocheirus* sp. have been recovered from the stomachs of sharks (Dunning & Stevens unpublished data) and probable spawning populations of *Enoploteuthis galaxias* have been sampled in demersal trawls (Dunning & Brandt 1985).

Riddell (1982) concluded from size frequencies and data on reproductive condition that *Pyroteuthis margaritifera* and *Pterygioteuthis gemmata* spawn during a single restricted period in summer in New Zealand waters and the largest mature females were larger than the males, as appears to be generally the case in enoploteuthids. In contrast, *Abraliopsis gilchristi* is believed to have a protracted summer spawning season. A trimodal size distribution in *Abralia astrolineata* suggested that the population may have three discrete spawning periods during the year. Off southern Japan, *A. andamanica* also displays a multimodal size distribution, and spawning apparently occurs in late summer to early winter (Kubota, Koshiga & Okutani 1982). Mature females of this species were caught off the Australian North West Shelf in late winter (Dunning & Lindholm unpublished data).

Females of enoploteuthine and pyroteuthine species that mature at about 50 mm mantle length are capable of producing between 10 000 and 20 000 eggs, typically with a maximum diameter of 1.2 mm (Kubota *et al.* 1982; Riddell 1982). Ripe eggs of mature *Ancistrocheirus* are large for oegopsids, reaching 3 mm over the long axis (Dunning unpublished data). Growth rates of enoploteuthid squids have not been studied although the preponderance of large females seen in populations of many species perhaps suggests that males have shorter life spans than females (Kubota *et al.* 1982; Riddell 1982; Brandt 1983).

Enoploteuthids are among the most commonly caught squids in midwater trawls. This abundance in the epipelagic and mesopelagic zones is reflected in their prevalence in the diets of tunas and lancetfishes, sharks and marine mammals (Rancurel 1970; Rancurel 1976; Wolff 1982; Okutani & Tsukada 1988; Dunning *et al.* 1993). Small enoploteuthids feed predominantly on pelagic crustaceans, particularly euphausiids, and larger individuals also take fishes and smaller squids (Riddell 1982). Representative radular arrangements are illustrated in Figure 13.12 for the three subfamilies.

Elsewhere, enoploteuthids are known to be diel vertical migrators and also show ontogenetic descent. Larval enoploteuthine squids are most abundant at depths of 100–150 m during the day, and at 30–50 m at night (Young, R.E. & Harman 1986). Adults occur at depths of 300–600 m during the day, migrating to the upper 150 m at night (Roper & Young 1975).

Although no enoploteuthids are fished in Australian waters, two species grow large enough to be of commercial interest. Individuals of an *Ancistrocheirus* species attain lengths in excess of 400 mm mantle length, but this species is unlikely to find local market acceptance because of the semi-gelatinous texture of its mantle. *Enoploteuthis galaxias* reaches 110 mm mantle length,

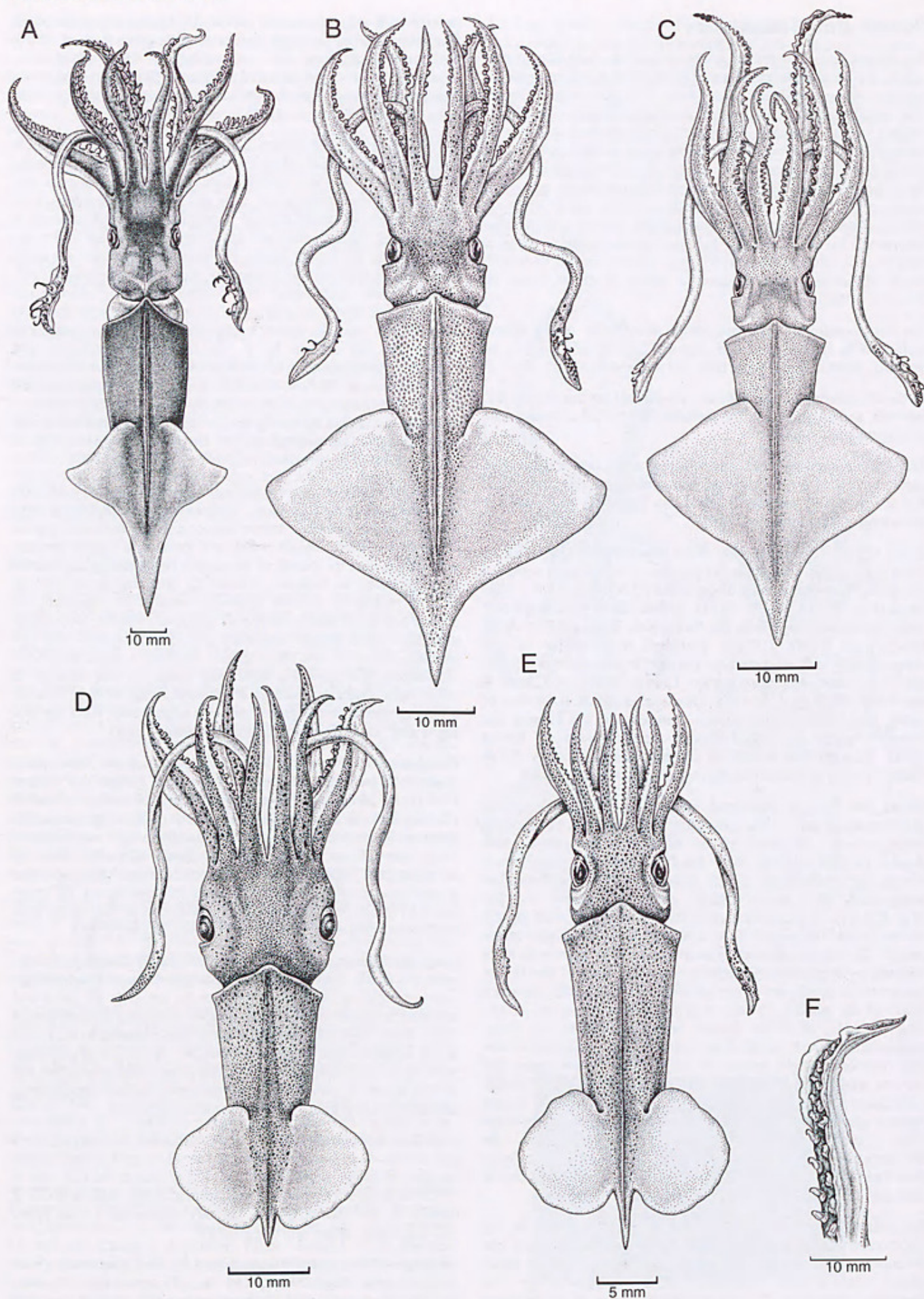


Figure 13.11 Family Enoploteuthidae. Members of this diverse, abundant family of oceanic squids occur from the surface to the bathypelagic zone. A–E, dorsal views: A, *Enoploteuthis galaxias*; B, *Abralia andamanica*; C, *Abraliopsis gilchristi*; D, *Pyroteuthis margaritifera*; E, *Pierygioteuthis gemmata*. F, hectocotylus of *Enoploteuthis galaxias*. [K. Hollis]

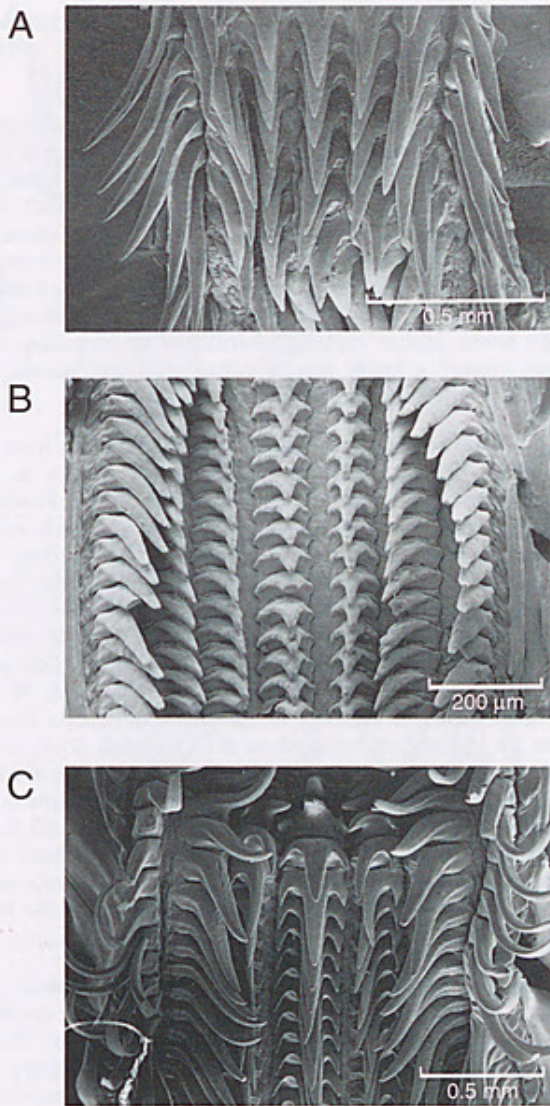


Figure 13.12 Family Enoploteuthidae. Representative enoploteuthine, pyroteuthine and ancistrocheirine radulae, showing several transverse tooth rows. A, *Enoploteuthis galaxias*. B, *Pyroteuthis margaritifera*. C, *Ancistrocheirus lesueurii*. [C.C. Lu]

similar to that of the commercially important enoploteuthid of Japanese waters, *Watasenia scintillans*, and is occasionally abundant in demersal trawl catches off the eastern Australian coast (Dunning & Brandt 1985).

None of the 12 species recorded from Australian waters is endemic, although *Enoploteuthis galaxias* appears to be restricted to southern Australia and New Zealand. Nesis (1979a) assigned nine pelagic enoploteuthid species from the Australian region to tropical, subtropical and peripheral groups. The distributional boundaries of these major groupings are defined largely by the Tropical and Subtropical Convergences. However, none of these species has been the subject of detailed study.

Enoploteuthids of all life stages are caught readily in good condition in sampling nets and, because of their size, can be kept in onboard aquaria. They have proven to be ideal subjects for the laboratory study of bioluminescence in Hawaiian waters (Young, R.E. 1983).

Family Octopoteuthidae

The family Octopoteuthidae includes two genera of medium-sized to large squids, up to more than 1000 mm mantle length, characterised by a broad, straight funnel locking apparatus and very broad fins extending almost the length of the mantle. The arms bear biserial hooks and sometimes small biserial suckers at their tips. The tentacles, which in all larvae carry a few distal club suckers, are lost in adults (Fig. 13.13). Buccal connectives attach to the ventral

borders of the ventral arms. Several small, spindle-shaped photophores are present on the tips of all eight arms in the genus *Octopoteuthis*. A single very large photophore is present at the tip of each dorso-lateral arm in the monotypic genus *Taningia*. Hectocotylisation in males is unknown (Roper *et al.* 1969). Species within the genus *Octopoteuthis* are poorly delineated, and the genus is badly in need of revision (Lu & Phillips 1985).

The genus *Octopoteuthis* was recognised first from the south-western Pacific by Rancurel (1970). Nesis (1979a) also reported *T. danae* from the Australian region. Further records of octopoteuthids are provided by Clarke (1980) from material in sperm whale stomachs from off Albany, Western Australia, and Zeidler (1981) reported large moribund *T. danae* from off South Australia.

In larval *Octopoteuthis* body proportions change rapidly during growth up to 15 mm mantle length. Eyes which appear stalked initially, become sessile at mantle lengths of 10–15 mm. By this size, most specimens have lost their tentacles also (Stephen 1986). The mantle of some *Octopoteuthis* species has a thick gelatinous layer over the pigmented skin-like layer; it is especially thick over the tail region. Clarke (1980) suggests that longitudinal grooving in the anterior mantle jelly is characteristic of females in at least one species and that this area of the mantle is where spermatophores are lodged by the males. Clarke (1967) estimated that a female of a species of *Taningia* of 1400 mm mantle length carried 250 000 ovarian eggs. No life history studies of octopoteuthids have been made in Australian waters or elsewhere. The radular arrangement in *Octopoteuthis sicula* is illustrated in Figure 13.13B.

Octopoteuthids form a significant part of the diet of sperm whales off south-western Australia and in the Tasman Sea (Clarke 1980; Clarke & MacLeod 1982). They are included also in the diet of lancetfishes in the Coral Sea (Rancurel 1970; Okutani & Tsukada 1988) and of hammerhead, blue and tiger sharks off eastern Australia (Dunning *et al.* 1993).

From their numbers in stomachs of individual sperm whales, Clarke (1980) concluded that *O. rugosa* is a schooling species, but that *Taningia* may be solitary or form only small groups. Small specimens of *Taningia* species occur in the upper 200 m, while adults are more abundant in depths of more than 1000 m, suggesting that ontogenetic descent may occur (Clarke 1967). Roper & Young (1975) concluded that larvae of *Octopoteuthis* species off California are distributed in a narrow depth band from 200–400 m during the day, and spread throughout the upper 500 m at night. However, Stephen (1986) was unable to find conclusive evidence of diel variation in the depth distribution of *Octopoteuthis* larvae collected primarily from the North Atlantic.

Until their taxonomy has been clarified, the distribution of octopoteuthid species in Australian waters will remain poorly known. *Octopoteuthis megaptera* is considered to occur from tropical waters to as far as 36°S off the east coast and to Cape Leeuwin in the west (Nesis 1979a). *Taningia* occurs as far south as 44°S.

Members of this family have soft gelatinous bodies and have no commercial fisheries potential, although some reach very large sizes. They are readily damaged during capture in sampling nets, and therefore are unsuitable for laboratory study.

Family Onychoteuthidae

Onychoteuthids are medium-sized to very large oceanic squids, up to 2 m mantle length, with a strong, muscular torpedo-shaped mantle (Fig. 13.14). The family is characterised by a simple, straight funnel locking cartilage, biserial and sometimes smooth suckers on the arms and biserial hooks. There are two rows of marginal suckers on the tentacular clubs in the immature stages. The buccal connectives attach to the ventral border of the ventral arms and visceral light organs are present in the genus *Onychoteuthis*. Hectocotylisation is not evident in males of this family (Roper *et al.* 1969).

13. SUBCLASS COLEOIDEA

Onychoteuthis rutilis, described by Gould (1852) from off Sydney, New South Wales, was the first-recorded onychoteuthid from Australian waters. Allan (1945) assigned onychoteuthid larvae from off New South Wales to this species. Additional species have been recorded from the Australian region by Rancurel (1970, 1976) and Nesis (1979a). The most recent checklist of Australian onychoteuthids includes all genera except the Antarctic *Kondakovia* (Lu & Phillips 1985). Animals assigned to the genus *Onykia* are now known to be immatures of a *Moroteuthis* species (Tsuchiya & Okutani 1991).

The large muscular fins are generally rhomboidal. In some species of the genera *Moroteuthis* and *Ancistroteuthis*, fins and mantle are attenuated posteriorly. In contrast to the typically muscular mantle of other genera, *Chaunoteuthis* has a soft gelatinous body. Numerous distinctive dorsal pleats are present in the neck region in *Onychoteuthis* and *Chaunoteuthis*, and the

skin of *Moroteuthis* and *Kondakovia* often contains subcutaneous papillae and ridges. Lateral arms have swimming keels in some of the larger species.

Reproductive organs are typically oegopsid and vary little within the family. Hectocotylisation has not been observed in any male onychoteuthid, although Gilly, Horrigan & Fraley (1986) noted that male *Moroteuthis* from off California had only a prominent fleshy keel on the ventral arms. Spermatophores appear to be introduced into the mantle of female *Onychoteuthis* and *Moroteuthis* from the elongate penis, through a longitudinal cut made midway between the head and fins of the female using the beak or perhaps the tentacular hooks. Mature copulated females of *O. borealijaponica* off Japan display a bright orange colour over the viscera and mantle (Clarke 1980; Murata, Iishii & Osaka 1982).

Age and growth of onychoteuthids in Australian waters have not been studied. Indeed the biology of only one species in this family, *O. borealijaponica*, is relatively well known. Reaching over 300 mm mantle length, this species inhabits temperate waters of the north-western Pacific, and apparently spawns from late autumn to winter in warmer subtropical waters to the south. Larvae have been found in the upper 150 m of the water column but not at the surface. The growth rate of adults is up to 20 mm per month and the life span approximately one year. Generally females are larger than contemporary males (Okutani & Murata 1983). *Moroteuthis* is believed to spawn in submarine canyon areas on the upper continental slope off California (Gilly *et al.* 1986). From examination of material collected from sperm whale stomachs, Clarke (1980) concluded that *M. robsoni* spawns in the austral autumn on the lower continental slope (2500 m) off South Africa. Clarke suggested that the young grow to more than 500 mm mantle length over a period of approximately two years, before a single spawning is followed by a wasting of the body musculature and death.

Onychoteuthids are oceanic forms, occasionally encountered in continental slope waters where they may be caught in demersal trawls. Elsewhere they feed on a broad range of fishes, crustaceans including krill, squids and other pelagic molluscs, and are at least partially cannibalistic. The radular arrangement in *Moroteuthis robsoni* is illustrated in Figure 13.14C. Known predators include lancetfishes and tunas, pelagic sharks, whales, dolphins, seals and albatrosses (Rancurel 1970; Rancurel 1976; Clarke 1983; Okutani & Tsukada 1988; Dunning *et al.* 1993).

Onychoteuthids form schools. Juvenile *Onychoteuthis* are able to leap above the surface to escape predators, as do ommastrephids, and sometimes are found on the decks of vessels. Off Japan, *O. borealijaponica* appears to make a north-south migration from feeding grounds to the warmer spawning grounds (Okutani & Murata 1983), although whether such migrations are typical, even of temperate onychoteuthids, remains to be confirmed. Little information regarding the vertical distribution of any onychoteuthid species is available. Immatures of *Moroteuthis* species share with the much larger ommastrephid, *Ommastrephes bartrami*, and some epipelagic octopods, the deep blue dorsal day colouration characteristic of the neuston generally (Roper & Young 1975).

The presence of immature *Moroteuthis* in the stomachs of lancetfishes and yellowfin tunas further confirms their epipelagic distribution (Rancurel 1970; Fujita & Hattori 1976; Rancurel 1976). Clarke & Lu (1974) recorded juvenile *Onychoteuthis banksi* from 100–1250 m in the North Atlantic.

In Australian waters, onychoteuthids are not fished commercially, although sometimes members of the genus *Moroteuthis* are caught incidentally in demersal trawls in continental slope waters (300–600 m) off both the north-western and southern coasts (Dunning & Brandt 1985). In Subantarctic waters off New Zealand, they make up a significant proportion of the trawled squid catch (Roberts 1978). The flesh of *Moroteuthis robsoni* caught off California proved to be unpalatable (Clarke 1966).

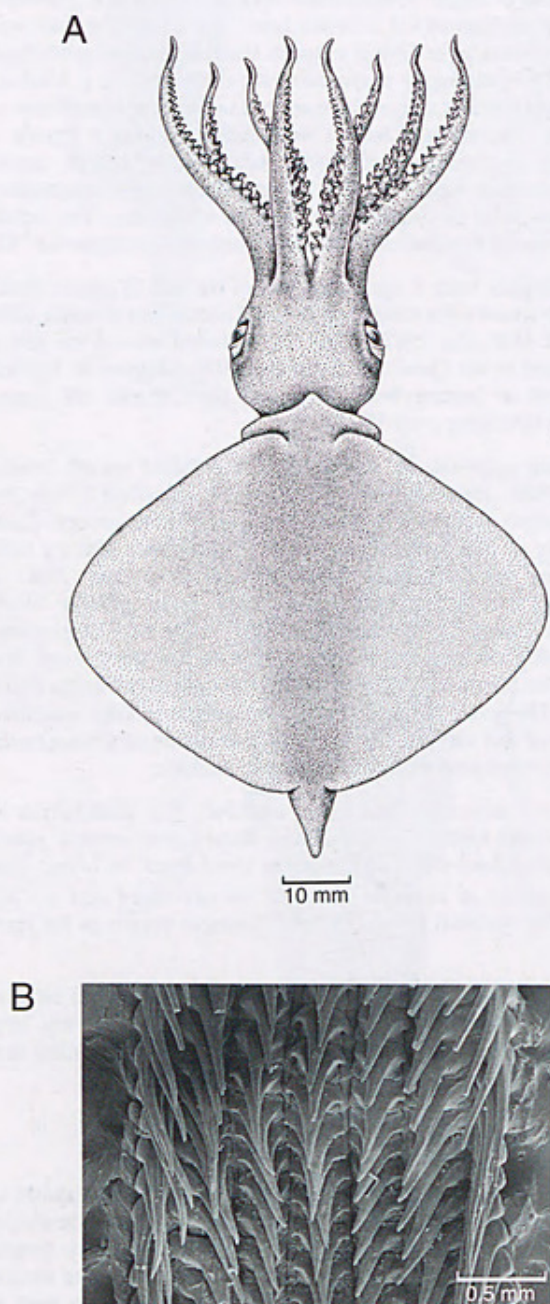


Figure 13.13 Family Octopoteuthidae. The large fins, biserial hooks on all arms and absence of tentacles in adults are typical of the family. A, *Octopoteuthis sicula*, dorsal view. B, portion of radula of *Octopoteuthis sicula*, showing several transverse tooth rows. [A, K. Hollis; B, C.C. Lu]

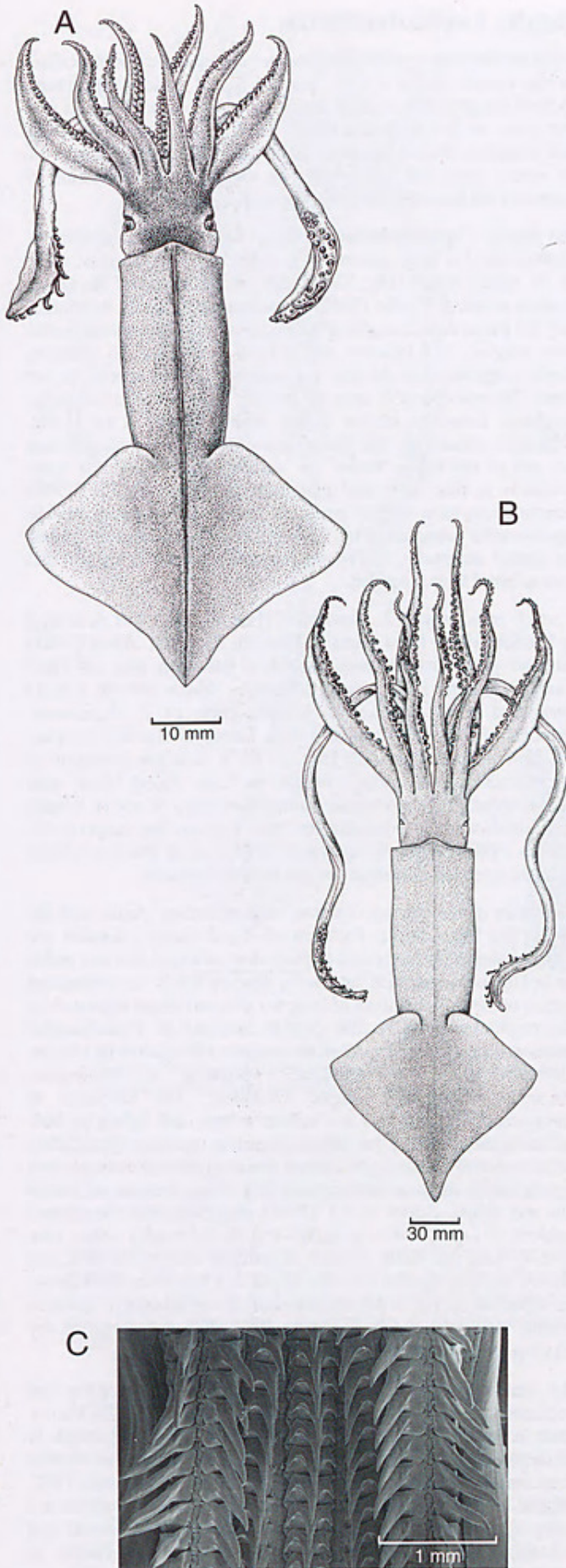


Figure 13.14 Family Onychoteuthidae. These oceanic squids are medium-sized to large epipelagic, mesopelagic or benthic inhabitants of the bathyl zones. A, *Onychoteuthis banksi*, dorsal view. B, *Moroteuthis loennbergi*, dorsal view. C, portion of radula of *Moroteuthis robsoni*, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

Onychoteuthid squids occur in all oceans. With the exception of *Kondakovia*, all currently recognised genera occur in Australian waters but generally their distributions are poorly defined. Nesis (1979a) considered *Onychoteuthis* to be a very eurythermal, mesopelagic and epipelagic tropical species, in waters as far south as 44°S. Fossil statoliths of late Pliocene *Moroteuthis* have been found in California (Clarke & Fitch 1979), although none has yet been discovered in Australia.

As was noted for ommastrephids, collection and laboratory maintenance of these muscular, highly mobile molluscs present major difficulties and have not been attempted in Australian waters. Large scale commercial trawls are necessary to catch the larger adults although larvae have been collected successfully using large tow nets and hand-held scoop nets.

Family Cycloteuthidae

The poorly known family Cycloteuthidae includes two genera of medium-sized to large squids, generally less than 500 mm in mantle length (Fig. 13.15). These apparently mesopelagic species have rarely been encountered in Australian waters. Cycloteuthids are characterised by a subtriangular funnel locking cartilage. The toothed or smooth suckers are arranged biserially on the arms and tetraserally on the tentacular clubs. Buccal connectives attach to the ventral border of the ventral arms, and light organs are present in adults around the eyes, on the ventral mantle and at the arm bases in some species. Fins extend anteriorly for more than 70% of the mantle length in adults. In the genus *Cycloteuthis*, the mantle is elongate posteriorly, forming a distinct tail (Fig. 13.15A) and the ink sac bears a single light organ. In *Discoteuthis*, a tail is lacking, the fins are very large and round (Fig. 13.15B), and mantle photophores only are present. No mature males of any cycloteuthids have been described in the literature, and the form or even the presence of hectocotylation is unknown (Young, R.E. & Roper 1969a).

This family was described first from Australian waters by Clarke (1980), who found specimens of *Cycloteuthis akimushkini* (perhaps a junior synonym of *C. sirventyi*) among the stomach contents of sperm whales caught off Albany, Western Australia. Later, *Cycloteuthis* and beaks assigned tentatively to *Discoteuthis* were also found in whales from the Tasman Sea (Clarke & MacLeod 1982). Lu & Phillips (1985) recorded *Discoteuthis discus* from off the south-eastern Australian coast.

The mantle of cycloteuthids is not strongly muscular. A central layer of gelatinous connective tissue lies between thin inner and outer layers of strong, circular muscle. The head is also covered with moderately thick semi-gelatinous tissue (Clarke 1980). In contrast to the superficially similar octopoteuthids, the fins of *Discoteuthis* are separate (Fig. 13.15B) and insert directly onto the shell sac of the gladius. Those of *Octopoteuthis* are fused and continuous across the dorsal midline, and pass over the shell sac. Corresponding differences in the structure of the gladius also occur. That of *Octopoteuthis* is thin and fragile, compared to the very thick, rigid supporting structure of *Discoteuthis* (Young, R.E. & Roper 1969a).

No studies of cycloteuthid life history have been undertaken in Australia or elsewhere, because they are rarely captured. Cycloteuthids form part of the diet of sperm whales in the Australian region (Clarke 1980; Clarke & MacLeod 1982) and elsewhere (Clarke 1983). The radular arrangement in *Discoteuthis laciniosa* is illustrated in Figure 13.15C.

The few records of this family from Australian waters and elsewhere are uninformative about their vertical distribution. Elsewhere all three species recognised by R.E. Young & Roper (1969a) have been captured in the upper 200 m at night.

Cycloteuthids have not been recorded in sufficient abundance in Australian waters to indicate any commercial fisheries potential or to assess adequately their geographic distribution.

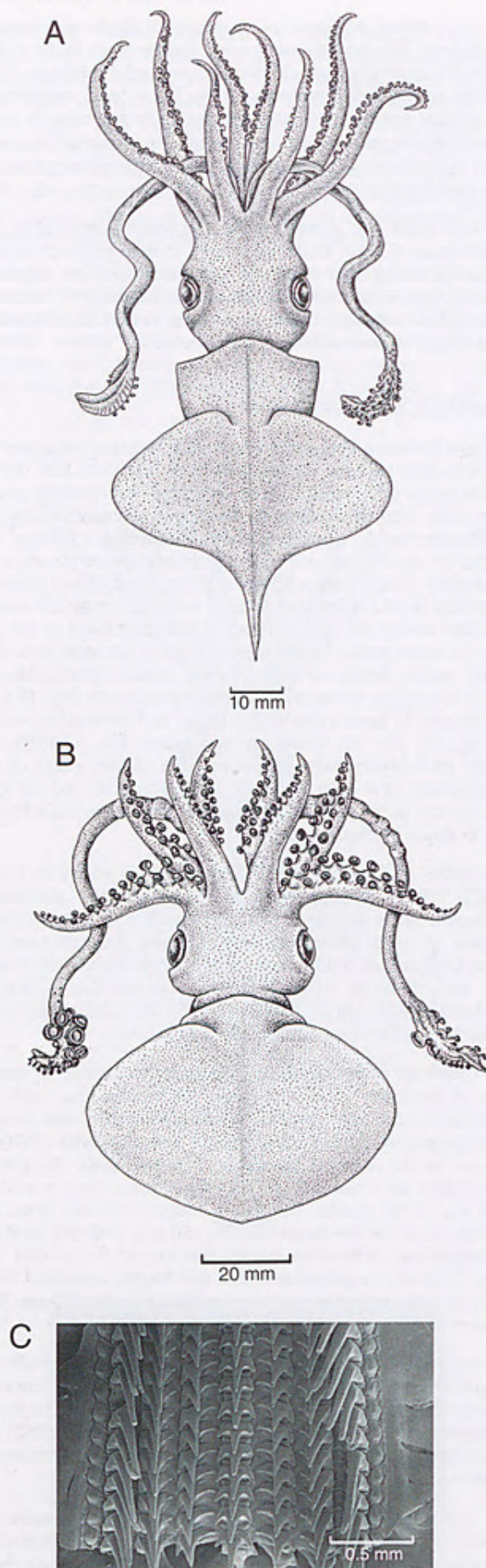


Figure 13.15 Family Cycloteuthidae. A, *Cycloteuthis sirventyi*, dorsal view. B, *Discoteuthis discus*, dorsal view. C, portion of radula of *Discoteuthis laciniosa*, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

Family Lepidoteuthidae

Lepidoteuthids are characterised by the presence of distinct 'scales' on the mantle and a simple, straight funnel locking apparatus. Suckers are generally toothed, and form two rows on the arms and four rows on the tentacular clubs. Adult *Lepidoteuthis grimaldii* lack tentacles. Buccal connectives attach to the ventral border of the ventral arms, and light organs are absent. Hectocotylisation in males has not been described (Roper *et al.* 1969).

The family Lepidoteuthidae currently includes three genera of medium-sized to large oceanic and continental slope species, up to 1.0 m mantle length (Fig. 13.16), but the taxonomy of the group requires revision. Clarke (1980) considered this family to contain only the genus *Lepidoteuthis*; *Pholidoteuthis* and *Tetronychoteuthis* were assigned to a separate family Pholidoteuthidae. In addition, Clarke suggested that the two currently recognised species in the genus *Tetronychoteuthis* may be growth stages of *Pholidoteuthis boschmai*. Based on studies of the 'scales', Roper & Lu (1989, 1990) also pointed out that the present grouping is not natural, and that use of the terms 'scales' or 'cartilaginous scales' for these structures is inaccurate and inappropriate. Roper & Lu (1990) introduced the term 'dermal cushions' to refer to these structures in *Lepidoteuthis grimaldii* (Fig. 13.16D) and *Pholidoteuthis adami*; the dermal structures on *Tetronychoteuthis* species (Fig. 13.16B) were referred to as tubercles.

A single specimen of *T. dussumieri* (Fig. 13.16A) was described by Pfeffer (1912) from south of Western Australia. Allan (1945) assigned juvenile specimens caught in plankton nets off New South Wales to *T. massyae*, a species which Pfeffer (1912) considered might represent a juvenile form of *T. dussumieri*. Rancurel (1970, 1976) reported both *Tetronychoteuthis massyae* and *Lepidoteuthis grimaldii* (Fig. 13.16C) from the stomachs of lancetfishes (*Alepisaurus*) caught in the Coral Sea, and lepidoteuthids were among the stomach contents of sperm whales from south-western Australia and the Tasman Sea respectively (Clarke 1980; Clarke & MacLeod 1982). Lu & Phillips (1985) included three lepidoteuthid species in their checklist.

The nature of the 'dermal cushions' and 'tubercles' varies with the genus. The large dermal cushions of *Lepidoteuthis grimaldii* are diamond-shaped to hexagonal in form, and arranged like fish scales but lacking bony structure. Internally, they are highly vacuolated and contain numerous chambers of irregular size and shape separated by thin membranous walls. The dermal cushions of *Pholidoteuthis adami* are irregularly rounded to roughly pentagonal in outline. Internally, they are vacuolated, consisting of continuous, thin-walled, irregularly shaped chambers. The tubercles of *Tetronychoteuthis massyae* are stellate, minute and tightly packed. Each tubercle is roughly mushroom-shaped in profile, with a slightly concave central disc and a thick base. Internally the tubercle consists of very dense material interspersed with small vacuoles of varied size and shape. Roper & Lu (1990) suggested that the dermal cushions of *Lepidoteuthis grimaldii* and *Pholidoteuthis adami* may serve to store less dense solution containing ammonium ions, and thereby function together with the mantle as a buoyancy mechanism. The tubercles on *Tetronychoteuthis massyae* are thought to maintain laminar flow along the boundary layer during locomotion by reducing hydrodynamic drag.

The small number of specimens available in collections has precluded any comprehensive studies of lepidoteuthid life history either in Australia or elsewhere. The presence of lepidoteuthids in stomachs of lancetfishes, yellowfin tunas and sperm whales (Rancurel 1970, 1976; Clarke 1980; Clarke & MacLeod 1982; Okutani & Tsukada 1988) has been noted above. These squids are also preyed upon by pilot whales, dolphins, deep-sea sharks and scabbard fish (Clarke 1966). The radular arrangement in *Lepidoteuthis grimaldii* is illustrated in Figure 13.16E.

Pholidoteuthis species have been caught in demersal trawls in continental slope waters, but only during the day. Therefore, it seems likely that this species leaves the near-bottom waters and disperses into midwater at night (Roper & Young 1975). Clarke

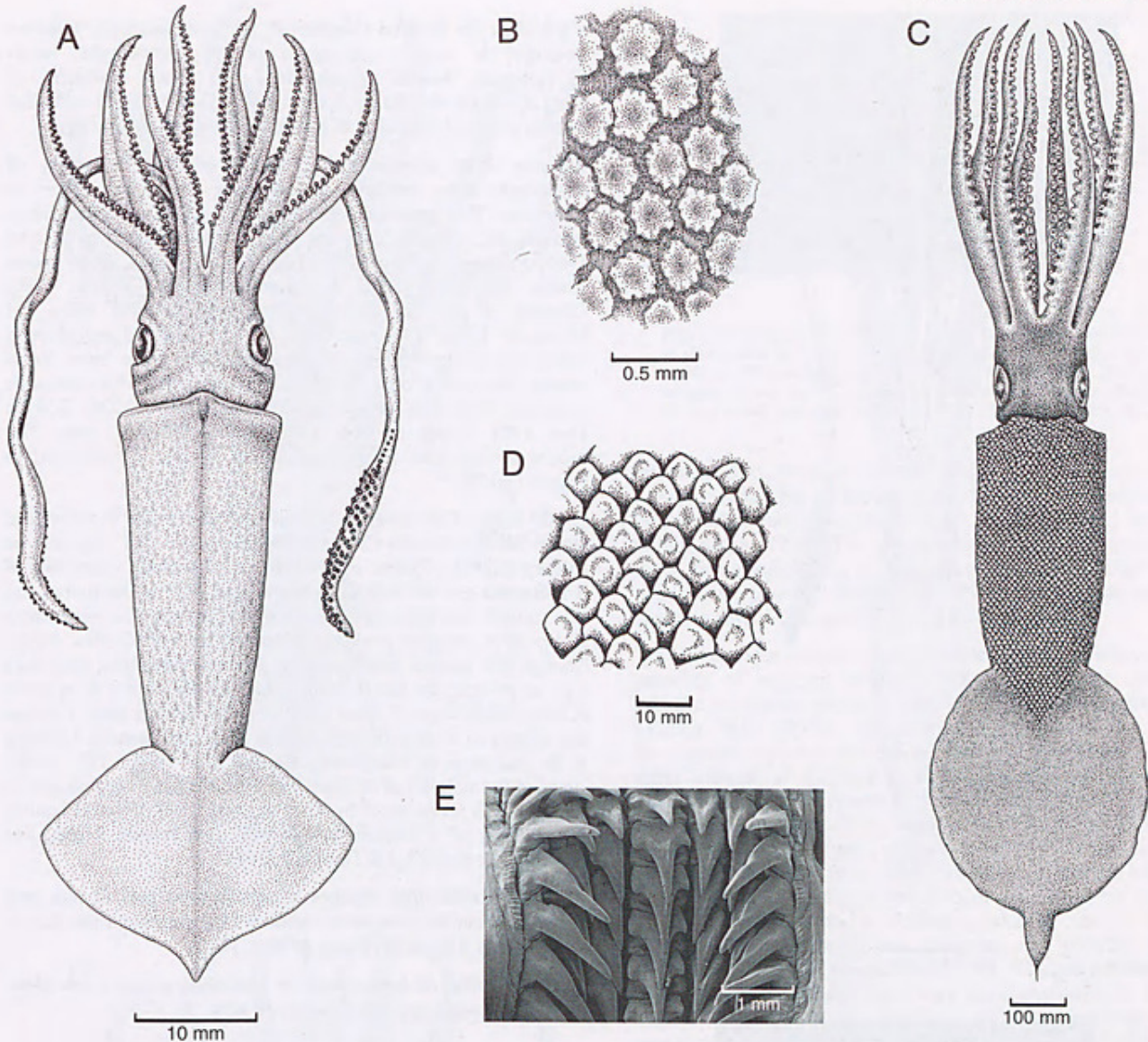


Figure 13.16 Family Lepidoteuthidae. These large squids are characterised by 'scales' on the mantle. A, B, *Tetranychoteuthis dussumieri*: A, dorsal view; B, section of mantle surface enlarged to show tubercles. C–E, *Lepidoteuthis grimaldii*: C, dorsal view; D, section of the mantle surface enlarged to show dermal cushions; E, portion of radula, showing several transverse tooth rows. [A–D, K. Hollis; E, C.C. Lu]

(1980) suggests that large individuals of *Pholidoteuthis* species may be solitary or occur in small groups. In the Gulf of Mexico however, schools of *P. adami* have been observed at the surface at night (Clarke 1966).

Although lepidoteuthids grow large enough to be of commercial interest, they have not been recorded in sufficient abundance in Australian waters to indicate any commercial fisheries potential, and too few specimens are available in existing collections to clarify their geographic distribution.

Family Architeuthidae

The 19 nominal species of giant squids within the monotypic family Architeuthidae are poorly defined and some workers have suggested that all specimens can be assigned to as few as three species (Roper & Boss 1982). The genus *Architeuthis* is characterised by a muscular mantle, short oval fins (Figs 13.17, 11.2) and a simple straight funnel locking cartilage. Suckers bearing many small, sharp teeth occur in two rows on the arms. A distinct cluster of small suckers and knobs is present at the proximal end of the tentacular club and larger quadrilateral suckers occur distally. Two longitudinal rows of alternating suckers and pads are present along the tentacular stalks. Photophores have not been described from any specimen and both

ventral arms are described as being hectocotylised in mature males (Knudsen 1957; Kjennerud 1958; Roper *et al.* 1969; Roper & Boss 1982).

A specimen of an *Architeuthis* species stranded in eastern Victoria, and assigned by Allan (1948) to *A. kirki*, was the first record of this family from Australian waters. A larval *Architeuthis* was caught in a midwater trawl in the upper 20 m off the central New South Wales coast in October 1981 and a live juvenile female was taken in this same region in the upper 300 m in January 1982 (Lu 1986).

Adults of species of *Architeuthis* are the largest living cephalopods (Fig. 11.2). They weigh more than 1 tonne, and have mantle lengths exceeding 4.5 m (Clarke 1966). A relatively high concentration of ammonium ions in the muscles of the mantle, head and arms provides buoyancy (Clarke, Denton & Gilpin-Brown 1979). The oxygen carrying capacity of the haemocyanin in the blood of *Architeuthis* is much less than that of other active oceanic squids, such as ommastrephids (0.3 versus 1.6–1.9 mM O₂). As haemocyanin's affinity for oxygen has a pronounced sensitivity to temperature, this low carrying capacity may limit the distribution of adults to low water temperatures. Their encounters with warm currents may result in suffocation and may explain the strong correlation of strandings in some areas with warm water inflow (Brix 1983).

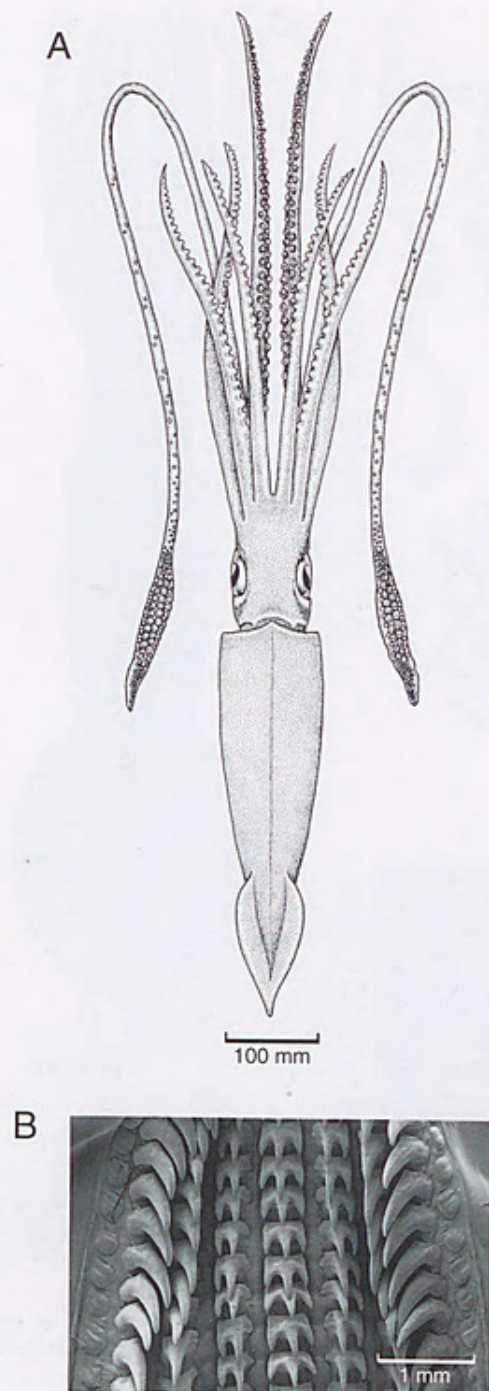


Figure 13.17 Family Architeuthidae. A, *Architeuthis* sp. from southern Australia, dorsal view. B, portion of radula of *Architeuthis* sp. showing several transverse tooth rows. [A, K. Hollis; B, C.C. Lu]

Size at maturity of male *Architeuthis* appears to be variable and may reflect specific differences. Specimens from 180 mm to more than 1 m mantle length elsewhere have been found with apparently viable spermatophores (Toll & Hess 1981). The size at which females first reach maturity is uncertain. Female *Architeuthis* do not have spermathecae. A recently captured female specimen with a mantle length of 2.4 m was found to be mated. Spermatophores were found embedded in the skin on both ventral arms. On one arm, the remains of several spermatophores up to 80 mm in length radiated under the skin from a single small entry point (ca 10 mm in diameter). They did not penetrate the arm musculature. It is unclear how the spermatophores are inserted; the male may inject the spermatophores with the large muscular penis or use his beak to make the entry wound through

which they are injected (Norman & Lu in manuscript). If either technique is correct, the status of the hectocotylus needs re-evaluation. Mature *Architeuthis* eggs reach diameters of 1.2–1.8 mm (Roeleveld & Lipinski 1991). Boyle (1986) estimated that the potential fecundity of a female at over 10 million eggs.

Because of its relative rarity, studies of the life history of *Architeuthis* have not been undertaken in Australian waters or elsewhere. The genus is recorded in the diets of lancetfishes, swordfishes, albacore tunas and sperm whales elsewhere (Clarke 1966; Roper & Young 1972; Toll & Hess 1981), from sperm whales and mako sharks in Australian waters (Clarke 1980; Dunning *et al.* 1993), and from sleeper sharks taken off Macquarie Island (Lu unpublished data). Fishes and cephalopods (including ommastrephids and histioteuthids) have been found among the stomach contents of the few specimens of *Architeuthis* examined elsewhere (Pérez-Gándaras & Guerra 1978; Toll & Hess 1981; Roper & Boss 1982; Lu unpublished data). The radular arrangement in an *Architeuthis* species is illustrated in Figure 13.17B.

On the basis of the numbers of *Architeuthis* remains in individual sperm whale stomachs Clarke (1980) suggested that they may be solitary animals. Recent examination of the blood chemistry of *Architeuthis* and the lack of strong musculature in the funnel and fins suggest that these animals are also relatively poor swimmers and passive, sluggish predators (Roper & Boss 1982; Brix 1983). Though the vertical distribution of adults is uncertain, they may live on or near the sea floor in depths of 500–1000 m or more (Clarke 1980; Roper & Boss 1982; Lu unpublished data). Perhaps the capture of a larva in near surface waters off eastern Australia is an indication of ontogenetic descent (Lu 1986). The growth rings on the statolith of *Architeuthis* were similar in appearance to daily growth rings found in other oegopsid and myopsid squids; the statolith of a juvenile female, 422 mm mantle length, had 153 rings (Jackson, Lu & Dunning 1991).

Although *Architeuthis* reaches a considerable size, it has little fisheries potential because ammonium ions present in the muscle tissue render it inedible (Roper & Boss 1982).

The distribution of *Architeuthis* in Australian waters is not clear, although all records are from south of 32°S.

Family Histioteuthidae

The monotypic family Histioteuthidae comprises medium-sized to large squids, less than 350 mm mantle length, characterised by a simple, straight funnel locking apparatus, unmodified toothed suckers arranged biserially on the arms, and in four and eight rows on the tentacular clubs. The family is readily distinguished by many large, anteriorly directed light organs over the surface of the mantle, head and arms (Fig. 13.18), more concentrated on the ventral surface. Buccal connectives attach to the dorsal border of the ventral arms and both the dorsal arms are usually hectocotylised in males. Adult histioteuthids have a large head, and the left eye is considerably larger than the right (Voss, N.A. 1969).

Berry (1918) described the first histioteuthid from Australian waters, *Histioteuthis miranda*, from a single adult specimen trawled off Gabo Island, Victoria. Larvae of this species were later reported from the New South Wales coast by Allan (1945) and additional species were recognised from the Tasman Sea by N.A. Voss (1969). At least eight histioteuthid species were identified from the stomach contents of sperm whales from south-western Australia and the Tasman Sea (Clarke 1980; Clarke & MacLeod 1982). In their checklist, Lu & Phillips (1985) listed ten Australian species.

R.E. Young (1975b) reviewed the function and peculiar modification of the asymmetrical eyes (Fig. 13.18), unique amongst oegopsid squids. The left eye is tubular, and in some specimens, may be twice the size of its smaller, hemispherical partner. It is thought to detect down-welling light during the day, primarily at depth. The mantle of most species of *Histioteuthis* is

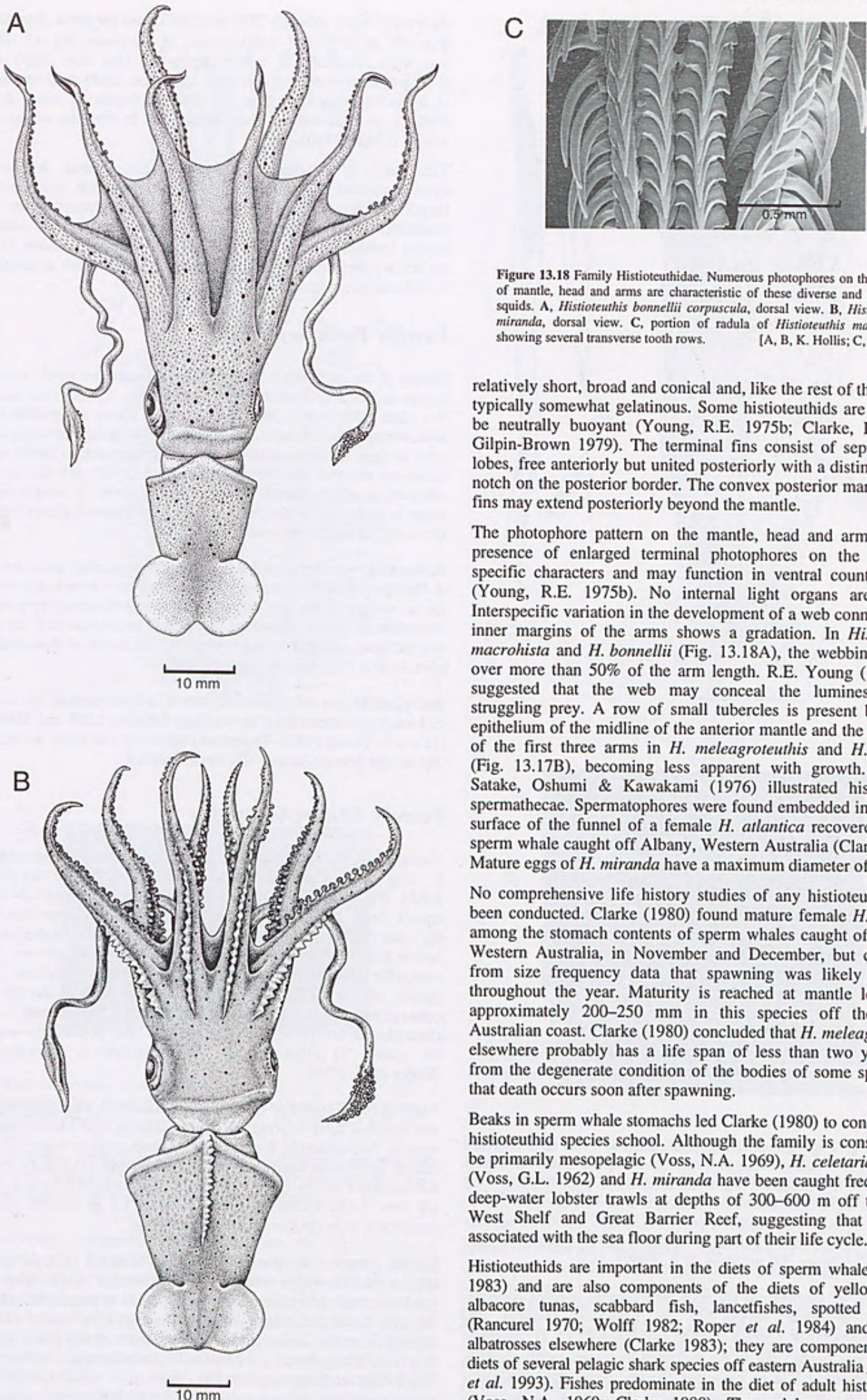


Figure 13.18 Family Histioteuthidae. Numerous photophores on the surface of mantle, head and arms are characteristic of these diverse and abundant squids. **A**, *Histioteuthis bonnellii corpuscula*, dorsal view. **B**, *Histioteuthis miranda*, dorsal view. **C**, portion of radula of *Histioteuthis macrohista*, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

relatively short, broad and conical and, like the rest of the body, is typically somewhat gelatinous. Some histioteuthids are known to be neutrally buoyant (Young, R.E. 1975b; Clarke, Denton & Gilpin-Brown 1979). The terminal fins consist of separate oval lobes, free anteriorly but united posteriorly with a distinct median notch on the posterior border. The convex posterior margin of the fins may extend posteriorly beyond the mantle.

The photophore pattern on the mantle, head and arms and the presence of enlarged terminal photophores on the arms are specific characters and may function in ventral countershading (Young, R.E. 1975b). No internal light organs are present. Interspecific variation in the development of a web connecting the inner margins of the arms shows a gradation. In *Histioteuthis macrohista* and *H. bonnellii* (Fig. 13.18A), the webbing extends over more than 50% of the arm length. R.E. Young (1983) has suggested that the web may conceal the luminescence of struggling prey. A row of small tubercles is present below the epithelium of the midline of the anterior mantle and the basal half of the first three arms in *H. meleagroteuthis* and *H. miranda* (Fig. 13.17B), becoming less apparent with growth. Okutani, Satake, Oshumi & Kawakami (1976) illustrated histioteuthid spermathecae. Spermatophores were found embedded in the inner surface of the funnel of a female *H. atlantica* recovered from a sperm whale caught off Albany, Western Australia (Clarke 1980). Mature eggs of *H. miranda* have a maximum diameter of 0.8 mm.

No comprehensive life history studies of any histioteuthid have been conducted. Clarke (1980) found mature female *H. miranda* among the stomach contents of sperm whales caught off Albany, Western Australia, in November and December, but concluded from size frequency data that spawning was likely to occur throughout the year. Maturity is reached at mantle lengths of approximately 200–250 mm in this species off the eastern Australian coast. Clarke (1980) concluded that *H. meleagroteuthis* elsewhere probably has a life span of less than two years and, from the degenerate condition of the bodies of some specimens, that death occurs soon after spawning.

Beaks in sperm whale stomachs led Clarke (1980) to conclude that histioteuthid species school. Although the family is considered to be primarily mesopelagic (Voss, N.A. 1969), *H. celetaria pacifica* (Voss, G.L. 1962) and *H. miranda* have been caught frequently in deep-water lobster trawls at depths of 300–600 m off the North West Shelf and Great Barrier Reef, suggesting that they are associated with the sea floor during part of their life cycle.

Histioteuthids are important in the diets of sperm whales (Clarke 1983) and are also components of the diets of yellowfin and albacore tunas, scabbard fish, lancetfishes, spotted dolphins (Rancurel 1970; Wolff 1982; Roper *et al.* 1984) and perhaps albatrosses elsewhere (Clarke 1983); they are components of the diets of several pelagic shark species off eastern Australia (Dunning *et al.* 1993). Fishes predominate in the diet of adult histioteuthids (Voss, N.A. 1969; Clarke 1980). The radular arrangement in *Histioteuthis macrohista* is illustrated in Figure 13.18C.

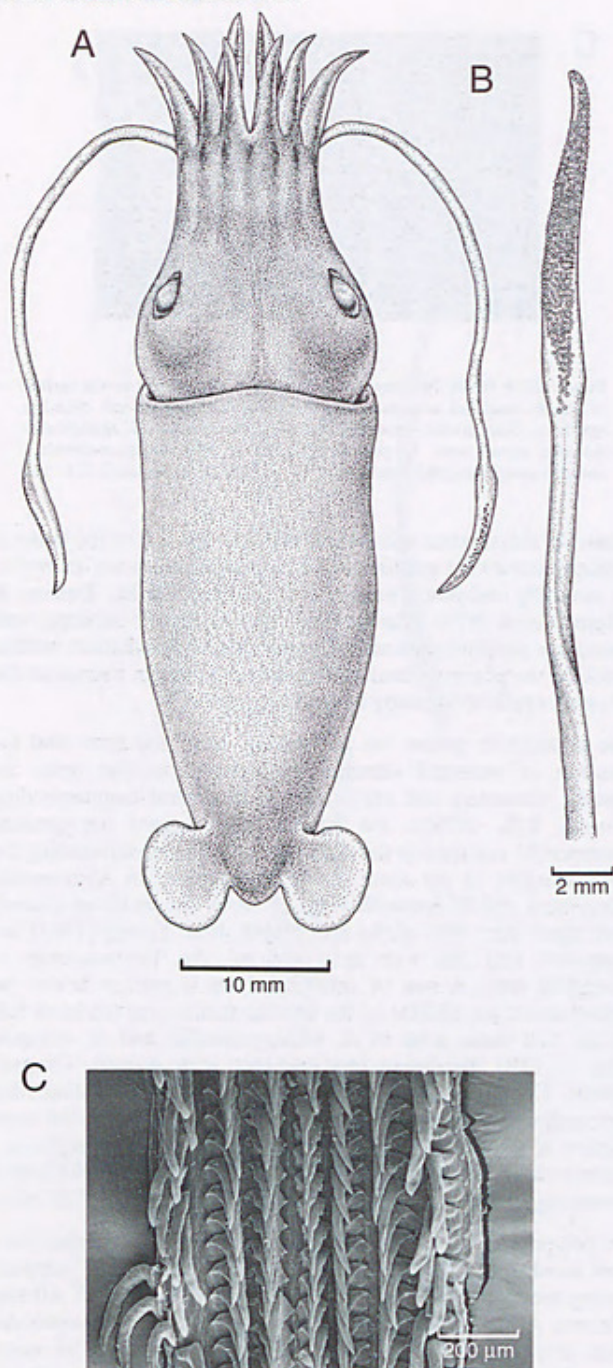


Figure 13.19 Family Bathyteuthidae. *Bathyteuthis abyssicola* is a cosmopolitan bathypelagic species, found even in the Antarctic: A, dorsal view; B, tentacular club; C, portion of radula, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

Off Hawaii, *Histioteuthis dofleini* shows both diel vertical migration and ontogenetic descent. Small squids occur at depths of 200–300 m during the night and descend to 400–700 m during the day. Larger adults have been caught at depths of up to 800 m and only occasionally deeper (Young, R.E. 1975b). Other species are more common in waters of 2000 m and are captured only rarely in the upper 200 m (Voss, N.A. 1969).

Nesis (1979a) considered the five histioteuthid species collected in the Australian region to be primarily tropical and subtropical/notalian species. Of the tropical species, *H. celetaria pacifica* was considered to be restricted to waters north of 30°S, *H. meleagroteuthis* to be more eurythermal occurring southwards to 38°S and *H. dofleini* even more so, occurring as far south as 44°. The subtropical/notalian *H. atlantica* and *H. macrohista*

reportedly occur between 35°S and 50°S, and are most abundant from 40° to 45°S. Off South Africa, *H. miranda* (Fig. 13.18B) was most abundant in water depths of less than 1000 m, *H. atlantica* in waters of between 1000 and 2500 m deep, and *H. bonnellii corpuscula* (Fig. 13.18A) at depths of more than 2000 m, as indicated by their abundance in the diet of sperm whales (Clarke 1980).

This family is not presently of commercial interest. Although some histioteuthid species attain in excess of 200 mm mantle length and are frequently, if not abundantly, encountered in Australian waters, the gelatinous nature of their bodies would detract from their market acceptance. For the same reason, they are readily damaged during capture, and therefore are unsuitable for laboratory study.

Family Bathyteuthidae

Squids of the monotypic family Bathyteuthidae are rarely caught except in Antarctic waters. Bathyteuthids (Fig. 13.19A) are small, less than 100 mm mantle length, with round or paddle-like subterminal fins, a simple, straight funnel locking cartilage, and arms suckers in irregular rows. The tentacular club is small with numerous rows of minute suckers (Fig. 13.19B) and the buccal connectives attach dorsally to the ventral arms. A single light organ is embedded at the base of each of the dorsal, dorso-lateral and lateral arms (Roper *et al.* 1969).

Bathyteuthis was first recorded from eastern Australian waters by Lu & Phillips (1985). Because so few specimens have been collected so far, no studies of life span or growth of this *Bathyteuthis* species in Australian waters or elsewhere have been undertaken and its diet and predators are not known. A portion of the radula of *Bathyteuthis abyssicola* is illustrated in Figure 13.19C.

Bathyteuthids are not vertical migrators in other parts of the world and most specimens have been caught between 1000 and 2500 m (Roper & Young 1975). Their small adult size and rarity precludes this family from commercial fisheries interest.

Family Ctenopterygidae

Ctenopteryx, the sole genus in this family, is easily recognised by its long ribbed fins, which extend the length of the mantle in adults (Fig. 13.20). Ctenopterygids are small to medium-sized squids, less than 100 mm mantle length; they have four to six rows of suckers on the distal half of all but the ventral arms, which have very few small suckers in a zig-zag pattern. The tentacular clubs bear eight to 14 rows of small suckers. The funnel locking cartilage is simple and straight and the buccal connectives attach to the ventral border of the ventral arms. Photophores are present on the ink sac and posteriorly within the mantle in some species. Hectocotylisation is unknown (Roper *et al.* 1969).

Allan's (1945) record of this genus from eastern Australian waters was the first from beyond the North Atlantic and Mediterranean regions. Subsequently, it was reported from tropical waters of the central and south-western Pacific by Rancurel (1970), from the north-eastern Indian Ocean by Fujita & Hattori (1976) and from off New South Wales by Brandt (1983). Lu & Phillips (1985) recorded it from the Coral and Tasman Seas.

During growth, the arms, tentacles and head all become longer relative to the body, which scarcely changes shape. The fins become relatively longer. They are terminal at mantle lengths of less than 5 mm and extend the whole length of the mantle when it reaches 30 mm (Clarke 1966). The structure of the fins suggests that ctenopterygids are not capable of sustained rapid movement. Undulating movements of the fins, much as in sepiid cuttlefishes, may provide the primary propulsive force. With sexual maturity, male *Ctenopteryx* develop a large photophore within the posterior

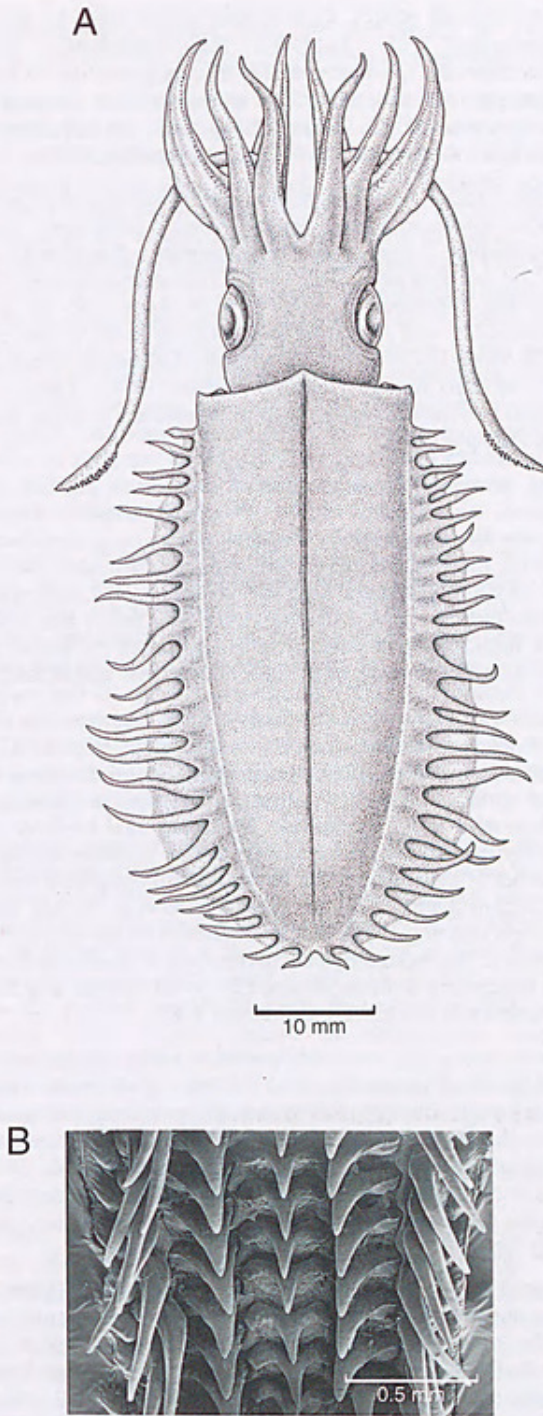


Figure 13.20 Family Ctenopterygidae. *Ctenopteryx sicula*: A, dorsal view, showing the characteristic ribbed fins; B, portion of radula, showing several transverse tooth rows. [A, K. Hollis; B, C.C. Lu]

region of the body. R.E. Young (1983) concluded that the light produced, which is of a wavelength poorly detected by many potential predators, may be used to attract a mate.

No detailed information is available on the life history of ctenopterygids. Larvae have been common, though not abundant in collections made off the New South Wales coast during both summer and winter, suggesting that the spawning season is broad. Elsewhere, ctenopterygids are preyed upon by lancetfishes (*Alepisaurus*), albacore, dolphins and mesopelagic viper-fishes (*Chauliodus*) (Clarke 1966; Rancurel 1970; Fujita & Hattori 1976). The diet of ctenopterygids is unknown. A portion of the radula of *Ctenopteryx sicula* is illustrated in Figure 13.20B.

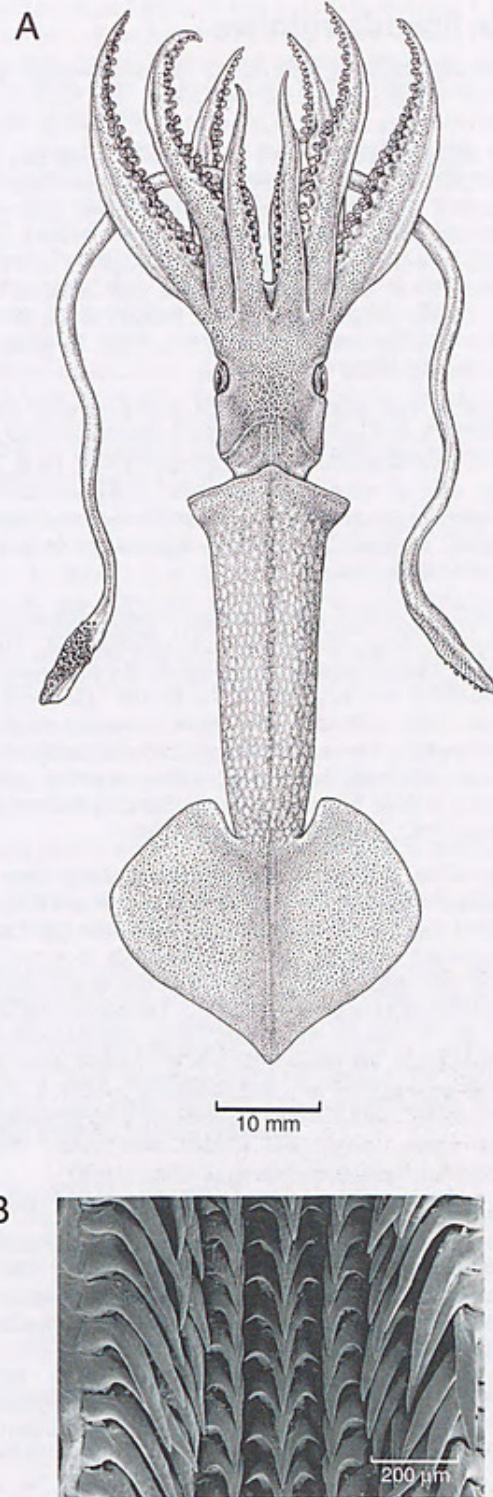


Figure 13.21 Family Brachioteuthidae. A, *Brachioteuthis cf. picta*, a small squid found on the continental slope of south-eastern Tasmania, dorsal view. B, portion of radula of *Brachioteuthis* sp., showing several transverse tooth rows. [A, K. Hollis; B, C.C. Lu]

Little is known regarding the vertical distribution of ctenopterygids. Most specimens from Australian waters and elsewhere have been caught in the upper 150 m, although day captures at more than 350 m have been made in the Atlantic. Roper & Young (1975) suggest that this genus inhabits near-surface waters at night. Ctenopterygids are regularly encountered off the east coast in tropical oceanic surface waters and in the East Australian Current system. They do not reach a suitable size or abundance to be of any commercial fisheries interest in Australia.

Family Brachioteuthidae

The taxonomy the monotypic family Brachioteuthidae is based mainly on larval characters, as adults are rarely caught. Brachioteuthids are small to medium-sized squids, less than 100 mm mantle length, with a slender muscular mantle, sometimes produced as a short tail. The terminal fins are rhombic, generally less than 50% of the mantle length (Fig. 13.21). Brachioteuthids have a simple, straight funnel locking cartilage and biserial suckers occur on the arms. Lateral arms have swimming keels in adults. The tentacular club is expanded, and numerous small suckers in the carpal region extend proximally along the club. The buccal connectives attach ventrally to the ventral arms. Light organs are absent.

Brachioteuthis riisei was recorded first from Australian waters by Allan (1945). It has since been taken in midwater trawls in an eddy of the East Australian Current (Brandt 1983). Lu & Phillips (1985) list only *B. riisei* from Australian waters although Nesis (1979a) assigned specimens in his net collections to *B. behni* and Clarke (1966) reported *B. picta* from the southern Indian Ocean and around New Zealand.

The unusually long neck of *Brachioteuthis* larvae distinguish them from all other larvae except those of chiroteuthids. The neck appears to be a single muscular, fluid-filled tube continuous with a large fluid-filled reservoir within the mantle. The neck in the *Dorotopsis* 'larva' of chiroteuthids is elongate also, but is supported by many separate chambers. Larval *Brachioteuthis* are believed to orientate in a head down position generally, resembling a drifting bell with hanging tentacles ready to capture prey (Young, R.E., Harman & Mangold 1986).

The eggs of a species of *Brachioteuthis* have been taken occasionally in plankton nets in Hawaiian waters and R.E. Young *et al.* (1986) suggested that females spawn single eggs (as in the Enoploteuthinae). Unlike the enoploteuthids however, adult females do have nidamental glands. No studies of age and growth of brachioteuthids have been undertaken. The occurrence of larvae suggests that in eastern Australian waters *Brachioteuthis riisei* spawns throughout the year (Allan 1945); the diet is not known. The radular arrangement in a *Brachioteuthis* species is illustrated in Figure 13.21B. *Brachioteuthis* species are a dietary component of sperm whales caught off Iceland after recent migration northwards from the tropics (Martin & Clarke 1986).

Larval *Brachioteuthis* are diel vertical migrators off Hawaii, where they occur in the upper 50 m at night and descend to 100–150 m during the day (Young, R.E. *et al.* 1986). The distribution of adults is unknown, although they have been caught in midwater trawls in subtropical oceanic waters off central New South Wales.

The studies of Nesis (1979a) and Brandt (1983) indicate that *Brachioteuthis riisei* is primarily a tropical species, carried southwards by the East Australian Current off the Australian east coast.

Their small adult size and rarity precludes brachioteuthids from commercial fisheries interest. Eggs collected in plankton nets have been successfully hatched in onboard aquaria off Hawaii (Young, R.E. *et al.* 1986). In the East Australian Current north of 32°S, eggs ready to hatch and early hatchlings have been caught in abundance during the summer months, and may lend themselves to laboratory studies of early growth and development.

Family Ommastrephidae

Ommastrephids are medium-sized to large oegopsids, more than 500 mm mantle length, with a strong, muscular, torpedo-shaped mantle (Fig. 13.22A–F). They are characterised by an inverted, T-shaped funnel locking cartilage and biserial suckers on the arms (Fig. 13.22M–R). The tentacular clubs in all Australian representatives have tetraserial suckers. The buccal connectives attach to the dorsal border of the ventral arms and light organs are

present in some genera. One or both ventral arms in males are hectocotylised (Fig. 13.22G–L). Three subfamilies, Illicinae, Todarodinae and Ommastrephinae, are recognised on the basis of the presence and structure of the foveola and side pockets in the funnel groove (Fig. 13.22M, S–U). All are represented in Australian waters (Wormuth 1976; Lu & Dunning 1982).

In 1888, McCoy described the first ommastrephid from Australian waters, *Ommastrephes gouldi*. Two additional species, *Ommastrephes gigas* and *Ommastrephes oualaniensis*, were recorded by Brazier (1892) in the first comprehensive list of Australian cephalopods. The first of these two is a misidentification, and *Dosidicus gigas* occurs only in the eastern Pacific. Nesis (1979b) provided records of additional species from the Australian region. Dunning (1988a, 1988b, 1988c, 1993) reported two ommastrephid species, in addition to those listed by Lu & Phillips (1985).

Sharp, strongly developed conical teeth are present on the chitinous sucker rings of the arms and tentacles. The large muscular fins are generally rhomboidal, except in *Ornithoteuthis* in which the fins and mantle are strongly attenuated posteriorly (Fig. 13.22C). The lateral arms are strongly keeled, particularly in oceanic species (Lu & Dunning 1982). The family has a distinct larval form, the rhynchoteuthion, characterised by fusion of the tentacles which separate over a size of 5–10 mm mantle length.

Nototodarus, *Todaropsis* and *Todarodes* species typically display a dark, narrow mid-dorsal stripe on the mantle (Fig. 13.22D–F), which is replaced in oceanic species by a general darkening of the dorsal surface. Large light organs are present in *Sthenoteuthis*, *Eucleoteuthis* and *Hyaloteuthis*. These are oval or form stripes ventrally or dorsally on the mantle and/or ventrally on the head and bases of the ventral arms. Juveniles of these genera have oval light organs ventrally on the eyes and between the ink sac and intestine (Dunning 1985). Adult *Ornithoteuthis* have an additional midventral, luminous stripe along the viscera. Small subcutaneous light organs are distributed ventrally on the mantle and head of *Ommastrephes* species (Lu & Dunning 1982).

All ommastrephids are active predators; they use the arms and tentacles for grasping food and the heavily chitinated beak for dividing prey. The reproductive organs are typically oegopsid. All species in Australian waters have buccal seminal receptacles for storage of sperm bulbs during copulation. The presence of sperm bulbs in the spermathecae of immature females of several species suggests that copulation may precede spawning by some time in this group.

No direct studies of age and growth of ommastrephids in Australian waters have been undertaken. From examination of population size structure, it appears probable that most species reproduce for a single season only and die after reaching reproductive maturity at less than two years of age. In some species, males mature at considerably smaller sizes than females. Spawning locations remain unknown although larvae have not been found away from continental shelf and slope waters.

Ommastrephids occupy all major marine habitats, including the tropical and temperate continental shelf and slope, and oceanic waters. They feed on a broad range of crustaceans, fishes, squids and other pelagic molluscs, and are at least partially cannibalistic (O'Sullivan & Cullen 1983). The radular arrangement in *Ommastrephes bartrami* is illustrated in Figure 13.22V. Known predators include seabirds, teleosts and sharks, whales, dolphins and seals (Dunning & Brandt 1985; Okutani & Tsukada 1988; Dunning *et al.* 1993). Ommastrephids form schools, which decrease in size as the animals grow. Evidence from commercial fishing operations suggests that neritic species congregate close to the bottom during the day, and move up through the water column at night. Oceanic species have been seen feeding at the surface at night, where large individuals of *Ommastrephes* species have been observed hunting for prey. Juveniles of several species are able to glide like exocoetid flying fishes to escape predators, for distances in excess of 10 m. There is evidence for long distance migration associated with

spawning by *Ommastrephes* elsewhere (Dunning & Brandt 1985), and perhaps on a smaller scale by *Nototodar* in southern Australian (Smith, H.K. 1983) and New Zealand waters (Sato 1985).

Ommastrephid squids occur in all oceans, with the exception of polar waters. Of the 11 recognised genera, nine occur in Australian waters and one subspecies appears to be endemic. Significant distributional overlap occurs for many species, particularly in East Australian Current waters where juveniles of up to five genera have been taken in the same trawl catch (Dunning & Brandt 1985). *Todarodes pacificus pucillus* (Fig. 13.22D) occurs in continental shelf waters north of 27°S. The genus *Nototodar* is represented in northern slope waters by *N. hawaiiensis* and in shelf waters south of 25°S by *N. gouldi*. The distribution of the former species overlaps with that of the less abundant *Todaropsis eblanae* (Fig. 13.22F). Between 18° and 35°S, *Ornithoteuthis volatilis* (Fig. 13.22C) is common in trawl catches from slope waters. The Subantarctic shelf species, *Martialia hyadesi*, has occasionally been found stranded on the beach after storms at Macquarie Island, sometimes in large numbers.

Hyaloteuthis pelagica and *Eucleoteuthis luminosa* occur in tropical and subtropical oceanic waters off the east coast respectively. *Ommastrephes bartrami* (Fig. 13.22B) is the dominant ommastrephid in the south-eastern Indian Ocean and Tasman Sea north of 40°S, replaced to the south by *Todarodes filippovae* and *T. angolensis* (Dunning 1993). This species is also caught in continental slope waters around the southern Australian coast. Fossil statoliths of late Pliocene *Sthenoteuthis* have been found in California (Clarke & Fitch 1979), although none has yet been discovered in Australia.

Nototodar *gouldi* (Fig. 13.22E; Pl. 18.11) is caught incidentally for human consumption in trawling operations around the southern Australian coast (Dunning 1979), and more than 200 tonnes are sold on the domestic market annually. Since 1978, this species has been the target also of a directed jig fishery in Bass Strait by Japanese, Taiwanese and Korean vessels. The highest catch taken during the summer months of 1979/1980 exceeded 8000 tonnes (Dunning 1982). Several species are intermediate hosts for ascaridoid nematodes. Ommastrephids are a source of anisakiasis in man in Japan, where squid is often eaten raw (Hochberg 1983); these parasites pose no public health risk after cooking. Because of their abundance, large adult size and consequently the maximum diameter of their giant nerve axons, this family is of interest to neurophysiologists (Hixon, Ramirez & Villoch 1981).

Collection and laboratory maintenance of these large highly mobile molluscs present major difficulties. Large scale commercial fishing gear is necessary to catch the larger adults and some information has been gained from examination of the stomach contents of squid predators. Larvae have been collected successfully in large plankton nets designed for larval tunas (Dunning 1985). Future laboratory maintenance in large aquarium facilities, such as those used to maintain the ommastrephid *Illex illecebrosus* in Canada (O'Dor, Durward & Balch 1977), may lead to better understanding of the life cycles of Australian species.

Family Thysanoteuthidae

Of the two genera included in this family, only the monotypic genus *Thysanoteuthis* is well known. *Cirrobrachium* is known from larval forms and fragments of adults from the Atlantic only and its taxonomic status is not clear. *Thysanoteuthis rhombus* has a muscular mantle and rhombic fins which extend the length of the mantle in adults (Fig. 13.23A). The funnel locking cartilage has a long narrow longitudinal groove and a short broad transverse groove (Fig. 13.23B). Toothed suckers are present in two rows on the arms and four rows on the tentacular clubs. The lateral arms are strongly keeled in large specimens. Long, cirrate trabeculae on the arms support a well-developed web, and buccal connectives attach to the ventral borders of the ventral arms. The left ventral arm in males is hectocotylied (Pfeffer 1912). No photophores are present (Roper *et al.* 1969).

Rancurel (1970) and Fujita & Hattori (1976) recorded *T. rhombus* in the stomach of lancetfishes from the south-western Pacific and north-eastern Indian Ocean. Net-caught specimens are known from the Australian region (Nesis 1979a), including nearshore waters (Dunning 1982).

Adults may grow to more than 800 mm mantle length. Females spawn gelatinous, sausage-shaped egg masses, 150–200 mm in diameter and up to 1 m long, which have been found near the surface. A spiral, double row of eggs of up to 2 mm diameter is contained in the external layers. Around Japan, spawning occurs during summer. The smallest larvae hatch at 1.1 mm mantle length (Misaki & Okutani 1976; Suzuki, Misaki & Okutani 1979). No studies of age and growth of this species have been undertaken. Lancetfishes (*Alepisaurus*), yellowfin tunas, spotted dolphins and blue marlin prey on *T. rhombus* elsewhere (Clarke 1966; Rancurel 1970; Fujita & Hattori 1976; Rancurel 1976; Wolff 1982). The radular arrangement in *Thysanoteuthis rhombus* is illustrated in Figure 13.23C.

Thysanoteuthis rhombus is an oceanic species, generally caught in the upper 50 m of the water column. Juveniles are apparently capable of leaping out of the water but do not glide in the same manner as ommastrephids and onychoteuthids. Adults are slow swimmers (Nishimura 1966). In Australian waters, *T. rhombus* has been observed singly or in pairs, although groups of up to 20 have been observed elsewhere (Clarke 1966; Dunning 1988c).

This species occurs circumglobally in tropical surface waters and in the East Australian Current system as far south as north-eastern Tasmania. Juveniles have been recorded also from tropical waters off the North West Shelf.

Although not fished in Australian waters, *T. rhombus* is caught using drifting jigs and set nets in the Sea of Japan and is renowned for its tender flesh which is sometimes eaten as sashimi (Okutani 1977).

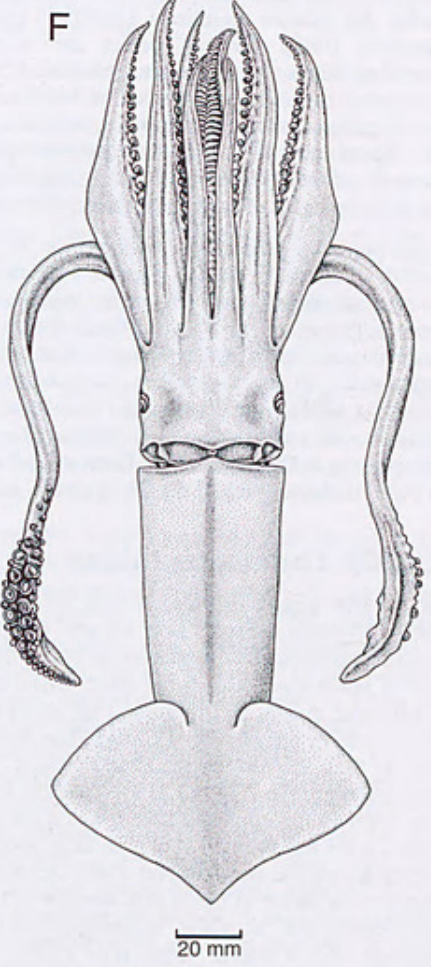
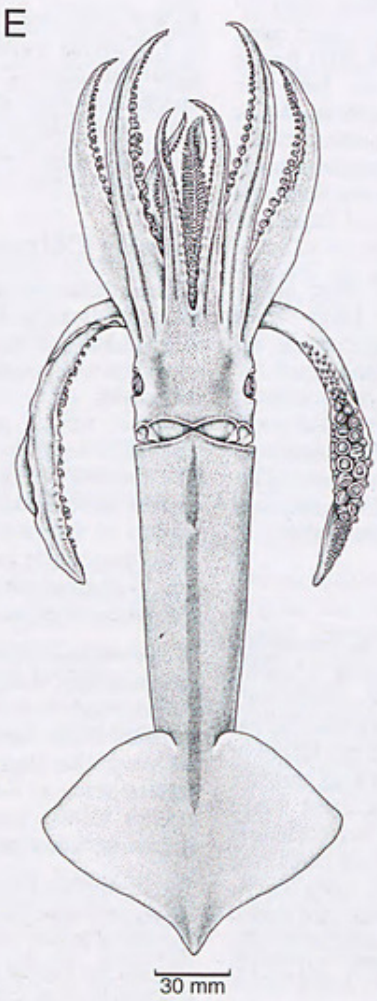
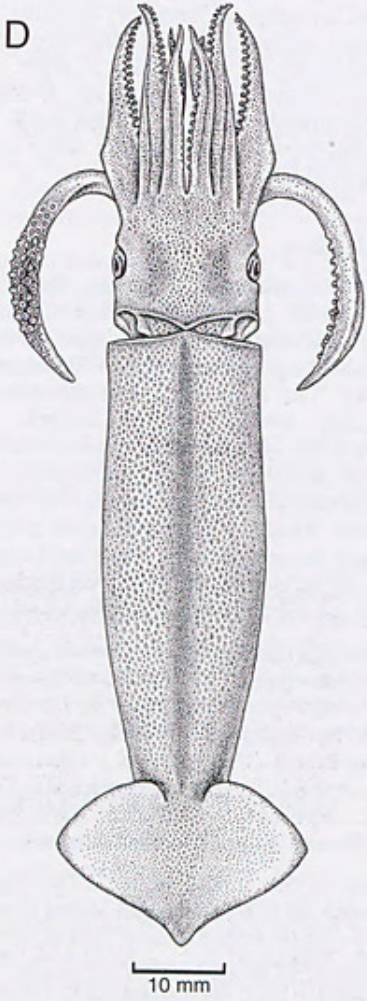
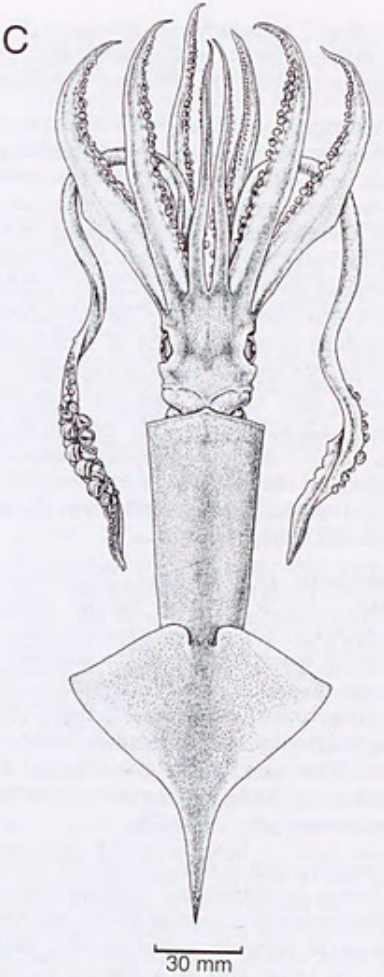
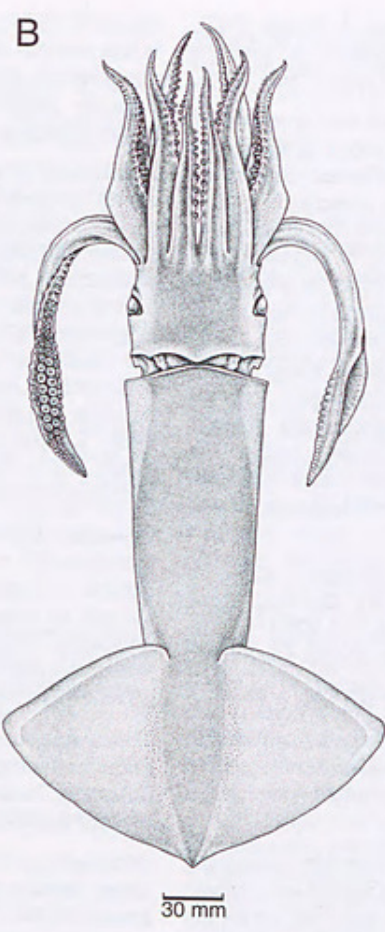
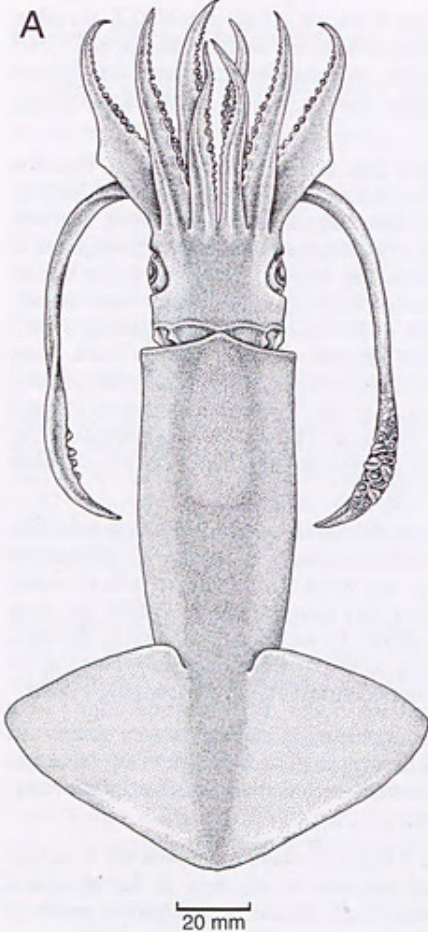
As with other large mobile cephalopods, laboratory maintenance of *T. rhombus* could present major difficulties. However, these squids are regularly encountered on the surface at night and smaller individuals can sometimes be caught in hand-held scoop nets. They may represent suitable subjects for the study of locomotion and social behaviour in oceanic squids when large aquarium facilities become available.

Family Chiroteuthidae

Chiroteuthids are small to medium-sized squids, less than 400 mm mantle length, with somewhat gelatinous bodies (Fig. 13.24A). They are characterised by an oval funnel locking apparatus with one or two knobs projecting towards the centre of the cavity (Fig. 13.24B). The arms, including the greatly enlarged ventral pair, bear biserial, toothed suckers. All Australian representatives have very elongate tentacles (up to five times the mantle length) and distinctive clubs with tetraserial suckers on long stalks. Buccal connectives attach to the ventral borders of the ventral arms. Abundant photophores are present along the tentacle stalks and the ventral arms. Large light organs are also present ventrally on the eyes, at the tips of the tentacular clubs and embedded in the ink sac on both sides of the intestine.

A *Chiroteuthis* species was reported among the stomach contents of lancetfishes from the south-western Pacific and north-eastern Indian Ocean (Rancurel 1970; Fujita & Hattori 1976; Okutani & Tsukada 1988). Nesis (1979a) recorded *Chiroteuthis picteti* from the Australian region and Brandt (1983) caught a *Chiroteuthis* species inside an East Australian Current warm-core eddy. Lu & Phillips (1985) listed *C. imperator* and another *Chiroteuthis* species from the Tasman Sea and off north-western Australia.

The distinctive larval form of this family, termed a *Doratopsis*, attains an unusually large size, up to 60 mm mantle length in some species. It has an elongate spindle-shaped mantle, almost circular fins and the gladius projects posteriorly as a narrow rod. The head is attached to an extraordinarily long, transparent neck. The neck



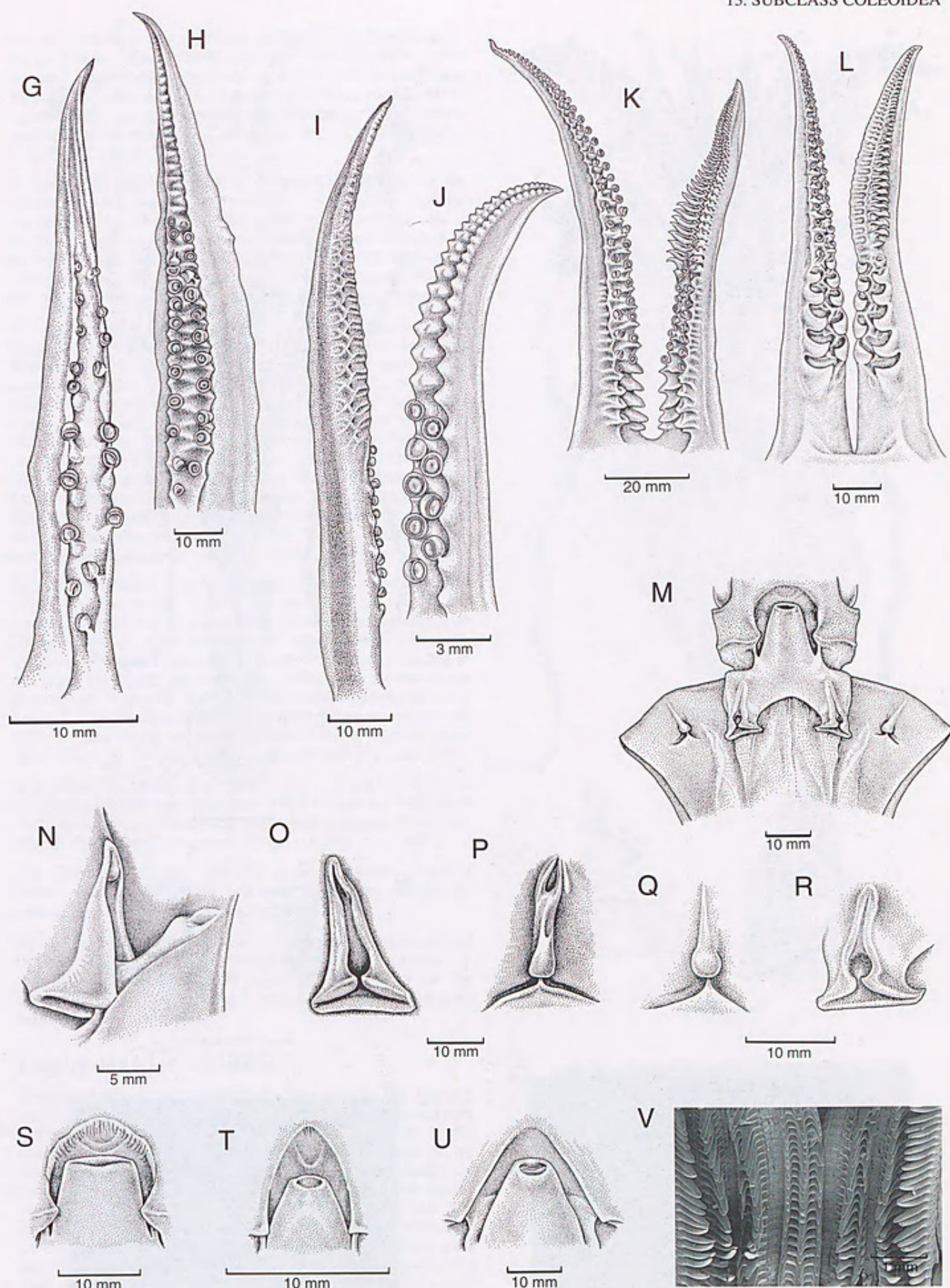


Figure 13.22 Family Ommastrephidae. Members of this diverse family live in surface, mid and bottom waters of the continental shelf and slope, and in the open ocean. A-F, external appearance, dorsal view. G-L, hectocotylised arm. M-R, funnel-mantle locking apparatus. S-U, funnel groove in the three subfamilies. A, G, N, *Sthenoteuthis oualaniensis*. B, H, Q, R, V, *Ommastrephes bartrami*. C, I, M, O, P, *Ornithoteuthis volatilis*. D, J, *Todarodes pacificus pusillus*. E, K, *Nototodaros gouldi*. F, L, *Todaropsis eblanae*. S, Ommastrephinae. T, Todarodinae. U, Illicinae. V, portion of radula showing several transverse tooth rows. [A-U, K. Hollis; V, C.C. Lu]

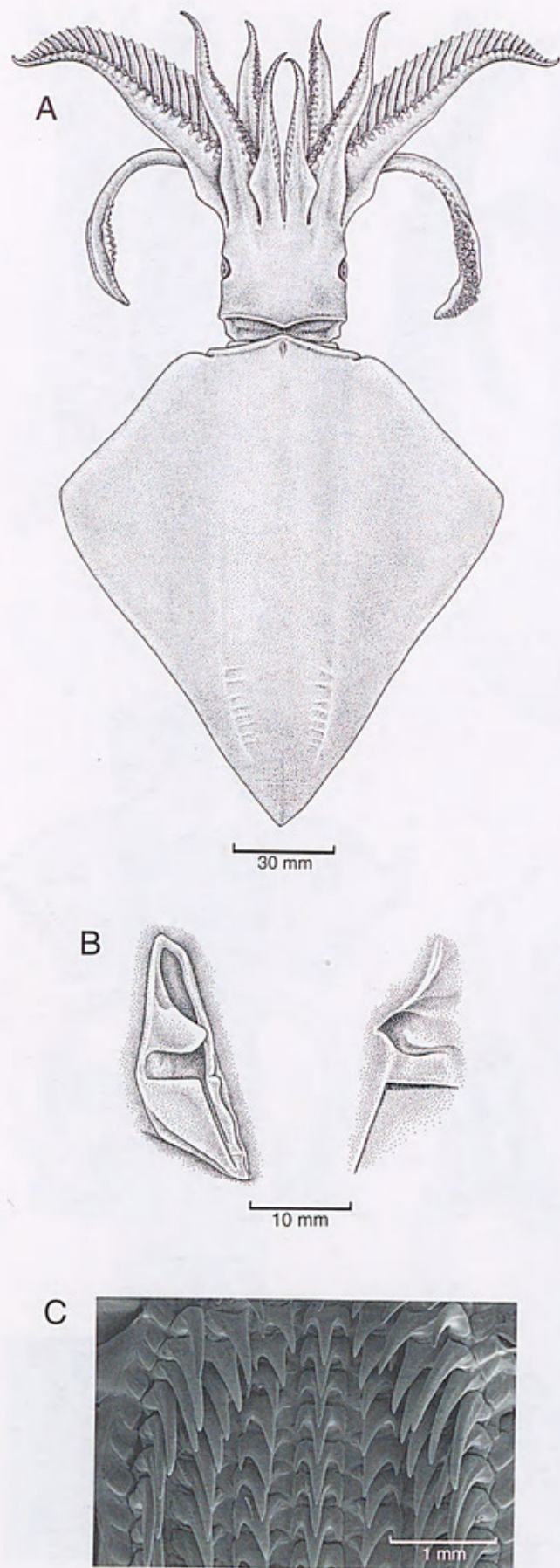


Figure 13.23 Family Thysanoteuthidae. *Thysanoteuthis rhombus*, a large oceanic squid of the tropical and subtropical waters worldwide: A, dorsal view; B, funnel-mantle locking apparatus; C, portion of radula, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

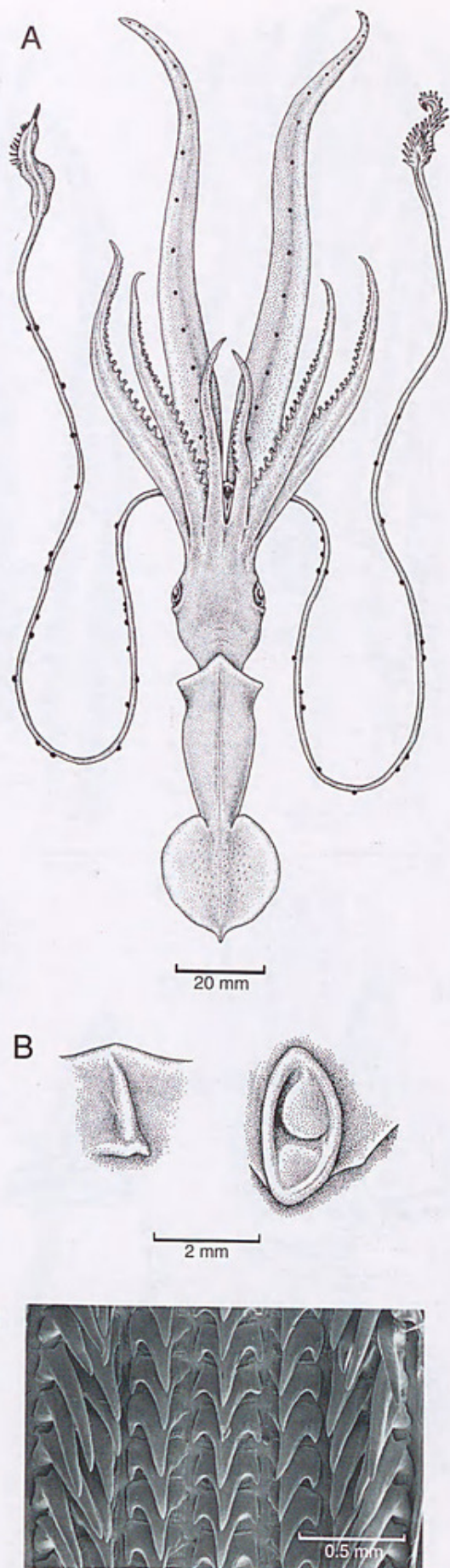


Figure 13.24 Family Chiroteuthidae. A, B, *Chiroteuthis calyx*, a species found regularly off south-eastern Tasmania: A, dorsal view; B, funnel-mantle locking apparatus. C, portion of radula of *Chiroteuthis imperator*, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

has many membranous partitions, unlike that of *Brachioteuthis* larvae. Clarke *et al.* (1979) concluded that the neck region provides buoyancy for the whole animal. In smaller specimens, the long tentacles and the ventral arms may be up to 60% of the mantle length, and approximately equal in length. The remaining arms are poorly developed. Light organs are not readily apparent in the larval stages.

In post-larval stages, the head is shortened through loss of the post-orbital neck, and the mantle and fins broaden. The advanced development of the ventral arms seen even in larval stages is maintained with growth, and these structures contribute most to the buoyancy of adult chiroteuthids. It is likely that adults float with these uppermost (Clarke *et al.* 1979). Some species lose the tail, and in others a cylindrical gelatinous projection is retained.

No comprehensive life history studies of chiroteuthids have been undertaken. The broad size distribution of specimens examined by Kubota, Koshiga & Okutani (1981) may indicate an extended spawning season for *C. imperator* in Japanese waters. No information on the life span or growth rate of any chiroteuthid species is currently available. Chiroteuthids form part of the diet of sperm whales off south-western Australia and in the Tasman Sea (Clarke 1980; Clarke & MacLeod 1982) and of lancetfishes and yellowfin tunas in the Coral Sea and north-eastern Indian Ocean (Rancurel 1970; Fujita & Hattori 1976; Rancurel 1976). Off Japan, *C. imperator* feeds on micronektonic crustaceans, molluscs and fishes (Kubota *et al.* 1981). The radular arrangement in *Chiroteuthis imperator* species is illustrated in Figure 13.24C.

From its abundance among sperm whale stomach contents, Clarke (1980) concluded that *Chiroteuthis joubini* forms schools off southern Africa, but it is unknown whether this behaviour is characteristic of other members of the family. *Chiroteuthis* displays ontogenetic descent. The smallest larvae are abundant in the upper 100 m and those metamorphosing to the subadult stage predominate at depths of 500–700 m. Adults apparently occur below 500 m during the day but are distributed throughout the water column during the night. Diel vertical migration of larvae and adults is also evident in some species (Roper & Young 1975).

A *Chiroteuthis* species was taken recently in bottom trawls in continental slope waters at depths of 300–600 m off the North West Shelf, although considered to be predominantly oceanic. It has been trawled also in nearshore waters off Japan (Kubota *et al.* 1981).

The distribution of this family in Australian waters is poorly known; *Chiroteuthis picteti* is considered to be restricted to oceanic waters north of 30°S (Nesis 1979a).

Chiroteuthids have soft gelatinous bodies and have no commercial fisheries potential. They are readily damaged during capture in sampling nets, because of the nature of their bodies and the protruding tail in larvae of many species, and therefore are poor subjects for laboratory study.

Family Mastigoteuthidae

Mastigoteuthids are medium-sized to large squids (Fig. 13.25A), attaining 0.5–1.0 m mantle length, with a gelatinous body consistency. The funnel locking cartilage is oval, with inward projecting knobs (Fig. 13.25B). Unlike those of chiroteuthids, the posterior knob generally and the medial knob occasionally are poorly developed. The arms bear biserial, toothed suckers and the ventral arms are greatly enlarged, like those of chiroteuthids. The long, whip-like tentacles, bearing many hundreds of minute suckers, are characteristic of the family. The buccal connectives attach to the ventral borders of the ventral arms. The fins are large. Many species have photophores on the surface of the mantle, and the ventral surfaces of the head, the ventral arms and on the eyeball.

Seventeen species belonging to two genera, *Mastigoteuthis* and *Echinoteuthis*, have been described. The taxonomy of the family, on a worldwide basis, is badly in need of revision. Allan (1945) recorded the first *Mastigoteuthis* species from Australian waters. Four nominal species were listed by Lu & Phillips (1985).

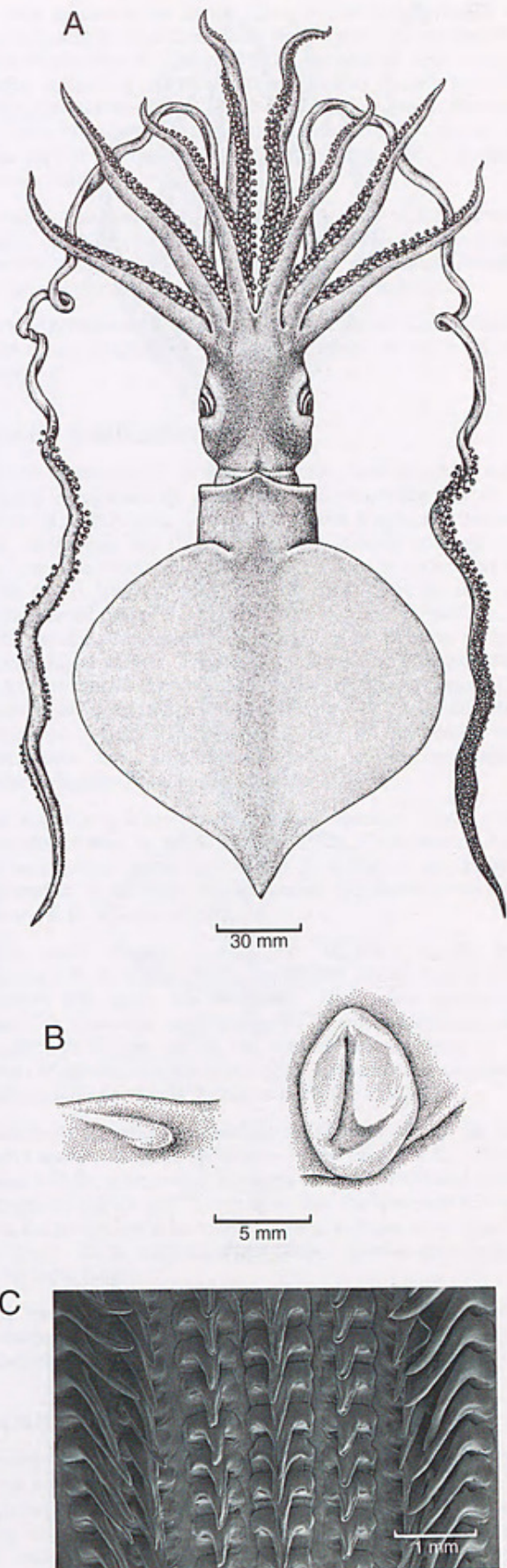
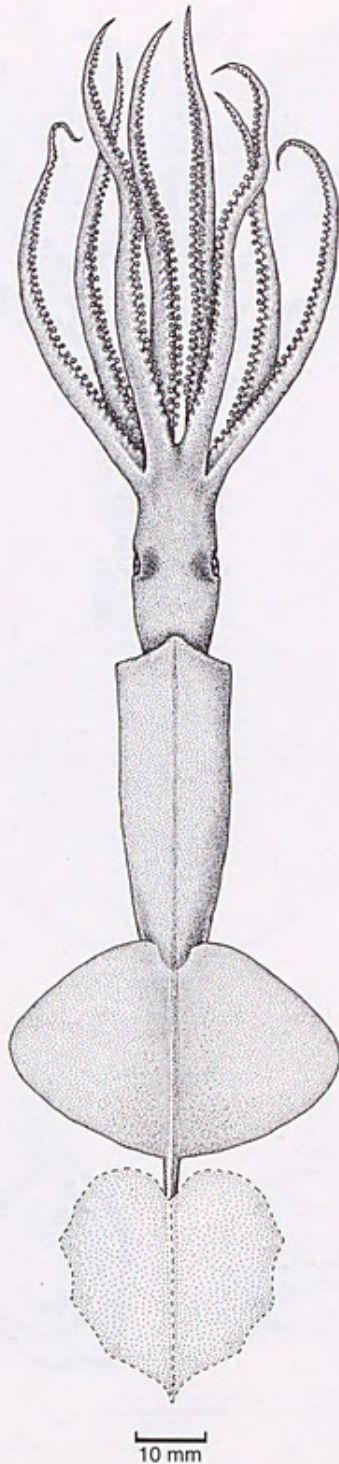


Figure 13.25 Family Mastigoteuthidae. Members of this family are named whip squids, for their long, slender tentacles which bear numerous minute suckers. *Mastigoteuthis cordiformis*, a large species commonly found on the continental slope of north-western Western Australia: A, dorsal view; B, funnel-mantle locking apparatus; C, portion of radula, showing several transverse tooth rows. [A, B, K. Hollis; C, C.C. Lu]

A



B

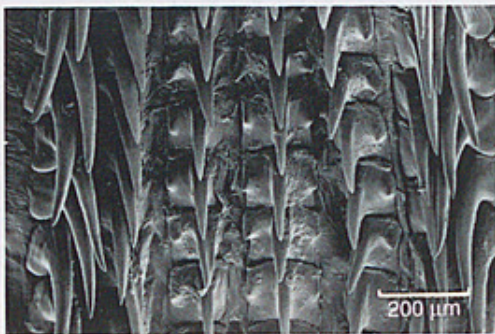


Figure 13.26 Family Grimalditeuthidae. *Grimalditeuthis bonplandii*, a rare squid, is one of the two species with an accessory fin: A, dorsal view; B, portion of radula, showing several transverse tooth rows.

[A, K. Hollis; B, C.C. Lu]

The body in *Mastigoteuthis* species is often pink or brick red in colour. Some species have minute dermal tubercles covering the body surface. These structures consist of elastic cartilage or fibro-cartilage in *Mastigoteuthis cordiformis* and *M. hjorti*, and may aid in the reduction of drag, at least in *M. cordiformis* (Roper & Lu 1990).

The tissues at the front of the head, and in the arms, mantle, fins and cartilage of *Mastigoteuthis* are highly vacuolated (Dilly, Nixon & Young 1977). On the other hand, the tentacles have a dense musculature. The vacuolated tissues containing ammonium-rich fluid provide buoyancy (Clarke *et al.* 1979). Based on the distribution of vacuolated tissue, Dilly *et al.* (1977) suggested that a stationary mastigoteuthid lies vertically in the sea with arms held upwards, and tentacles hanging downwards.

No comprehensive information on the biology of mastigoteuthids is available. Verrill (1882) and Rancurel (1971) found crustacean remains among the stomach contents of *Mastigoteuthis agassizii* and *M. grimaldi*. The radular arrangement in *Mastigoteuthis codiformis* is illustrated in Figure 13.25C. Although various species of *Mastigoteuthis* have been captured frequently in mid-water trawl tows, they are rarely found among the stomach contents of predators (Clarke 1986). The known predators of various species of *Mastigoteuthis* include *Alepisaurus ferox*, *Globicephala melas*, *Hyperoodon planifrons*, *Mesoplodon carlhubbsi* and *Physeter catodon* (Rees & Maul 1956; Clarke 1986).

Male mastigoteuthids do not have a hectocotyliised arm. There is no distinctive larval stage.

Mastigoteuthids are deep living squids occurring from the tropical waters to the polar regions. Closing net data indicate that all species live at depths of 500–1000 m in daytime and may ascend to shallower water at night, even to as shallow as 50–100 m (Clarke & Lu 1975; Lu & Clarke 1975b; Roper & Young 1975). With increased fishing effort using bottom trawls on the continental slopes of Australia in recent years mastigoteuthids have been captured, the largest of which was a specimen of *M. cordiformis* of 0.7 m mantle length (Roper & Lu 1990).

Several mastigoteuthid species (at least four) have been recorded from Australian waters but their detailed distributions are unknown. None of the species is endemic in Australian waters, and some may have cosmopolitan distribution (Nesis 1982).

Members of this family have no commercial fisheries potential because of their gelatinous body consistency and the ammonium content of the mantle and arms. No specimen has ever reached the deck of a research vessel alive from the great depths at which these animals live. They are easily damaged during trawling operations also, particularly the long tentacles, and consequently they are not good subjects for laboratory study.

Family Grimalditeuthidae

This rare, monotypic family of medium-sized oceanic squids, less than 250 mm mantle length, is recognised easily by the fused funnel locking cartilages and free dorsal nuchal locking apparatus. The body and mantle are soft, delicate and semitranslucent. The long slender tail bears a delicate accessory fin, which may be lost during capture (Fig. 13.26A). The presence of an accessory fin is unique among cephalopods and whether it functions in concert with the primary fin remains to be clarified.

Biserial suckers, some with attenuate teeth, are present on the long slender arms, which lack protective and swimming membranes and trabeculae. Tentacles are lacking; stubs which may have a sensory function are generally present. Buccal connectives attach to the ventral border of the ventral arms and photophores may be present at the tips of the arms. Little pigmentation is evident on the body (Roper *et al.* 1969; Young, R.E. 1972a).

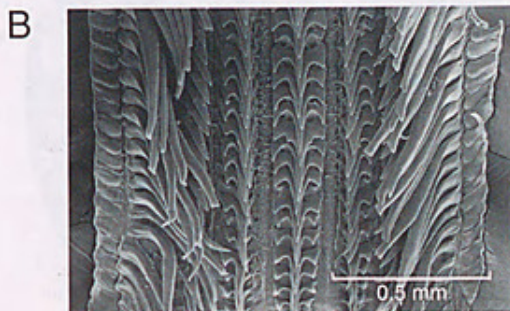
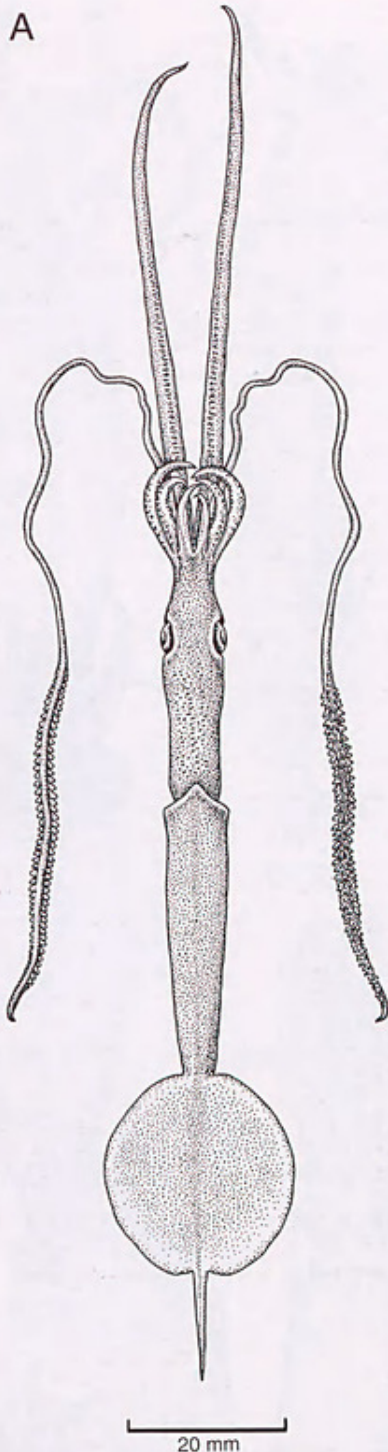


Figure 13.27 Family Joubiniteuthidae. *Joubiniteuthis portieri*, characterised by the elongate tail: A, dorsal view; B, portion of radula, showing several transverse tooth rows. [A, K. Hollis; B, C.C. Lu]

The only species in this family, *Grimalditeuthis bomplandii*, was recorded recently from continental slope waters off southern New South Wales (Lu & Phillips 1985). Because of their rarity in existing collections, no information regarding the life history of *G. bomplandii* is available. The radular arrangement is illustrated in Figure 13.26B. Like many other oceanic squids, this species forms part of the diet of lancetfishes (Clarke 1966; Okutani & Tsukada 1988).

Grimalditeuthis bomplandii has been caught at the surface elsewhere (Clarke 1966) but the vertical distribution of this species remains unknown. Clarification of the distribution of *Grimalditeuthis* in Australian waters awaits the collection of further specimens.

The soft gelatinous body and low capture rate of *Grimalditeuthis* removes all potential for laboratory study or as a fisheries resource.

Family Joubiniteuthidae

The sole species in this monotypic family, *Joubiniteuthis portieri*, is easily recognised by its slender tail, projecting beyond the mantle by slightly more than its own mantle length, and the small, oval, subterminal fins (Fig. 13.27A). The slender arms are more than twice the mantle length, and bear six rows of suckers on each of the dorsal, lateral and dorso-lateral arms. There are four rows on the ventral arms. The tentacles are long and thread-like, and each laterally compressed club carries up to 12 rows of small, smooth-ringed suckers. The distal tip of the club is bordered by a distinct protective membrane with no apparent supports. The funnel locking cartilage is small and oval and the buccal connectives attach to the ventral border of the ventral arms. Photophores are absent and males show no apparent hectocotylisation (Young, R.E. & Roper 1969b).

Joubiniteuthis portieri was recorded recently from eastern Australian waters by Lu & Phillips (1985). Collection of further specimens from Australian waters is necessary to clarify its distribution. Less than 20 specimens are known worldwide (Young, R.E. & Roper 1969b).

Males reach maturity at less than 105 mm mantle length (Young, R.E. & Roper 1969b); an 85 mm mantle length female collected off Japan was immature. The female reproductive system is typically oegopsid with paired nidamental glands (Okutani & Kubota 1972). No information regarding the life history of this rare species is available. The radular arrangement in *Joubiniteuthis portieri* is illustrated in Figure 13.27B.

Because of its rarity, the vertical distribution of this species is poorly known. Atlantic specimens examined by R.E. Young & Roper (1969b) were caught at depths of between 330 and 2500 m. Okutani & Kubota (1972) concluded that the specimen recovered from the stomach of a lancetfish stranded in Japan was captured in the upper 150 m, suggesting that adult *J. portieri* may occupy a broad depth range.

This species has a soft gelatinous body, and is rarely caught. Consequently, it has no potential for laboratory study or as a fisheries resource.

Family Cranchiidae

Members of the ubiquitous and abundant family Cranchiidae range in size from small to very large oceanic squids more than 1 m mantle length, which display great morphological diversity (Fig. 13.28). The mantle of all cranchiids is fused to the head in the nuchal region and to the funnel at its two posterior lateral corners. Generally, the arms bear biserial, sharp-toothed suckers, and the armature of the tentacular clubs has four rows of suckers, hooks or hook-like suckers. Buccal connectives attach to the ventral borders of the ventral arms, and photophores are present on the eyes and on the arm tips in some species (Roper *et al.* 1969). Several rows of the radula of *Cranchia scabra* are shown in Figure 13.29.

13. SUBCLASS COLEOIDEA

The 13 cranchiid genera currently recognised are divided into the subfamilies Cranchiinae (Fig. 13.28A-E) and Taoniinae (Fig. 13.28F-L). The Cranchiinae are characterised by one or two cartilaginous strips which extend posteriorly from the anterior apex of the funnel-mantle fusions and the fusion of the funnel to the head laterally (Fig. 13.28B, D). The eyes bear four or more small, round or oval photophores. The right or left ventral arms are hectocotylised in mature males.

In the Taoniinae, no cartilaginous strips are present and the funnel is free from the head laterally. One to three crescent-shaped light organs, dissimilar in size, are present on the eyes. Hectocotylisation does not occur.

Secondary sexual modification of the ends of the arms in mature males and development of brachial end-organs on the arms of mature females may occur in both subfamilies. The recent generic revision (Voss, N.A. 1980) and detailed studies of individual genera (Voss, N.A. 1985) provide a more comprehensive treatment of this complex group.

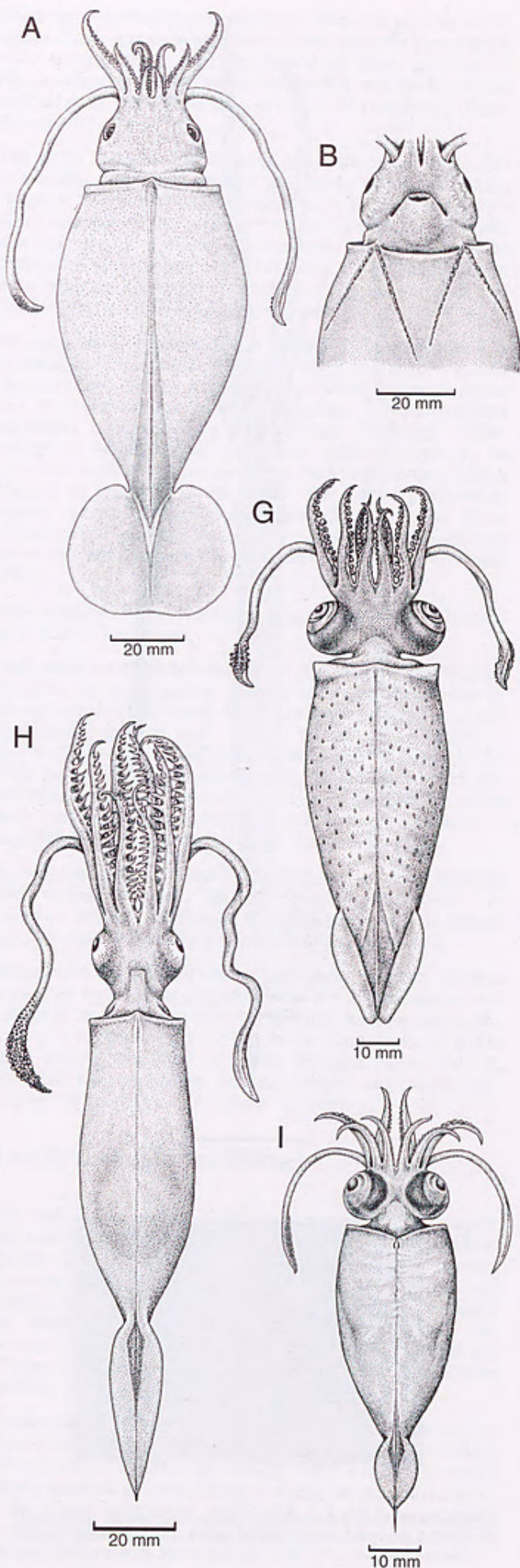
Cranchiids were first recorded from eastern Australian waters by Allan (1940, 1945), with '*Pyrgopsis pacificus*' (probably *Leachia* sp.) being the most numerous cephalopod in her plankton collections. Brandt (1983) recorded at least five cranchiid species from both subfamilies in a warm-core eddy of the East Australian Current. Recently, Lu & Phillips (1985) listed some 13 species and species groups from off the east coast.

The taxonomic confusion surrounding this family remained until the recent work of N.A. Voss (1980, 1985) was partially the result of the major morphological changes which accompany growth in many cranchiids. The different early larval characters, such as stalked eyes and paddle-shaped fins, are lost or modified at varying stages during growth (Clarke 1966; Voss, N.A. 1980, 1985; Rodhouse & Clarke 1986).

Cranchiid reproductive systems show typical oegopsid characteristics, with the exception of the four nidamental glands in a female *Asocranchia joubini* from the North Atlantic (Voss, G.A. 1962). Female cranchiids have no spermathecae. In *Teuthowenia pellucida* (Fig. 13.28G), a species abundant in eastern Australian waters, spermatophores are embedded externally on the anterior half of the mantle, either dorsally or ventrally. The sperm reservoirs penetrate the inner wall and release sperm into the mantle cavity, where fertilisation of mature eggs leaving the oviducal glands apparently occurs. The large, swollen nidamental glands seen in mature females suggest that the eggs are deposited in one or more gelatinous egg masses. An estimated 6000-8000 eggs of 3.0 mm maximum length were carried by two mature female *T. pellucida* of 177 and 187 mm mantle length (Voss, N.A. 1985).

No comprehensive life history studies of cranchiids from Australian waters have been undertaken. Nixon (1983) reviewed available information on the life cycle of North Atlantic *T. megalops*. N.A. Voss (1985) concluded that female *T. pellucida* probably shed all their eggs over a short period and do not survive beyond one spawning period. Males may mate more than once, but like the females, do not survive past one limited mating season. No information on the life span and growth rates of any cranchiid species is available. The radular arrangement in *Cranchia scabra* is illustrated in Figure 13.29. Cranchiids form a minor part of the diet of sperm whales off south-western Australia and in the Tasman Sea (Clarke 1980; Clarke & MacLeod 1982). They are included also in the diets of lancetfishes and yellowfin tunas from the Coral Sea and north-eastern Indian Ocean (Rancurel 1970, 1976; Fujita & Hattori 1976; Okutani & Tsukada 1988), and elsewhere they are eaten by seabirds (Imber 1978), blue sharks (Clarke & Stevens 1974), albacore tunas and dolphins (Clarke 1966).

Some cranchiids show ontogenetic descent. The smallest larvae of *T. pellucida* are more abundant in the upper 600 m, and those metamorphosing to the subadult stage predominate at depths of 700-800 m. Adults generally occur below 500 m and as deep as 2400 m. Mature *T. pellucida* have only been caught in water depths of more than 3800 m (Voss, N.A. 1985). *Leachia pacifica*



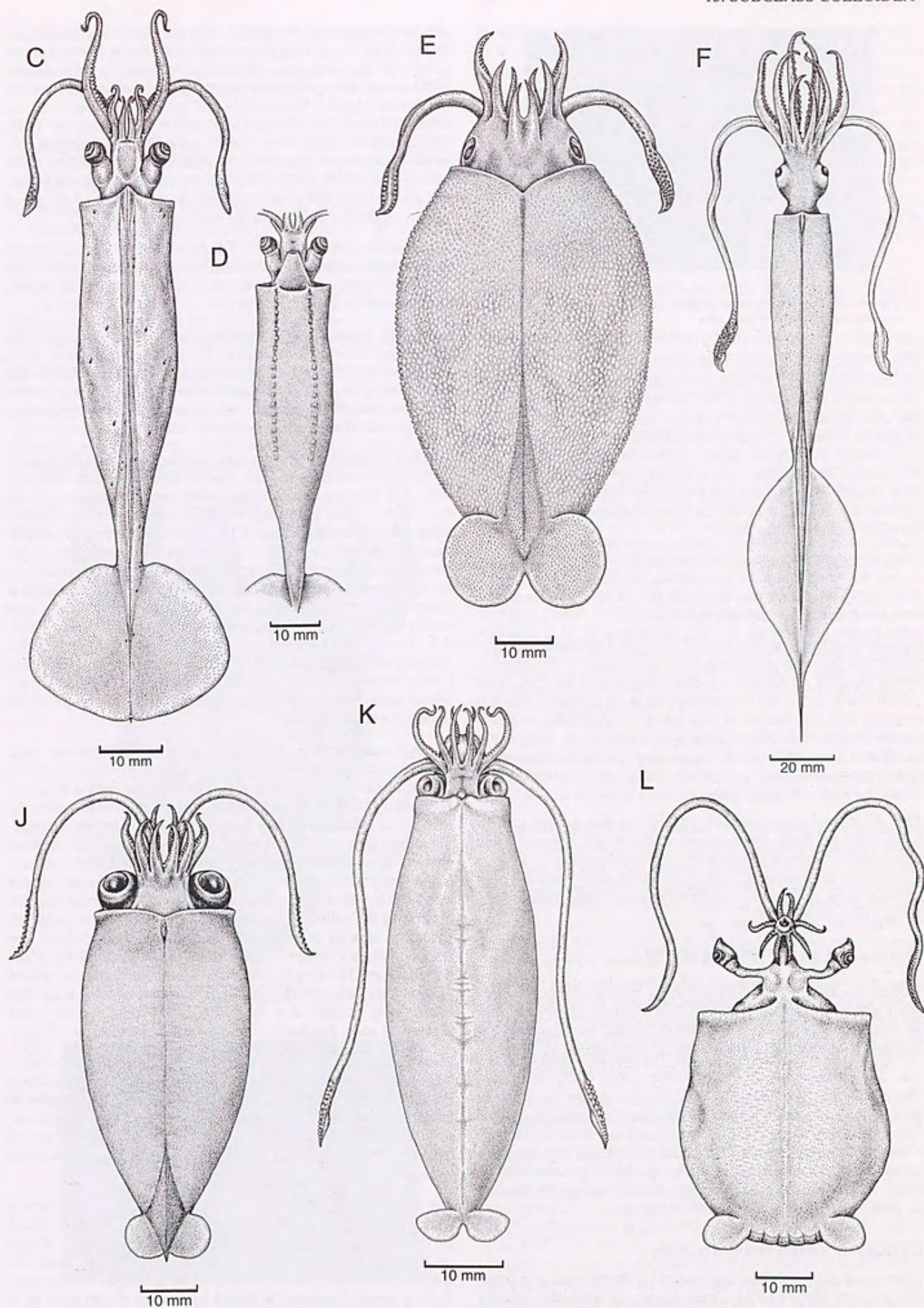


Figure 13.28 Family Cranchiidae, a large, diverse, cosmopolitan group of oceanic squid. A, C, E–L, dorsal view. B, D, ventral view, showing cartilaginous stripes. A–E, subfamily Cranchiinae: A, B, *Liocranchia reinhardti*; C, D, *Leachia* cf. *pacificus*; E, *Cranchia scabra*. F–L, subfamily Taoniinae: F, *Taonius* sp.; G, *Teuthowenia pellucida*; H, subadult and I, juvenile of *Megalocranchia abyssicola*; J, *Sandalops melancholicus*; K, *Helicocranchia pfefferi*; L, *Bathothauma lyromma*. [A–L, K. Hollis]

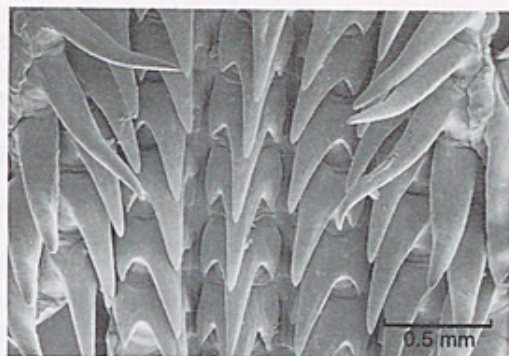


Figure 13.29 Family Cranchiidae. Portion of the radula of *Cranchia scabra*, showing several transverse tooth rows. [C.C. Lu]

(Fig. 13.28C) off Hawaii lives in near-surface waters until it reaches about 80% of its maximum length. Both males and females then descend to depths of up to 2300 m where they mature, mate and then apparently spawn (Young, R.E. 1975a). Diel vertical migration of larval or adult cranchiids has not been demonstrated conclusively elsewhere (Roper & Young 1975; Young, R.E. 1975a). The recent capture in a demersal trawl of a *Taonius* species (Fig. 13.28F) off north-western Australia perhaps suggests that this species is associated with the sea floor in continental slope waters during at least part of the day.

Often abundant, most representatives of this family in Australian waters are small and have thin-walled mantles, sometimes filled with highly ammoniacal body fluids (Pl. 18.10), and hence they have no commercial fisheries potential.

Cranchiids are among the most speciose and abundant oegopsid squids and occur in all oceans from the surface to depths of in excess of 3500 m. Of the 13 genera recognised by N.A. Voss (1980), eight are known from Australian waters, none of which is endemic. The distribution of most species in Australian waters is poorly known. N.A. Voss (1985) concluded that *T. pellucida* is distributed circumglobally in the mixed waters of the Subtropical Convergence, its local occurrence being affected by surface winds, currents and water depth.

The abundance of cranchiids in near surface waters off the Australian coast and the resilient nature of the body of some species suit cranchiids to shipboard laboratory studies of flotation physiology, luminescence, functional morphology and behaviour as have been conducted elsewhere (Clarke 1962; Young, R.E. 1975c; Voss, N.A. 1980).

Order VAMPYROMORPHA

These deep-water (bathypelagic) animals have four pairs of arms. A pair of special additional appendages is located on the outer side of the web between the first and second arms. These long, thread-like filaments are retractable into pockets, and lack suckers. The arms are connected by a moderately deep web. The arm suckers align in one row, between two rows of cirri which lie parallel to the sucker row. The suckers lack chitinous rings, and are absent from the proximal parts of the arms. One elongate, paddle-like fin is situated on each side of the mantle (Fig. 13.30A). The larvae may have two pairs, one of which disappears by the end of the larval stage. The mantle is always fused with the head in the occipital area but not with the funnel. Numerous, small simple photophores of composite structure are present. The gladius is a wide, very thin plate.

Family Vampyroteuthidae

This monotypic family is characterised by the presence of a single pair of fins (Fig. 13.30A), and a pair of retractile, sensory filaments in addition to the eight sessile arms. The suckers are arranged in a single row and alternate with lateral cirri along most of the arm. The mantle is fused to the head and the mantle opening is wide. Photophores are present.

The sole member of the family, *Vampyroteuthis infernalis* was described from a specimen from the Guinea Basin, South Atlantic (Chun 1903), and was originally regarded as an octopod. Subsequently the species has been taken in the Pacific Ocean and the Indian Ocean (Young, R.E. 1972a) and elsewhere in the Atlantic Ocean. The family was erected by Thiele in 1915. Transferred to a new order of its own, Vampyromorpha, the species was studied extensively by Pickford (1939a, 1939b, 1940, 1946, 1949a, 1950, 1952, 1959). Her reports on the natural history and distribution (Pickford 1946) and external anatomy (Pickford 1949a) remain the most extensive studies on the species.

The first Australian records of *Vampyroteuthis infernalis* were from the *Dana* Expedition in 1929 in the western Tasman Sea (Pickford 1946). The species was reported off south-eastern Tasmania by Lu & Phillips (1985).

Externally *Vampyroteuthis infernalis* is jet black in colour. The body is gelatinous in consistency. The mantle is broad and short, and fused with the head on its dorsal side. The large, paddle-like fins are located laterally and subterminally towards the posterior end of the mantle. In adults, a pair of small pockets, representing the degenerated larval fins, is present behind the fins.

The head is broad and the eyes are very large (Fig. 13.30A). Each of the eight arms bears a single row of suckers that lack chitinous rings. The arms are connected by a deep web that extends to about two thirds of arm length. Paired cirri alternate with the suckers along most of the oral surface of the arms. About four to 10 pairs of primary cirri occur proximal to the first sucker. Between the dorsal and dorso-lateral arms, a slender filament extends from a pocket on the dorsal surface of the web. The filament is retractile and often is completely retracted within the pocket. These filaments were considered to be homologous with arms (Pickford 1940). R.E. Young (1967) studied their nerve innervation and concluded that they are not homologous with the arms. However, J.Z. Young (1977) believed that the filaments are indeed the modified second pair of arms of a decapod. Thus presently, the true origin of the filaments remains unclear.

Vampyroteuthids have a shell-sac which runs from the neck backwards to the apex of the body where it bends towards the ventral surface. The following description of the shell is based on Pickford's (1949a) thorough studies. The shell, located within the shell sac is a thin, plate-like, transparent, non-calcified structure. There is a little cup-shaped conus, but no trace of a chambered phragmocone. There are no significant differences between sexes in the shape and structure of the shell. The shell of larvae is more slender than that of adults. The posterior three-quarters of the shell consists of the united lateral plates and conus vanes and is arched so that it appears boat-shaped when viewed from below. The anterior quarter is formed largely of the broad middle plate of the pro-ostracum. The thin middle plate is separated from the lateral plates in the posterior region by the inner asymptotic zone. The lateral plate is separated from the conus vane by the outer asymptotic zone. The function of the shell is unknown.

Many photophores are scattered over the surface of the head, mantle, fins and arms, particularly on their ventral surfaces. Posterior to each fin is a single large photophore. An oval patch of thickly packed, small photophores is located on the dorso-lateral surface of the mantle (Fig. 13.30A) at the level of the mantle opening. Photophores are absent on the web area and the oral surface of the arms.

The mantle musculature of *V. infernalis*, particularly the circular muscle, is poorly developed, and bundles of radial muscle fibres are interspersed with gelatinous material. According to R.E. Young (in Roper & Brundage 1972), *V. infernalis* swims at a moderate speed with the arms pointed forward to the direction of motion and the fins provide propulsion. Rapid swimming is produced by a medusoid action of the arms and web. Slow swimming is achieved by water ejection through the funnel, with the fins spread as stabilisers. R.E. Young also stated that the first is the primary method. The second method is rarely used and the third method



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