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Identification guide for cephalopod
paralarvae from the Mediterranean Sea



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Authors

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1 Introduction

Cephalopods are key components of marine trophic webs, where they constitute major food resources for a large variety of predators including fish, other cephalopods, marine mammals, and seabirds (e.g. Clarke, 1996; Piatkowski *et al.*, 2001; Cherel *et al.*, 2009). Cephalopods are, in turn, voracious predators of fish and crustaceans (Boyle and Rodhouse, 2005). Octopuses, squid, and cuttlefish are also important living marine resources, maintaining relevant fisheries around the world (FAO, 2012). Despite their economic and ecological importance, the number of studies on these molluscs, until relatively recently, has been small compared to other taxonomic groups such as fish, crustaceans, or marine mammals (Piatkowski *et al.*, 2001). The lack of knowledge is even worse in the case of larval stages, which have been little studied worldwide and represent, without doubt, a challenge for future studies on cephalopods. The difficulties in sampling (low abundance and patchy distribution), the uncertainties of species identification, and problems related to their maintenance in captivity are major limitations to those studies (Vecchione, 1987; Boyle and Rodhouse, 2005). The taxonomy is probably the biggest obstacle to overcome, since the identification of virtually all larval and juvenile stages of cephalopods has been, and still is in many cases, confusing and problematic (Sweeney *et al.*, 1992).

Cephalopod hatchlings rarely have specializations and do not undergo metamorphosis, so they are not true larvae (Young and Harman, 1988; Sweeney *et al.*, 1992). However, there are significant changes in certain body features during the early developmental stages that complicate the identification of these phases compared to more advanced stages and subadults of their own species (Figure 1.1). Therefore, the early stages of post-embryonic development of some groups have been called paralarvae (Young and Harman, 1988).

Despite the publication of a manual for the identification of cephalopod paralarvae and juveniles in the early 1990s (Sweeney *et al.*, 1992), larval forms of many species and some whole families are currently still unknown. Pending future improvements on taxonomic aspects, most of the existing studies have focused on the effects of oceanographic parameters on the distribution of paralarvae in different areas of the world's oceans (e.g. Vecchione *et al.*, 2001; Diekmann and Piatkowski, 2002; Zeidberg and Hamner, 2002; González *et al.*, 2005; Martins and Pérez, 2006; Moreno *et al.*, 2009; Otero *et al.*, 2009). To a lesser extent, studies exist on the taxonomy and systematics (Sweeney *et al.*, 1992; Nixon and Mangold, 1998; Piatkowski, 1998; Boletzky, 2003), aspects related to the maintenance in captivity (Villanueva, 1995; Villanueva and Bustamante, 2006), or growth during the early stages of larval development (Villanueva *et al.*, 2007).

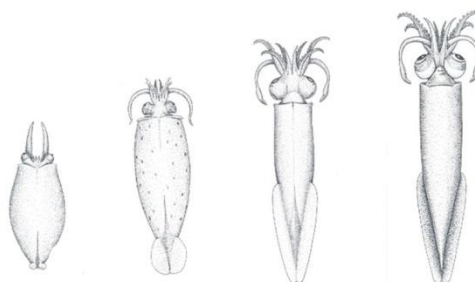


Figure 1.1. Change in form during growth of an oceanic species of cephalopod (from Guerra, 1992).

The identification and analysis of cephalopod larval stages is interesting, not only from a systematic point of view and for a comprehensive understanding of the biological cycle of the species, but also for studies on population dynamics, especially to estimate the recruitment of certain commercially important stocks (Guerra, 1992). In the Mediterranean, cephalopods are important resources for certain fisheries. The most important in terms of biomass is the common octopus (*Octopus vulgaris*), which may represent 20–40% of the bottom trawl landings (Quetglas *et al.*, 1998). The seasonal fishery for cuttlefish (*Sepia officinalis*) is vital for the maintenance of the small-scale fleet, since a large number of vessels throughout the Mediterranean target this species. Finally, although the importance of the common squid (*Loligo vulgaris*) for the commercial fleet is limited in relative terms, it is one of the main targets for recreational fishers (Morales-Nin *et al.*, 2005). The remaining commercially sought species have negligible economic importance owing to low catches or scarce flesh quality (Sartor *et al.*, 1998).

Until now, a total of 67 cephalopod species has been reported in the Mediterranean Sea (Bello, 2008), from which only 53 are represented by well established populations (Bello, 2003). Despite having well-cataloged the Mediterranean teuthofauna from their adult forms (e.g. Belcari and Sartor, 1993; Sánchez *et al.*, 1998; Quetglas *et al.*, 2000; González and Sánchez, 2002), studies on larval stages are very scarce (Roper, 1972, 1974; Sánchez and Molí, 1985; Bello, 2004; Lefkaditou *et al.*, 2005). As mentioned, such studies are limited by a lack of taxonomic information for many species, which is essential for the proper identification of specimens. The only available paralarva guide was produced more than 20 years ago (Sweeney *et al.*, 1992), but valuable taxonomic information has been published since then. To assist with the identification of cephalopods in plankton samples collected in the Balearic Sea (western Mediterranean), we compiled the currently available information on paralarvae and early life stages of the cephalopod species inhabiting our study area. This CRR is the result of such a compilation, which also incorporates new, unpublished pictures from our own material. We hope this work will also assist scientists and students interested in identifying cephalopod paralarvae.

2 Checklist of species

Taxonomic list of the cephalopods recorded in the Mediterranean.

Class CEPHALOPODA Cuvier, 1795

Subclass COLEOIDEA Bather, 1888

Order SEPIIDA Zittel, 1895

Family SEPIIDAE Leach, 1817

Genus *Sepia* Linnaeus, 1758

Sepia officinalis Linnaeus, 1758

Sepia elegans Blainville, 1827

Sepia orbignyana Férussac, 1826

Order SEPIOLIDA Fioroni, 1981

Family SEPIOLIDAE Leach, 1817

Subfamily ROSSINAE Appellöf, 1898

Genus *Rossia* Owen, 1834

Rossia macrosoma (Delle Chiaje, 1830)

Genus *Neorossia* von Boletzky, 1971

Neorossia caroli (Joubin, 1902)

Subfamily HETEROTEUTHINAE Appellöf, 1898

Genus *Heteroteuthis* Gray, 1849

Heteroteuthis dispar (Rüppell, 1844)

Genus *Stoloteuthis* Verrill, 1881

Stoloteuthis leucoptera (A. E. Verrill, 1878)

Subfamily SEPIOLINAE Appellöf, 1898

Genus *Rondeletiola* Naef, 1921

Rondeletiola minor (Naef, 1912)

Genus *Sepiola* Leach, 1817

Sepiola rondeletii Leach, 1817

Sepiola robusta Naef, 1912

Sepiola ligulata Naef, 1912

Sepiola intermedia Naef, 1912

Sepiola affinis Naef, 1912

Genus *Sepietta* Naef, 1912

Sepietta oweniana (d'Orbigny, 1841)

Sepietta obscura Naef, 1916

Sepietta neglecta Naef, 1916

Order TEUTHIDA Naef, 1916

Suborder MYOPSIDA d'Orbigny, 1845

Family LOLIGINIDAE Lesueur, 1821

Genus *Loligo* Lamarck, 1798

Loligo vulgaris Lamarck, 1798

Loligo forbesii Steenstrup, 1857

Genus *Alloteuthis* Wülker, 1920

Alloteuthis media (Linnaeus, 1758)

Alloteuthis subulata (Lamarck, 1798)

Suborder OEGOPSIDA d'Orbigny, 1845

Family CHTENOPTERYGIDAE Grimpe, 1922

Genus *Ctenopteryx* Appellöf, 1890

Ctenopteryx sicula (Vérany, 1851)

Family ENOPLOTEUTHIDAE Pfeffer, 1900

Genus *Abralia* Gray, 1849

Abralia veranyi (Rüppell, 1844)

Abraliopsis morisii (Vérany, 1839)

Family ANCISTROCHEIRIDAE Pfeffer, 1912

Genus *Ancistrocheirus* Gray, 1849

Ancistrocheirus lesueurii (d'Orbigny, 1842)

Family OCTOPOTEUTHIDAE Berry, 1912

Genus *Octopoteuthis* Rüppell, 1844

Octopoteuthis sicula Rüppell, 1844

Genus *Taningia* Joubin, 1931

Taningia danae Joubin, 1931

Family ONYCHOTEUTHIDAE Gray, 1847

Genus *Onychoteuthis* Lichtenstein, 1818

Onychoteuthis banksii (Leach, 1817)

Genus *Ancistroteuthis* Gray, 1849

Ancistroteuthis lichtensteinii (Férussac [in Férussac & d'Orbigny], 1835)

Family HISTIOTEUTHIDAE Verril, 1881

Genus *Histioteuthis* d'Orbigny, 1841

Histioteuthis reversa (Verril, 1880)

Histioteuthis bonnellii (Férussac, 1835)

Family BRACHIOTEUTHIDAE Pfeffer, 1908

Genus *Brachioteuthis* Verrill, 1881

Brachioteuthis riisei (Steenstrup, 1882)

Family OMMASTREPHIDAE Steenstrup, 1857

Subfamily ILLICINAE Posselt, 1890

Genus *Illex* Steenstrup, 1880

Illex coindetii (Vérany, 1839)

Genus *Todaropsis* Girard, 1890

Todaropsis eblanae (Ball, 1841)

Subfamily TODARODINAE Adam, 1960

Genus *Todarodes* Steenstrup, 1880

Todarodes sagittatus (Lamarck, 1798)

Subfamily OMMASTREPHINAE Steenstrup, 1857

Genus *Ommastrephes* d'Orbigny, 1835

Ommastrephes bartramii (Lesueur, 1821)

Family THYSANOTEUTHIDAE Keferstein, 1866

Genus *Thysanoteuthis* Troschel, 1857

Thysanoteuthis rhombus Troschel, 1857

Family CHIROTEUTHIDAE Gray, 1849

Genus *Chiroteuthis* d'Orbigny, 1841

Chiroteuthis veranii (Férussac, 1835)

Family CRANCHIIDAE Prosch, 1847

Subfamily CRANCHIINAE Prosch, 1849

Genus *Cranchia* Leach, 1817

Cranchia scabra Leach, 1817

Subfamily TAONIINAE Pfeffer, 1912

Genus *Teuthowenia* Chun, 1910

Teuthowenia megalops (Prosch, 1849)

Genus *Galiteuthis* Joubin, 1898

Galiteuthis armata Joubin, 1898

Order OCTOPODA Leach, 1818

Suborder CIRRATA Grimpe, 1916

Family OPISTHOTEUTHIDAE Verrill, 1896

Genus *Opisthoteuthis* Verrill, 1883

Opisthoteuthis calypso Villanueva, Collins, Sánchez & Voss, 2002

Suborder INCIRRITA Grimpe, 1916

Family OCTOPODIDAE d'Orbigny, 1839

Subfamily OCTOPODINAE d'Orbigny, 1845

Genus *Octopus* Cuvier, 1798

Octopus salutii Vérany, 1836

Octopus vulgaris Cuvier, 1797

Genus *Callistoctopus* Iw. Taki, 1964

Callistoctopus macropus (Risso, 1826)

Genus *Macrotritropus* Grimpe, 1922

Macrotritropus defilippi (Vérany, 1851)

Genus *Scaevurgus* Troschel, 1857

Scaevurgus unicirrhus (Delle Chiaje [in de Férussac & d'Orbigny], 1841)

Genus *Pteroctopus* P. Fischer, 1882

Pteroctopus tetracirrhus (Delle Chiaje, 1830)

Subfamily ELEDONINAE Grimpe, 1921

Genus *Eledone* Leach, 1817

Eledone cirrhosa (Lamarck, 1798)

Eledone moschata (Lamarck, 1798)

Subfamily BATHYPOLYPODINAE Robson, 1929

Genus *Bathypolypus* Grimpe, 1921

Bathypolypus sponsalis (P. Fischer & H. Fischer, 1892)

Family TREMOCTOPODIDAE Brock, 1882

Genus *Tremoctopus* delle Chiaje, 1830

Tremoctopus violaceus Delle Chiaje, 1830

Family OCYTHOIDAE Gray, 1849

Genus *Ocythoe* Rafinesque, 1814

Ocythoe tuberculata Rafinesque, 1814

Family ARGONAUTIDAE Tryon, 1879

Genus *Argonauta* Linnaeus, 1758

Argonauta argo Linnaeus, 1758

3 Identification key of early life stages of cephalopods

1. • Mantle without fins; arm crown without tentacles..... **Order Octopoda** 16
 - Mantle with fins or fin rudiments; one pair of tentacles or a trunk-like structure (proboscis) exists 2
2. • Mantle with lateral fins..... 3
 - Mantle with subterminal or terminal fins, sometimes dorsally attached **Order Teuthoidea** 5
3. • Arm crown with eight subequal arms with suckers only (cirri develop in later juvenile stage). Suborder Cirrata **Opisthoteuthidae**
 - Arm crown with 6–8 arms and two tentacles between arm III and IV; all appendages with stalked suckers 4
4. • Fins long and narrow (not paddle-shaped); extend laterally from near posterior end to near anterior margin of mantle, but never united posteriorly **Sepiidae**
 - Fins paddle or ear-shaped, each fin at least as wide as long (antero-posteriorly) **Sepiolidae**
5. • Eye covered by a transparent membrane (cornea), tentacular clubs with clubs with four rows of suckers, no external photophores. Suborder Myopsida **Loliginidae**
 - Eye without cornea, thus, in contact with seawater, many species with external photophores. Suborder Oegopsida 6
6. • Tentacles fused into trunk like structure (proboscis) **Ommastrephidae**
 - Pair of tentacles; no proboscis 7
7. • Head with long neck 8
 - Head without long neck 9
8. • Neck with dorsal hump; arm crown not stalked **Brachioteuthidae**
 - Neck multiple chambered and without dorsal hump; long tail with secondary fin (often missing); arm crown stalked **Chiroteuthidae**
9. • Funnel locking cartilage and mantle fused in nuchal region **Cranchiidae**
 - Funnel locking cartilage and mantle not fused; mantle always free in nuchal region 10
10. • Transverse T-shape funnel locking-cartilage; mantle densely covered with small chromatophores, even visible in preserved specimens **Thysanoteuthidae**
 - Funnel locking-cartilage of other shape (straight, round or subtriangular) 11
11. • Fins with muscular ribs; tentacular club in small paralarvae **Ctenopterygidae**
 - Fins without ribs 12
12. • Mantle sharply pointed posteriorly; funnel locking-cartilage straight; head often withdrawn into mantle up to eye lenses; in juvenile stages arm pair IV rudimentary **Onychoteuthidae**

- Features other than above 13
- 13. • Eyes stalked, tubular, anterolaterally directed; tentacles present only in early stage, generally lost in older stage; tentacular club with two rows of suckers **Octopoteuthidae**
- Eyes not stalked, tubular, or anterolaterally directed; tentacular club with 4–8 rows of suckers 14
- 14. • Integumental light organs around margin of eye lid; in large juvenile to adult individuals, left larger than the right one **Histioteuthidae**
- Integumental light organs absent around eye lid; in large juvenile to adult individuals, eyes of equal size 15
- 15. • Light organs on mantle, arms and/or intestine, but no on eyes **Ancistrocheiridae**
- Light organs on mantle, arms and/or intestine and eyes, well defined even in early juvenile stages, but no light organs on viscera **Enoploteuthidae**
- 16. • Mantle muscular, arms of equal length or only slightly enlarged 17
- Mantle muscular, arm pairs I, or I and IV greatly enlarged 18
- 17. • Specialized funnel locking cartilage present (groove with a small knob below), conspicuous even in hatchlings; in juvenile females arm pair I slightly enlarged; dwarfed males with hectocotylus enveloped in a small sac **Argonautidae**
- No specialized funnel locking cartilage (roughly a small “bump”), mantle locking apparatus absent; arms not modified in juvenile males; arms equal in length and generally short and compact **Octopodidae**
- 18. • Arm pairs I and IV greatly enlarged; in early juvenile stages, not enclosed in brachial membrane; funnel elongated **Ocythoidae**
- Arm pair I greatly enlarged and robust, arm pair III reduced; in hatchlings, head and arms enveloped by brachial membrane **Tremoctopodidae**

4 Glossary of terms (from Sweeney *et al.*, 1992)

- **Antitragus:** Small knob-like cartilaginous projection from the posterior wall of the funnel locking-cartilage in some families (e.g. Chiroteuthidae). See tragus.
- **Arms:** Eight circumoral appendages in adults of coleoid cephalopods. (One pair of modified appendages called "tentacles" lies between the ventral and ventrolateral arms in the "decapodous" Sepioidea and Teuthoidea).
- **Arm crown:** Inclusive term encompassing all circumoral appendages (arms, tentacles). See circumoral appendages.
- **Arm-crown stalk:** Elongation of the head between the eyes and the arm crown. Common in many "larval" and juvenile squids (e.g. Brachioteuthidae, Chiroteuthidae, Cranchiidae). Sometimes referred to as armcrown pillar.
- **Band:** Unbroken transverse line or series of chromatophores; may be simple or complex.
- **Bar:** Short transverse line of chromatophores that represents broken or interrupted bands.
- **Buccal connectives:** Muscular rods that connect the supports of the buccal membrane to the bases of the arms.
- **Buccal lappet:** Small, subtriangular flap formed by the tip of the buccal membrane support and the adjoining buccal membrane; may bear suckers.
- **Buccal membrane:** Thin web of tissue that encircles the mouth, reinforced by 6–8 buccal supports.
- **Bullet-shape:** Refers to posteriorly blunt, rounded, rather broad body (mantle) form common in "larval" cephalopods.
- **Calamus:** Conical papilla or projection on the hectocotylus of octopods at the distal terminus of the sperm groove, distal to the last sucker and proximal to the ligula. See ligula.
- **Carpal cluster (Carpal pad):** Usually distinct group of suckers and knobs on the carpus of the tentacular club.
- **Carpal suckers:** Small suckers on the carpus of the club that usually adhere to knobs on the opposite carpus during the locking of the clubs.
- **Carpus:** Proximal zone of suckers and/or knobs on the tentacular club.
- **Cartilage (-inous):** Solid concentration of connective tissue-derived material occurring in funnel-mantle locking apparatus, nuchal attachment, integumental "scales", cranium, etc.
- **Chitinous:** Generalized term for some hard structures in cephalopods that may contain chitin.
- **Chromatophore:** Organs consisting of pigment-filled sacs with associated muscles and nerves that provide much of the background color, color patterns, and pattern changes in cephalopods.
- **Chromatophore fields:** Suites of chromatophores that produce species-specific patterns in discrete regions of the body, namely arm, arm base, head, eye, mantle, viscera, and funnel.

- **Circumoral appendages:** Eight arms (squid, cuttlefish, and octopuses) and (squid and cuttlefish) or the very numerous tentacles (*Nautilus*) that protrude from the head and encircle the mouth of cephalopods.
- **Cirri:** Arm – elongate, fleshy tendrils along the lateral edges of the oral surface of the arms, especially in cirrate octopods. Body – fleshy protuberances of skin that can be erected as papillae, usually dorsal to the eyes.
- **Club:** See tentacular club.
- **Complex band or stripe:** Single irregular or multiple series of chromatophores forming a thick but distinct line.
- **Cone, conus:** Spoon-like or cup-like conical posterior terminus of the gladius or cuttlebone; homologous to the phragmacone of fossil teuthoids.
- **Cuttlebone:** Calcareous, oblong, supporting plate in the dorsal part of the mantle of cuttlefish.
- **Dactylus:** Distal, terminal section of the tentacular club, often characterized by suckers of reduced size.
- **Fins:** Muscular flaps that arise along the lateral or dorsolateral surface of the mantle of sepioids, teuthoids, vampyromorphs, and cirrate octopods; used for locomotion, steering, and stabilization.
- **Fin lobe:** Portion of each fin that protrudes anteriorly from the anterior point of attachment of the fin to the mantle.
- **Funnel:** Ventral, subconical tube through which water is expelled from the mantle cavity during locomotion and respiration (reproductive and waste products; ink also passes through the funnel). (Archaic term: siphon).
- **Funnel locking-cartilage:** Cartilaginous pad that contains variously shaped grooves, pits, pockets, or depressions on each ventrolateral side of the posterior part of the funnel that joins with the mantle component to lock the funnel and mantle together during locomotion. See mantle locking-cartilage.
- **Funnel organ:** Glandular structure on the inside of the funnel, generally a single W-shape form in octopods and a dorsal inverted V-shape component with opposed ventral oblong components in decapods.
- **Funnel valve:** Semilunar muscular flap, a one-way valve, on the inner, dorsal surface near the distal opening of the funnel.
- **Gill lamellae:** Leaf-like convoluted individual components of the gill through which gas exchange occurs.
- **Gills:** In decapods and octopods (other than cirromorphs), the gills are not flattened; the inner and outer demibranchs are attached to a narrow central axis and typically are arranged vertically in two diverging rows or are oriented parallel to the gill axis (lamellae perpendicular to axis). In sepioids, the gills have free lamellae (not attached at tip) and have no branchial canal.
- **Gladius:** Feather or rod-shape chitinous supporting structure in the dorsal midline of teuthoids and nonsepiid sepioids; the homolog of the shell of ancestral forms. Formerly termed pen.

- **Hectocotylus:** One (or more) arm(s) of male cephalopods modified for transferring spermatophores to the female; modifications may involve suckers, sucker stalks, protective membranes, trabeculae, and arm shape. Not all species have a hectocotylus. See calamus, ligula.
- **Hooks:** Chitinous, claw-like structures ontogenetically derived from the suckers on the arms and/or clubs of some oegopsids.
- **Ink sac:** Organ that produces and stores the ink of cephalopods; it generally lies along the intestine (sometimes imbedded in the digestive gland) and empties via a duct into the rectum.
- **Koelliker organs:** Minute, bristle-like structures that cover the body of planktonic octopod larvae.
- **Lanceola:** Expanded portion of the gladius vane.
- **Light organ:** Simple or complex structure that produces bioluminescence by intrinsic (self-generated) or extrinsic (bacterial) means. Also termed photophore.
- **Ligula:** Spatulate to spoon-shape, terminal structure of the hectocotylus of octopods, which includes the calamus proximally (basally) and usually a series of transverse ridges and grooves on the oral surface. See calamus, hectocotylus.
- **Mantle:** Fleishy (muscular) tubular or sac-like body of cephalopods; contraction provides propulsion through jet-like expulsion of water as well as respiration; contains the viscera.
- **Mantle length (ML):** In decapods, measured dorsally from anterior most point of mantle to posterior apex of mantle or tip of united fins, whichever is longest. In octopods, measured dorsally from midpoint between eyes to posterior end of mantle. For exceptions, see Introduction.
- **Mantle locking-cartilage:** Cartilaginous ridge, knob, or swelling on each side of the ventrolateral, internal surface of the mantle that locks into a corresponding funnel cartilage during locomotion. See funnel locking-cartilage.
- **Manus:** Central portion of club between the dactylus distally and the carpus proximally.
- **Nuchal folds:** Series of longitudinal folds or pleats of skin on the nuchal region.
- **Nuchal region:** Dorsolateral area around the posterior part of the head, normally covered by the anterior mantle wall.
- **Pedichel:** Cylindrical stalk that supports a sucker in sepioids and teuthoids.
- **Photophore:** Organ of greater or lesser complexity that produces and distributes bioluminescence, either intrinsically through biochemical reaction or extrinsically through luminescent bacteria. See light organ.
- **Protective membrane:** Thin fold of integument along the lateral angles of the oral surface of the arms and clubs lateral to the suckers, usually supported by muscular rods called trabeculae. See trabeculae.
- **Rachis:** Thickened central axis that usually extends the entire length of the gladius. Free rachis is the portion that does not support vanes. See gladius, vane.
- **Radula:** Chitinous, ribbon-like band in the mouth of cephalopods containing numerous transverse rows of teeth.

- **Rostrum:** See spine.
- **Sepion:** See cuttlebone.
- **Simple band or stripe:** Single unbroken series of chromatophores forming a straight line.
- **Spine:** Sharp, spike-like extension on the posterior tip of the gladius or cuttlebone (= rostrum).
- **Spot:** Regular color marking, typically circular, of fixed diameter that may occur anywhere on the body, may be either darker or lighter than the background color of the cephalopod. Dark spots consist of either single large chromatophores or clusters of small chromatophores, and light spots are defined by concentrations of leucophores in the skin.
- **Suckers:** Muscular, suction-cup structure on the arms and tentacles (rarely on the buccal membrane) of cephalopods; some are stalked, placed on muscular rods that contract (squid and cuttlefish); some are sessile, embedded without stalks on the oral surface of the arms (octopuses); are usually counted either in longitudinal or in transverse (oblique) rows.
- **Sucker ring:** Chitinous, often serrated or denticulate ring that encircles the opening of suckers of squid and cuttlefish.
- **Tail:** Posterior extension generally of the gladius and mantle epithelium, frequently elongate. Fins may extend posteriorly along the tail, and the tail may be swollen by the inclusion of vacuolated tissue.
- **Tentacles:** Elongate, fourth circumoral appendages of cuttlefish and squid used to capture prey; divided into a proximal stalk and a distal club; clubs generally expanded with arrangement of suckers (or hooks); stalks commonly devoid of suckers. Tentacles can retract into pockets on the head of cuttlefish, or merely contract, as in squid.
- **Tentacular club:** Terminal portion of a tentacle; armed with suckers (or suckers and/or hooks), used for capturing prey.
- **Trabeculae:** Muscular rods that support the protective membranes on the arms and clubs of cephalopods; occasionally membranes are reduced and/or trabeculae are elongated, so they extend beyond the edge of the membrane, papilla-like.
- **Tragus:** Small, cartilaginous, knob-like projection from the inner wall of the funnel locking-cartilage in some families (e.g. *Chiroteuthidae*, *Mastigoteuthidae*). See antitragus.
- **Vane:** Thin lateral expansion of the gladius that arises from the rachis. See rachis.
- **Visceral chromatophores:** Large tegumental chromatophores located deep in the mantle region in the integument (skin) covering the dorsal surface of the visceral mass.
- **Water pores:** Small orifices at the base of the web of some pelagic octopuses, e.g. *Tremoctopus*.
- **Web:** Thin, muscular fold of skin of greater or lesser extent that extends between the arms of many octopuses and a few squid, giving an umbrella-like appearance when the arms are spread (e.g. *Cirroteuthidae*, *Histioteuthidae*).

5 Description and illustration of paralarvae

5.1 Family Sepiidae Leach, 1817

Family characters: Cuttlebone (shell or sepion) internal, usually calcareous, porous, and finely laminate; mantle broad, robust, oval to circular in outline, and slightly flattened dorso-ventrally (Figure 5.1); fins narrow, lateral, and occupy almost entirely the mantle length; posterior fin lobes free, not connected at midline; arms with 2–4 rows of suckers and tentacular clubs with 4–8 rows or more longitudinal rows of suckers; retractile tentacles into pockets on ventro-lateral sides of the head; funnel locking-apparatus curved to angular, not straight.

Remarks: Three species of this family inhabit the Mediterranean (*Sepia officinalis*, *Sepia elegans*, and *Sepia orbignyana*). Hatchlings of all three species are not found in plankton samplings because they have benthonic habits. There are not paralarvae forms, since hatchlings are like miniature adults.

References: Sweeney *et al.* (1992).

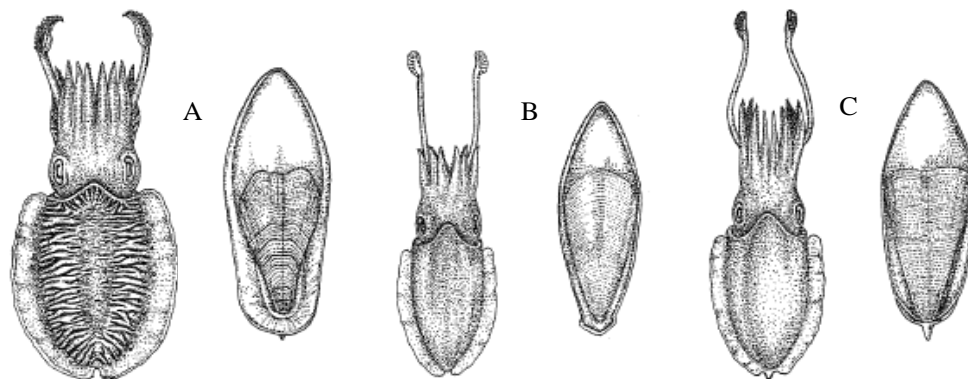


Figure 5.1. Family Sepiidae: dorsal views of adult specimens and cuttlebones of *Sepia officinalis*, size not available (A); *S. elegans*, size not available (B); *S. orbignyana* (C), size not available. From Yau (1994).

Sepia officinalis Linnaeus, 1758

Species characters (Figures 5.1A and 5.2): Mantle projects forward into an obtuse angle behind head; posterior part of cuttlebone widened and with a small apical spine (Figure 5.2D); fins starting directly at anterior edge of mantle and extending anteriorly beyond edge to posterior level of eyes; fins widened posteriorly; five longitudinal rows of suckers on club, with 5–7 median club suckers enlarged (Figure 5.2E).

References: Yau (1994).

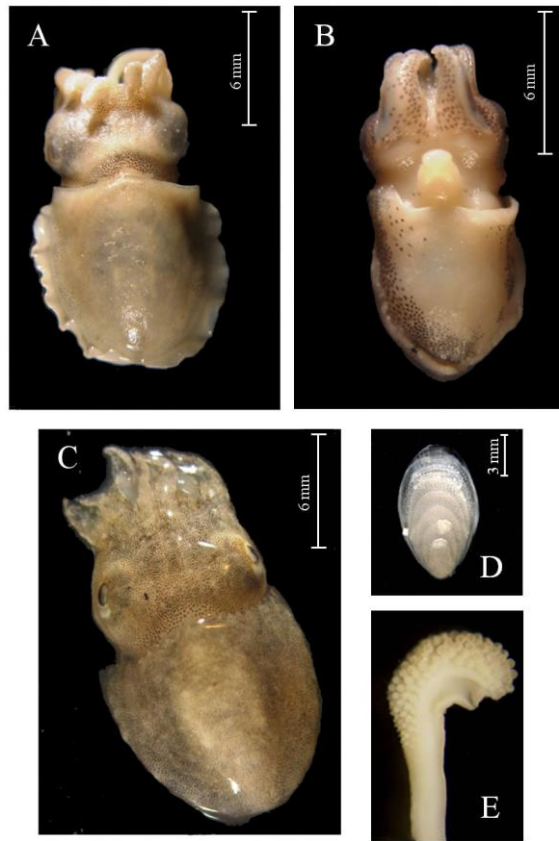


Figure 5.2. *Sepia officinalis* hatchlings from egg incubation: dorsal side, 8.3 mm ML (A); ventral side, 8.6 mm ML (B); dorsal side, 9.2 mm ML (C); cuttlebone (D), and tentacular club (E).

Sepia elegans Blainville, 1827

Species characters (Figure 5.1B): Mantle projects forward in an acute angle behind head; posterior part of cuttlebone not widened; fins starting a small distance from anterior edge of mantle, not exceeding mantle's anterior edge and not widening posteriorly; proximal parts of arms with two rows of suckers, four rows of arm suckers distally; very small apical spine on posterior of cuttlebone; cuttlebone rhomboidal, greatly narrowed anteriorly and posteriorly; three greatly enlarged median suckers on tentacle club.

References: Yau (1994).

Sepia orbignyana Férussac, 1826

Species characters (Figure 5.1C): Mantle projects forward in an acute angle behind head; posterior part of cuttlebone not widened; fins starting a small distance from anterior edge of mantle, not exceeding mantle's anterior edge and not widening posteriorly; arms with four rows of suckers, well-developed apical spine on posterior of cuttlebone, spine may protrude out of mantle in preserved specimens; cuttlebone lanceolate, narrowed gradually anteriorly and posteriorly; five greatly enlarged median suckers on club, central sucker being largest.

References: Yau (1994).

5.2 Family Sepiolidae Leach, 1817

Family characters: Mantle short, broad, sac-like, rounded posteriorly; fins large, round, separated; funnel locking-cartilage simple, straight; shell absent or reduced to a chitinous gladius; eye covered by transparent skin.

Remarks: The characters used here for most sepiolid paralarvae descriptions are those of juveniles or adults.

References: Sweeney *et al.* (1992); Nesis (1999).

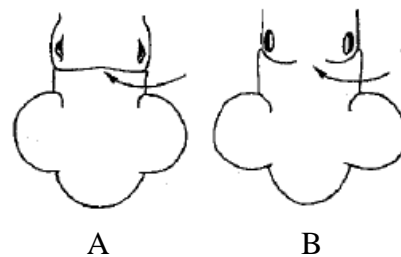


Figure 5.3. Rossiinae (A) and Sepiolinae (B): dorsal head-mantle union. From Bello (1995).

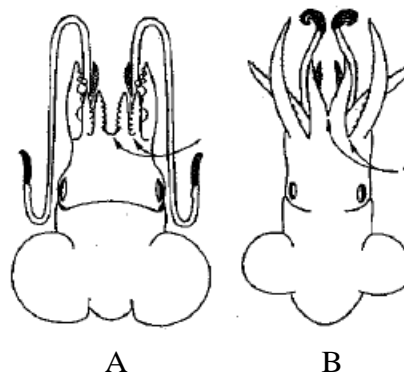


Figure 5.4. Heteroteuthinae (A, *Heteroteuthis dispar*) and Sepiolidae other than Heteroteuthinae (B): dorsal views showing the web joining the first three pairs of arms (lacking in B) and the length of fins. From Bello (1995).

5.2.1 Subfamily Rossiinae Appellöf, 1898

Subfamily characters: No web joining the arms; fins short, not exceeding the mantle; dorsal mantle edge not fused to the head (Figure 5.3A).

References: Bello (1995).

Rossia macrosoma (Delle Chiaje, 1830)

Species characters (Figure 5.5): Arms with four rows of suckers; well developed, functional ink sac with regular anal flaps.

References: Bello (1995).

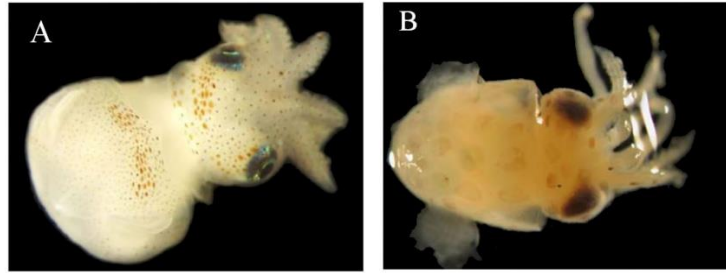


Figure 5.5. *Rossia macrosoma*: dorsal views of a pre-hatchling after incubation (A) and a paralarva of 2.7 mm ML (B). From Moreno (2008).

Neorossia caroli (Joubin, 1902)

Species characters: Arms with two rows of suckers; no functional ink sac; anal flaps vestigial.

References: Bello (1995).

5.2.2 Subfamily Heteroteuthinae Appellöf, 1898

Subfamily characters: A deep web joining the first three pairs of arms (Figure 5.4A); fins long, either the posterior or the anterior edge of fins reaches or exceeds the mantle.

References: Bello (1995).

Heteroteuthis dispar (Rüppell, 1844)

Species characters (Figure 5.6): Body short and egg-like; mantle muscular, not fused with head; anterior mantle margin in paralarvae and early juveniles straight, in later juveniles and adults strongly protruding forward on the ventral side, reaching the level of the anterior eye margin and almost covering the funnel from below; anterior fin attachment posterior to dorsal midpoint of mantle; fins tongue-like, wide (fin width in hatchings exceeding mantle width), large, and extended to the posterior end of the mantle; arms very short, the first three arm pairs connected at bases with a deep membrane (Figure 5.4A and 5.6C); gladius absent; large, oval bilobed photophore inside the mantle cavity (partly covered by funnel), noticeable even in hatchings (Figure 5.6D); colour very bright, vivid, with white fin bases and metallic iridescences on head and body.

References: Sweeney *et al.* (1992); Diekmann *et al.* (2002).

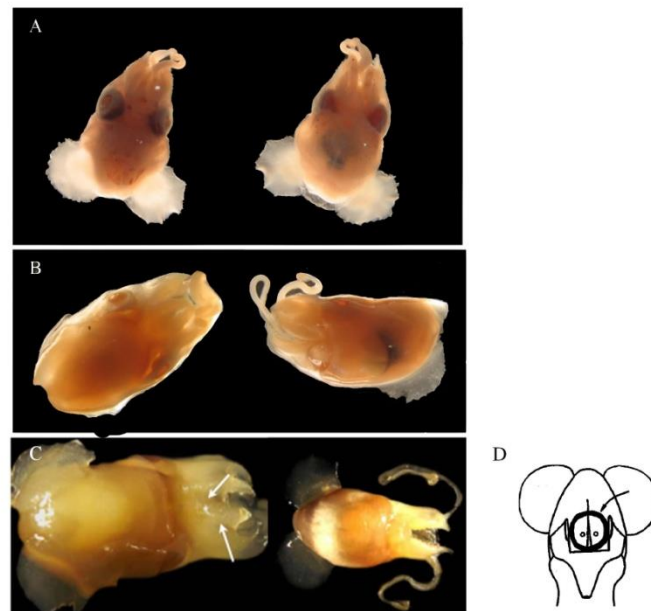


Figure 5.6. *Heteroteuthis dispar*: dorsal (left) and ventral (right) views of paralarvae measuring 2.7 mm ML (A), 6.6 mm ML (B), and 10.6 mm ML (C); light organ rounded inside the mantle cavity (funnel partly removed) (D). In C, arrows indicate the web joining the first three pairs of arms. C from Moreno (2008); D from Bello (1995).

Stoloteuthis leucoptera (A. E. Verrill, 1878)

Species characters (Figure 5.7): Mantle muscular, globular, fused dorsally to head (Figures 5.7A and 5.7D); ventral mantle margin (ventral shield) protrudes anteriorly to level of eye opening; dark, broad stripe of densely packed chromatophores along dorsal midline, more scattered laterally; ventral shield covers the entire ventral surface of mantle, very darkly pigmented with closely set chromatophores; lateral and posterior surfaces covered with golden reflective tissue; fins long (>90% ML), widely separated, broad, elongate-rounded; fin base attached to anterior part of mantle; posterior edges do not extend posteriorly to mantle; funnel tip narrow, barely extends anterior to ventral mantle opening; base broad, muscular; head short (50–60% ML), broad (head width similar to mantle width); eyes large; eyelids distinct; arms short, robust, bluntly tipped; deep web connects arms I–IV, but not present between arms IV (Figures 5.7B and 5.7E); arm formula: III=II>IV>I; suckers biserial, globular, reduced in diameter toward tip, closely packed; tentacles robust, especially on proximal half, clubs short, tip bluntly pointed, suckers very small, closely packed in 12–16 rows (Figure 5.7F); narrow median adductor muscle connects ventral mantle wall to viscera; large bilobed photophore covers ventral surface of ink sac; no light organ inside the mantle cavity.

References: Bello (1995); Vecchione *et al.* (2001).

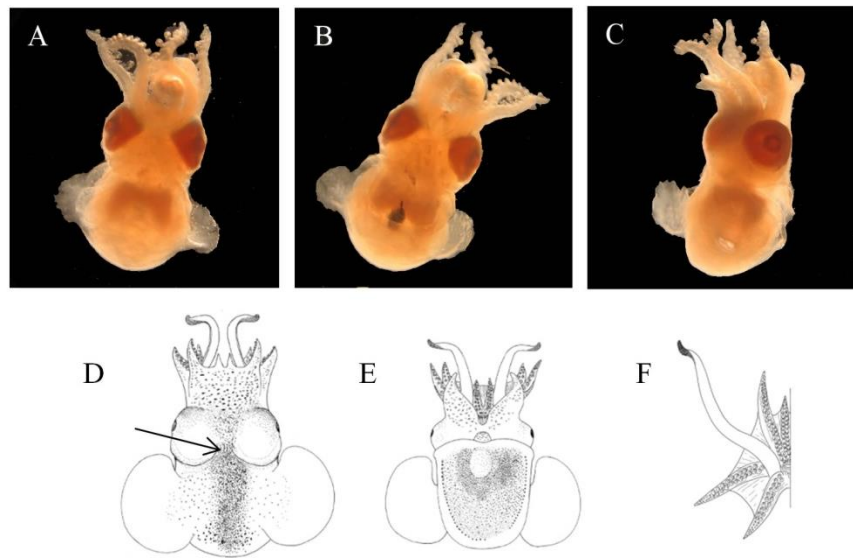


Figure 5.7. *Stoloteuthis leucoptera*: dorsal (A), ventral (B), and lateral (C) views, 3.2 mm ML; dorsal (D), ventral (E), and right half of oral (F) views, 9.8 mm ML. D–F from Vecchione *et al.* (2001).

5.2.3 Subfamily Sepiolinae Appellöf, 1898

Subfamily characters: Dorsal edge of mantle fused with head (Figure 5.3B); no web joining the arms (Figure 5.4B); fins short, not exceeding the mantle.

References: Bello (1995).

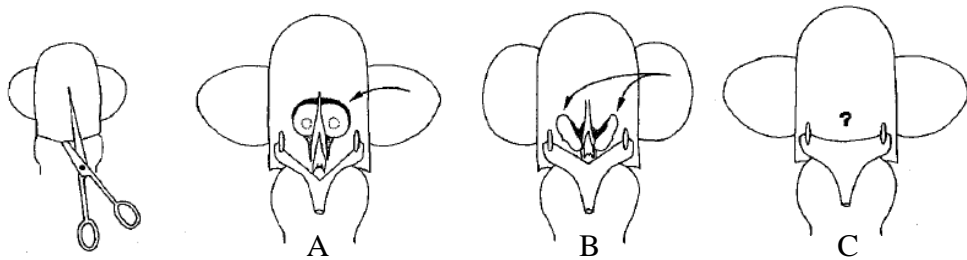


Figure 5.8. Subfamily Sepiolinae: mantle cavity showing the light organs in *Rondeletiola minor* (A), *Sepiola* spp. (B), and *Sepietta* spp. (C). From Bello (1995).

Rondeletiola minor (Naef, 1912)

Species characters (Figure 5.9): Body short, rounded; its anterior end on the ventral side not protruded anteriorly and not covering the funnel; fins kidney-like, much shorter than the longitude of mantle; first and second arms not connected by a membrane; large photophore in the anterior part of the ink sac (Figures 5.8A and 5.9C), bilobed in juveniles, compact in adults.

References: Bello (1995); Nesis (1999).

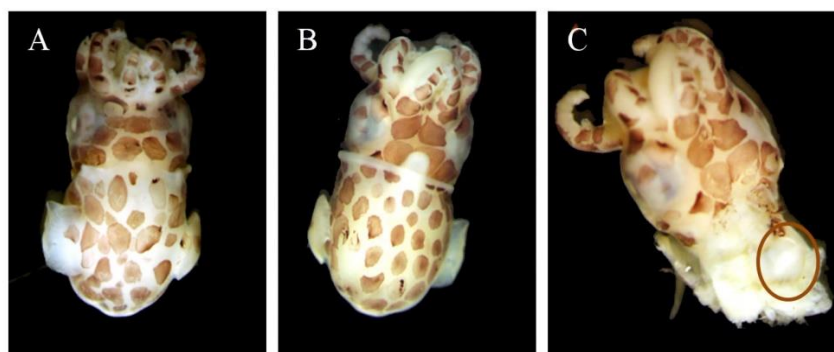


Figure 5.9. *Rondeletiola minor*: dorsal (A), ventral (B), and ink sac light organ (C; mantle and funnel removed to expose the ink sac), 3.3 mm ML.

Sepiola spp. Leach, 1817

Generic characters: A pair of kidney-shaped light organs inside the mantle cavity (Figure 5.8B).

References: Bello (1995).

Sepietta spp. Naef, 1912

Generic characters (Figure 5.10): No light organs inside the mantle cavity (Figure 5.8C).

References: Bello (1995).

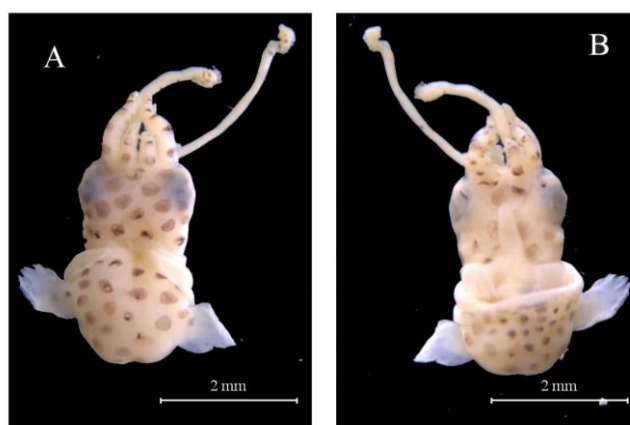


Figure 5.10. *Sepietta* sp.: dorsal (A) and ventral (B) views, 1.8 mm ML.

5.3 Family Loliginidae Lesueur, 1821

Family characters: Body form of hatchlings bullet-shaped; mantle elongated, its anterior margin with mid-dorsal projection; fins paddle-shaped, broad with short bases, much wider than long; ventral arms (arms IV>I) and tentacles with four rows of suckers, without hooks; tentacular club broad, much wider than stalks; tentacles not retractile; minute suckers may be present on the buccal membrane; buccal membrane with

eight lappets, connectives to arms IV attached ventrally; funnel cartilage straight, elongated; gladius feather-like, with short free rachis; in some species, two (rarely one) photophores on ink sac; head squarish; eyes covered by transparent corneal membrane with only a minute pore at its anterior end; the number of chromatophores decreases from the ventral to dorsal side.

Remarks: The paralarvae of this family are very similar and distinguishable mainly by number and position of chromatophores. Since chromatophores may fade after fixation, it is very difficult to identify the species when the individuals have been stored in formalin for a long time (Figure 5.11).

References: Sweeney *et al.* (1992); Nesis (1999); Moreno (2008).

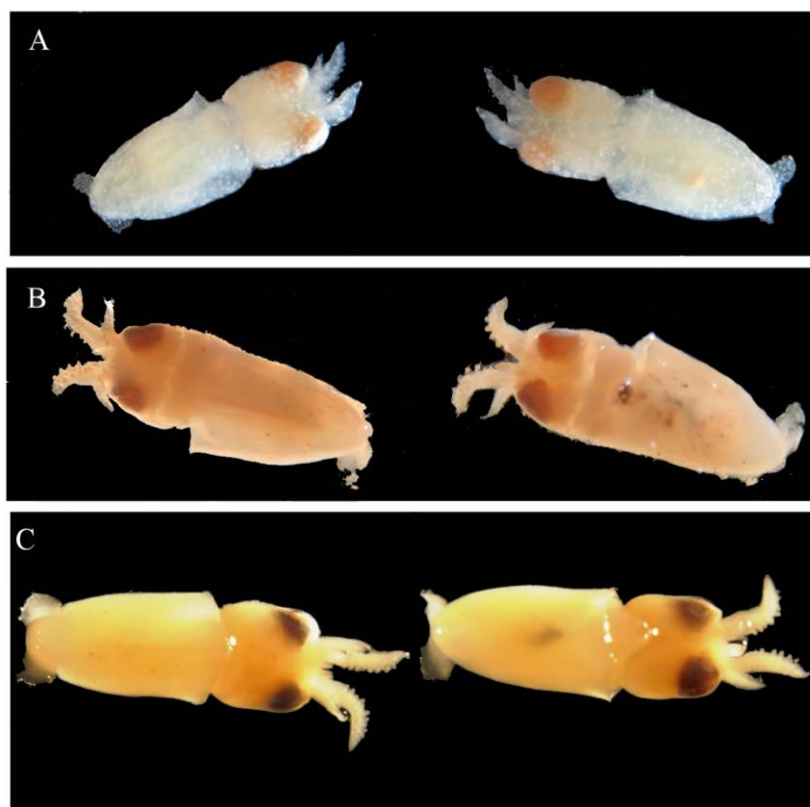


Figure 5.11. Loliginidae: dorsal (left) and ventral (right) views of individuals measuring 2.5 mm ML (A), 3.2 mm ML (B), and 4.5 mm ML (C). C from Moreno (2008).

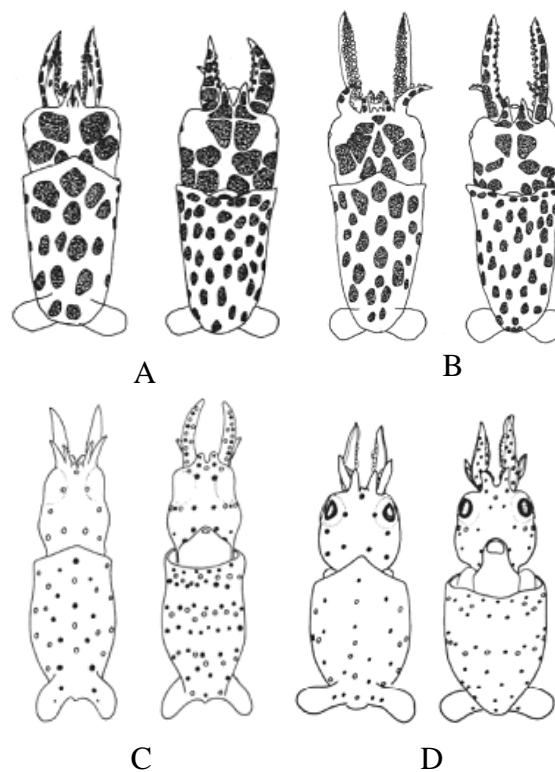


Figure 5.12. Loliginidae, dorsal (left) and ventral (right) views: *Loligo vulgaris*, 3.1 mm ML (A); *Loligo forbesii*, 3.7 mm ML (B); *Alloteuthis media*, live hatchlings (C); and *Alloteuthis subulata*, 2.0 mm ML (D). A, B, and D from Sweeney *et al.* (1992); C from Fioroni (1965).

Loligo vulgaris Lamarck, 1798

Species characters (Figures 5.12A, 5.13A,B, 5.14, and 5.15): Mantle cylindrical in the anterior half, conical in the posterior half; mid-dorsal mantle projection tongue-like; fins transversely tongue-like in paralarvae and oval in juveniles, fin length equal to or longer than width; in early juveniles, central club suckers much larger than the marginal ones (Figure 5.14A), however, this difference is not noticeable in hatchlings (Figure 5.14B,C); buccal membrane with small suckers; lateral sides of gladius bent arch-like, without marginal ribs; the arrangement of red/brown chromatophores on the mantle is variable, but 5–6 are generally located on the ventral border and only one on the dorsal mantle border; on the ventral head, ten red chromatophores are arranged in two cheek patches of four posterior to eyes and a pair between the eyes (Figures 5.13A and 5.15A,C); on the dorsal surface of head, two brown chromatophores are located between the eyes and two above each eye; below the eyes, yellow chromatophores are present in variable numbers (Figures 5.13B and 5.15B,D).

Remarks: Live hatchlings measure 2.8–3.9 mm ML (Turk *et al.*, 1986; Villanueva, 2000) and are smaller once preserved in ethanol (2.1–2.8 mm ML) or formalin (1.6–3.0 mm ML). They last 2–3 months in the plankton (Moreno *et al.*, 2012).

References: Nesis (1999); Moreno (2008).

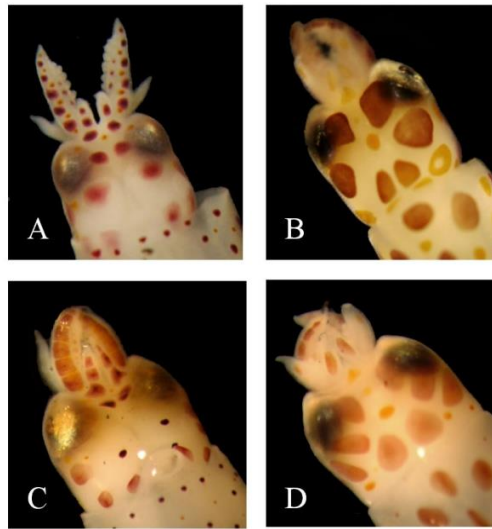


Figure 5.13. Detail of ventral (left) and dorsal (right) head in hatchlings of *Loligo vulgaris* (A,B) and *Loligo forbesii* (C,D).

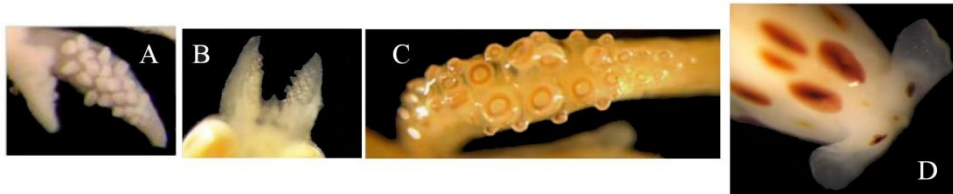


Figure 5.14. *Loligo vulgaris*: detail of the tentacular club of individuals measuring 20.6 mm ML (A), 2.6 mm ML (B), and 2.7 mm ML (C); and posterior end of the dorsal mantle and fins of a hatchling (D). From Moreno (2008).

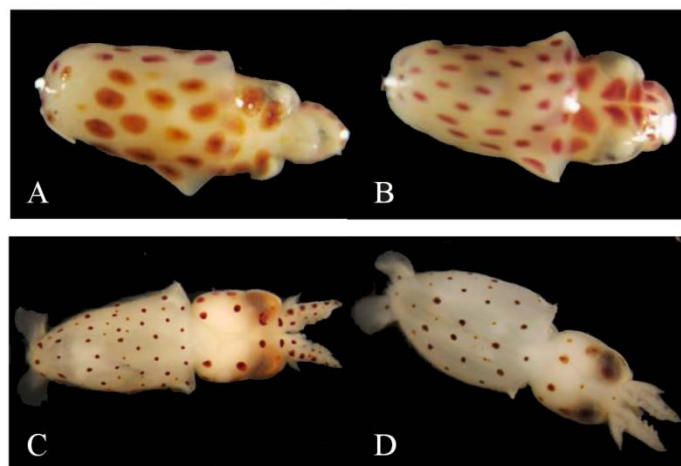


Figure 5.15. *Loligo vulgaris*: dorsal (left) and ventral (right) views. Individual sizes are 2.4 mm ML (A), 2.7 mm ML (B), and 2.9 mm ML (C,D). From Moreno (2008).

***Loligo forbesii* Steenstrup, 1857**

Species characters (Figure 5.12B and 5.13C,D): Body form bullet-shaped with well-developed, paddle-shape terminal fins; mantle with few large dorsal chromatophores and numerous ventral chromatophores; the arrangement of chromatophores in hatchlings is similar to *L. vulgaris*, but in higher numbers in each body part; e.g. on the ventral surface of head, three red chromatophores are located on each arm IV (Figure 5.13C).

Remarks: Hatchling sizes range from 3.5–4.1 mm ML (mean 3.7 mm ML).

References: Sweeney *et al.* (1992); Moreno (2008); Yau (1994).

***Alloteuthis* spp. Wülker, 1920**

Generic characters (Figure 5.12C,D): Juveniles have bullet-shaped body; paddle-shaped terminal fins that form a simple point at the tip at this stage, which develops into a tail in the subadult stage; in early juveniles, the median rows of suckers of the tentacle club are three–four fold larger than marginal suckers; however, such a difference in sucker size is not noticeable in hatchlings.

Remarks: Juvenile stages are nearly indistinguishable from *Loligo* spp., but hatchlings show a different chromatophore arrangement with a greater number of yellow chromatophores than *L. forbesii*. Two species of this genus (*Alloteuthis media* and *A. subulata*) inhabit the Mediterranean (Bello, 2008). Hatchlings measure 2.0–2.8 mm ML and last 15–30 d in the plankton.

References: Yau (1994); Hastie *et al.* (2013).

5.4 Family Ctenopterygidae Grimpe, 1922

Since this family is monotypic, family/species characters are described for the only currently known species.

***Ctenopteryx sicula* (Vérany, 1851)**

Species characters (Figures 5.16 and 5.17): mantle short, wide, slightly depressed dorso-ventrally, rounded behind; head short and half-retractable (up the midline of eye); eyes small, widely separated; funnel straight, large; fins separate dorsally, fringe mantle laterally; hatchlings with transversely elongate fins, result of first trabeculae; fins clearly with muscular trabeculae (at 3.5 mm ML); fins length increase with size, but much shorter than mantle, consisting of a series of flexible muscular ribs joined by thin transparent membrane; arms short, arms IV longer and wider than others; arms suckers small, in two rows in proximal, 4–6 rows in distal part of arms I–III, 1–2 zig-zag rows on arms IV; tentacles short and robust with broad, oval clubs with suckers forming a distinct circular pad (at <4 mm ML), and the sucker surface directed towards the front (already visible in hatching ~1 mm ML; Figure 5.16A–C); pointed tip develops and becomes dactylus (at >4 mm ML), equal length of manus (at 6 mm ML); buccal membrane with seven lappets, with 12–15 minute suckers in two rows on lappets, connectives to arms IV attached ventrally; gladius with long rachis and wide vane, without end conus; a single chromatophore occurs on the aboral surface of the club (at ≥2 mm ML); photophores on eye-ball (one elongated) and ink sac (large, round, resembling a fried egg on a black frying pan); ink sac photophore appearing in late paralarvae.

Individuals ca. 2.0 mm ML (Figure 5.16D,E): Mantle large, muscular, broad, tapers to a point posteriorly; mantle much longer than head and arms combined; head dorso-ventrally compressed; eyes prominent, tubular, subspherical; slightly dorso-ventrally elongate; funnel large, robust, muscular, extends to level of mid-eye; fins minute, terminal flaps; arms IV longest; arms II and III subequal, very short, stubby at bases; sudden attenuate papilla-like tips; 2–3 suckers; arms I are minute papillae, just developing; clubs terminal, broad, round, nearly equal in diameter to eyes, with about 25 suckers in round cluster of 5–6 suckers across; digestive gland subspherical; ink sac well-developed (Figure 5.16F), spherical, with concentration of bronze reflective tissue on ventral surface (precursor to photophore).

Individuals ca. 3.5 mm ML (Figure 5.17A-E): Head very short; eyes tubular, directed antero-laterally, slightly elongate dorso-ventrally; funnel very large, robust; extends anterior to base of arms; fins very small, with short bases; fins extend well posterior to mantle tip, about 10 (at 3.2 mm ML) to 12 (at >3.5 mm ML) short muscular supports (ribs) extend from muscular bases, connected by thin, easily torn membrane, giving comb-like appearance to fins; arms short with attenuate tips and few very small suckers; tentacle stalks, longer than arms; clubs terminal, expanded, round, with about 20 suckers and a papilla-like dactylus; digestive gland globular, slightly elongate dorso-ventrally; photophore anlage a round, reflective, bronze patch at ventral tip, ringed with black.

Remarks: The species is easily identifiable at all developmental stages by its distinctive clubs and the typical ribbed fins made of muscular supports joined by a thin membrane.

References: Sweeney *et al.* (1992); Nesis (1999); Diekmann *et al.* (2002); Haimovici *et al.* (2002); Moreno (2008).

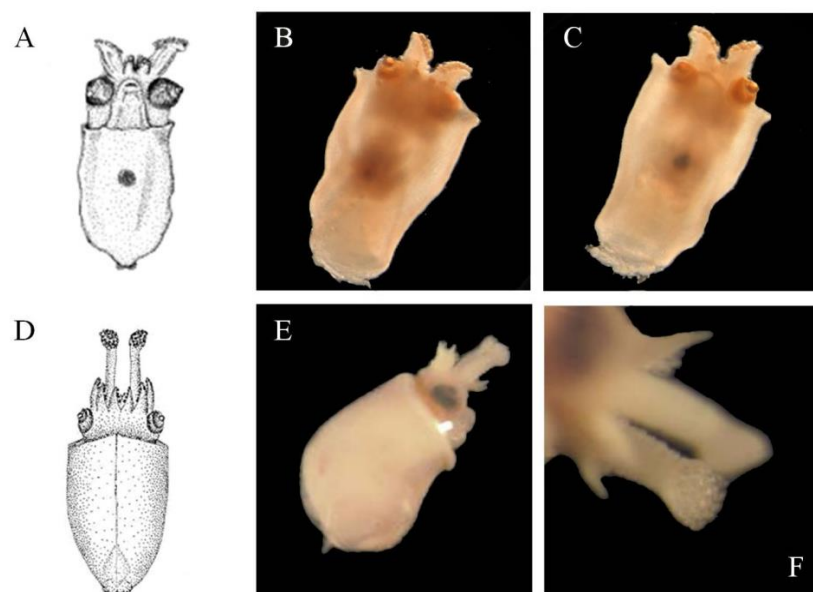


Figure 5.16. *Ctenopteryx sicula*: ventral view, 1.3 mm ML (A); dorsal (B) and ventral (C) views, 1.4 mm ML; dorsal view, 2.5 mm ML (D); lateral view (E), and detail of the tentacular club (F), 2.1 mm ML. A from Diekmann *et al.* (2002); D from Haimovici *et al.* (2002); E,F from Moreno (2008).

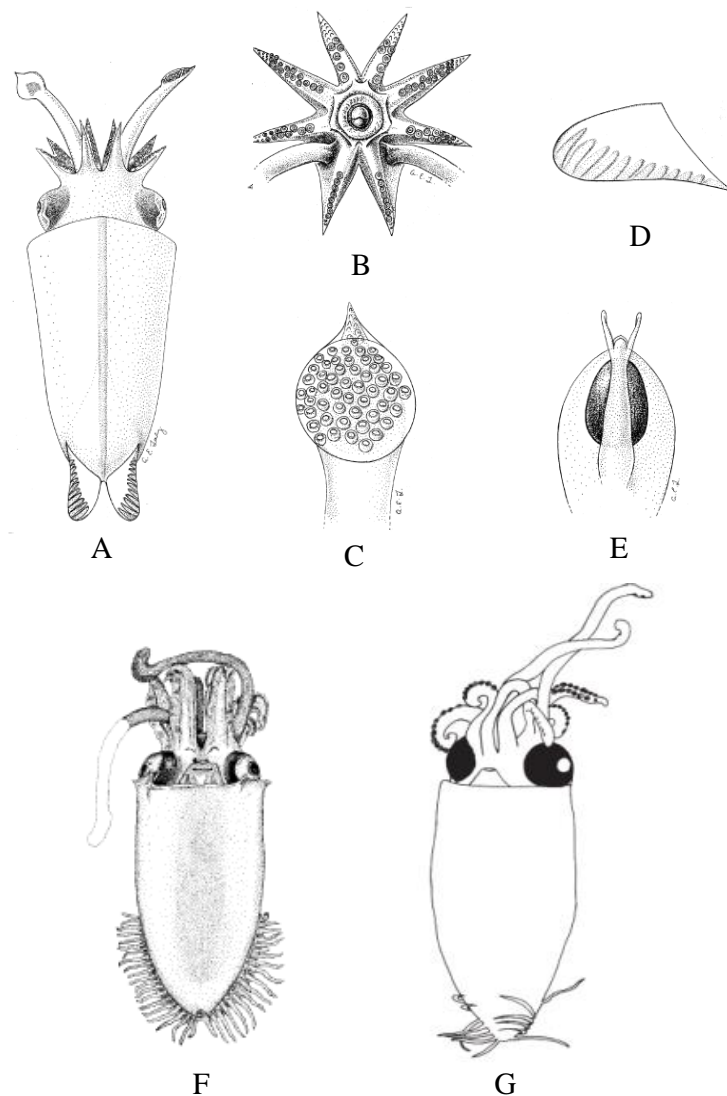


Figure 5.17. *Ctenopteryx sicula*: dorsal view, 3.6 mm ML (A) and oral view (B), detail of tentacular club (C), fin (D), and visceral light organ (E); dorsal views, 7.5 mm ML (F), and 9.0 mm ML (G). A–E from Vecchione *et al.* (2001); F from Diekmann *et al.* (2002); G from Salman *et al.* (2003).

5.5 Family Enoploteuthidae Pfeffer, 1900

Family characters: Photophores developed in a single row on each eye at >3 mm ML and numerous small photophores on the ventral surface of mantle; funnel, head, and arms begin to appear at about 3–4 mm ML; photophores absent from the tentacles and viscera; cone-shaped mantle (generally everted in fixed individuals); eyes prominent; arm crown short; tentacles and arms moderately long.

Remarks: The characters useful for classification include the chromatophore pattern, size of the largest club suckers relative to arm suckers, relative sizes among club suckers, number of club suckers, photophore pattern, and photophore sizes. The juvenile stages are difficult to separate because the characteristic photophore patterns do not develop before 4–5 mm ML.

References: Sweeney *et al.* (1992); Diekmann *et al.* (2002); Haimovici *et al.* (2002); Moreno (2008).

***Abralia veranyi* (Rüppell, 1844)**

Species characters (Figures 5.18 and 5.19): Arms I–III long, but never as long or longer than the ML, and attenuate, with about 14–20 suckers at <4.5 mm ML; chromatophores on aboral surface of arms I–III; arms IV much less developed, with 6–16 suckers at <4.5 mm ML, no hook; arm formula $II > I = III > IV$; tentacular stalks long and robust with a row of large aboral chromatophores; three photophores forming a single row on the ventral surface of eyes occurring at >3.0 mm ML, anterior largest, posterior intermediate, central smallest (Figures 5.18D,E); in juveniles, posterior photophore different from the others; no trace of light organs in positions two or four; absence of light organs on the arm tips (key characteristic to distinguish between *Abralia* and *Abraliopsis*).

Individuals ca. 3.0 mm ML: Club region undifferentiated, minute suckers along distal one fourth of tentacle; a few small, integumentary photophores, evenly distributed over ventral and ventro-lateral surface of head, mantle, and funnel, most in association with small chromatophores; fins very small, terminal flaps; meet posteriorly.

Individuals ca. 4.5 mm ML: Carpus with 4–5 suckers, four rows of suckers on manus with 6–8 median suckers enlarged and no hook development; head narrower than mantle opening; seven large dark chromatophores on dorsal and lateral surface of head; small photophores in longitudinal rows on ventral and lateral surface of head; one row extends into arms IV; funnel strongly developed, extends to the level of posterior edge of eye; six small photophores on ventral surface of funnel; mantle elongated and muscular, with broad opening that tapers to blunt posterior end; many small chromatophores evenly distributed over ventral and ventro-lateral surface of mantle; large chromatophores in bands around mantle, corresponding to photophores on ventral and lateral surfaces; very large chromatophore on each postero-lateral end of mantle ventral, to posterior part of fins; fins terminal, muscular, short, triangular with rounded angles and meet at posterior end of mantle.

Remarks: Late juveniles and adults are characterized by one series of hooks and two series of suckers on the manus club. Hooks are not yet formed in paralarvae.

References: Vecchione *et al.* (2001); Haimovici *et al.* (2002); Moreno (2008).

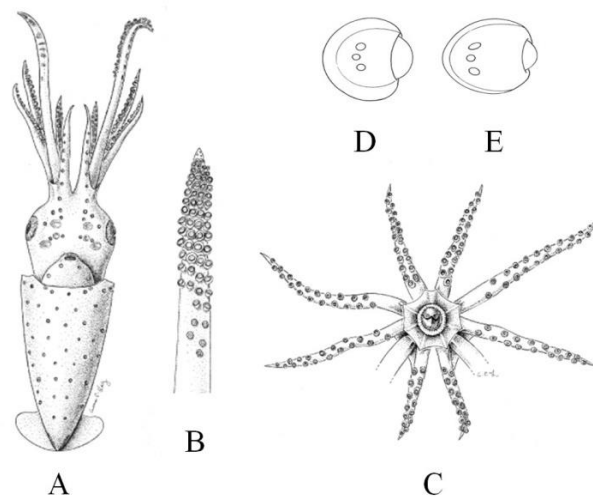


Figure 5.18. *Abralia veranyi*: ventral (A), tentacular club (B), and oral (C) views, 4.5 mm ML; light organs on ventral surface of eye (D, 3.1 mm ML; E, 4.5 mm ML). From Vecchione *et al.* (2001).

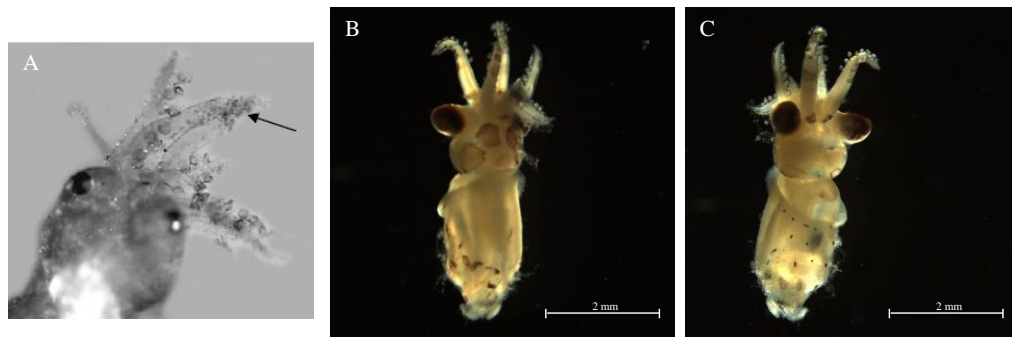


Figure 5.19. *Abralia veranyi*: arrow in head detail indicates the tentacle club with very small suckers, 2.1 mm ML (A); dorsal (B), and ventral (C) views, 2.7 mm ML. A from Moreno (2008).

Abraliopsis morisii (Vérany, 1839)

Species characters (Figures 5.20 and 5.21): Mantle muscular, three conspicuous, dark, large photophores (green in living specimens) on the tips of arms IV (absent at <4 mm ML); arms and tentacles extremely long, greater than or equal to mantle length; tentacles stalk robust; tentacular club has >4 rows of suckers and hooks visible at specimens >4 mm ML; fins small and round; funnel large extending until the posterior level of the eyes.

Individuals ca. 3.0 mm ML (Figure 5.21B): Arms IV with slight swelling near tip, the precursor of the light organ; on arms I–IV, only suckers (9–16), no hooks; arm formula III>II>I>IV; integumentary photophores originally present, but deteriorated during preservation; club with ten biserial suckers proximally, then three hooks developing in the next three pairs of suckers (two ventral, one dorsal), followed by about 20 suckers diminishing in diameter distally, some in three rows, with sucker anlagen at the tip; eye light organs one (anterior), three, five developing as dark bronze reflective swellings.

Individuals ca. 5.0 mm ML: Arms IV with two small terminal light organs and median row of photophores on proximal half, but hooks absent; four hooks present on arms I, seven hooks on arms II, nine hooks on arms III; photophores absent on arms I–III; three rows of photophores on head, row on ventral midline most conspicuous; eye photophores one (anterior), three, and five developed, two and four anlagen present.

Individuals ca. 13.0 mm ML (Figure 5.20C): Arms IV with three terminal light organs, two rows of photophores that extend to one half of arm length, and 16 hooks; arms I with 13 hooks, II with 17 hooks and no photophores; arm formula IV>III>II>I; tentacular club with four large hooks in ventral row and five small hooks in dorsal row (Figure 5.20D), carpus with eight suckers, dactylus with 3–4 rows of small suckers; aboral keel of club developing; two kinds of photophores (large, spherical, dark; and small, spherical, translucent) in about nine indistinct rows on ventral surface of head; ventral periphery of eyes with five photophores in single row; one and five largest, two and four small, three intermediate; 13 small integumentary photophores around eyelids; photophores on mantle and funnel similar to those on head, kinds in indistinct rows; dense ventrally, sparse dorsally on mantle; ventral midline devoid of photophores.

Remarks: In juveniles and adults, five round photophores of similar structure develop on the ventral side of each eye; they form a typical row with the posterior and anterior photophore enlarged; the manus of the club presents two series of hooks in specimens >9 mm ML.

References: Sweeney *et al.* (1992); Diekmann *et al.* (2002); Vecchione *et al.* (2001); Moreno (2008).

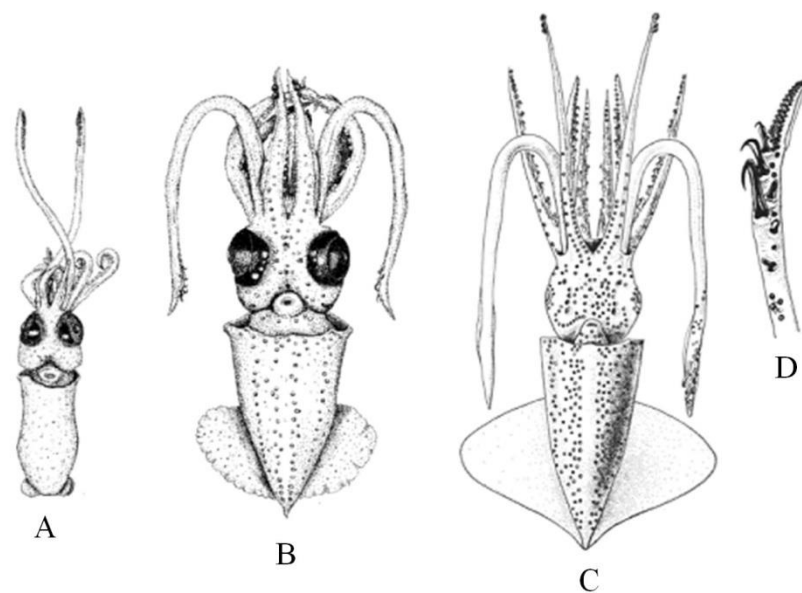


Figure 5.20. *Abraliopsis morisii*: ventral views, 3.6 mm ML (A), 8.5 mm ML (B), 13 mm ML (C), and tentacular club of individual C (D). A,B from Diekmann *et al.* (2002); C,D from Vecchione *et al.* (2001).



Figure 5.21. *Abraliopsis morisii*: dorsal (left) and ventral (right) views, 2.1 mm ML (A) 3.1 mm ML (B).

5.6 Family Ancistrocheiridae Pfeffer, 1912

Since this family is monotypic, family/species characters are described only for the currently known species.

Ancistrocheirus lesueurii (d'Orbigny, 1842)

Species characters: Mantle rather wide, conical; fin tongue-like in paralarvae, very wide transverse-elliptical in juveniles; tentacular suckers few, but large; relatively small, broadly spaced eyes, the separation of the eyes from the arm bases, with space between filled by gelatinous head tissue; arms and tentacular hooks developed at >8 mm ML; arms robust and strong, with two rows of suckers in juveniles and hooks in adults; tentacles long and robust, central part of club in paralarvae with two rows of suckers, in juveniles two rows of hook (median) and two rows of very large suckers (marginal), and in adults only hooks (8–9 in row); digestive gland kidney bean-shape, located in posterior of mantle cavity; head and mantle photophores present at >5 mm ML; diagnostic tentacular photophores at >7 mm ML.

Individuals ca. 3.0 mm ML (Figure 5.22A): Mantle rounded, cup-shaped, devoid of photophores; fins terminal, small, weakly muscled; tentacles long, robust, without photophores; 11 suckers, no hooks on club, proximal sucker small, next five enlarged almost to diameter of tentacle stalk, distal five small with several anlagen distally; no hooks or photophores on arms; arm suckers few and large; no suckers on proximal portions of arms; five suckers on arms I, six suckers on arms II (none on proximal one third), two suckers on arms III; arms IV very short with only a few sucker anlagen;

photophores absent on head; eyes and buccal assemblage stalked with gelatinous material filling spaces between stalks.

Individuals ca. 4.0 mm ML (Figures 5.22B and 5.23A): Mantle without obvious photophores; fins small, rounded; tentacles long, robust, without photophores; 15 suckers on club plus several distal anlagen, no hooks; all suckers large except proximal one and distal two; arm formula $II>I=III>>IV$; arm suckers large, few in number, none on proximal sections of arms; eight suckers on arms I, 12 on arms II, nine on arms III, none on arms IV; head lacks detectable photophores; eyes and buccal assemblage stalked with gelatinous material between stalks.

Individuals ca. 5.5 mm ML (Figures 5.22C and 5.23B–G): Mantle short, broad, bluntly rounded posteriorly, muscular; 12 photophores on ventral surface: four along anterior margin, four pairs that form two zig-zag rows posteriorly to the tip; fins small, elongate, semilunar, posterior; funnel tubular, base broad; head broad; two rows of five photophores on ventral surface of head in an arc from posterolateral corner to base of arms IV; arms long, robust, attenuate; arm formula $III>II>I>IV$ (Figure 5.23F); number of suckers on arms: 15 (I), 16 (II), 22 (III), eight (IV); no hooks; suckers relatively large, on long stalks; tentacles long, robust to the attenuate tip; suckers on club begin with one small proximal sucker, set apart from the rest; manal suckers relatively large, biserial proximally, enlarge gradually to maximum diameter in third–sixth pairs, then diminish to tip; lateral suckers larger than medial suckers; about 27 suckers in total, no hooks (Figure 5.23G); six small spherical photophores embedded along the tentacular stalk.

Individuals ca. 8.0 mm ML: Mantle muscular, broadest anteriorly, tapers evenly to bluntly rounded posterior tip; 18 small, spheroidal photophores on ventral surface of mantle in distinct pattern of transverse rows, anterior to posterior: four, two, two, four, two, two, two; the posterior-most photophores form at the very tip as elevated knobs (Figure 5.23H); fins rounded, triangular, terminal; funnel large, base broad, tube extends to posterior level of eyes; head large, wider than mantle; eyes prominent, no ocular photophores; at least five photophores in arc on each side of ventral surface of head; arms very long, robust, attenuate; arms I–III subequal, longer than IV; armature on arms I: one proximal sucker, five hooks, 13+ distal suckers; arms II: 8–9 hooks, 14+ suckers; arms III: 11 hooks, 16+ suckers; arms IV: none hooks, about 20 suckers; tentacles long, robust to tip; club with four pairs biserial carpal suckers; four transverse rows with two medial hooks and two large marginal suckers each (i.e. eight hooks) on manus, 8–10 diminishing biserial suckers on dactylus; low aboral keel extends from level of first manal row to tip of dactylus; tentacular stalk with nine small embedded spheroidal photophores.

References: Sweeney *et al.* (1992); Nesis (1999); Vecchione *et al.* (2001); Moreno (2008).

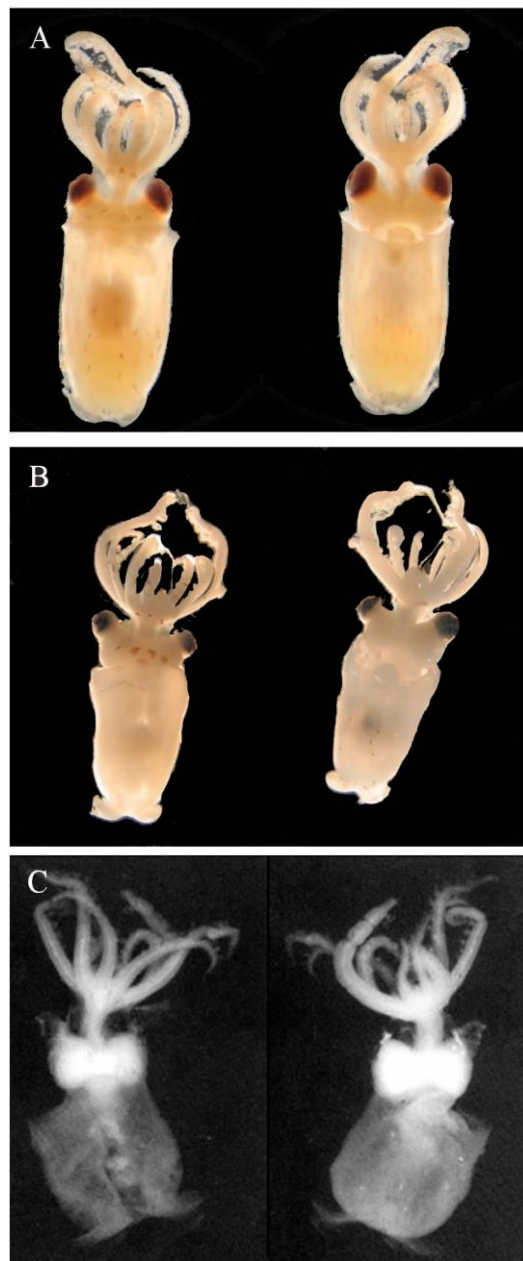


Figure 5.22. *Ancistrocheirus lesueurii*: dorsal (left) and ventral (right) views, 2.7 mm ML (A), 4.0 mm ML (B), and 5.0 mm ML (C). C from Lefkaditou *et al.* (1999).

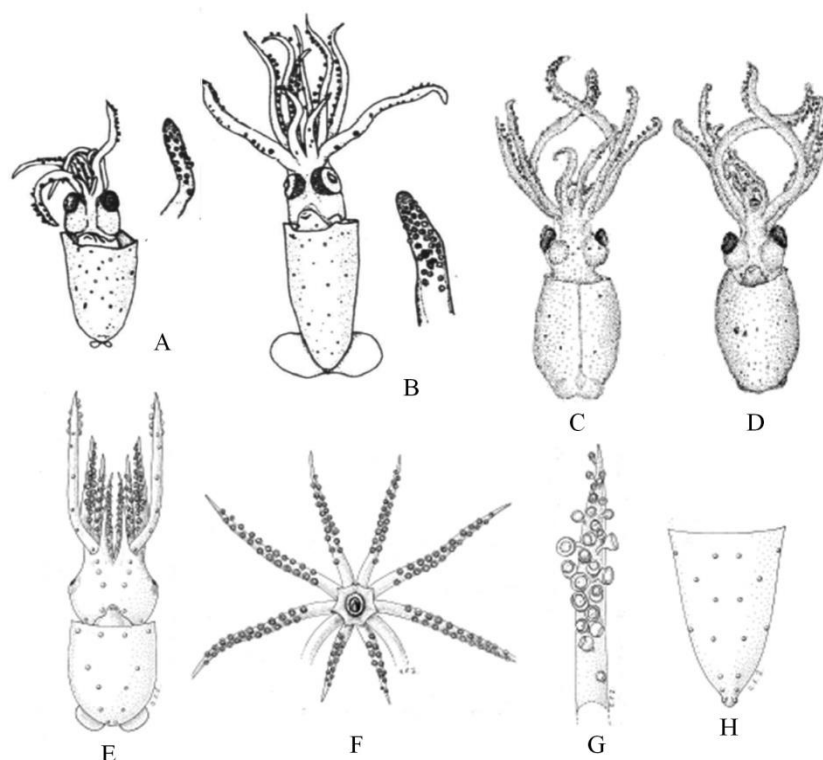


Figure 5.23. *Ancistrocheirus lesueurii*: ventral view and tentacular club of 3.3 mm ML (A) and 5.5 mm ML (B) paralarvae; dorsal (C) and ventral (D) view, 5.0 mm ML; ventral (E), and oral (F–G) views, 5.6 mm ML; and ventral mantle view (H), 8.2 mm ML. A,B from Kubodera and Okutani (1981); C,D from Haimovici *et al.* (2002); E–H from Vecchione *et al.* (2001).

5.7 Family Octopoteuthidae Berry, 1912

Family characters: Body conical, acute posteriorly; tentacles present only in paralarvae and early juveniles, lacking in adults; tentacular clubs short, spatulate, with eight suckers (several very large) in two rows; narrow pigmented keels extend laterally along each side of club; fins very long and wide, reaching or barely short of anterior margin and posterior end of mantle, joined dorsally along longitudinal midline; fins very broad in specimens >3 mm ML; buccal membrane with six lappets, connectives to arms IV attached ventrally; photophores present on some arm tips by 3–5 mm ML (but arm tips frequently missing); in "paralarvae", all arms with suckers; funnel locking-cartilage straight, elongated, widened posteriorly; gladius with wide vane, beginning near anterior end.

References: Sweeney *et al.* (1992); Nesis (1999).

Octopoteuthis spp. Rüppell, 1844

Species characters (Figures 5.24 and 5.25): Mantle short, conical, with gelatinous outer layer; fins very wide (apparent as small as 2.5 mm ML), tongue-like in paralarvae, transverse-oval in juvenile, length approaching 100% ML by 10 mm ML; funnel short initially, extending to between eyes by 10 mm ML; tentacles thin and longer than arms, with weak, gelatinous stalks; tentacular club with bunch of rather larger suckers on tip (eight in two rows); club reduced at ~12 mm ML, stems at 25 mm ML; arms rather short, weak, usually proportionally longer, their tips usually broken upon collection;

gelatinous tissue layer on head gives smaller specimens appearance of short arm-crown stalk and short, wide eye-stalks; one and two photophores on ventral mantle, anterior to body end; all arms with one elongate brown photophore at distal tip; some poorly noticed (except in live animals) photophores on head and in mantle cavity; paired photophores on ink sac.

Individuals ca. 3.0 mm ML: Mantle short, broad, round posteriorly, mantle width about 75% ML; fins terminal, very short, broad, laterally ovoid, fin length about 33% ML, fin width of both fins about 45% ML; tentacles long, robust proximally, thin distally with eight suckers; from proximal to distal, first two suckers minute, next two strikingly large (>tentacle diameter), followed by two intermediate in size, one slightly smaller, then one minute terminal sucker (Figure 5.24A–C); arms long, attenuate, with swollen areas at tips (anlagen to light organs); biserial suckers on arms developing into hooks, some well-developed; eyes and buccal assemblage stalked, with stalks embedded in gelatinous tissue of anterior head.

Individuals ca. 6.0 mm ML (Figures 5.24D,E and 5.25B): Mantle thin walled, muscular, conical, widest at anterior opening, tapers to blunt tip, mantle width 60% ML; fins very muscular, fused along dorsal midline of mantle, blunt mantle tip extends very slightly beyond posterior border of fins; fins longest at point of fusion with mantle, fin length 60% ML; fins very broad, oval, fin width 112% ML; funnel long, tapers to narrow opening that reaches mid-level of head, posterior to eyes, head width 60% ML; eyes on antero-laterally directed stalks; buccal stalk elongate; eye and buccal stalks embedded in gelatinous matrix; no photophores anlagen present on mantle or head; arms long, attenuate; arm formula: II>III>I>IV, (most tips broken); arms II and III, especially, are very robust in proximal half; arms with biserial globular suckers that develop into hooks; hooks and suckers present on arms II and III, suckers only on I and IV arms; arm tips with swellings that are anlagen to photophores; tentacles with robust stalks, but not nearly as muscular as arms; body length approximately equal to length of arm I; club region unexpanded; 2–3 minute biserial suckers on proximal club, followed by two enormous suckers, each with a diameter greater than that of the tentacle where they are attached; proximally are two more enlarged suckers, then one intermediate and one small sucker at the bluntly rounded tip of the club; no sucker anlagen occur on the tip; all sucker rings have relatively narrow openings and very broad walls; anlagen of photophores on ink sac beginning to differentiate as a different appearance of the ventral-most reflective tissue.

Individuals ca. 9.0 mm ML (Figure 5.25C): Fin length 72% ML; fin width 136% ML; tentacles missing, but long shreds of tissue remain; biserial hooks on all arms; arm tips damaged, apparently from abrasion, causing loss of photophores; eyes and buccal assemblage stalked, embedded in gelatinous tissue.

Remarks: Only one species of this genus (*Octopoteuthis sicula*) inhabits the Mediterranean.

References: Sweeney *et al.* (1992); Nesis (1999); Vecchione *et al.* (2001).

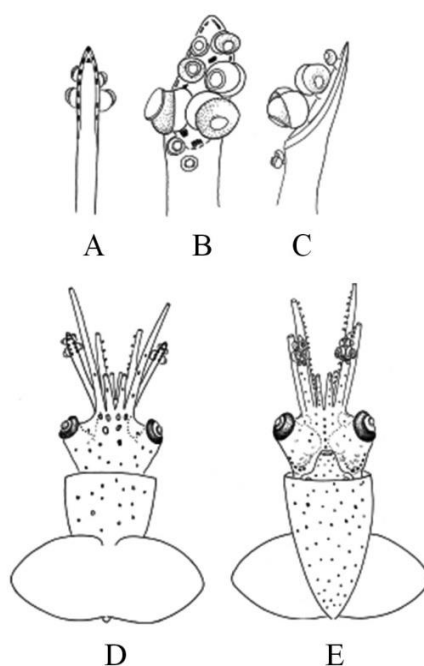


Figure 5.24. *Octopoteuthis* sp.: aboral (A), oral (B), and lateral (C) views of club, 3 mm ML; dorsal (D) and ventral (E) views, 6 mm ML. From Vecchione *et al.* (2001).

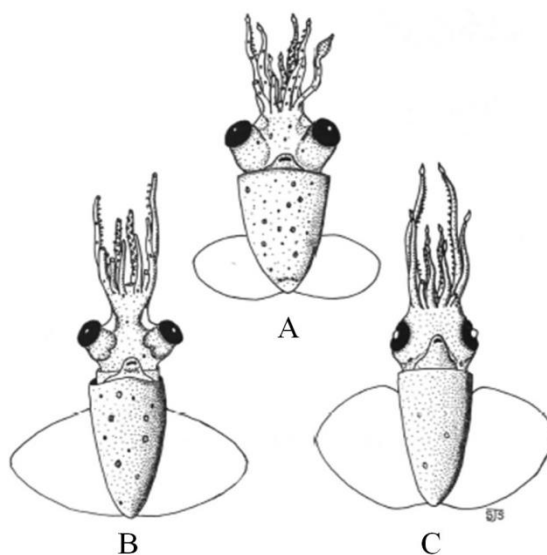


Figure 5.25. *Octopoteuthis* sp.: ventral views of development series, 4.5 mm ML (A), 6.0 mm ML (B) and 8.0 mm ML (C). From Stephen (1985).

Taningia danae Joubin, 1931

Species characters (Figure 5.26): Mantle short, broadly conical, tapering into short tail, with gelatinous outer layer; fins very wide, in paralarvae transverse-oval (length approaching 100% ML by 3 mm ML), in juveniles and adults diamond-shaped, barely short of anterior (but not posterior) mantle margin; eyes in early paralarvae on short

wide stalks, subsequently not stalked; funnel locking-cartilage straight; tentacles much shorter than arms II; tentacular clubs with eight rather large suckers on the tip; club reduced at ~40–45 mm ML, but stems remaining until much later; arms short, thick; arms hooks appearing rather early (at >5 mm ML), and then suckers remaining only on very tips of arms; arms II devoid of suckers, with one large, complex photophore on distal tips, whose central yellowish luminescent part may be covered by black lobes (“lips”); no photophores on the other arms; large unpaired photophore on ink sac, developed at ~5 mm ML; gladius with parallel lateral sides.

Remarks: Easily distinguishable by extremely wide fin and photophore on tips of arm II developing at ~4.5–5.0 mm ML.

References: Sweeney *et al.* (1992); Nesis (1999).

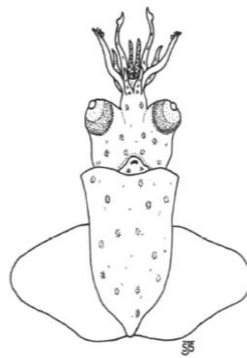


Figure 5.26. *Taningia danae*: ventral view, 2 mm ML. From Sweeney *et al.* (1992).

5.8 Family Onychoteuthidae Gray, 1847

Family characters (Figures 5.27 and 5.28): Mantle relatively broad, conical or cylindrical and muscular, but sharply pointed posteriorly, often constricted anteriorly relative to the midpoint; mantle surface often with fine longitudinal wrinkling of its outer layer; head often withdrawn into the mantle up to the eye lenses and the funnel tip in some species; fins on posterior half, transverse-oval, heart- or diamond-shaped; tentacles thick and slightly longer than arms I and II; fixing apparatus of tentacles well developed, oval; buccal membrane with seven lappets, connectives to IV arms attached ventrally; funnel cartilage straight, elongated; large, dark chromatophores may occur on the dorsal mantle and head; mantle with one conspicuous chromatophore on the ventral side at a midpoint of the basis of the fins; two rows of suckers with smooth rings on the arms and one large photophore on the ventral surface of each eye, except in the smaller specimens; photophores may appear on eyeball and near hindgut; gladius with narrow vane and chitinous or cartilaginous end conus and a pointed rostrum.

Remarks: Two species of this family inhabit the Mediterranean, *Onychoteuthis banksii* and *Ancistroteuthis lichtensteinii*. These species are easily confused at sizes smaller than 11 mm ML, because both are characterized by few large suckers on the tentacular clubs and by eyes and buccal assemblages on stalks embedded. *Onychoteuthis banksii* greater than 11 mm ML can be distinguished from *Ancistroteuthis lichtensteinii* by significantly larger fins, greater than 30% ML; gladius visible dorsally as distinct line; tentacular club hooks differentiated at slightly greater ML; presence of photophores.

References: Sweeney *et al.* (1992); Nesis (1999); Vecchione *et al.* (2001); Haimovici *et al.* (2002).

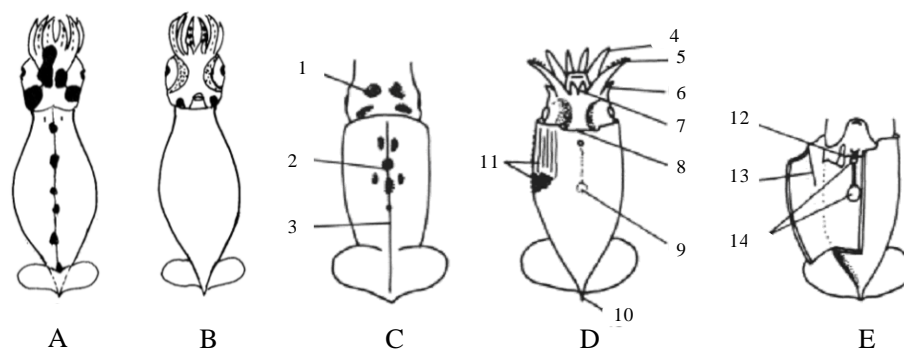


Figure 5.27. Onychoteuthidae paralarvae: dorsal (A) and ventral (B) views, 7.5 mm ML; dorsal (C), ventral (D), and ventral with mantle opened (E) views, sizes not available. 1, large chromatophores on the head; 2, large chromatophores on mantle; 3, gladius visible in the dorsal midline; 4–7, relative sizes of arms; 8, mantle edge between connectives; 9, photophores on the intestine; 10, protruding rostrum of the gladius, "spike"; 11, wrinkling or papillation of the mantle surface; 12, elongate funnel connective; 13, long mantle connective; and 14, photophores ventral to the intestine. A,B from Lefkaditou *et al.* (1999); C–E from Sweeney *et al.* (1992).

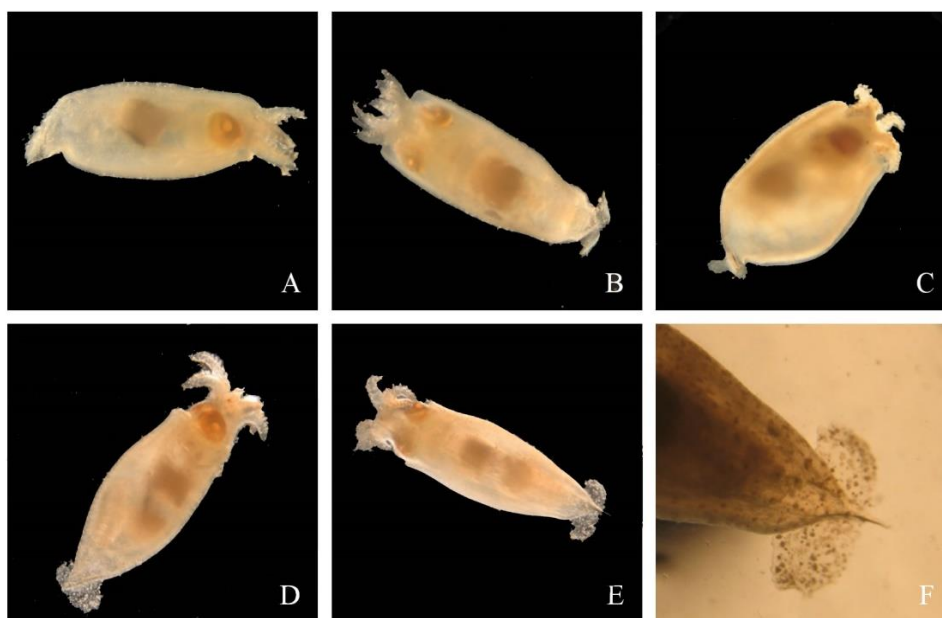


Figure 5.28. Onychoteuthidae paralarvae: lateral (A) and dorsal (B) views, 2.8 mm ML; lateral view (C), 2.9 mm ML; lateral (D) and dorsal (E) views, 3.0 mm ML; detail of the posterior mantle tip, 6.8 mm ML (F).

Ancistroteuthis lichtensteinii (Férussac [in Férussac & d'Orbigny], 1835)

Species characters: Surface of muscular mantle and head smooth; nuchal folds; gladius not visible along the dorsal midline; conus consists of minute spoon (not a deep conical end part as in *Onychoteuthis* spp.) and a long cartilaginous rostrum, 1/7 gladius length;

fins longer than 1/3 ML at 16 mm ML; carpal pad with 8–12 suckers and knobs; photophores absent.

References: Sweeney *et al.* (1992).

Onychoteuthis banksii (Leach, 1817)

Species characters (Figure 5.29): Mantle muscular, elongated, narrow, cylindrical in anterior, conical in posterior half; gladius very narrow, with strong longitudinal dorsal rib easily visible from dorsal, with chitinous needle behind, directed diagonally dorsally and protruding through skin upon fixation; terminal fins small tongue-like; head of paralarvae <10 mm ML is generally retracted inside the mantle, with only the arms and tentacles outside of a constricted mantle opening; arms rather short, strong; only I and II arms in early paralarvae, III appearing later only at ~5 mm ML; tentacles long; tentacular club with four rather irregular rows of suckers, two central rows transformed later into hooks, those of the ventral row first (at ~12–15 mm ML); nuchal folds on head well developed; skin smooth; paralarvae almost transparent, with sparse chromatophores, red-brown; one elongate photophore on ventral side of eyeball, two near the hindgut (one small near anus, one large and round in an arch-like bend of gut near its beginning, developed at ~9–11 mm ML).

Individuals ca. 2.0 mm ML (Figure 5.29A–D): Mantle very elongate, narrow, muscular; posterior third of gladius and mantle bent ventrally; posterior “spike” of gladius extends beyond very small, paddle-shaped, laterally directed fins; funnel very large, well-developed, covers much of postero-ventral surface of head, extends anteriorly to level of lenses of eyes; head narrow and dominated by large, sessile, laterally oblong eyes; arms III and IV not well developed, arms II>I; five suckers on arms I, six on arms II; tentacles slightly longer than arms, with eight suckers; no hooks on clubs nor light organs on viscera or eyes.

Individuals ca. 3.5 mm ML: Head completely retracted inside mantle, which is tightly sealed around head; only arms and tentacles protrude; posterior third of gladius bent ventrally, and “spike” bent back dorsally; fins small, round, well-developed; arms III and IV mere protuberances; arms I and II and tentacles short, stubby, all approximately of equal length; suckers on arms and tentacles small, 12 each on arms I and II and tentacles; tentacular suckers appear to be biserial.

Individuals ca. 5.5 mm ML (Figures 5.29E,F and 5.30A): Head narrow, partially withdrawn into mantle; eyes lateral, relatively large; mantle opening constricted to about two-thirds maximum mantle width; widest mantle width at its posterior half; fins well-developed, broadly heart-shaped; gladius tip still protrudes as “spike” beyond posterior end of mantle and fins; arm formula: I=II>>III>>IV; arm suckers small, numerous on arms I and II, few on arms III, none on arms IV; tentacles slightly longer than longest arms; small biserial suckers along entire oral surface of tentacles, a few in central region beginning to elongate into hooks; nuchal folds not yet developed; intestinal light organs undeveloped.

Remarks: Paralarvae easily distinguishable by acute needle protruding from posterior end, light in colour, and usually head retracted.

References: Nesis (1999); Vecchione *et al.* (2001); Diekmann *et al.* (2002); Haimovici *et al.* (2002).

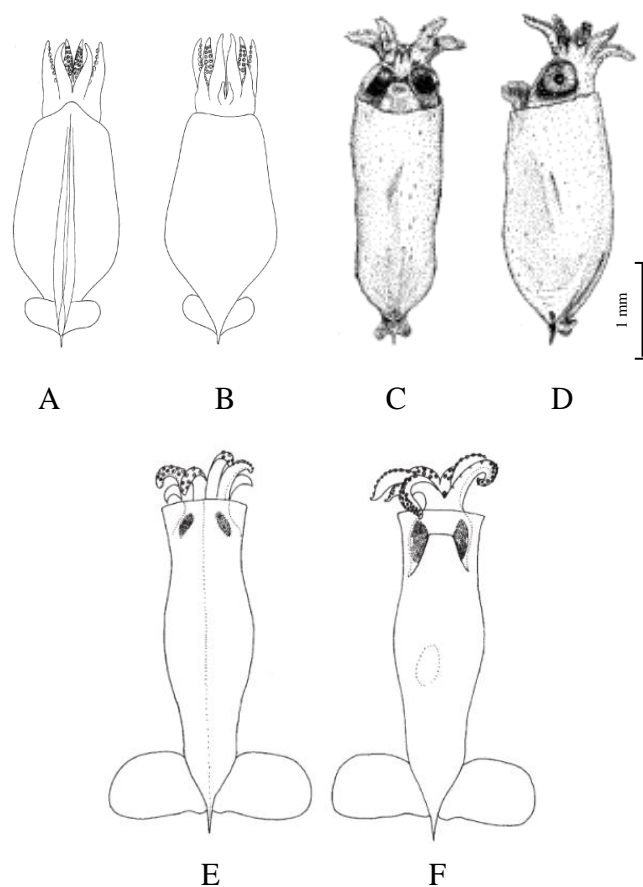


Figure 5.29. *Onychoteuthis banksii*: dorsal (A) and ventral (B) views, 2 mm ML; ventral (C) and lateral (D) views, 2.7 mm ML; dorsal (E) and ventral (F) views, 5.0 mm ML. A,B from Vecchione *et al.* (2001); C,D from Diekmann *et al.* (2002); E,F from Salman *et al.* (2003).

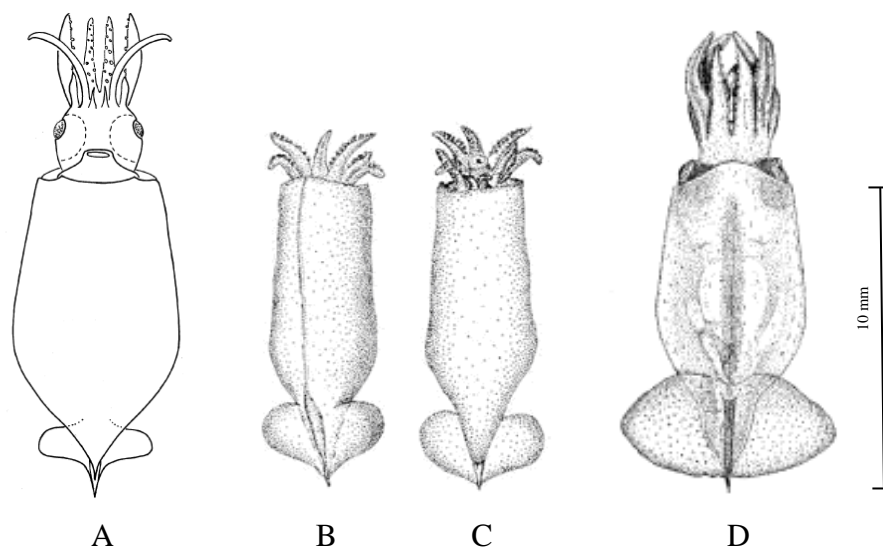


Figure 5.30. *Onychoteuthis banksii*: ventral view (A), 5.4 mm ML; dorsal (B) and ventral (C) views, 7.2 mm ML; and dorsal view (D), 11.7 mm ML. A from Vecchione *et al.* (2001); B,C from Haimovici *et al.* (2002); D from Diekmann *et al.* (2002).

5.9 Family Histioteuthidae Verril, 1881

Family characters (Figures 5.31 and 5.32): Mantle muscular, usually thick-walled, short and conical; mantle tissue usually thick and firm; head narrower than mantle and long; eyes “subtubular”, antero-laterally directed; in large juvenile to adult individuals, large eyes asymmetrically developed, left larger than the right one; funnel cartilage, straight, large, broad slightly curved, and widened caudally; fins terminal, medium to large, together transversally oval in outline, united posteriorly with a median notch; arms long, conical, with two rows of suckers, in some species joined by web near bases from outer and/or inner side; tentacles very long, club with 4–8 rows of suckers commonly of strongly unequal size; fixing apparatus long, consisting of knobs and suckers; buccal membrane with 6–7 lappets, connectives to IV arms attached dorsally; gladius with thin rachis and wide vane, without end conus; photophores numerous, small, anteriorly directed, on the mantle (often in diagonal rows), head and aboral surface of arms, more concentrated on the ventral surface; only fins and tentacles are devoid of photophores; also lacking on eyeball and inside mantle cavity; skin colour of juvenile to adult specimens brownish red.

Individuals ca. 1.5 mm ML (Figure 5.31A,B): Mantle very short, broad (Figure 5.32D); fins very small in proportion to mantle, close-set, wide, rounded only at tips; funnel very large, muscular, broad, extend anteriorly nearly to base of arms; eyes dorso-ventrally elongate; arms I and II robust, attenuate, each with 12 suckers, central six somewhat enlarged and globular; arms III small, with eight suckers, only 2–4 slightly enlarged; arms IV very short with two minute suckers; tentacles missing distally (broken off), but proximal stalks robust.

Individuals ca. 3.0 mm ML (Figure 5.31C,D and 5.32E): Mantle very broad, rounded, much longer dorsally than ventrally (Figure 5.32F); fins attached to each other, round, muscular, large; extend posteriorly well beyond mantle; reddish chromatophores thickly distributed on mantle, head, and funnel, especially on dorsal surface; funnel with tapers to small opening; arms long, slender, tapered, bluntly attenuate; arm formula: II>I>III>IV (Figure 5.32G); arms III only about two-thirds the length of II; arm suckers large and few, except for arms II which have much smaller suckers; arms I with 18–20 suckers, proximal six pairs enlarged; arms II with 24 suckers, seven pairs enlarged; arms III with 16–18 suckers, five pairs slightly enlarged; arms IV very short with 4–6 small suckers plus a few anlagen; enlarged suckers very globular, spherical, with narrow openings; tentacles robust, long, about one-fourth longer than arms II, suckers very small, proportionately few; tentacular stalk with two single suckers near base; pairs of suckers begin sparsely at mid-stalk, then increase in number, first as pairs, then in more than two rows, up to 6–8 rows across distal manus where suckers become smaller; minute suckers and anlagen buds only at dactylus (Figure 5.32H).

Remarks: The early life stages of this family are difficult to classify at the species level; generally, juveniles may be identifiable at ≥ 10 mm ML. One useful feature to recognize *Histioteuthis* is the much smaller size of the tentacular suckers compared with the arm suckers. Two species are present in the Mediterranean: *H. reversa* and *H. bonnellii*.

References: Sweeney *et al.* (1992); Nesis (1999); Vecchione *et al.* (2001); Diekmann *et al.* (2002).

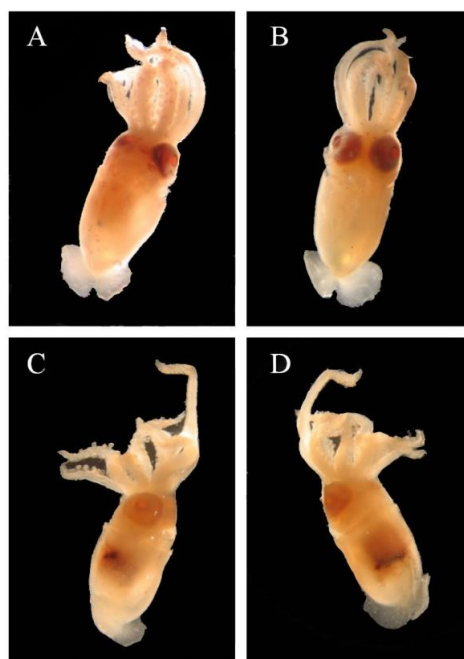


Figure 5.31. *Histiototeuthis* sp.: dorsal (A) and ventral (B) views, 1.6 mm ML; lateral (C) and dorso-lateral (D) views, 3.6 mm ML.

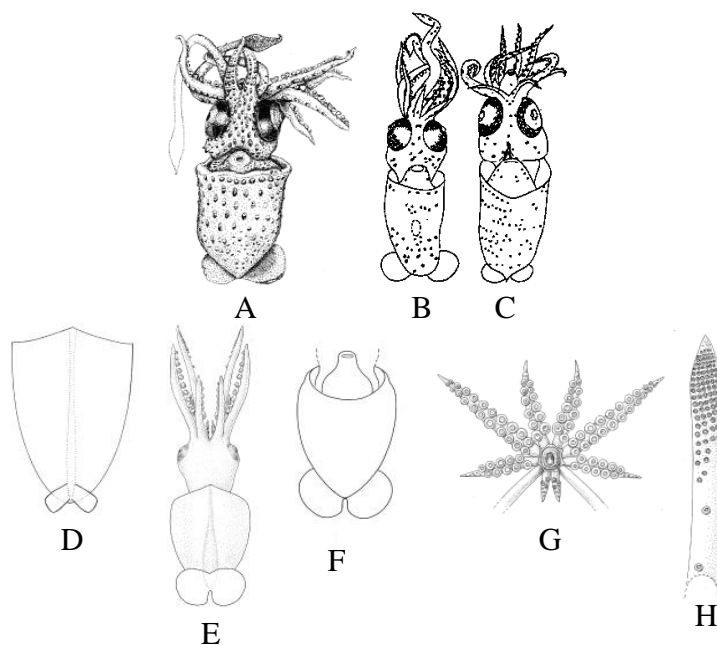


Figure 5.32. Family Histiototeuthidae: ventral views of *Histiototeuthis celetaria celetaria*, 7.1 mm ML (A) and *Histiototeuthis* sp., sizes not available (B, C); *Histiototeuthis* sp., dorsal view, 1.6 mm ML (D); dorsal (E), ventral (F), detail of oral (G), and tentacular club (H) views, 3.2 mm ML. A from Diekmann *et al.* (2002); B,C from Nesis (1999); D–H from Vecchione *et al.* (2001).

***Histioteuthis reversa* (Verrill, 1880)**

Species characters (Figure 5.33A,B): Mantle short, cup-like; arms shorter than mantle; outer arm web absent, inner vestigial; large eyes; globular arms suckers; arm suckers rather large in juveniles; club suckers in four rows on manus of equal size; buccal membrane with seven lappets; ventral surface of the mantle with intermixed large and small photophores (developed at 5 mm ML), large ones distributed in about seven diagonal rows, each with nine photophores; four photophores along midline of ventral side of head; three rows of large photophores at base of IV arms and dorsal marginal row of small photophores (such dorsal row usually not seen in juveniles <15 mm ML); 2–3 rows of photophores on I–III arms; no elongate black photophores on arms end; 18 photophores (17 large and one small; occasionally 18 large and one small) around the right eye (Figure 5.33C) (small photophore often not seen in juveniles <8 mm ML, but an open space is present); an arch of seven large photophores anterior to, and 10–14 small ones lateral and posterior to left eye; dorsal pad of the funnel organ with separate, longitudinal, median ridge on each lateral arm (sometimes seen as early as 9 mm ML); skin not papillate.

References: Sweeney *et al.* (1992); Nesis (1999).

***Histioteuthis bonnellii* (Férussac, 1835)**

Species characters (Figure 5.33D): Mantle short, cup-like; arms as long as mantle; inner web between arms I–III deep (~16–37% of the longest arm length at 8–10 mm ML, ~19–58% at >10–20 mm ML), outer web poorly developed; large eyes; arms suckers rather small in juveniles, globular, with low, barely noticeable teeth; tentacles thick and very long; club suckers in 5–6 rows of equal size; buccal membrane with six lappets (Figure 5.33E), connectives to arms IV attached to dorsal parts of arms IV and to middle of web joining arms III and IV; mantle covered with many large chromatophores (developed at 5 mm ML); large ventral photophores distributed in 7–8 diagonal rows, each with seven photophores, gradually diminishing posteriorly; 4–5 photophores along midline of ventral head surface; three longitudinal rows at the base of all arms; single enlarged, long, dark photophore on end arms I–III or I–IV (seen in juveniles as small as 7 mm ML; at 15–20 mm ML, photophore measures ~12–15% of the arm length); 17 large photophores around right eye (Figure 5.33F); an arch of seven large photophores anterior to, and ca. ten small ones lateral and posterior to left eye; 2–4 conspicuous large around black photophores posterior to left eye on ventral side of head; skin not papillate.

References: Sweeney *et al.* (1992); Nesis (1999).

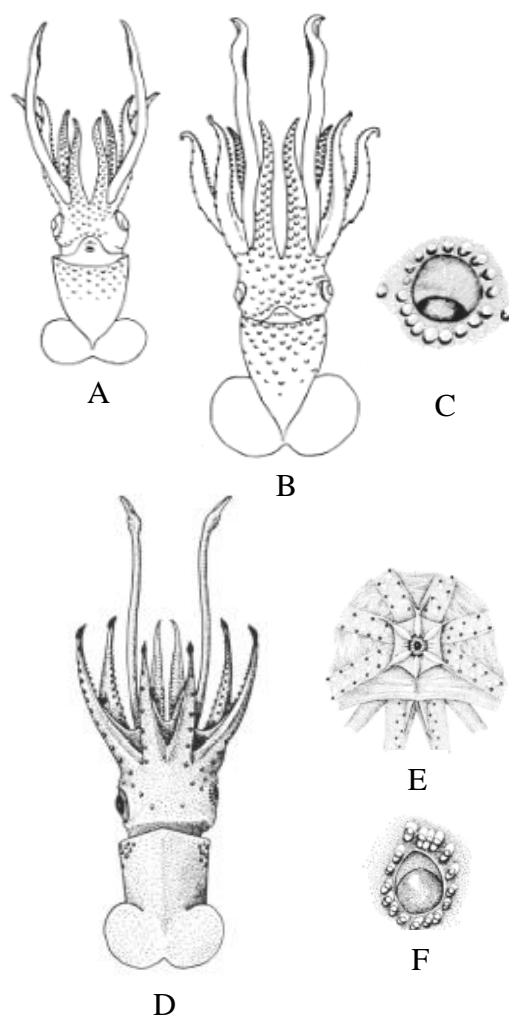


Figure 5.33. *Histioteuthis reversa*: ventral views, 6 mm ML (A) and 9 mm ML (B); detail of photophore of the right eye, 29 mm ML (C); *Histioteuthis bonnellii*: dorsal view (D), buccal view with 6-membered buccal membrane (E), and right eye (F), 9 mm ML. A,B from Voss and Voss (1962); C–F from Voss (1969).

5.10 Family Brachioteuthidae Pfeffer, 1908

This is a monogeneric family with a single species present in the Mediterranean.

Brachioteuthis riisei (Steenstrup, 1882)

Species characters (Figures 5.34 and 5.35): Mantle long, narrow, cylindrical or becoming conical ahead of the end of the anterior fin; head narrow, but not retractable into mantle; distinctive long, slender neck (no arm-crown stalk); neck contains a fluid-filled sac that extends as a reservoir into the body; contraction of the reservoir can greatly increase the length of the neck, thereby extending the head from the mantle; mantle opening wide relative to neck; eyes below midline of head; distinctive swelling or hump on the dorsal surface of the head; fins paddle-shape, separated, straight or weakly tapering behind, fin length less than width, not exceeding half ML; arms short, with two rows of suckers; tentacles large, present at hatching, prominent, robust and much longer than arms; terminal club wide; club suckers develop at hatching, with 2–4 rows of rather large suckers in carpal, 6–8 rows of knobs in distal part (Figure 5.34F–H); transition from larval to adult pattern at >10 mm ML; fixing apparatus with two

rows of small suckers along stem; buccal membrane with seven lappets, connectives to arms IV attached ventrally; funnel cartilage straight, simple; gladius with thin, very long rachis and narrow vane; in some forms, a photophore on ventral eyeball.

Individuals 3.0 mm ML (Figure 5.34A and 5.35A): Clubs with suckers in 2–3 rows, arms I and II very short, and arms III and IV just small papillae.

Remarks: Paralarvae easily distinguishable by a narrow head, long neck, and many rows of carpal club suckers, light in color, with sparse chromatophores.

References: Sweeney *et al.* (1992); Nesis (1999); Moreno (2008).

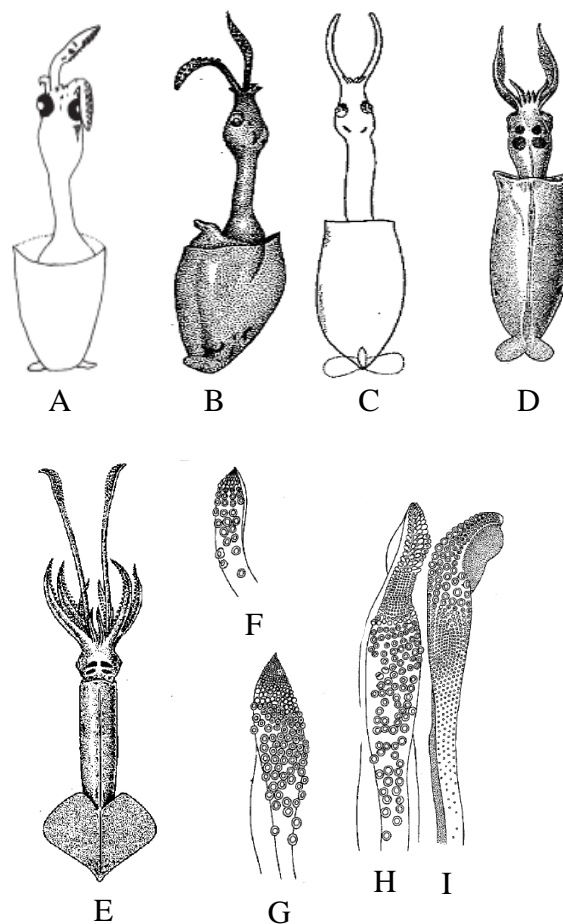


Figure 5.34. *Brachiooteuthis riisei*: general view of paralarvae (A–D) and a juvenile (E) (A: 3.5 mm ML, B–E sizes not available); tentacular club of paralarvae of different sizes, 2.5 mm ML (F), 6.5 mm ML (G), 10 mm ML (H), and size not available (I). A from Salman *et al.* (2003); B–I from Nesis (1999).

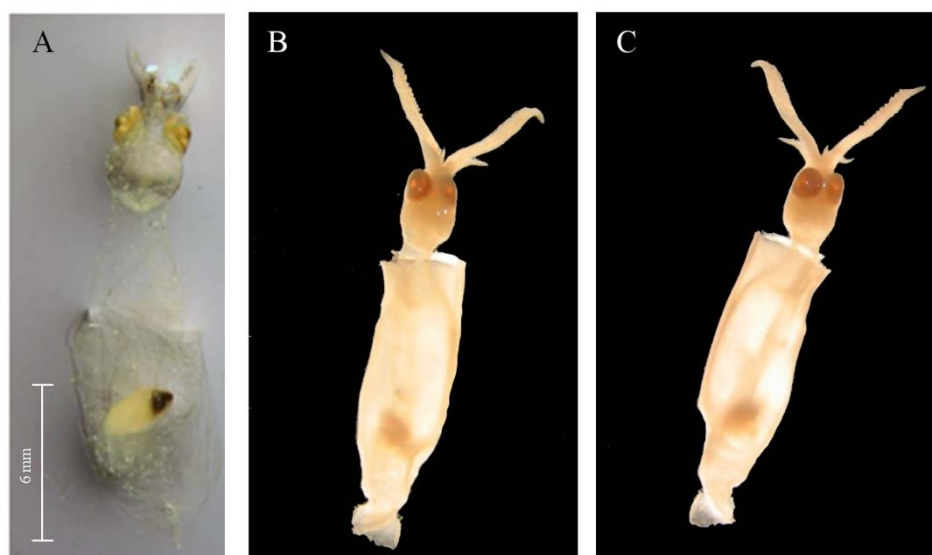


Figure 5.35. *Brachioteuthis riisei*: general view, 3.18 mm ML (A); dorsal (B) and ventral (C) views, 10.1 mm ML. A from Moreno (2008).

5.11 Family Ommastrephidae Steenstrup, 1857

Family characters (Figure 5.36): Distinctive paralarval form, the “rhynchoteuthion”, characterized by the fusion of the tentacles into a trunk-like structure named proboscis; proboscis present at hatching (about 1 mm); as the squid grows, the proboscis begins to divide with a splitting groove forming at its base; depending on the species, the separation into the two tentacles is completed at 6–10 mm ML; up to the inception of the division, distal tip of proboscis with eight suckers; in some species, two opposing distal suckers larger than the others; locking cartilage as in adults; mantle in paralarvae is at first barrel-shaped, later cylindrical; fins short, petaloid; relative length of the proboscis, size relationships of lateral to other suckers, and presence/absence of ocular or visceral photophores are characters used for the identification of paralarvae.

Remarks: Three species of this family inhabit the Mediterranean (*Illex coindetii*, *Todarodes sagittatus* and *Todaropsis eblanae*) and a forth (*Ommastrephes bartramii*) is only sporadically caught. To date, *T. sagittatus* and *T. eblanae* paralarvae have not been described.

References: Sweeney *et al.* (1992); Nesis (1999); Moreno (2008).

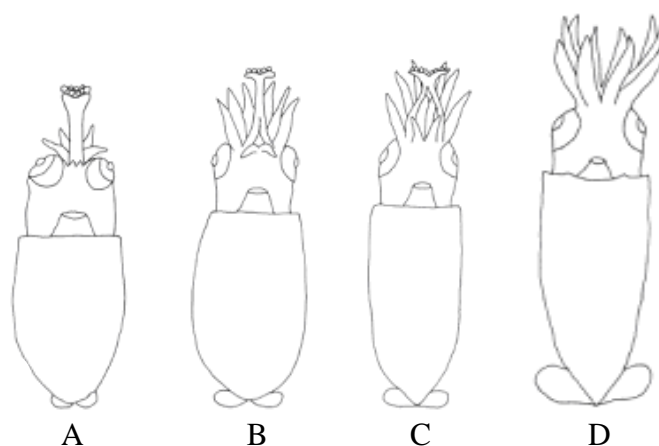


Figure 5.36. Growth series of a typical paralarvae of the family Ommastrephidae: 1.5 mm ML (A), 4.0 mm ML (B), 8.0 mm ML (C), and 15.0 mm ML (D). From Sweeney *et al.* (1992).

Owing to the difficulties in identifying the paralarvae of this family to species level, several rhynchoteuthion types (A, B, and C) have been described according to different morphological characters.

Rhynchoteuthion type A

This rhynchoteuthion type has been ascribed to different species of the genera *Illex*: *I. illecebrosus* (Roper and Lu, 1979), *Illex argentinus* (Haimovici *et al.*, 1995), and *I. coindetii* (Salman *et al.*, 2003; Moreno, 2008).

Species characters (Figures 5.37 and 5.38): No ocular or visceral photophores; slender and long proboscis (see remarks below) with eight suckers on tip nearly equal in size (Figure 5.37B,G,J); proboscis length typically 50–75% ML (<4–8 mm ML); proboscis is always longer than the longer arms; proboscis division begins at about 4–5 mm ML, and the tentacles separate at 6–10 mm ML; bulbous liver is slightly elongated, pear-shaped, narrowed anteriorly (Figure 5.37C); post-proboscis juveniles are characterized by the presence of more than four rows of suckers on the dactylus and many closely packed suckers and/or sucker buds.

Remarks: Differences in proboscis length and width could be due to differences among species, since it is relatively short and robust (Figure 5.37E) according to Roper and Lu (1979), but slender and long (Figures 5.37F,H,I and 5.38B) according to Haimovici *et al.* (1995) and Moreno (2008).

References: Roper and Lu (1979); Sweeney *et al.* (1992); Haimovici *et al.* (1995); Salman *et al.* (2003); Moreno (2008).

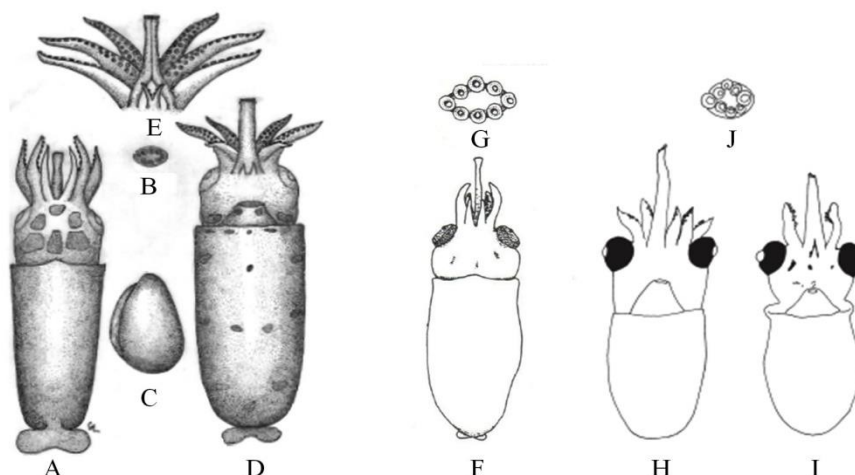


Figure 5.37. Rhynchoteuthion type A, ascribed to the following species according to different authors: 1) *Illex illecebrus* (A–D; Roper and Lu, 1979); 2) *Illex argentinus* (F, G; Haimovici *et al.*, 1995); and 3) *Illex coindetii* (H–J; Salman *et al.*, 2003). Dorsal view (A, 3.13 mm ML; F, ~3.0 mm ML), ventral view (D, 4.69 mm ML; H, 2.5 mm ML; I, 5.3 mm ML), suckers on tip of proboscis (B, G, J), lateral view of liver and ink sac (C), and ventral view of arm crown (E).

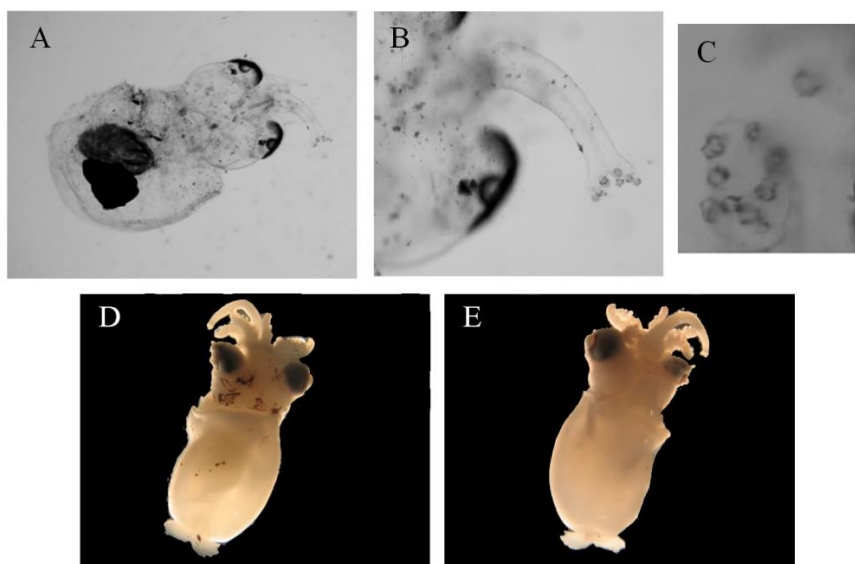


Figure 5.38. Rhynchoteuthion type A: 2.25 mm ML paralarva (A) and detail of the proboscis (B); proboscis tip of a 2.86 mm ML paralarva (C); dorsal (D) and ventral (E) views of 3.2 mm ML paralarva. A–C from Moreno (2008).

Rhynchoteuthion type B

Species characters (Figure 5.39): Thick and short proboscis with eight suckers of equal size; proboscis starts splitting in paralarvae >4 mm ML; proboscis measure on average 35% ML (± 8.7) in paralarvae <5 mm ML; tentacular index ranges between 0.16 and 0.53.

References: Moreno (2008).

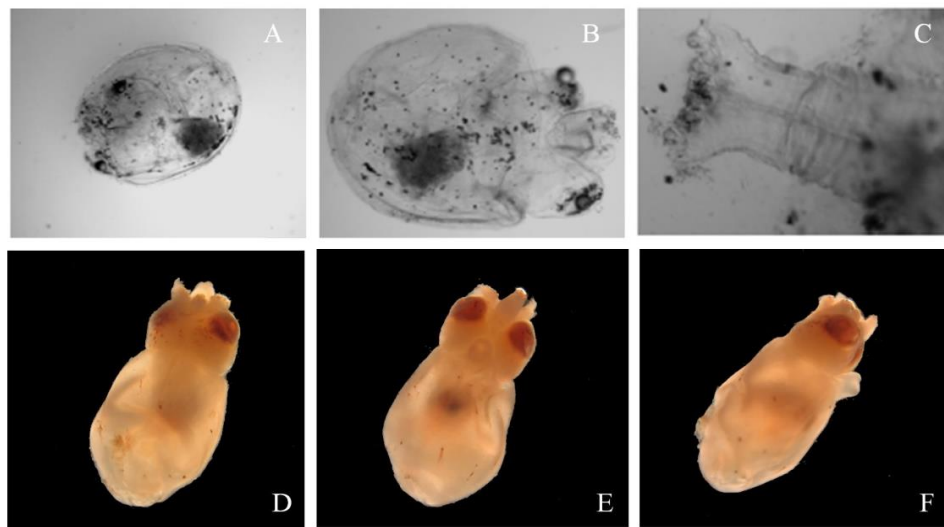


Figure 5.39. Rynchoteuthion type B: 2.04 mm ML paralarva (A, B) and detail of the proboscis of a 3.42 mm ML paralarva (C); dorsal (D), ventral (E) and lateral (F) views of a 3.0 mm ML paralarva. A–C from Moreno (2008).

Rhynchoteuthion type C

Species characters (Figure 5.40): Proboscis thick and short with eight suckers, six of similar size and two lateral suckers larger than the others; proboscis measure on average $38 \pm 7.8\%$ ML (and is longer than the arms in paralarvae < 3 mm ML; tentacular index ranges between 0.27 and 0.50; only arms II and III are formed at < 1.5 mm ML, each with one large sucker close to the base; eyes prominent; mantle as wide as long and ends as a pointed apex; fins small; 14 red chromatophores on the dorsal surface of mantle (two isolated on the posterior end) and three on the dorsal surface of head (one central and one above each eye); 16 chromatophores on the ventral surface of mantle, of which one isolated on the posterior end.

References: Moreno (2008).

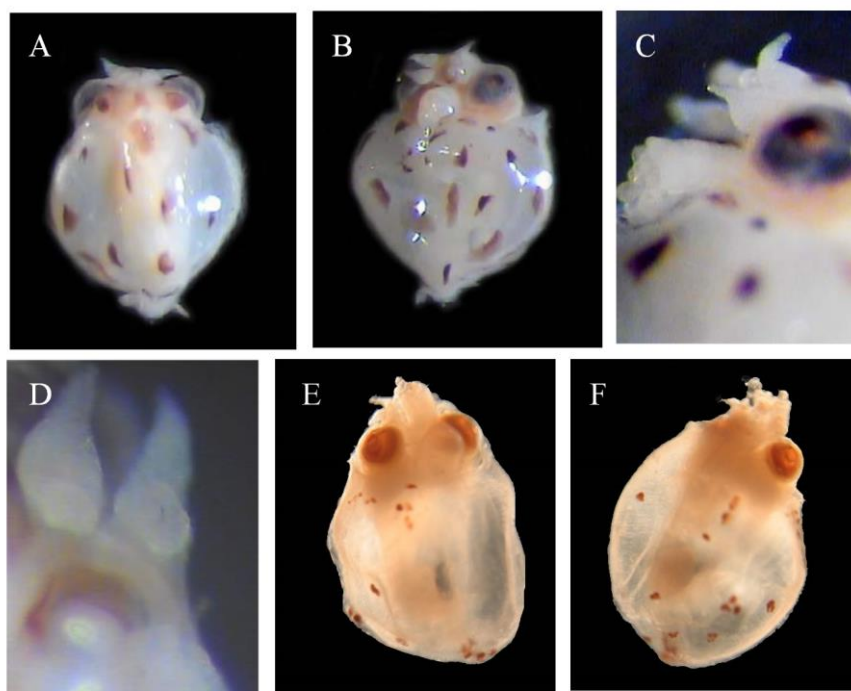


Figure 5.40. Rynchoteuthion type C: dorsal (A) and ventral (B) views, details of the proboscis (C) and arms (D), 1.43 mm ML; dorsal (E) and ventral (F) views, 2.4 mm ML. A–D from Moreno (2008).

Ommastrephes bartramii (Lesueur, 1821)

Species characters (Figure 5.41): No ocular or visceral photophores; proboscis thin, rather long (1/2–2/3 ML), may be equal to ML in early paralarvae, usually longer than arms; diameter of lateral (distal) two suckers on the proboscis tip up to twofold larger than of the remaining 6 suckers (Figure 5.41C); division of the proboscis begins at 5 mm ML and tentacles are separated at 7–9 mm ML; third and fourth arm pairs developed at about 1.5 and 2.5–3.0 mm ML, respectively; mantle in paralarvae barrel-shaped, in juveniles very narrow, cylindrical, pencil-like; head not retractable into mantle; mantle in paralarvae with dispersed large brown chromatophores, in juveniles with crimson and brown chromatophores.

References: Sweeney *et al.* (1992); Nesis (1999).

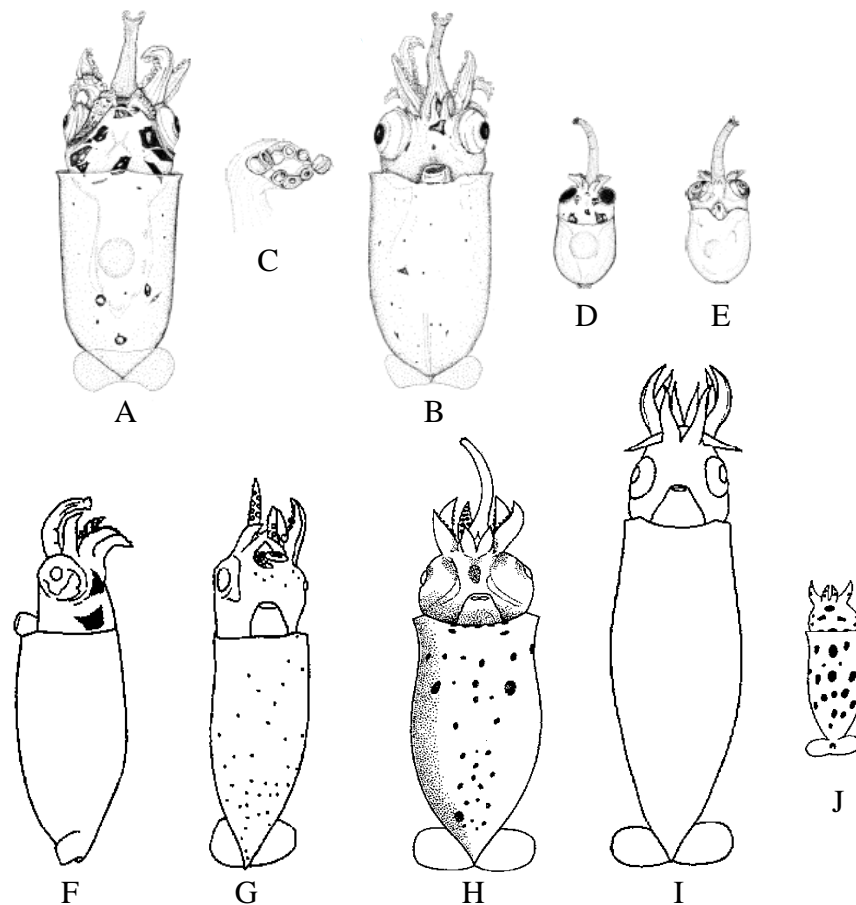


Figure 5.41. *Ommastrephes bartramii*: dorsal (A), ventral (B), and end of the proboscis (C) views of a 5.2 mm ML paralarva; dorsal (D) and ventral (E) views of a 1.4 mm ML paralarva; lateral (F), ventral (G, H, I) and dorsal (J) views, sizes not available. A–E from Diekmann *et al.* (2002); F–J from Nesis (1999).

5.12 Family *Thysanoteuthidae* Keferstein, 1866

Since this family is monotypic, family/species characters are described only for the currently known species.

Thysanoteuthis rhombus Troschel, 1857

Species characters (Figures 5.42 and 5.43): Mantle stout and short, in paralarvae sac-like, in juveniles broadly cup-like; sideways T-shape funnel locking-cartilage, with narrow projection in upper and rectangular in lower part; head wider than mantle and may retract into it only in hatchlings paralarvae; small, broadly separated eyes that protrude in specimens <5 mm ML; fins small and petaloid in paralarvae, kidney-shaped in juvenile; by 14 mm ML, fin length 64% ML; head, mantle and arms with densely speckled large violet chromatophores (fading after prolonged fixation); arms short but strong, with two rows of suckers, in juveniles relatively longer than paralarvae; arms III are longest, arms IV widened at base; all arms bear wide protective membranes with long cirrus-like trabeculae by 10 mm ML; tentacles short, stouter and longer than the arms at 1.5 mm ML, attenuate by 5 mm ML; club widened, with four rows of suckers; fixing apparatus: two rows of alternating knobs and suckers along stem; buccal membrane with seven lappets, connectives to arms IV attached ventrally; nuchal cartilage with two knobs fitting two pits near anterior margin of the mantle; gladius is like tip

of arrow with short stem; no photophores except probably one on the ink sac in juveniles, lacking in paralarvae.

Individuals ca. 1.5–2.0 mm ML (Figure 5.43A–D): Mantle oval, short and blunt posteriorly, anterior margin of the mantle concave on both the dorsal and ventral sides, more so ventrally; fins subterminal, small and paddle-shaped, located somewhat anteriorly to the mantle's posterior end and separated from each other; fin length is 6.6% ML; head trapezoid with small eyes broadly separated, slightly protruding with four reddish chromatophores at their base; mostly head inside the mantle cavity, showing only the arms and the tentacles externally; funnel locking cartilage with short, broad transverse groove and a long relatively wide, longitudinal groove; each tentacle with 16–18 reddish chromatophores disposed in one row and three more at the base; arm formula: $II > I > IV > III$; arms II about 35% ML; arms III and IV rudimentary; developed arms with small suckers arranged in two rows; an incipient swimming keel membrane present on arms I and II; trabeculae protective membrane absent in arms and tentacles; two suckers with chitinous rings on the proximal ends of arms I and II (Figure 5.45A); tentacles compressed 60% ML and stouter and slightly longer than the longest arm (II); tentacular club not differentiated, with 13–14 suckers on the third of the tentacle length, arranged in two transverse and four longitudinal rows on the proximal half of the tentacle; distal position of the tentacle avoids armatures, and terminates in an acute tip (Figure 5.45G); paralarvae with two types of chromatophores: the first, large and reddish densely concentrated on the dorsal, lateral and ventral sides of the mantle, and the second, with yellow chromatophores on the dorsal sides of the arms; dorsally, at the anterior end of the mantle, a line of 16 chromatophores, and 150 more posterior to these forming a mosaic; ventrally, at the anterior end of the mantle, a line of 16–20 chromatophores and about 250 posteriorly; dorsal surface of the head with seven chromatophores, two at the attachment of the first pair of arms, another two situated laterally, and the remaining ones very close to and ventral to the others; single lines of 3–5 chromatophores on arms; fins lack chromatophores.

Individuals ca. 2.5–3.5 mm ML (Figure 5.43E–H): Mantle width index: 91.7%; arm formula: $II > I > III > IV$; protective membrane of arm IV; four large suckers with chitinous rings developed proximally and 12–20 small suckers without chitinous rings in the middle (Figure 5.46A), no suckers on the distal tip of arm II (Figure 5.45E,F); tentacular club occupies 70% of the total tentacle length and expanded slightly, with suckers arranged in eight transverse and four longitudinal rows; tips of the upper and lower beak's rostrum developed slightly; minute dentitions on the cutting edge of the lower beak (Figure 5.46B), and cilia around the entire lip.

Individuals ca. 4.0–5.5 mm ML (Figure 5.43I,J and 5.44A,B): Mantle dome-shaped; fins grow longitudinally, with a fin length index of 31%, and reach the mantle's posterior end; mantle width index 73.8%; protective membranes of arms I–III developed and clearly differentiated; arm formula: $II > III > I > IV$, and arm II grow to 60% ML (Figure 5.45C); 16 transverse and four longitudinal rows of tentacular suckers on the manus, whereas five pairs of suckers in double rows on the carpus (Figure 5.45I); lower beak blunt, but beak serrations smooth and lip cilia disappear (Figure 5.46C).

Individuals ca. 6.0–7.0 mm ML (Figure 5.44C): Mantle cylindrical and tapered abruptly in posterior direction; mantle width index: 58.6%; head subcubic and eyes become sessile; arm formula: $III > II > I > IV$; arm III equals the mantle in length.

Individuals ca. 9.5 mm ML (Figure 5.44D): Suckers developed on the distal tips of the arms (Figure 5.45D); tentacular suckers arranged in 17 transverse and four longitudinal rows on the manus, but six pairs in double rows on the carpus (Figure 5.45J).

Individuals ca. 15.0 mm ML: Mantle spindle-shaped and similar to adult; length of arm III increases to 120% ML; fin length index: 86%; fins extend to almost the entire length of the lateral mantle; mantle cylindrical, tapered abruptly in the posterior direction; mantle width index: 58.6%; rostra of the upper and lower beaks of the paralarvae pointed.

Remarks: According to Miyahara *et al.* (2006), the chromatophores of the hatchlings are usually retracted and appear as small dots (Figure 5.47), whereas they are generally expanded in specimens fixed in formalin (Guerra *et al.*, 2002).

References: Yamamoto and Okutani (1975); Sweeney *et al.* (1992); Guerra *et al.* (2002); Wakabayashi *et al.* (2005); Miyahara *et al.* (2006).

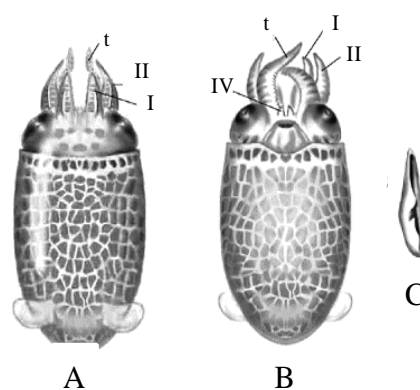


Figure 5.42. *Thysanoteuthis rhombus*: dorsal (A) and ventral (B) views of paralarvae showing the shape and disposition of chromatophores on the head, mantle, arms, and tentacles, no sizes available; funnel locking-cartilage (C). Labels refer to arms (I, II, IV) and tentacles (t). From Guerra *et al.* (2002).

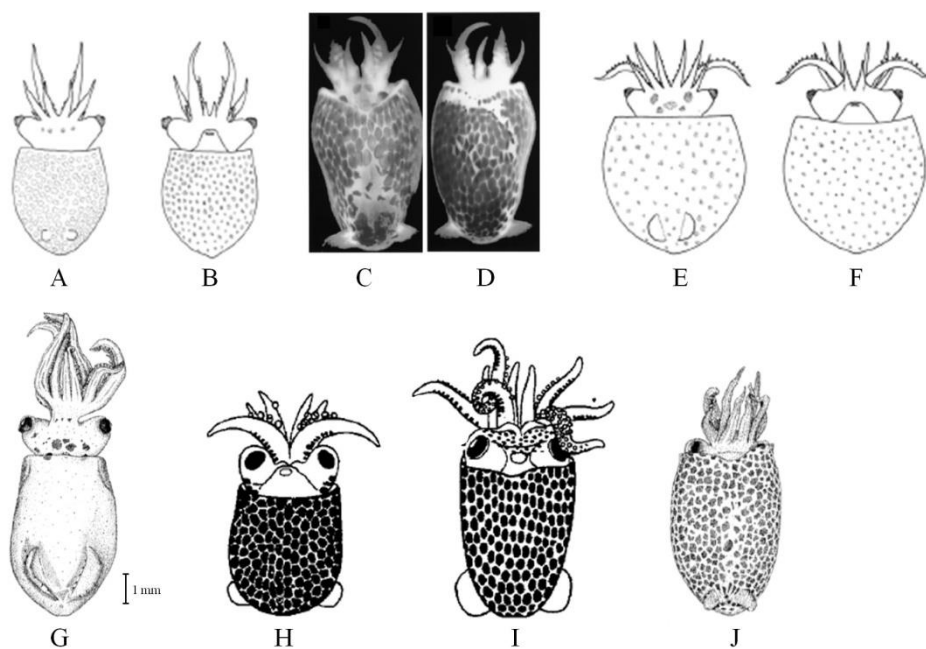


Figure 5.43. *Thysanoteuthis rhombus*: dorsal (A) and ventral (B) views, 1.4 mm ML; dorsal (C) and ventral (D) views, 1.5 mm ML; dorsal (E) and ventral (F) views, 2.4 mm ML; dorsal view, 2.7 mm ML (G); ventral views, 3.0 mm ML (H) and 4.0 mm ML (I); and dorsal view, 5.6 mm ML (J). A,B and E,F from Wakabayashi *et al.* (2005); C,D from Guerra *et al.* (2002); G and J from Diekmann *et al.* (2002); H,I from Nesis (1999).

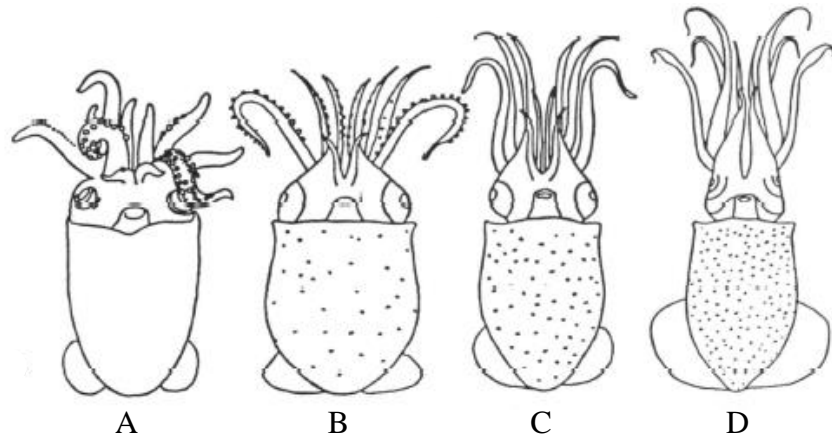


Figure 5.44. *Thysanoteuthis rhombus*: changes in form during growth, 4.0 mm ML (A), 4.5 mm ML (B), 6.0 mm ML (C), and 10.0 mm ML (D). From Clarke (1966).

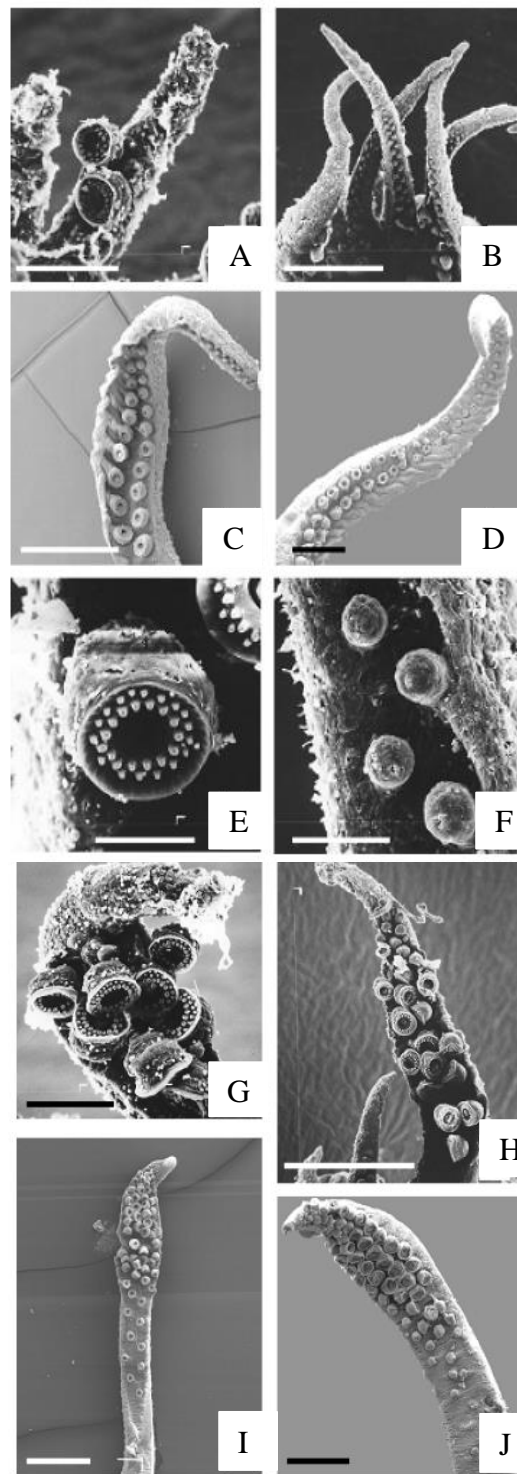


Figure 5.45. Scanning electron micrographs of *Thysanoteuthis rhombus*. A: arm II, 1.4 mm ML, scale bar = 0.1 mm; B: arms I-III, 2.9 mm ML, scale bar = 0.5 mm; C: arm II, 5.4 mm ML; scale bar = 0.5 mm; D: arm II, 9.6 mm ML, scale bar = 0.5 mm; E: proximal sucker of arm II, 3.3 mm ML, scale bar = 0.05 mm; F: medial suckers of arm II, 3.3 mm ML, scale bar = 0.05 mm; G: tentacle, 1.4 mm ML, scale bar = 0.1 mm; H: tentacle, 3.4 mm ML, scale bar = 0.5 mm; I: 5.4 mm ML, scale bar = 0.5 mm; and J: 9.6 mm ML, scale bar = 0.5 mm. From Wakabayashi *et al.* (2005).

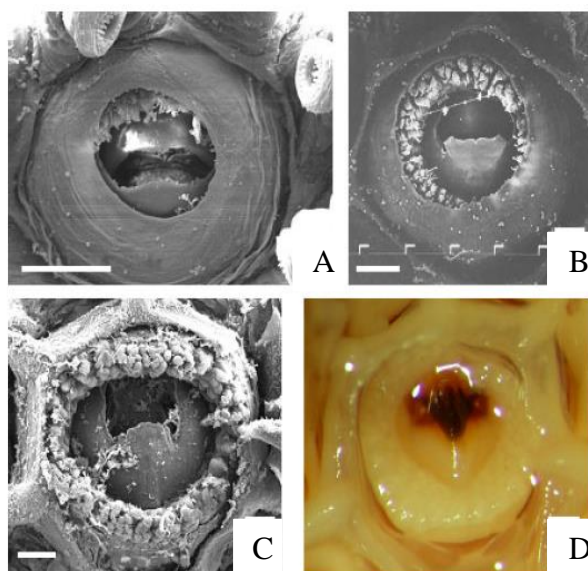


Figure 5.46. Scanning electron micrographs and biological micrographs of mouth part in *Thysanoteuthis rhombus* paralarvae of different sizes: 2.4 mm ML (A), 3.4 mm ML (B), 5.4 mm ML (C), and 15.0 mm ML (D). Scale bars = 100 µm. From Wakabayashi *et al.* (2005).

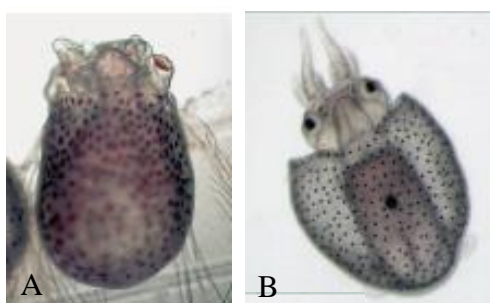


Figure 5.47. *Thysanoteuthis rhombus*: hatchling embryos (A, B). From Watanabe *et al.* (1996).

5.13 Family Chiroteuthidae Gray, 1849

Since this family is monotypic in the Mediterranean, the family/species characters are described only for the currently known species.

Chiroteuthis veranii (Férussac, 1835)

Species characters (Figure 5.48): Mantle almost transparent, elongate, rod-like, and cylindrical, tapering into long thin tail; gladius very thin, rod-like, with long conus, extends well posterior to fins (frequently broken); on conus behind fin are 1–3 small additional fins, but frequently lost; primary fin butterfly-like, then transverse-oval; head very narrow, with extremely long, transparent neck, subdivided by many transverse septa, columnar, vesiculate, and long (but shorter than neck) narrow “snout” (arm-crown pillar); eyes near middle of head; arms I–III very short, arms IV far longest, much wider than others (>11 mm ML), with widened ventral protective membrane; arms suckers on arms I–III in two rows, on arms IV in two rows only in basal half, then zigzag-like and in one row near the end; arm suckers with acute teeth on distal margin; arm suckers on arms IV slightly smaller than on arms I–III; definitive club wide, without keel, with four rows of very peculiar suckers (nearly 20 in row) on thick, long, dark-

colored pedicels, widening at the middle, located so that pedicels of inner rows appear to grow from those of marginal rows; club suckers with long acute median tooth and some smaller ones; tentacles developed early with very elongate, thick stalks; tentacular club narrow, keeled, club and part of stem with four rows of ordinary suckers on short pedicels, resorted during transition to juveniles which occurs at ~50 mm ML, although some larval features discernible at ~75 mm ML; no fixing apparatus; buccal membrane with seven lappets, connectives to arms IV attached ventrally; mantle cartilage nose-like; funnel cartilage ear-shaped with two projections: *tragus* (on ventral side) and *antitragus* (on posterior side); funnel valve present; two large round photophores on ink sac; two parallel elongate luminous stripes, two large oval and one small round photophore on ventral eyeball, a longitudinal row of round photophores along ventral protective membrane of arms IV, one large complex photophore on end of tentacular club, some small ones on stalk.

Remarks: The paralarvae of chiroteuthids are known as “doratopsis”.

References: Sweeney *et al.* (1992); Nesis (1999).

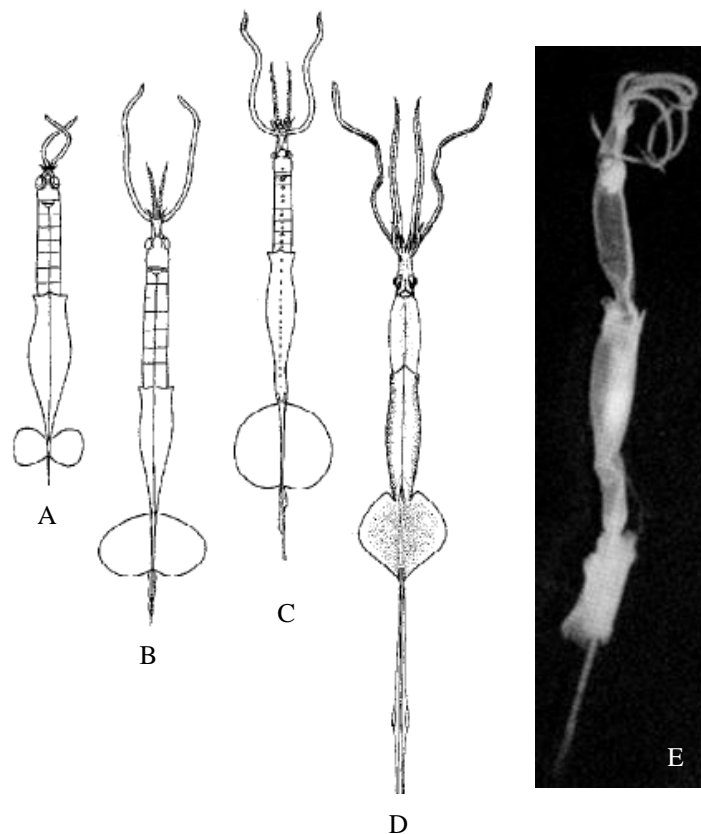


Figure 5.48. *Chiroteuthis veranii*: dorsal views of paralarvae of different sizes, 4 mm ML (A), 7 mm ML (B), 17 mm ML (C), 35 mm ML (D); dorso-lateral view, 31 mm ML (E). A–D from Nesis (1999); E from Lefkaditou *et al.* (1999).

5.14 Family Cranchiidae Prosch, 1847

Family characters: Mantle thin-walled, membranous, semigelatinous or leathery, smooth or bearing small cartilaginous tubercles either circumscribed in some areas or distributed through most of the body; mantle fused to head at nuchal region and to

funnel at postero-lateral corners; fins of very variable form and size, from separate, small, paddle-shape, subterminal, to medium-large, round, terminal, to ovate or lanceolate, terminal, or terminal-lateral; funnel moderately large to very large; head short and narrow; eyes small to large with photophores, commonly with ventrally directed rostrum and without photophores, stalked and tubular in paralarvae and juveniles of most genera; arms short to medium length with protective membranes and weak keel suckers in two rows; tentacles long with two rows (except in *Teuthowenia*, with four rows) of carpal suckers on major portion of stalks; tentacular club short, not wide, with four rows of denticulate suckers, hooks appear with growth in *Galiteuthis*; fixing apparatus well developed, stretched along the stalk; buccal membrane with seven lappets, connectives to arms IV attached ventrally; gladius thin, rod-like, with diamond-shaped caudal widening (lanceola); rear end mantle may not reach tail end; fins attached to rear sides of lanceola, in some genera, their anterior ends may reach in front of lanceola on mantle sides; funnel valve present or absent; photophores always present, located usually on ventral side of eyeball, on arms ends; the coelom is very voluminous, closed and filled with a weak solution of NH_4Cl , forming a float like in a bathyscaph ("bathyscaphoid squids"); mantle cavity subdivided by thin horizontal membrane into two chambers, upper (including coelom) and lower, both connected by two round openings over gills; paralarvae clear, while adults usually purple, brown, or yellow, but transparent in some genera.

Remarks: The family (with the exception of *Cranchia*) displays a special "larval" stage characterized by stalked eyes and a short to long arm-crown.

References: Sweeney *et al.* (1992); Nesis (1999).

5.14.1 Subfamily Cranchiinae Prosch, 1849

Subfamily characters: Ventral surface of mantle with two hyaline, cartilaginous strips in inverted V-shaped pattern extending posteriorly from anterior apex of funnel mantle fusions (usually not apparent in *Cranchia* <10 mm ML); head without arm-crown stalk; eyes sessile; mantle surface with widely or densely set, cross shape cartilaginous tubercles (>4 mm ML); funnel valve present; eye photophores numerous, in 1–2 arcs.

Remarks: A single individual of *Cranchia scabra* has been reported to date in the Mediterranean (Quetglas *et al.*, 1999).

References: Sweeney *et al.* (1992); Nesis (1999).

Cranchia scabra Leach, 1817

Species characters (Figure 5.49 and 5.50): Stout, balloon-shape elongate mantle; all mantle surface and upper side of fins covered with very numerous scattered cross-shaped, cartilaginous tubercles, formed in paralarvae at ~4–5 mm ML and becoming more numerous with growth (few widely scattered tubercles confined to anterior half of the mantle at ~4–5 mm ML); four short, non tubercular, hyaline, cartilaginous stripes on ventral mantle near mantle-funnel fusion, in form of an inverted V, usually not apparent until ~10–15 mm ML; head may retract into mantle up to eyes; protruding, but not stalked, small oval eyes; eyes with 14 oval photophores, seven in outer half circle, one midway, and six in inner full circle (outer photophores first seen ~15–17 mm ML); small, separated, paddle-shape fins (Figure 5.50D), which gradually become round and unite posteriorly with growth; arms short; tentacular stalks bear suckers along entire length; club with four rows of suckers; funnel valve present; outer and inner eyeball photophores developed in paralarvae at 10 and 15–17 mm ML, respectively.

Remarks: Paralarvae easily distinguishable by cartilaginous tubercles.

References: Sweeney *et al.* (1992); Nesis (1999).

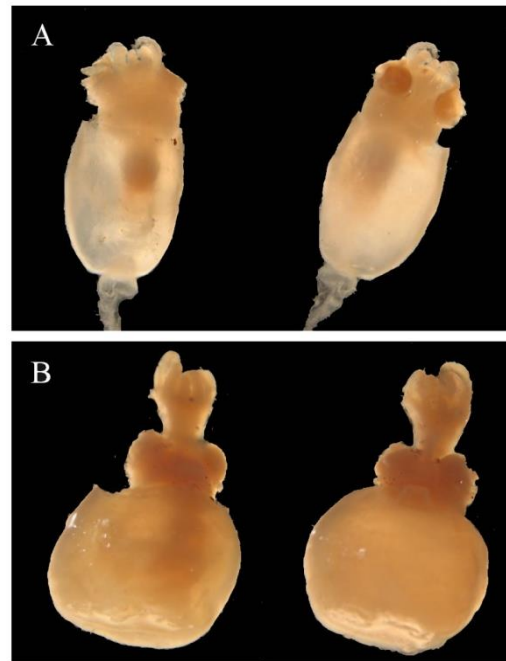


Figure 5.49. *Cranchia scabra*: dorsal (left) and ventral (right) views, 4.1 mm ML (A) and 5.2 mm ML (B).

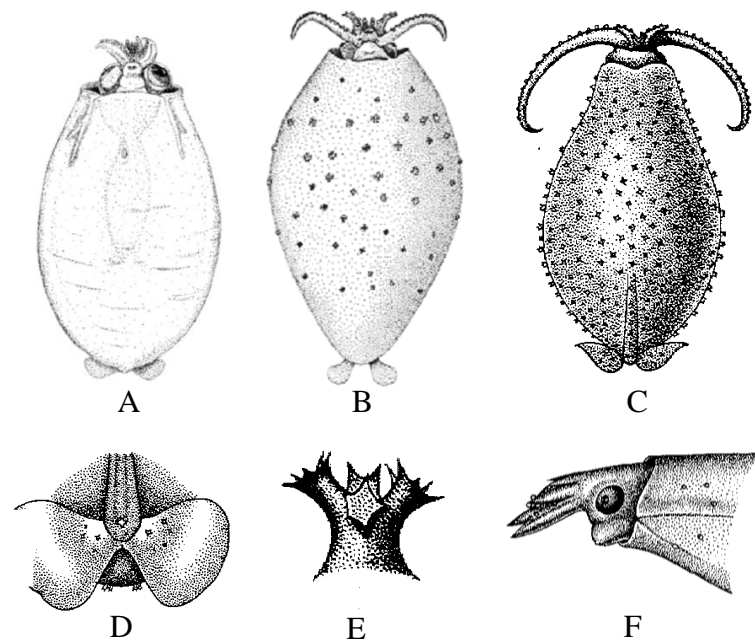


Figure 5.50. *Cranchia scabra*: ventral views, 5.5 mm ML (A) and 8 mm ML (B); dorsal view, 11 mm ML (C); detail of fins (D) and cartilaginous tubercle (E), sizes not available; lateral view of anterior part of body, 5 mm ML (F). A from Diekmann *et al.* (2002); B from Voss (1980); C–F from Nesis (1999).

5.14.2 Subfamily Taoniinae Pfeffer, 1912

Subfamily characters: May have cartilaginous tubercles at points of funnel-mantle fusion in some genera, but not in elongate strips; funnel-mantle fusion area narrow; funnel valve absent; tubercles sometimes present on straight, oval, subtriangular, spindle-shape, or postero-lateral margins of blunt or sharp-pointed, diamond-shape lanceola; lanceola narrow or of medium width, diamond-shape, with narrow, sharp-pointed end; eyes stalks with one large crescent-shaped and usually one (rarely two) much smaller, usually rod-shaped photophores; arm-crown stalk short or moderately long.

References: Sweeney *et al.* (1992); Nesis (1999).

Teuthowenia megalops (Prosch, 1849)

Species characters (Figure 5.51): Mantle stout and sac-like at <11 mm ML, becomes increasingly conical with growth; mantle with large (if expended), widely spaced, reddish brown, and oval chromatophores beginning at early paralarval stages; head with short, stout arm-crown stalk with very small arms; tentacles moderately large with small part with two rows of suckers, followed by four rows of suckers extending nearly entire length of tentacle; eyes oval, with short ventral rostrum, on short, stout stalks; tentacles medium length, usually stout, with four rows of suckers extending near the entire length of the stalk; funnel-mantle fusion cartilages with single-point tubercle first seen in “larvae” at ~30–60 mm ML.

Individuals ca. 6.0 mm ML (Figure 5.51A): mantle blunt posteriorly; fins very small, separate; funnel very large, broad; no tubercles on funnel-mantle fusion at this stage; head small, but eye stalks stout, relatively short; eyes small, dorso-ventrally elliptical, reflective tissue developing (Figure 5.51B), very slight ventral rostrum; arms very small; arms formula: I=II>>III=IV; arms I and II stout, conical with 5–6 suckers, globular grading; arms III and IV very small, conical; 2–3 minute suckers and 2–4 sucker anlagen on III, 1–2 sucker anlagen on IV; tentacles moderately large, stalks covered with suckers from proximal base in two rows that rapidly become four rows along stalk near tip (Figure 5.51C).

Remarks: The paralarval period is prolonged and ends when the eyes become sessile, at sizes of 75–95 mm ML.

Note: Only in this genus, carpal suckers occur in four rows on major portion of tentacular stalk.

References: Sweeney *et al.* (1992); Vecchione *et al.* (2001); Moreno (2008).

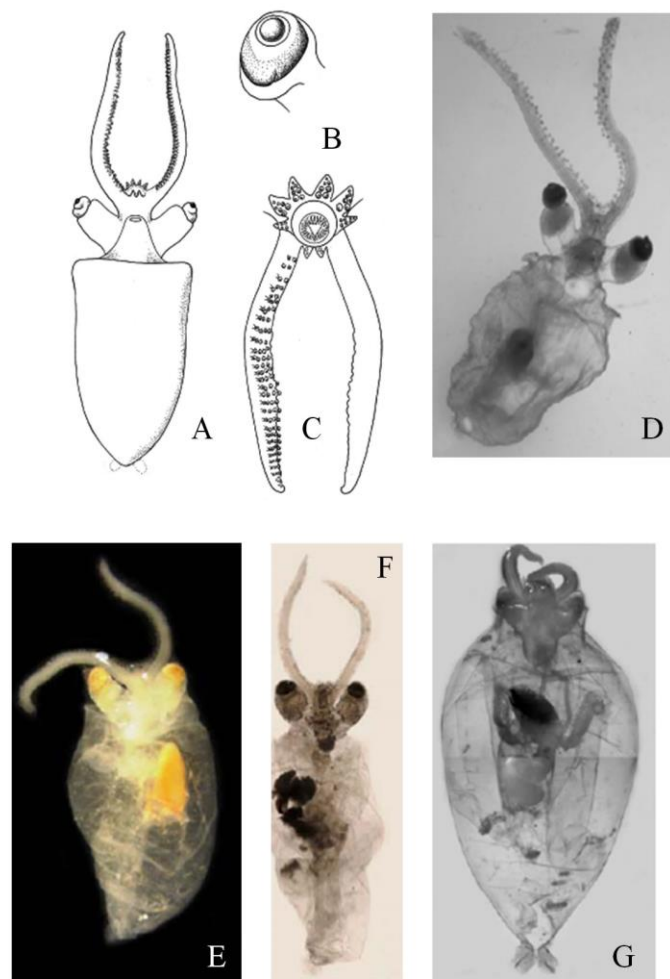


Figure 5.51. *Teuthowenia megalops*: ventral view (A), detail of oral view (B) and eye with ocular light organ (C), 6.2 mm ML; paralarval growth series, 8.18 mm ML (D), 12.5 mm ML (E), 15.2 mm ML (F), and 28 mm ML (G). A–C from Vecchione *et al.* (2001); D–G from Moreno (2008).

Galiteuthis armata Joubin, 1898

Species characters: Mantle moderately stout, spindle-shaped; fins small, paddle-shaped at <15 mm ML, change with growth to lanceolate with stout, glacial spine; head with short to medium length arm-crown stalk; eyes oval, without ventral rostrum, on stout, short to medium length stalks in “paralarvae”; inner ocular photophores stout, barrel-shaped; funnel-mantle fusion cartilages each with 1–3 pointed tubercles (>25 mm ML); glacial tail long in juveniles; club manus with median suckers changing into hooks (first seen at ~35–60 mm ML); arms IV typically the longest; glacial tail long in juveniles; inner ocular photophore stout, bar-shaped.

Note: Useful features to identify the genus *Galiteuthis* are: pattern of tubercles, or lack of tubercles, on the funnel-mantle and nuchal fusion cartilages; and the shape of the small, inner ocular photophore.

Remarks: Since *Galiteuthis armata* paralarvae have not been drawn before, we show an illustration of *G. glacialis* (Figure 5.52).

References: Sweeney *et al.* (1992).

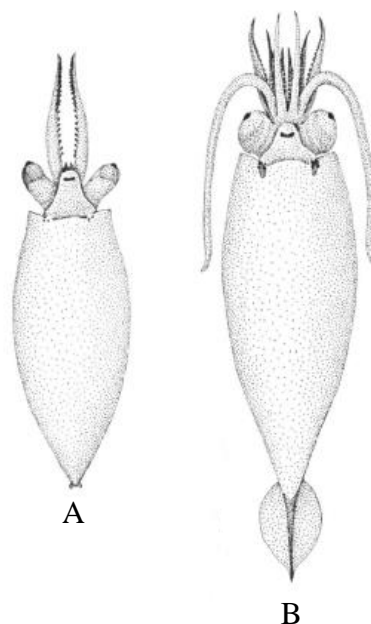


Figure 5.52. *Galiteuthis glacialis*: ventral view, 11 mm ML (A) and 54 mm ML (B). From Voss (1980).

5.15 Family Opisthoteuthidae Verrill, 1896

Family characters: Body semigelatinous to firm, anteriorly–posteriorly compressed, disk-shape, or bell-shape; mantle aperture small; funnel short; funnel organ inverted V; cirri short; eyes large; web single, deep; secondary web absent; fins small, shorter than head width or large; fin support straight, V- or U-shape; radula present or absent; crop absent; posterior salivary glands reduced in size or absent; gills “half orange” type.

Remarks: The paralarva of the single species inhabiting the Mediterranean [*Opisthoteuthis calypso* (Villanueva, Collins, Sánchez and Voss, 2002)] has not been described until now. Information of paralarvae of other species in this family also is limited. Therefore, descriptions herein are based on generic characters.

References: Sweeney *et al.* (1992).

Opisthoteuthis sp. Verrill, 1883

Species characters: Body semigelatinous to firm, anteriorly–posteriorly compressed, flattened, disk-shape; mantle aperture small; funnel short; funnel organ inverted V; cirri short; eyes large; web single, deep; secondary web absent; fins small, shorter than head, subterminal; fin support straight; radula absent; in juvenile individuals (Figure 5.53), arms with suckers only in smallest specimens, cirri develop in later juvenile stage; juveniles compressed compared to adults.

Remarks: The only available illustration of a small planktonic juvenile (15 mm ML) comes from Berry (1912).

References: Sweeney *et al.* (1992).



Figure 5.53. Opisthoteuthidae: ventral view of a juvenile, 15 mm ML. From Berry (1912).

5.16 Family Octopodidae d'Orbigny, 1839

Family characters: Body muscular to gelatinous; arms muscular, much longer than body, suckers uniserial or biserial; web usually not longer than half maximum arm length; mantle opening not reduced; mantle locking-apparatus absent; radula heterodont, occasionally homodont, not comb-like; digestive gland anterior to stomach and gonad; ink sac present, vestigial, or absent; light organs absent; shell vestige present in some species as a pair of cartilage-like (conchiolin) stylets in mantle; Koelliker's bristles present or absent in juvenile stage; functional chromatophores of several colors present.

Remarks: The Octopodinae is the largest contributor to the planktonic octopod fauna. The hatchlings of species with planktonic paralarvae measure 2–8 mm ML and characteristically are covered by bunches of short bristles (Koelliker's bristles; Figure 5.54). The eyes large and prominent; arms typically short and stubby, but in some species, they taper to delicate thread-like tips beyond the sucker-bearing part. Typically only a few suckers (3–4) present in a single, straight row. The mantle generally short and rounded, without fins. The ratio of mantle length to arm length is 3:1–2:1. During growth in plankton or at the time of settlement, the mantle elongates, the bristles are lost, the arms become long and unequal; with many suckers in one or two rows, a web develops, and colour becomes variable. Hatchlings from small eggs swim to near-surface waters where they develop for a period of time until ready to settle.

Planktonic paralarvae of bottom octopuses are all rather alike, distinguished by:

- the number and relative size of suckers per arm in hatchlings (Figure 5.55D–H). In the elledonines, such as *Eledone*, suckers are added in a single row as the arms elongate. If added in two rows, the paralarvae belong to one of a number of species of octopodines;
- the number of suckers vs. mantle length;
- the number and distribution of integumental chromatophores in the skin covering the arms, funnel, mantle, and head are species-specific (Figures 5.55 and 5.56). It should be noted that light (red and yellow) chromatophores fade shortly after fixation in formalin or ethyl alcohol; only the brown ones remaining.

The following definitions are used throughout for hatchling and paralarval chromatophore fields in octopod paralarvae. Similar fields are seen in other cephalopod paralarvae.

- **Arm chromatophores:** Small integumental chromatophores located in the skin covering the aboral surface of each arm. Specific chromatophore patterns are counted from the base of the arm toward the tip (Figure 5.55A,I–O).

- **Arm-base chromatophores:** Single large additional integumental chromatophore located at the base of the brachial crown of each arm, deep in the head region in the connective tissue covering the muscles where the arms join the head (Figure 5.55A,I–O).
- **Funnel chromatophores:** Small integumental chromatophores located in the skin covering the ventral surface of the funnel. Specific chromatophore patterns are counted from the lip of the funnel orifice toward the base of the funnel located under the anterior margin of the ventral mantle (Figure 5.55A,P–U).
- **Mantle chromatophores:** Small integumental chromatophores located in the skin covering the dorsal, ventral, lateral, and posterior mantle. Specific patterns are counted across the mantle and/or from the mantle margin (Figures 5.55A and 5.56A–N).
- **Visceral chromatophores:** Large integumental chromatophores located deep in the mantle region in the tegument (skin) covering the dorsal surface of the visceral mass (Figure 5.56O–Q).
- **Eye chromatophores:** Large extrategumental chromatophores located in the head region in the connective tissue covering the dorsal and ventral surfaces of the eye (Figure 5.56R–V).
- **Head chromatophores:** Large extrategumental chromatophores located deep in the head region in the connective tissue covering the muscle of the dorsal and ventral head. Specific chromatophore patterns in the dorsal surface of head are counted from the base of the arm crown toward the dorsal mantle margin (anterior to posterior). Additional, smaller integumental chromatophores may be located in the skin covering the dorsal surface of the head (Figure 5.56R–X).

References: Sweeney *et al.* (1992); Nesis (1999).

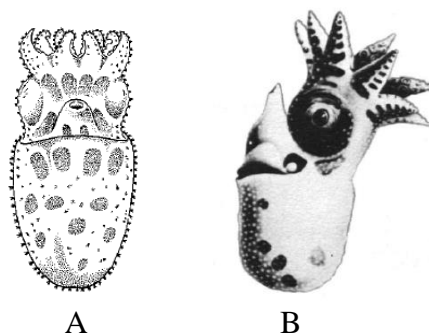


Figure 5.54. *Octopus vulgaris*, recent hatchling covered with Koelliker's bristles: A, ventral view 2.6 mm ML; B, lateral view, 3 mm ML. A from Rees (1953); B from Chun (1915).

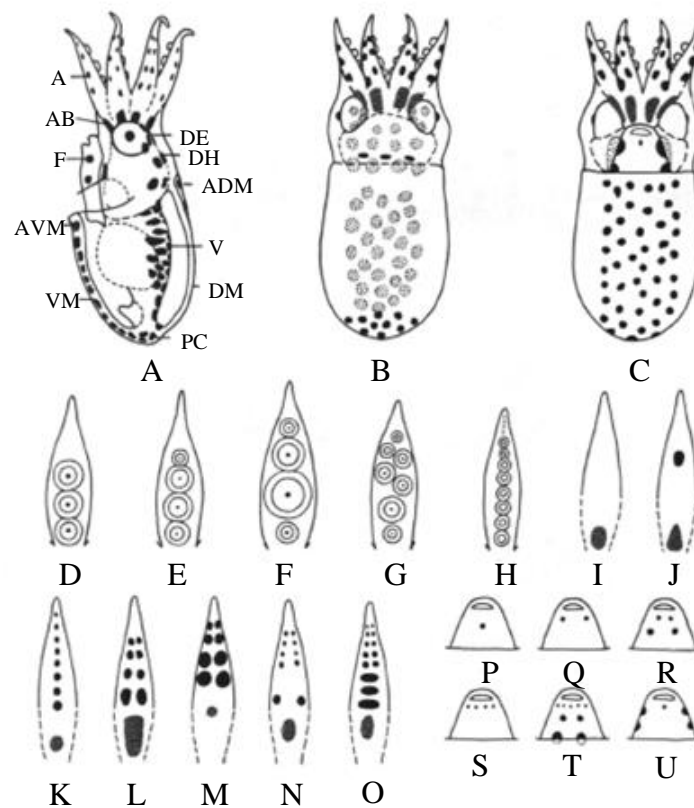


Figure 5.55. Octopodidae, terminology for species-specific sucker and chromatophore patterns. Abbreviations for chromatophore fields: A = arm; AB* = arm base; ADM = anterior margin of dorsal mantle; AVM = anterior margin of ventral mantle; DE* = dorsal eye; DH* = dorsal head; DM = dorsal mantle; F = funnel; PC = posterior cap; V* = visceral; VH* = ventral head; VM = ventral mantle (* = extrategumental chromatophores). *Octopus* spp., distribution of chromatophore fields, 2.0 mm ML: left lateral (A), dorsal (B) and ventral views (C) (superficial or tegumental chromatophores are represented by stippled spots); *Octopus* spp., variations in number and size of arm suckers at the time of hatching (D–G); *Eledone cirrhosa* (H); variations in number, size, and distribution of arm base and aboral arm chromatophores in hatchlings: none (I), one spot (single chromatophore) (J), one row (K), two rows (L–N) and 1+2 rows (O); variations in number, size, and distribution (not all patterns represented) of funnel chromatophores in hatchlings: one (P), two (Q), 2+2 (R), 4 (S), 5+2+2 (T); 1+2+2 (U). A–G from Young *et al.* (1989); H–U from Sweeney *et al.* (1992).

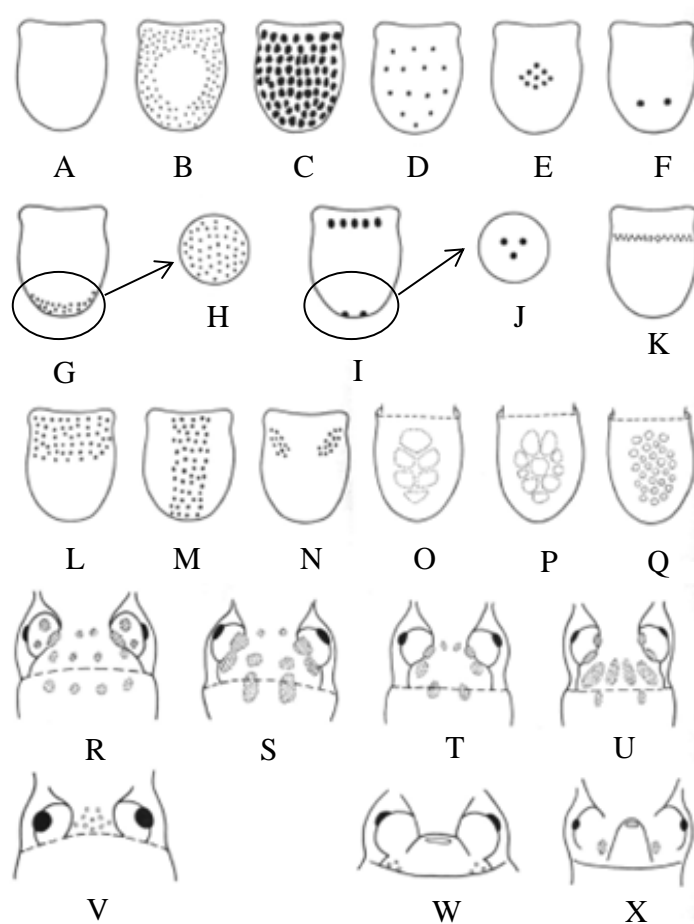


Figure 5.56. Octopodidae, terminology for species-specific chromatophore patterns. Variations in number, size, and distribution of dorsal and/or ventral surfaces of mantle chromatophores: entirely absent (A); absent in midregion, small chromatophores (B); densely covered, large chromatophores (nine across) (C); sparsely covered, medium chromatophores (four across) (D); mid region patch (E); two spots (F); posterior margin (G); posterior cap, end view of figure above (H); anterior margin, simple band (five across) plus posterior cap (I); posterior cap with three large chromatophores, end view of figure above (J); narrow, complex band (14–15 across, two rows) (K); wide, complex band (8–9 across) (L); wide, complex midline stripe (4–5 across, 12–13 in length) (M); diagonal patches (N). Visceral chromatophores viewed through dorsal mantle, variations in number and size: few (six) large chromatophores (O); few (ten) large chromatophores (P); many (20+) medium chromatophores (Q). Variations in number, size and distribution of dorsal surface of head and eye chromatophores: head 2+4+4 (large), eye three (R); head 2+4+2, eye 1 (S); head 2+2+2, eye 1 (T); head 2+4+2, eye 2 (U); head, do not pattern (scattered, small), eye cero (V). Variations in number, size and distribution of ventral surface of head chromatophores: head, 3+/side (small), eye cero (W); head, 1/side (large), eye cero (X). From Sweeney *et al.* (1992).

5.16.1 Subfamily Octopodinae d'Orbigny, 1845

Subfamily characters: Body muscular; arm suckers in two rows; ink sac present; right arm III hectocotylized in males, with well-differentiated ligula and calamus.

References: Sweeney *et al.* (1992); Nesis (1999).

Octopus vulgaris Cuvier, 1797

Species characters: Mantle elongated and conical, representing 60–70% ML; head wide and squarish, represents 51–56% ML; eyes protruding, conspicuous, and slightly ventral; arms short, subequal with tapering tips; number of suckers on arms increases with size, rearranged into two rows; funnel well-developed and occupies almost the entire length of the head, reaching the base of the fourth pair of arms and represents 40–45% ML; funnel with 2+2 chromatophores, two near the orifice and two adjacent to the mantle edge; head, eyes, mantle surface of chromatophore number and pattern change with the paralarva size; web vestigial; 8–10 gill lamellae per demibranch; the colour depends on the expansion level of the elastic sacculus where the granules of pigments are contained; however, incipient chromatophores are reddish and then become darker, brown, or black; dorsal surface of mantle slightly red; visceral chromatophores black or quite dark, ventral black, dorsal and ventral head black, funnel black, eyes black in dorsal view and red in ventral view, dorsal arms mostly red and ventral arms black.

Due to the availability of detailed information on *O. vulgaris* paralarvae, descriptions are presented in order of increasing sizes.

Individuals ca. 1.5–2.0 mm ML (newly hatched and 1 d old; Figures 5.57A, 5.58A–F and 5.59A): Arms with three suckers; the length of the arm I right represents 47% ML; arms I and II with 2–4 chromatophores and arms III and IV with 2–3 chromatophores, all arranged in a single row; dorsal surface of head with eight chromatophores, two between the eyes mid-head, two others at the basis of the eyes, and four covered by the mantle edge; ventral surface of head with four chromatophores, two behind the funnel and other two near the base of the arms; eyes with one postero-dorsally and one on mid-ventral; dorsal surface of mantle with 10–12 chromatophores, 2–3 on the mantle edge; underneath the mantle and above the digestive gland, there are 6–7 large visceral chromatophores distributed in oval form, and two on the posterior cap; ventral surface of mantle, with 16–19 randomly distributed.

Individuals ca. 2.5–3.5 mm ML (5–10 d old; Figures 5.57B, 5.58G,H,J, 5.59B,C and 5.60A,B): Arms with 3–6 suckers; length of the arm I right represents ~50% ML; dorsal and ventral surface of arms with 3–4 chromatophores distributed in a single row; head, eyes, and mantle chromatophore number and pattern do not change.

Individuals ca. 3.5 mm ML (14–15 d old; Figures 5.59D and 5.60C): Arms with 4–8 suckers; length of the arm I right is 49% ML; dorsal surface of arms with 3–9 chromatophores distributed in a single row near the base, but in two rows at the tips; ventral surface of arms with 3–6 chromatophores following the same pattern as in the dorsal view; dorsal surface of mantle with 10–23 chromatophores, four near the mantle edge, and with 6–17 visceral chromatophores; ventral surface of mantle, head, and eyes chromatophore number and pattern do not change.

Individuals ca. 4.0 mm ML (17–20 d old; Figure 5.58K, 5.59E–F): Arms with 5–10 suckers; length of the arm I right is 57–59% ML; dorsal surface of arms with 5–13 chromatophores and ventral surface of arms with 4–11 distributed in the same pattern described above; dorsal surface of head with 10–13 chromatophores, four additional small ones appear laterally in the connective tissue under the eyes; ventral surface of head with six chromatophores; dorsal surface of mantle with 15–30 chromatophores, of which 10–22 are over the viscera; ventral surface of mantle and eyes number and pattern do not change.

Individuals ca. 4.5 mm ML (27 d old; Figure 5.61A–C): arms with 7–14 suckers; dorsal surface of arms with 7–13 suckers and ventral surface of arms with 7–11 distributed in

the same pattern as described above; dorsal surface of head with ~16 chromatophores, 2–3 smaller ones appeared on the lateral surface of the head in the connective tissue under the eyes; ventral surface of head chromatophore number and pattern do not change; dorsal surface of eyes with three chromatophores, from 1–2 additional ones; dorsal surface of mantle, with 25–34 chromatophores, several small additional ones; ventral surface of mantle with 18–24 chromatophores.

Individuals ca. 5.5 mm ML (36 d old; Figure 5.61D–F): arms with 10–20 suckers; dorsal surface of arms with 10–15 chromatophores and ventral surface of arms with 11–14 distributed in the same pattern described above; dorsal surface of head with ~18 chromatophores, several small additional ones on the laterals of the head; ventral surface of head and eyes chromatophore number and pattern do not change; dorsal surface of mantle with 32–40 chromatophores and ventral surface of mantle with ~22–24 chromatophores, several small additional ones appeared both in dorsal and ventral views.

Individuals ca. 6.5 mm ML (45 d old; Figures 5.58L–M and 5.61G–I): arms with ~27 suckers; dorsal surface of arms with ~20 chromatophores and ventral surface of arms with ~17 chromatophores distributed in the same pattern as described above; dorsal surface of head with 28 chromatophores; dorsal surface of mantle with ~46 chromatophores, several additional small ones close to the mantle edge; ventral surface of mantle with ~33 chromatophores; ventral surface of head and eyes chromatophore number and pattern do not change.

Remarks: Large paralarvae ready to settle on bottom at 7.5–11.0 mm ML (usually 8.0–10.0 mm ML), normally at the age of 7–8 weeks.

References: Sweeney *et al.* (1992); Nesis (1999); Vidal *et al.* (2010); Moreno (2008).



Figure 5.57. *Octopus vulgaris*: dorsal (left) and ventral (right) views of paralarvae of 1.4 mm ML (A) and 2.7 mm ML (B). B from Moreno (2008).

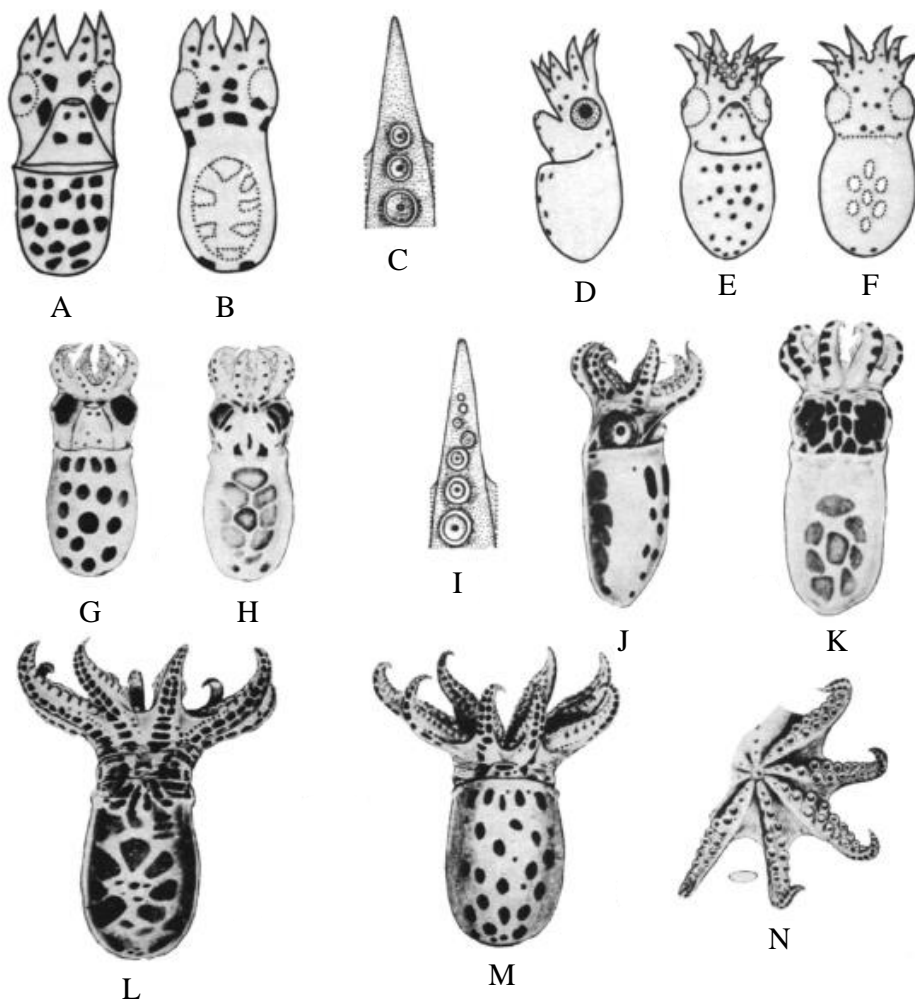


Figure 5.58. *Octopus vulgaris*: ventral (A) and dorsal (B) views, 1.5 mm ML; oral surface of arm from a hatchling, size not available (C); lateral (D), ventral (E), and dorsal (F) views, 2.0 mm ML; ventral (G) and dorsal (H) views, 2.4 mm ML; oral surface of arm with developing suckers buds from a juvenile, size not available (I); right lateral view, 3.15 mm ML (J); dorsal view, 3.75 mm ML (K); dorsal (L), ventral (M), and oral (N) views, 6.0 mm ML. A–B and D–F from Sweeney *et al.* (1992); C and I from Fioroni (1978); G,H and J–L from Rees (1950).

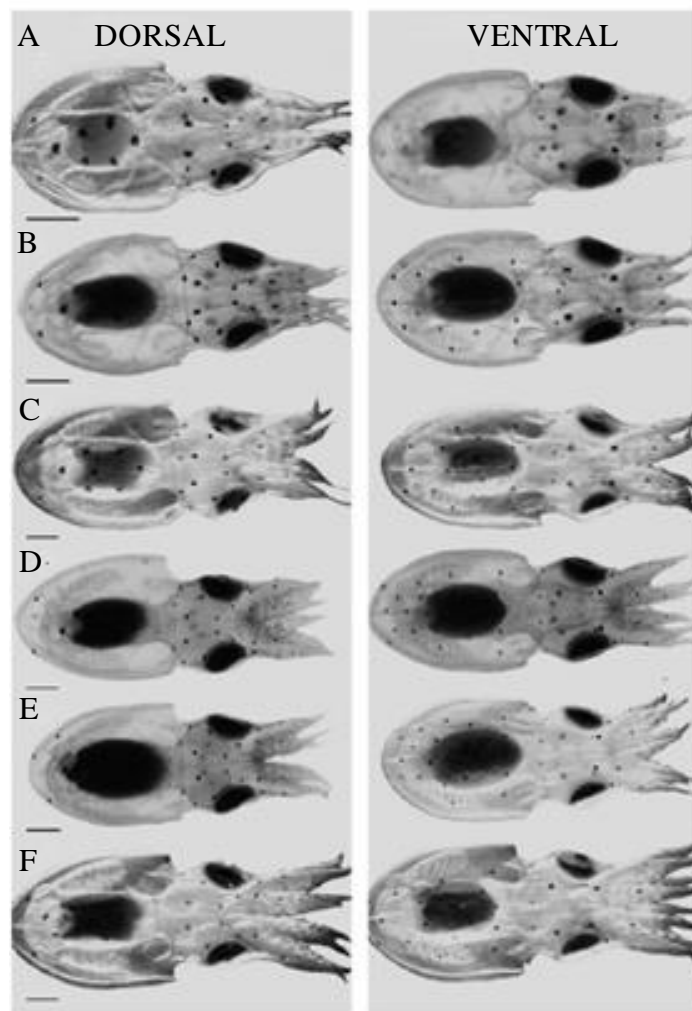


Figure 5.59. *Octopus vulgaris*: chromarophore development, arrangement and patterning of paralarvae from the Northeast Atlantic; newly-hatched to one day old (A); six (B), ten (C), 15 (D), 17 (E) and 20 (F) days old. Scale bar = 0.5 mm. From Vidal *et al.* (2010).

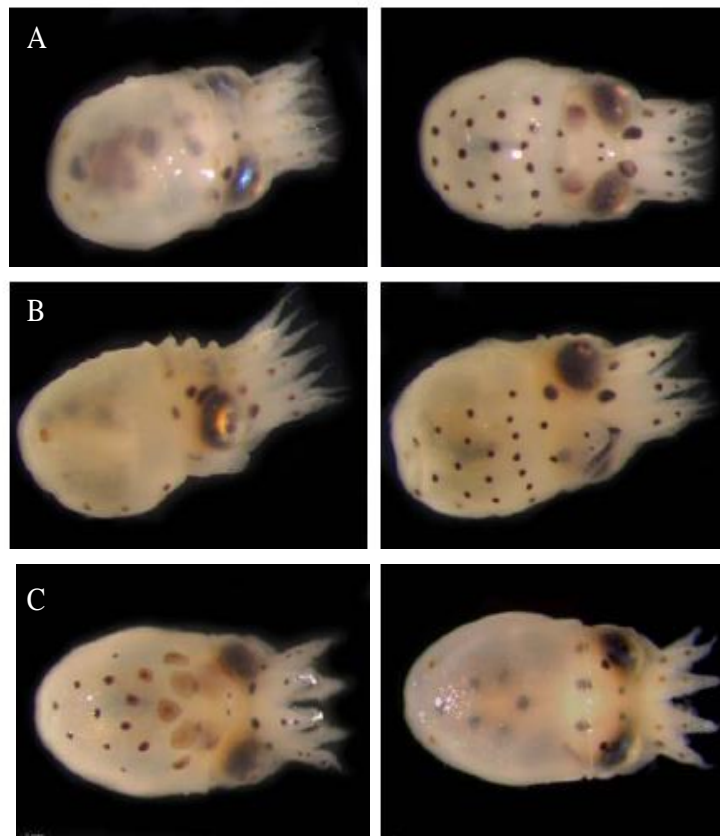


Figure 5.60. *Octopus vulgaris*: dorsal (left) and ventral (right) views of a five (A), ten (B), and 14 (C) days old paralarvae, hatched and reared at the laboratory. From Moreno (2008).

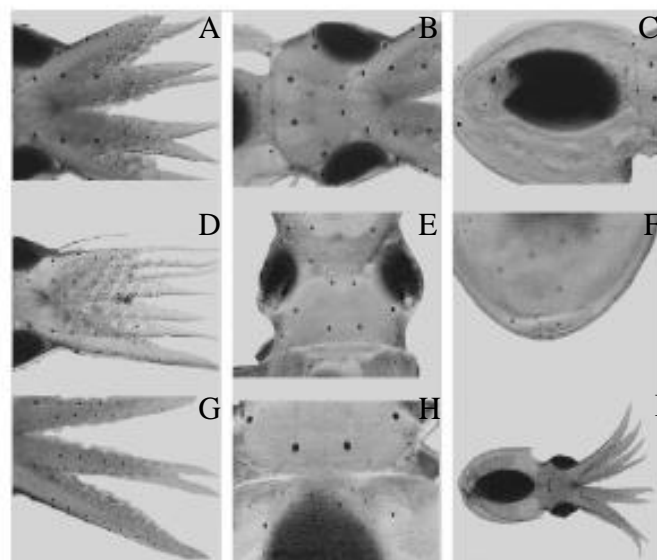


Figure 5.61. *Octopus vulgaris*: detail of the dorsal chromatophore fields of paralarvae from the Northeast Atlantic: arms (A), head (B), and mantle (C) of a 27 days old paralarvae; arms (D), head (E), and mantle (F) of a 36 days old paralarvae; arms (G), head (H), and dorsal view (I) of a 45 days old paralarvae. From Vidal *et al.* (2010).

Octopus salutii Vérany, 1836

Species characters: Only the individuals of ca. 3.0–3.5 mm ML have been described (Figure 5.62). Arms short, subequal, 1.5 mm long, with 4–5 suckers; surface of arms with chromatophores in two rows; chromatophores uniformly distributed over the entire body surface; skin densely packed with Kolliker's bristles, surface appears granular; gills with seven lamellae per outer demibranch.

Remarks: Older stages in plankton unknown.

References: Sweeney *et al.* (1992); Moreno (2008).



Figure 5.62. *Octopus salutii*: dorsal (A) and ventral (B) views, 3.08 mm ML; lateral (C) and dorsal (D) views, 3.5 mm ML. A,B from Moreno (2008); C,D from Sweeney *et al.* (1992).

Callistoctopus macropus (Risso, 1826)

Species characters (Figures 5.63 and 5.64): The availability of detailed information on this paralarva allows descriptions at different individual sizes.

Individuals ca. 2.5 mm ML (Figure 5.63A–D): Arms short, subequal, with seven suckers; surface of arms with 4–6 chromatophores in one row; funnel with four chromatophores on the lip; dorsal surface of mantle with 12 chromatophores in two lateral diagonal patches in the anterior region and 20+ chromatophores in the posterior region; ventral surface of mantle with 35+ chromatophores in distinct two-row band on the anterior margin and in two-row midline stripe in midregion plus distinct posterior cluster with 20+ chromatophores; dorsal surface of head with 14 chromatophores; eye chromatophore number unknown; ventral surface of head chromatophore pattern and number unknown; visceral chromatophore number unknown; iridophores do not visible.

Individuals ca. 3.5 mm ML (Figure 5.63E–G): Body elongated, ovoid, tending toward conical; arms subequal with ten suckers; arm with 16–20 chromatophores in 1+2 row pattern, second row starts distal to the end of the hatchling arm; dorsal surface of mantle number increases to 30+ chromatophores, dorsal surface of mantle pattern of chromatophores remains the same, but diagonal patches increase in size; midline stripe may disappear; dorsal surface of head increases to 18 chromatophores; ventral surface of head chromatophore pattern and number unknown; visceral chromatophore number unknown; surface of funnel number, posterior surface of cap number and ventral surface of mantle pattern of chromatophores remain the same.

Individuals of 15.0–20.0 mm ML (older stages in plankton; Figures 5.63H and 5.64C): Body elongate, tapered, and distinctly conical; arm pairs I and II become distinctly elongate in later larval stages.

References: Sweeney *et al.* (1992).

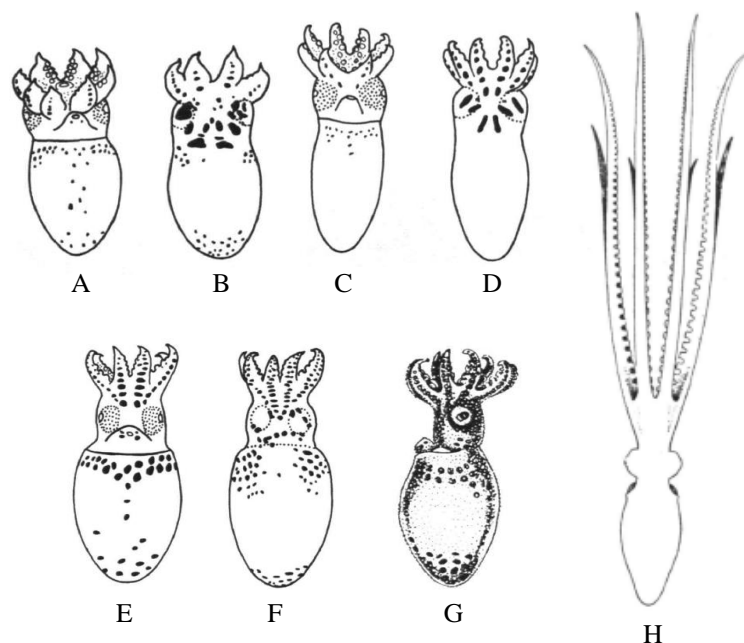


Figure 5.63. *Callistoctopus macropus*: ventral (A) and dorsal (B) views, 2.4 mm ML; ventral (C) and dorsal (D) views, 2.8 mm ML; ventral (E), dorsal (F), and lateral (G) views, 3.3 mm ML; dorsal view, recently settled juvenile, 22 mm ML (H). A–F from Sweeney *et al.* (1992); G from Fioroni (1978); H from Naef (1921–1923).

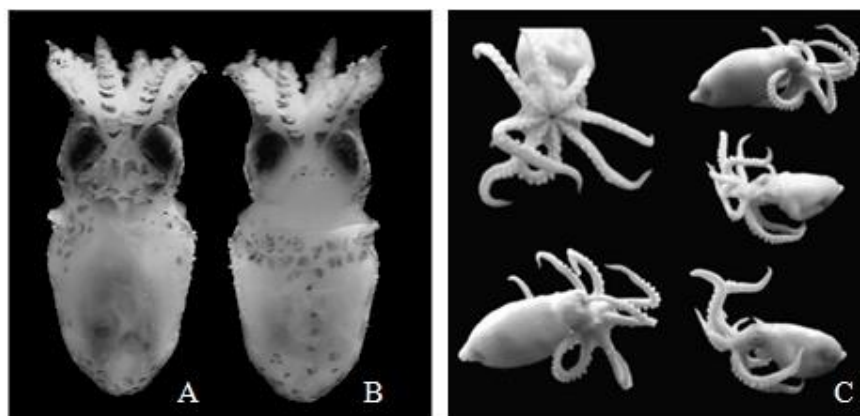


Figure 5.64. *Callistoctopus macropus*: dorsal (A) and ventral (B) views of paralarvae, sizes not available; different views of juvenile sizes not available (C). From Salman (2012).

Macrotritopus defilippi (Vérany, 1851)

Species characters: The availability of detailed information on this paralarva allows descriptions at different individual sizes.

Individuals ca. 1.5–2.0 mm ML (Figure 5.65A–G): Mantle round, head wide; arms subequal, ~50% ML; three primary suckers on each arm; arms III slightly elongated (as long as ML at 2.5 mm), in later paralarvae much longer than others (three-fourfold); second arms 1.5–threefold shorter than arms III; arms thick, their ends in late paralarvae tapering and fragile; arms with additional sucker bud present; outer surface of arms with one row of dark chromatophores, plus one chromatophore at base of each

sucker; dorsal surface of head chromatophores often visible, pattern unknown; additional chromatophore patterns unknown.

Individuals ca. 2.0–2.5 mm ML (Figures 5.65H–K and 5.66A): Arms III conspicuously elongated with 11–15 suckers, other arms only with 4–5 suckers; chromatophore pattern unknown.

Individuals ca. 3.0–3.5 mm ML (Figure 5.67A–F): Arms surface I, II, and IV with four chromatophores and arms surface III with 14–16 chromatophores in one row; one chromatophore at the base of each sucker; funnel with 2+2 chromatophores; dorsal surface of mantle without chromatophores in the midregion, but two chromatophores in the posterior region; ventral surface of mantle with small cluster of 6–8 chromatophores in the midregion; dorsal surface of head with eight chromatophores (2+4+2 pattern); ventral surface of head with two chromatophores, one small over each eye and one large at base of each arm; dorsal surface of the digestive gland with 11 large visceral chromatophores; gold iridophores around the eyes; gills with 11 lamellae per demibranch; digestive gland with 11 large dorsal visceral chromatophores.

Individuals ca. 10.0–15.0 mm ML (Figure 5.67J,K): Body elongated and tubular, bluntly rounded; arms I, II, and IV with >20 chromatophores and arms III with >40 chromatophores in one row; one chromatophore at the base of each sucker; dorsal surface of head with 2+2+4 pattern; funnel with 2+2 chromatophores; dorsal surface of mantle without chromatophores in the midregion, but >20 chromatophores in the posterior region; ventral surface of mantle chromatophores pattern and number unknown, web vestigial; eleven (rarely 12) gill lamellae per demibranch.

Remarks: Large paralarvae ready to settle on bottom at 9–11 mm ML, rarely at 15 mm ML.

References: Sweeney *et al.* (1992); Nesis (1999).

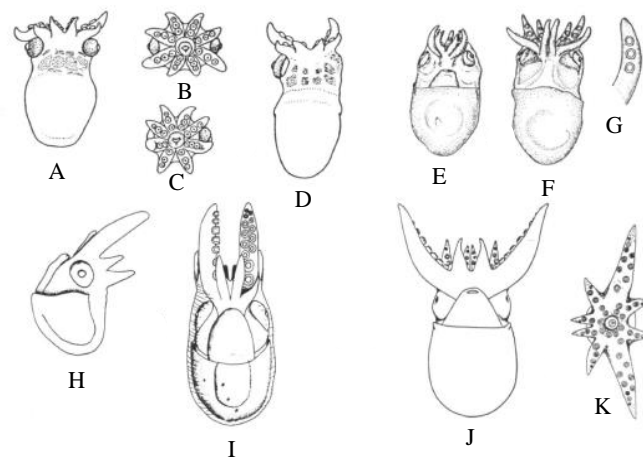


Figure 5.65. *Macrotritopus defilippi*: dorsal (A) and oral (B) views, 1.5 mm ML; oral (C) and dorsal (D) views, 1.7 mm ML; ventral (E), dorsal (F), and oral surface of arm III (G) views, 1.7 mm ML; lateral (H) and ventral (I) views, 2.2 mm ML; ventral (J) and oral (K) views, 2.5 mm ML. A–D from Hanlon *et al.* (1985), E–G from Nesis and Nikitina (1981); H,I from Clarke (1969); J,K from Vecchione *et al.* (2001).

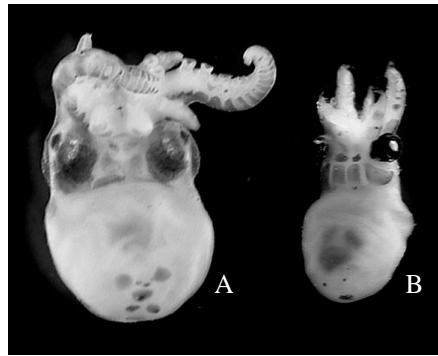


Figure 5.66. *Macrotritopus defilippi*: dorsal views, 2.1 mm ML (A) and 3 mm ML (B). From Salman (2012).

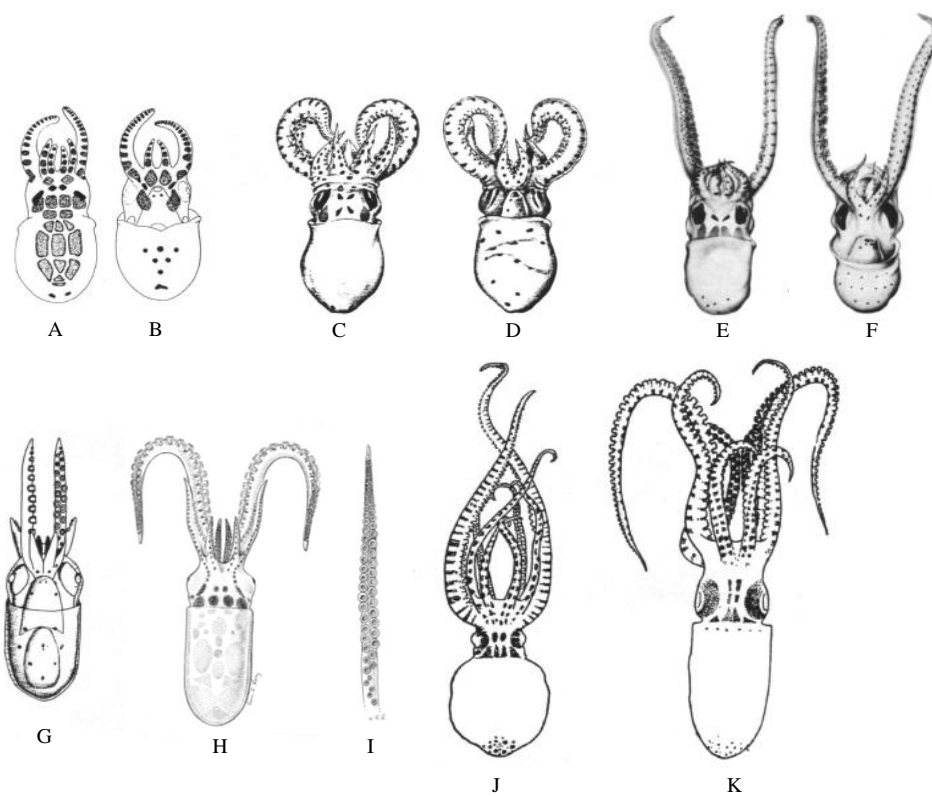


Figure 5.67. *Macrotritopus defilippi*: dorsal (A) and ventral (B) views, 3.2 mm ML; dorsal (C) and ventral (D) views, 3.45 mm ML; dorsal (E) and ventral (F) views, 3.75 mm ML; ventral (G) view, 4.5 mm ML; dorsal (H) and oral surface of arm III (I) views, 6.6 mm ML; dorsal views, 10 mm ML (J) and 13.2 mm ML (K). A,B from Fioroni (1965); C–F from Rees (1954); G from Clarke (1969); H,I from Vecchione *et al.* (2001); J from Sweeney *et al.* (1992); K from Joubin and Robson (1929).

Scaeurus unicirrhus (Delle Chiaje [in de Férussac & d'Orbigny], 1841)

Species characters: The availability of detailed information on this paralarva allows descriptions at different individual sizes.

Individuals ca. 2.5 mm ML (Figure 5.68): Body squat and globose; arms short, subequal with four suckers; arms with 3–4 chromatophores in one row; one arm base chromatophore per arm; funnel with 2+2 chromatophores; dorsal surface of mantle clear, with ca. ten chromatophores in posterior region; ventral surface of mantle with large cluster of 35–40 chromatophores in mid posterior region; dorsal surface of head with 14 chromatophores (4+4 pattern); eye chromatophores unknown; ventral surface of head with two large chromatophores; dorsal surface of digestive gland with 20 visceral chromatophores; iridophores are not visible; skin appears densely packed with calcareous granules; gills with seven lamellae per outer demibranch.

Individuals ca. 9.5–10.0 mm ML: Ventral mantle length ~7–8 mm, total length ~17–18 mm, head width ~6–7 mm; arms subequal, short; mantle globose; interbrachial membrane extended on the arms somewhat more than halfway; funnel prominent; whole body covered by swollen skin, which opens above the eye lens; skin loose on the body and finely papillate all over its surface, more abundantly so on the dorsal side; no Kölliker organs present on the skin surface; chromatophores are expanded and placed on the deepest layers of the skin, regularly spaced on the whole body; there are two types of chromatophores, red-brownish and ochre; not visceral chromatophore visible; ink sac present, gills with 11 lamellae per outer demibranch; each arm bears 14–15 two-sucker rows, the first suckers are in a single row.

Remarks: Number of gill lamellae increases during the planktonic life from seven (hatchlings) to at least 11.

References: Sweeney *et al.* (1992); Bello (2004).

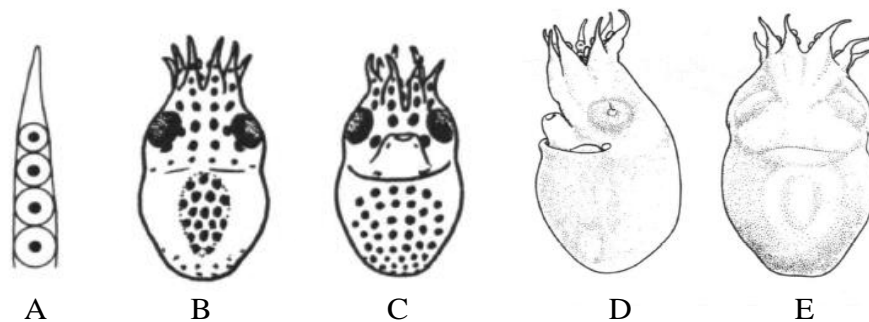


Figure 5.68. *Scaevargus unicirrhus*: oral view of arm with suckers (A), dorsal (B), and ventral (C) views, 2.0 mm ML; lateral (D) and dorsal (E) views, 2.5 mm ML. A,C from Boletzky (1984); D,E from Sweeney *et al.* (1992).

Pteroctopus tetracirrhus (Delle Chiaje, 1830)

To our knowledge, the paralarva of this species has not been described until now. In spite of this, Lefkaditou *et al.* (2005) classified a paralarvae of 1.8 mm ML as *P. tetracirrhus* (Figure 5.69) according to the baggy mantle and the relatively long (shallow) web between the arms.

References: Sweeney *et al.* (1992); Lefkaditou *et al.* (2005).

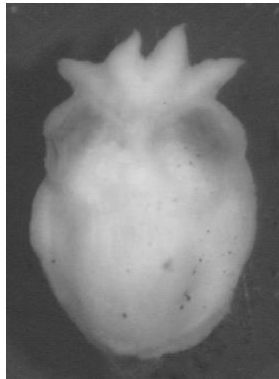


Figure 5.69. *Pteroctopus tetracirrhus*: dorsal view, 1.8 mm ML. From Lefkaditou *et al.* (2005).

5.16.2 Subfamily Eledoninae Grimpe, 1921

Subfamily characters: Similar in size and shape to *Octopus* paralarvae; entire body covered with large chromatophores; as suckers are added, they never form two rows; ink sac present; short hectocotylus on right arm III of males, ligula and calamus almost undifferentiated; ends of all other arms in males with modified suckers.

References: Sweeney *et al.* (1992); Nesis (1999).

Eledone cirrhosa (Lamarck, 1798)

Species characters: The availability of detailed information on this paralarva allows descriptions according to different sizes.

Individuals ca. 3.5 mm ML (Figure 5.70): Body globose to slightly elongate and conical; arms subequal, 2.5–2.8 mm long, with eight suckers in one row; arms with 8–11 chromatophores in row; funnel with two chromatophores, located laterally on the lip; dorsal surface of mantle densely covered with 50+ chromatophores, but may have a clear area over the digestive gland; ventral surface of mantle densely covered with 50+ chromatophores; dorsal surface of head with 6+ chromatophores (2+4 pattern); 8+ chromatophores per eye; ventral surface of head chromatophore number and pattern unknown; dorsal surface of the digestive gland with 13 visceral chromatophores; silver iridophores around the eyes.

Individuals ca. 12.0 mm ML: Arms subequal, 16.0 mm long, with >28 suckers in one row; chromatophore number and pattern appear to be the same as the paralarvae of 3.7–4.0 mm ML.

References: Sweeney *et al.* (1992).

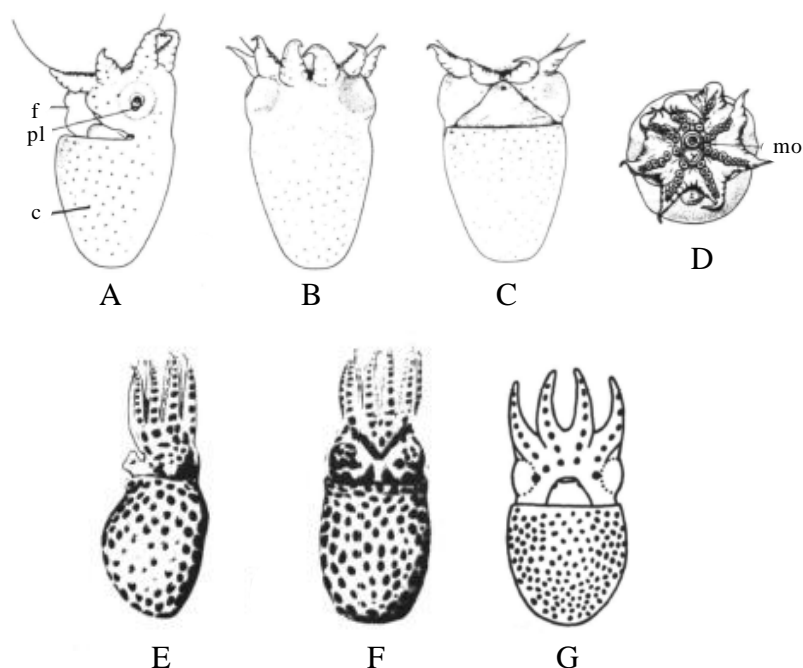


Figure 5.70. *Eledone cirrhosa*: lateral (A), dorsal (B), ventral (C), and oral (D) views, 3.2 mm ML (c = chromatophores; f = funnel; mo = mouth; pl = primary lid); lateral (E), dorsal (F), and ventral (G) views, 3.8 mm ML. A–D from Mangold *et al.* (1971); E,F from Rees (1956); G from Sweeney *et al.* (1992).

Eledone moschata (Lamarck, 1798)

To our knowledge, the paralarva of this species has not been described until now.

5.16.3 Subfamily Bathypolypodinae Robson, 1929

A single species of this subfamily inhabits the Mediterranean [*Bathypolypus sponsalis* (P. Fischer and H. Fischer, 1892)]. To our knowledge, the paralarva of this species has not been described until now.

5.17 Family Tremoctopodidae (Brock, 1882)

This family is monogeneric. Since only one species of this family inhabits the Mediterranean (*Tremoctopus violaceus*), the family/species characters are described for this single species.

Tremoctopus violaceus Delle Chiaje, 1830

Species characters (Figures 5.71 and 5.73): Smallest paralarval stages without jelly coating, but head and arms enveloped by cuff-shaped brachial membrane (skirt very similar to that of the smallest paralarvae of *Argonauta*); mantle semiovoid or subtriangular in juveniles, fused with head and connected with funnel by connective apparatus; body firm, muscular, mantle surface smooth; head wide, eyes large; mantle opening wide, its upper edges reaching level of upper eye margin; funnel long, its anterior end reaching anterior eye margin; funnel free; two pairs of skin pores (water pores) on the head, dorsally between bases of arms I and II and ventrally beside funnel opening; arms short,

arms I longest, arms II and IV shorter, arms III very short; web very short in paralarvae, deep between arms I and II in juveniles, these two arm pairs bordered by a film narrowing toward the arms ends; some suckers on the middle of arms I enlarged (last ones in one row), suckers on arms I larger than those on arms II and IV; web begins to form between the dorsal arms by ~10 mm ML; one row of chromatophores along outer side of arms I in paralarvae, two in juveniles; males dwarfed, their arms III right wholly modified and enclosed in sac under skin, thus appearing that immature males (even hatchlings) have seven arms; during maturation (13–15 mm ML), hectocotylus everts and becomes longer than specimen itself, detaches during mating; ends of arms I and II in males thin, without film; 13–16 lamellae per demibranch in females, 9–11 in males; paralarvae, juveniles, and males semitransparent; dorsal surface of mantle densely patterned with chromatophores; ventral surface of mantle patterned with a band of 4–6 chromatophores along anterior margin; distinct, dense cluster of chromatophores posteriorly; chromatophores absent on the mid-ventral mantle and on the funnel; second row of chromatophores present on the distal end of the arms, and single large chromatophore present on the inner edge of each sucker; eyes surrounded by gold iridophores.

Note: Males and juveniles (to ~15 mm ML) usually with pieces of stinging tentacles of *Physalia*, the Portuguese Man O'War in the arms I–II suckers, as an additional method of defense (Figure 5.72B).

Vecchione *et al.* (2001) describe this species according to different size classes from individuals taken in the western North Atlantic. Such descriptions are reproduced in the following paragraphs.

Individuals ca. 2.5 mm ML (Figure 5.71C–G): Mantle short, broad, covered with small, evenly spaced chromatophores; large internal chromatophores on viscera visible through dorsal mantle; funnel extends to base of arms IV; head short, broad, with 12 large chromatophores on dorsal surface; arms I disproportionately enlarged, length greater than ML, all but distal two suckers are large, globular; third from base greatly enlarged, about twofold diameter of next largest; proximal 3–4 suckers on arms I uniserial, remainder biserial; arms II–IV much shorter, thinner, with small suckers, uniserial proximally, but biserial toward tips; arm formula I>>>II>IV>>III; sucker counts: arms I–15, arms II–6, arms III–2, arms IV–5; narrow web connects all arms, deepest between arms I, proportionally shallower with each pair ventrally; single row of large chromatophores on aboral surface of each arm; one large chromatophore on base of each sucker.

Individuals ca. 7.5 mm ML (Figure 5.73B,D): Two pairs of pores on head: one pair between bases of arms I and II, one pair at bases of arms IV on each side of funnel opening; mantle plump, triangular; mantle opening very wide, extends dorsally to level with eye lens; head wider than mantle opening; eyes large, occupy entire lateral surface of head; funnel large, tapers to anterior of eyes, tip free; arms I and II extremely long; arm formula: I>II>>IV>III; suckers on all arms small, numerous, biserial, widely separated; deep web connects dorsal arms and arms I and II.

References: Sweeney *et al.* (1992); Nesis (1999); Vecchione *et al.* (2001).

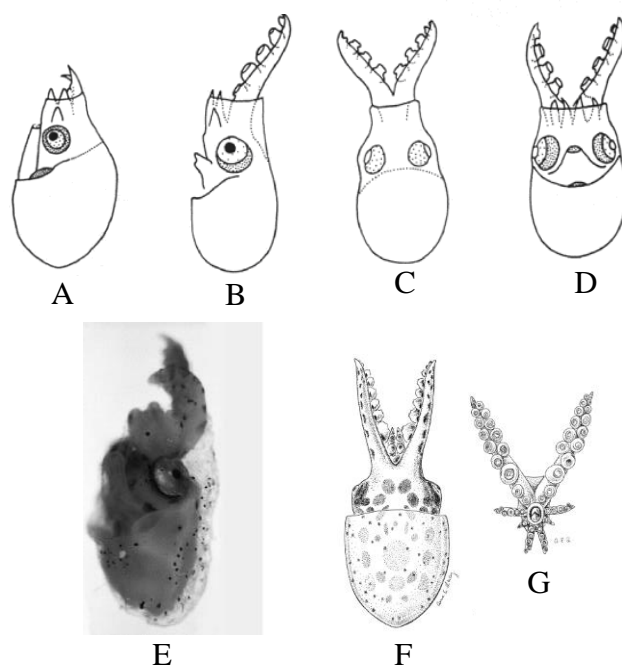


Figure 5.71. *Tremoctopus violaceus*: lateral view, 1.5 mm ML (A); lateral (B), dorsal (C), and ventral (D) views, 2 mm ML; ventro-lateral view, 2.2 mm ML (E); dorsal (F) and oral (G) views, 2.3 mm ML. A–D from Sweeney *et al.* (1992); E from Diekmann *et al.* (2002); F,G from Vecchione *et al.* (2001).

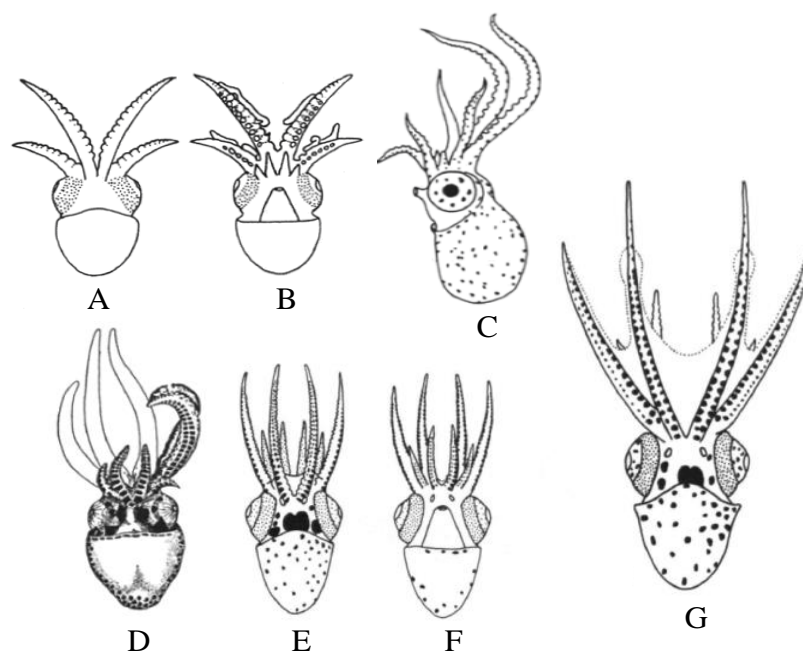


Figure 5.72. *Tremoctopus violaceus*, female growth and development: dorsal (A) and ventral (B) views, 4 mm ML, notice pieces of *Physalia* tentacles on arms in paralarvae B; lateral view, 5 mm ML (C); ventral view, 5.3 mm ML (D); dorsal (E) and ventral (F) views, 6.7 mm ML; dorsal view, 10.0 mm ML (G). A–C and E–G from Sweeney *et al.* (1992); D from Joubin (1902).

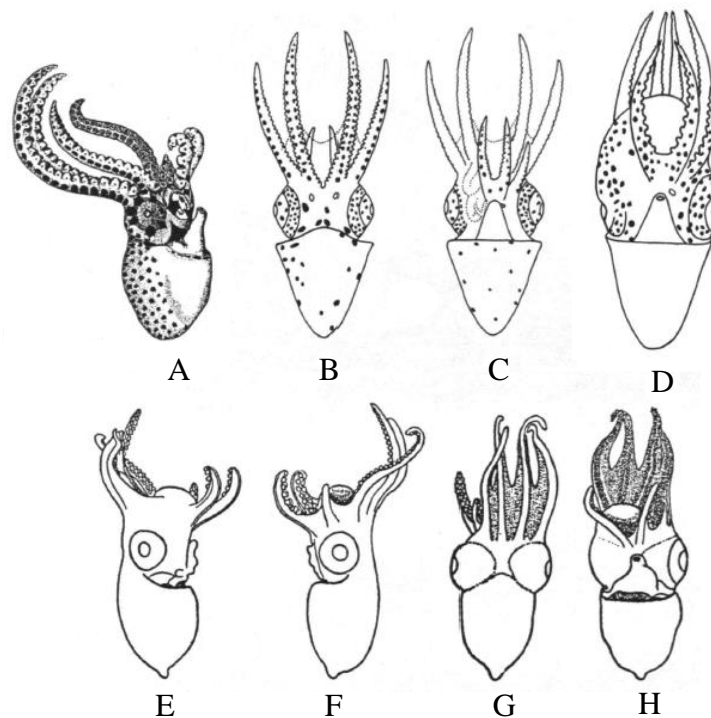


Figure 5.73. *Tremoctopus violaceus*, male growth and development: lateral view, 6 mm ML (A); dorsal (B) and ventral (C) views, 7.1 mm ML; ventral view, 13.2 mm ML (D); lateral (E–F), dorsal (G), and ventral (H) views, 11 mm ML. A from Joubin (1902); B–D from Sweeney *et al.* (1992); E–H from Adam (1937).

5.18 Family Ocythoidea Gray, 1849

Ocythoe tuberculata Rafinesque, 1814

Species characters (Figures 5.74 and 5.75): Distinctive at all sizes; body firm, muscular; head wide; mantle fused with head and connected with funnel by well-developed, strong connective apparatus; head and arms of smallest larval stages not enclosed in cuff-shape brachial membrane (see *Tremoctopus* and *Argonauta*); distinctive arm length formula (arms I and IV greatly elongated) evident even in the hatchlings; eyes large; mantle opening wide, reaching level of upper eye margin; funnel long, conical, extending beyond bases of arms IV; not sunken into tissues; skin pores (water pores) besides funnel near bases of both arms IV; arms short in paralarvae, long in juveniles and adults, arms I and IV subequal, much longer than arms II and III; web and arm membranes almost absent; suckers small, numerous, three primary ones small, in one row, others in two rows; ink sac present, photophores absent; third right arm hectocotylized, in paralarvae and juvenile males appears as a stalked sac; hectocotylus develop inside sac, released at maturity, detached during mating; 19–20 lamellae per demibranch; reticulate pattern on ventral mantle evident in juveniles at ~10 mm ML, water pores at all stages; dorsal surface of mantle covered with uniform pattern of tiny chromatophores; ventral surface of mantle devoid of chromatophores.

Remarks: Paralarvae are distinguishable by long arms I and IV, short arms II and III. Males are dwarf and distinguishable by the characteristic appearance of hectocotylus.

References: Sweeney *et al.* (1992); Nesis (1999).

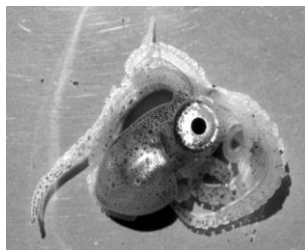


Figure 5.74. *Ocythoe tuberculata*: lateral view, 18 mm ML. From Diekmann *et al.* (2002).

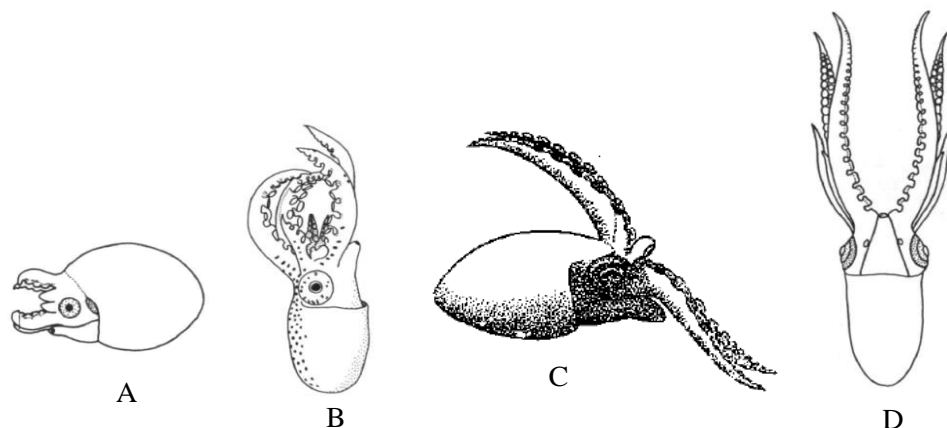


Figure 5.75. *Ocythoe tuberculata*: lateral views, 2.3 mm ML (A), 4.5 mm ML (B), and juvenile male of non-available size (C); ventral view, juvenile female of non-available size (D). A,B,D from Sweeney *et al.* (1992); C from Nesis (1999).

5.19 Family Argonautidae Tryon, 1879

This family is monogeneric. Since only one species of this family inhabits the Mediterranean (*Argonauta argo*), the family/species characters are described for this single species.

Argonauta argo Linnaeus, 1758

Species characters (Figures 5.76 and 5.77): Paralarvae clear with some (23–24 in hatchlings) sparsely distributed large chromatophores; early paralarvae (up to 3 mm ML) covered by jelly coat with only arm ends protruding; mantle semiovoid, caudal end curved slightly upwards; body firm, muscular, mantle surface smooth; mantle fused with head and connected with funnel by well-developed connective apparatus conspicuous even in hatchlings; head wide, eyes large and directed somewhat antero-ventrally; mantle opening reaching level of anterior eye margin; funnel free, broad and short, extends only to anterior edge of eye in paralarvae <2 mm ML; skin pores (water pores) lacking; arms in paralarvae short, arms I longest, others subequal, arms ends tapering; in males arms I, II, and IV subequal, III shortest, in females arms long, arms I much longer than others, arms IV and II shorter, arms III are the shortest, in maturing and mature females, distal section of arms I with every extensible wide membranous skin flap which secretes and holds the shell (secondary shell); web vestigial; three primary suckers in one row (two first larger than third), then two rows of small suckers on all arms; ink sac present, photophores absent; conspicuous cuff-shape brachial membrane surrounding arms of paralarvae <3.0 mm ML; mantle to arm ratio of paralarvae 2–5 mm ML, 2:1 or 3:1, approaches 1:1 in paralarvae >5 mm ML; membranous

shell flaps on elongate arms I of females detectable at >3 mm ML (dorsal arms of preserved female paralarvae often tightly coiled and reflexed over the head where their distinctive size and shape can be overlooked), developed at >4 mm ML; shell formation begins at ~5–7 mm ML; during subsequent life, beginning from ~8 mm ML, shell is enlarged; in juvenile females, the shell is small, ribs few, set far apart, keel wide, up to 10% shell length; males dwarfed, their left arm III totally modified and enclosed in sac on stalk (from ~1.5 mm ML), giving the impression that immature males (even hatchlings) have seven arms; during maturation, the hectocotylus everts and becomes much longer than male itself, detaches during mating; external shells present in females at least by 8 mm ML depending on species; hectocotylus can be recognized in males as small as 1.5 mm ML; left third arm short, blunt, enveloped by conspicuous sac by 1.5 mm ML; epidermis in most preserved small paralarvae loose, translucent.

Individuals ca. 1.0 mm ML (Figure 5.76A): Conspicuous cuff-shape brachial membrane; eyes small, directed slightly anteroventrally; arms short, subequal with three suckers; surface of arms with one chromatophore at the base of the brachial membrane; surface of funnel with 2+2 chromatophores; dorsal surface of mantle anterior and mid-region clear, with four chromatophores in the posterior cap; ventral surface of mantle clear, with four chromatophores in the posterior cap; ventral surface of mantle with 4–5 chromatophores on the anterior margin, mid- and posterior region clear; dorsal surface of head with two chromatophores; two chromatophores dorsally over each eye; one chromatophore ventrally over the eye; dorsal surface of the digestive gland with 9–11 large visceral chromatophores.

Vecchione *et al.* (2001) describes this species according to different size classes from individuals taken in the western North Atlantic. In the following paragraphs, such descriptions are reproduced.

Individuals ca. 1.5–2.0 mm ML (Figure 5.77A): General appearance very similar to paralarval *Octopus*-type octopodid; mantle short, very broad, widest at anterior end; head short, wider than mantle; eyes large, protrude laterally, covered with silvery reflective tissue; funnel moderately large, extends to anterior level of eyes, tip not yet free. Juvenile female (Figure 5.77B): arms very short, with 8–9 suckers each, biserial; arms I longest, distal elongations are devoid of suckers, probably a condition as precursor to the shell-secreting modifications of arms I of female (“shell web”); arms all connected by shallow web. Male, possibly mature (Figure 5.77C): much like immature specimen described above, but without naked elongations to arms I and with left arm III hectocotylized and contained in a large sac; all arms and hectocotylus sac connected by web.

Individuals ca. 13.0 mm ML (immature females; Figure 5.77D,E): Mantle very muscular, conical, very broad at anterior margin; attaches to head at postero-dorsal border of eyes; funnel very large, muscular, extends to base of arms IV; funnel tip free, but membrane from dorsal edge of arms IV connects to funnel just posterior to the tip; eyes very large, bulge laterally; all outer surfaces of mantle, funnel, head, and arms are covered with numerous dense, small chromatophores; arms II–IV long, slender, subequal in length; each has a single small basal sucker followed by biserial suckers, very numerous, closely-packed, the proximal 3–4 pairs particularly large; suckers toward the distal tip minute and very thickly set; arms I very long, thick, much longer than others, but much contorted and twisted in preservation due to strong contraction of “shell web”; basal 1–2 suckers small, next four pairs noticeably enlarged, following pairs with reduced diameters; suckers extremely minute distally with longitudinal series widely separated; distal tip devoid of suckers, a ridge-like supporting structure for “shell web”; “shell web” begins as narrow membrane at base of arms I, broadens noticeably

at level where suckers become small (about the fifth–sixth pair), then becomes very expanded in distal one-third of arm (full extent and dimension cannot be described because “shell webs” are very tightly contracted and covered with dense chromatophores); ovaries developing, ova extremely minute; viscero-pericardial membrane covered with dark chromatophores.

Remarks: The presence of a conspicuous cuff-shape membrane surrounding the arms of paralarvae <3.0 mm ML facilitates recognition of argonauts in the plankton. Also, the presence of a “pit-like” locking apparatus on the funnel clearly separates larval argonautids from larval octopodids. Argonauts are sexually dimorphic (males are dwarf) and are the only octopod species in which mature adults are commonly collected in plankton samples.

References: Sweeney *et al.* (1992); Nesis (1999); Vecchione *et al.* (2001).

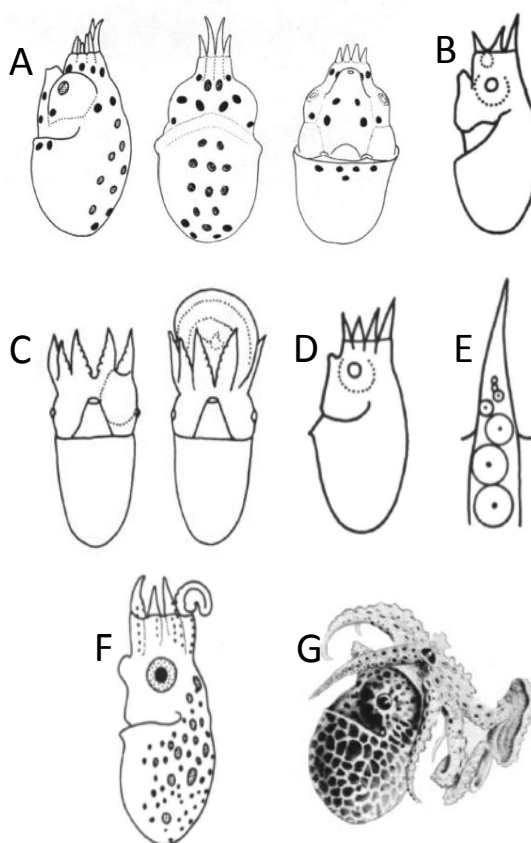


Figure 5.76. *Argonauta argo*: lateral, dorsal, and ventral views, hatchling 0.9 mm ML (A); lateral view, juvenile male, 2.5 mm ML (B); ventral views, juvenile males with small hectocotylus sac and with hectocotylus fully developed, but still in sac, both 4 mm ML (C); lateral view (D) and oral view of right arm III (E), juvenile female, 2.5 mm ML; lateral view, juvenile female with dorsal shell-producing arms differentiated, 4 mm ML (F); lateral view, juvenile female, 5 mm ML (G). A, lateral view from Sweeney *et al.* (1992), dorsal and ventral views from Fioroni (1965); B–G from Sweeney *et al.* (1992).

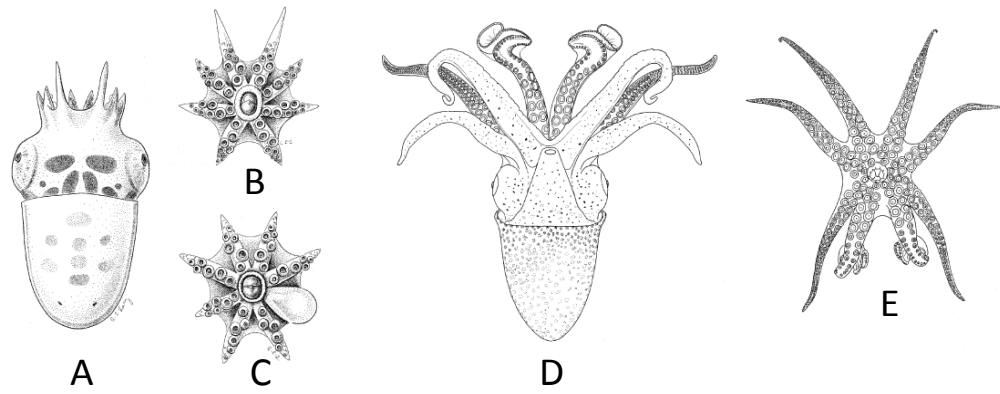


Figure 5.77. *Argonauta argo*: dorsal and oral views, 1.9 mm ML (A,B); oral view, 1.5 mm ML (C); ventral (D), and oral (E) views, 13 mm ML. From Vecchione *et al.* (2001).

6 Acknowledgements

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