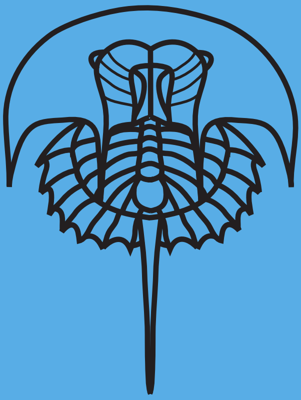

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The Gladius and its Vestiges in Extant Coleoidea

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PART M, CHAPTER 9A: THE GLADIUS AND ITS VESTIGES IN EXTANT COLEOIDEA

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INTRODUCTION

The presence of an internal shell is one of the most important functional and diagnostic features of Coleoidea. The structure and morphology of coleoid shells are highly variable (Fig. 1): some coleoids have calcified internal shells; others have decalcified shell (gladius); and in several unrelated coleoid groups, the shell has been lost completely.

Coleoidea with calcified shells always retain a gas-filled phragmocone. Within this group, the shell serves for buoyancy regulation as well as for support of the mantle-funnel and fin complexes. Among extant coleoids, calcified shells are found in *Spirula* Linnaeus, 1758 in 1758–1759, and sepiid cuttlefishes. The shell in Spirulida constitutes a planispirally ventrally coiled (endogastric) phragmocone with an even aperture lacking dorsal projection (Fig. 1.12). The shell in cuttlefishes (Sepiida) is a flattened, thick, porous oval plate (cuttlebone, sepion) with a highly modified phragmocone and wide flattened siphon (Fig. 1.13).

The second and considerably more diverse group of coleoids includes those taxa with completely decalcified shell vestiges and without a gas-filled phragmocone. These decalcified shells serve exclusively as skeletal elements to support the soft body and provide for muscular attachment and occur in most major groups of extant Coleoidea: loliginids, oegopsids, vampyroteuhids, sepiolids, and the cirrate and incirrate octopods (Fig. 1).

Finally, several groups within the Coleoidea have lost the shell entirely. These include some of the cuttlefishes (Idiosepiidae) and incirrate octopods (Argonautoidea, Bolitenoidea, some Octopodidae) (Voight, 1997; Bizikov, 2004, 2008).

Investigations of the chemical composition of decalcified internal shells in squids have shown that they are composed of beta chitin and proteins (Hunt & Nixon, 1981). Upon initial review, the decalcified shell vestiges in coleoids appear to have little in common with the ancestral shell. However, investigations of the embryology, development, and comparative morphology of the Coleoidea have demonstrated that the embryonic formation and development of the shell in Coleoidea closely follows the pattern of development of the shell found in other mollusk groups (Naef, 1928; Hopkins & Boletzky, 1994; Shigeno, Takenori, & Boletzky, 2010).

DECALCIFIED SHELLS: GENERAL MORPHOLOGY AND TERMINOLOGY

Various terms have been applied by investigators to identify the skeletal structures found among the Coleoidea. In squids, sepiolids, and vampire squids, the internal shell has most commonly been referred to as the gladius, based on its resemblance in some taxa to the Roman sword of gladiators (e.g., Pfeffer, 1912; Naef, 1921–1923; Pickford, 1940; Nesis, 1982–1987; Toll, 1982, 1988;

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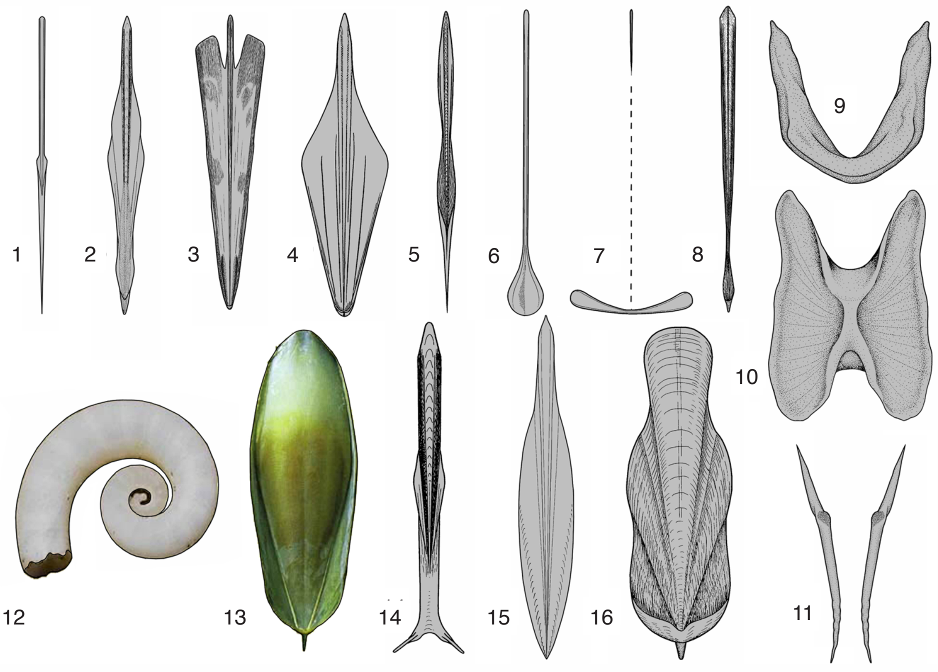

Fig. 1. Diversity of shells among the extant Coleoidea; *1, Chiroteuthis* Orbigny, 1841 in 1834–1846; *2, Berryteuthis* Naef, 1921 in 1921–1923; *3, Thysanoteuthis* Troshel, 1857; *4, Histioteuthis* Orbigny, 1834 in 1834–1846; *5, Lepidoteuthis* Joubin, 1895; *6, Bathothauma* Chun, 1906 (juvenile); *7, Bathothauma* Chun, 1906 (adult); *8, Ommastrephes* Orbigny, 1834 in 1834–1846 (*1–8,* Oegopsina); *9, Grimpoteuthis* Robson, 1932; *10, Cirroteuthis* Eschricht, 1836; *11,Octopus* Cuvier, 1797 (*9–11,* Octopoda); *12, Spirula* Linnaeus, 1758 in 1758–1759 (Spirulida); *13, Sepia* Linnaeus, 1758 in 1758–1759 (Sepiida); *14, Rossia* Owen, 1835 (Sepiolida); 15, *Loligo* Lamarck, 1798 (Myopsina); *16, Vampyroteuthis* Chun, 1903 (Vampyroteuthida) (new).

Bizikov, 1987a). Woodward (1851–1856), Steenstrup (1881–1882), and Chun (1910, 1915) referred to this structure as the pen or plate. Among the cirrate octopods, the vestigial shell has been variously termed the dorsal cartilage (Hoyle, 1886; Ijima & Ikeda, 1895), internal shell (Appellöf, 1899), shell vestige (Naef, 1921–1923; Robson, 1932; Bizikov, 2004), gladius (Nesis, 1982–1987; Bizikov, 2008), and fin support (Aldred, Nixon, & Young, 1983). Among the incirrate octopods, the shell vestiges, when present, Nesis (1982–1987) referred to them as the gladius, while Robson (1932), Voight (1997), and Bizikov (2004) termed them rods or stylets.

The variety of terms used by different contemporary investigators likely reflects the uncertainty of the true homology of these structures in the coleoidea. In general, the preferred term for all decalcified shells or mostly decalcified shell vestiges is modified gladius as it correctly identifies the common origin of these structures from the elongate internal shell of ancestral coleoids.

Gladii among different groups of coleoids are amazingly diverse in shape and structure. In loliginids, oegopsids, sepiolids and vampyroteuthids, the gladius represents a thin, narrow chitinous plate of variable shape that lies along and below the dorsal midline of the mantle. Typically, the pen-like gladius consists of a dorsal plate (pro-ostracum), which is variable in shape but always gradually tapering posteriorly, and a conical, thin-walled terminal cup, the conus (or primary conus), situated at the posterior end of the gladius (Fig. 2.1). Several authors reported

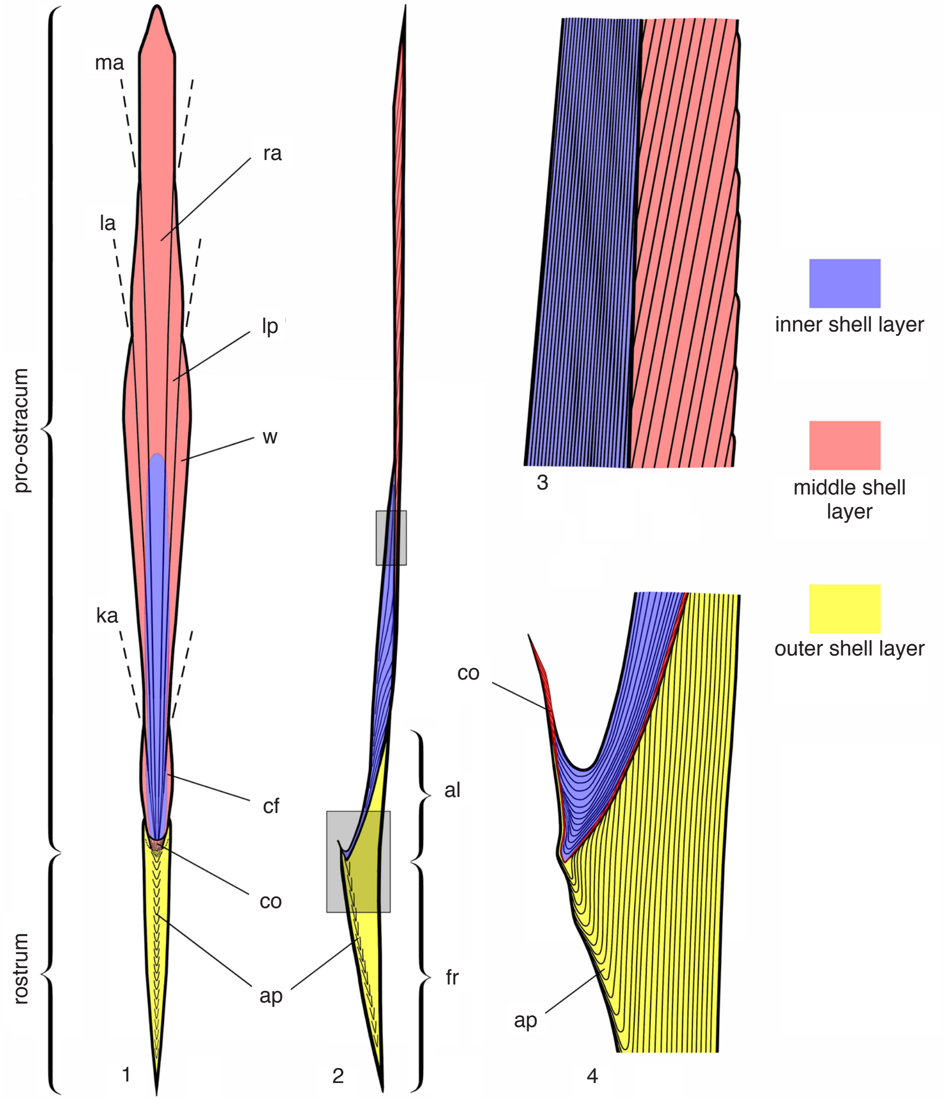

FIG. 2. Typical structure of the pen-like gladius; *1,* ventral view; *2,* sagittal section; 3, enlarged view of *smaller grey-shaded* rectangle in view *2,* illustrating two-layered structure of the pro-ostracum; *4,* enlarged view of *larger grey-shaded* rectangle in view *2,* illustrating the structure of conus and rostrum; *al,* alveolar part of the rostrum; *ap,* apical line; *co,* conus; *cf* conus flags; *fr,* free posterior part of the rostrum; *ka,* marginal asymptotes; *la,* lateral asymptotes; *lp,* lateral plates; *ma,* medial asymptotes; *ra,* rachis; *w,* wings (new).

the presence of the septa-like filling in the gladius conus of the squid families Gonatidae, Chiroteuthidae, and Ommastrephidae (STEENSTRUP, 1881–1882; HOYLE, 1886; CHUN, 1910). Recent studies (ARKHIPKIN, BIZIKOV, & FUCHS, 2012) confirmed earlier assumptions (NAEF, 1921–1923; JELETZKY, 1966) that these septa-like structures in the modern gladius conus are homologous to the septa in phragmocone-bearing coleoids. In some groups, the conus inserts deeply into a posterior spine, the rostrum, composed of a cartilaginous-like, highly hydrated form of chitin. In other groups the conus and rostrum are absent. The primary conus and rostrum represent plesiomorphic features of the posterior part of modern gladius. Toll (1982) described two advanced states, the secondary conus and pseudoconus. The secondary conus is formed by ventral curvature and midventral fusion of the posterolateral vanes of the gladius (some Enoploteuthidae). Being formed from the vanes, the secondary conus is presumed to be derived from the pro-ostracum portion of the ancestral shell and is never found in association with a rostrum. The pseudoconus state appears when posterior vanes of the gladius overlap ventrally but do not fuse (some Cranchiidae, Loliginidae). As with the secondary conus, the pseudoconus is never associated with a rostrum.

The pro-ostracum portion of the gladius (dorsal plate) typically consists of longitudinal plates diverging from the conus apex: the middle plate (rachis) and paired lateral plates, and paired wings (Fig. 2). The elements of the pro-ostracum are delimited by paired asymptotic lines that are formed by an acute angle of the growth lines. In some gladius-bearing groups—the Enoploteuthidae, Pyroteuthidae, Histioteuthidae, Architeuthidae, and Neoteuthidae (Bizikov, 2008), the lateral elements of the pro-ostracum are not differentiated into lateral plates and wings, but instead they form a single and usually wide vane on both sides of the rachis. In some families—Chiroteuthidae, Joubiniteuthidae, Batoteuthidae, and some Cranchiidae—the paired elements of pro-ostracum are absent (Bizikov, 2008).

The gladii typically comprise three structural layers: middle, inner, and outer (Fig. 2.2–2.4). All three layers are composed of chitin. The middle layer is formed from a firm, dense variety of chitin that is also present in the formation of the pro-ostracum and conus. The middle layer grows by accretion of successive layers (laminae) deposited on the anterior-ventral surface of the pro-ostracum and anterior-inner surface of the conus. Subsequent layers overlap previous ones, in some instances in an imbricated form, giving rise to stacked laminae that provide for growth relief on the dorsal side of the pro-ostracum and outer surface of the gladius. Prior laminae may indicate the growth contours as deposited during earlier ontogenetic stages of development (Bizikov, 1990, 1991).

The inner and outer layers of the gladius are made up of a less-dense, more-hydrated and cartilaginous-like form of chitin. The inner layer grows by adding increments to the ventral surface in the posterior half of the pro-ostracum and the inner surface of the conus, with each subsequent newer laminae shifted slightly forward, compared to the prior (older) one (Bizikov, 1991). The outer shell layer contributes to the development of the rostrum, a conical spine located apically and extending from the conus. Growth of the rostrum occurs in incremental, three-dimensional, conically-shaped layers that are deposited on the outer surface of the previous layer. All the layers can be seen in cross sections of the rostrum at the level of the conus apex (Fig. 2.4).

While middle, inner, and outer layers of the gladius have sometimes been referred to as the ostracum, hypostracum, and periostracum, respectively (Naef, 1921–1923; Bizikov, 1987a, 1995), their homologies with those typical layers of the molluscan shell have yet to be verified. Indeed, the homology of these layers remains problematic and speculative. The similar consistency and microstructure of the inner and outer layers in the gladii has provided some evidence that the outer layer could have originated from the same tissue layer that produced the inner layer, when the latter began to encapsulate the outer surface of the shell after its ontogenetic submergence within the mantle (Bizikov, 1996, 2008). If so, the use of the term periostracum for this layer is certainly incorrect and potentially highly misleading with regard to the true homologies involved.

The gladius of the Octopoda is highly divergent from that of other coleoids (Fig. 1.9–1.11). Octopod gladii are composed of concentric layers of a hydrated, cartilaginous-like form of chitin. These successive laminae are continuous along the outer surface of the structure, with each new layer completely enclosing the prior one. As such, the gladius grows by way of complete concentric accretions. In the finned octopods (suborder Cirrata), the gladius forms a thick, saddle-, butterfly-, or U-shaped structure that serves to support the paired fins (Fig. 1.9–1.10). The cirrate gladius entirely lacks the pro-ostracum and typically consists of a thick medial part (the saddle) and paired, widened lateral parts (the wings). In comparison, among the incirrate octopods (suborder Incirrata), the gladius is reduced to a pair of widely separated spindle-like rods, sometimes called stylets (Fig. 1.11). The stylets are embedded within the musculature along the dorsolateral sides of the mantle, oblique to longitudinal axis. Stylets appear to provide support to the insertion of the funnel retractor muscles (BIZIKOV, 2004, 2008).

Among extant Coleoidea, numerous anatomical, taxonomic, and phylogenetic studies of the shell have been published. Overall, the calcareous sepions of the Sepiidae have been studied more extensively than the shells of other coleoids because they are commonly used in taxonomic and phylogenic analyses of the group (ADAM & REES, 1966; NESIS, 1982–1987; KHROMOV, 1987; KHROMOV & others, 1998). The potential value of the use of the gladius in the taxonomy and phylogeny of Coleoidea also has been demonstrated for squids (TOLL, 1982, 1990, 1998; DONOVAN & TOLL, 1988; ALEXEEV, 1989; BIZIKOV, 1996), sepiolids (KHROMOV, 1990) and octopuses (ROBSON, 1929, 1932; COLLINS & HENRIQUES, 2000; COLLINS & others, 2001).

Investigations of the functional morphology of squid gladii have shown that the gladii provide general support for the soft body and specialized structural support during locomotory movements as the site for muscle attachment (TOLL, 1988; DONOVAN & TOLL, 1988; BIZIKOV, 1996, 2008). Gladii in the squid families Ommstrephidae, Onychoteuthidae, and Gonatidae have been used for age determination and individual growth reconstruction (BIZIKOV, 1991, 1996; JACKSON & others, 1993; ARKHIPKIN & BIZIKOV, 1991; BIZIKOV & ARKHIPKIN, 1997). Because the coleoid shell represents one of a few structures that can directly be compared between and among fossil and extant forms, the gladii have been used in general phylogenetic and coleoid evolutionary reconstructions (NAEF, 1921–1923; JELETZKY, 1966; BIZIKOV, 2004, 2008; see also *Treatise Online,* Part M, Chapter 9B).

SHELL-BODY INTERACTIONS

Among the extant Coleoidea, the anatomy of the soft body structure and the relationships of the soft structures to the shell are considerably more conserved than the morphological diversity of the shell itself (Fig. 3). Typically, the shell in coleoid cephalopods corresponds in size to the mantle and provides support for the mantle, fins, visceral sac, funnel retractors, and head retractors (BIZIKOV, 1987b, 2000; TOLL, 1988). The anterior part of the shell supports the head through the nuchal cartilage. The mantle musculature attaches via the shell sac to the dorsal surface of the shell along its entire length. The head retractor muscle typically consists of one median and two lateral segments, which attach via the shell sac to the inner paired elements of the shell (lateral plates). The funnel retractor muscles are thick and robust, attaching to the outer paired elements of the shell (wings). Muscular fins typically attach to the posterior part of the gladius by means of basal cartilages and epithelial gliding pockets, the latter representing derivates of the shell sac (NAEF, 1921–1923). Thus, the majority of all muscular organs in coleoids receive support from the shell, directly or indirectly.

In all extant Coleoidea the muscular system is arranged according to the general Bauplan as described in detail by CUVIER

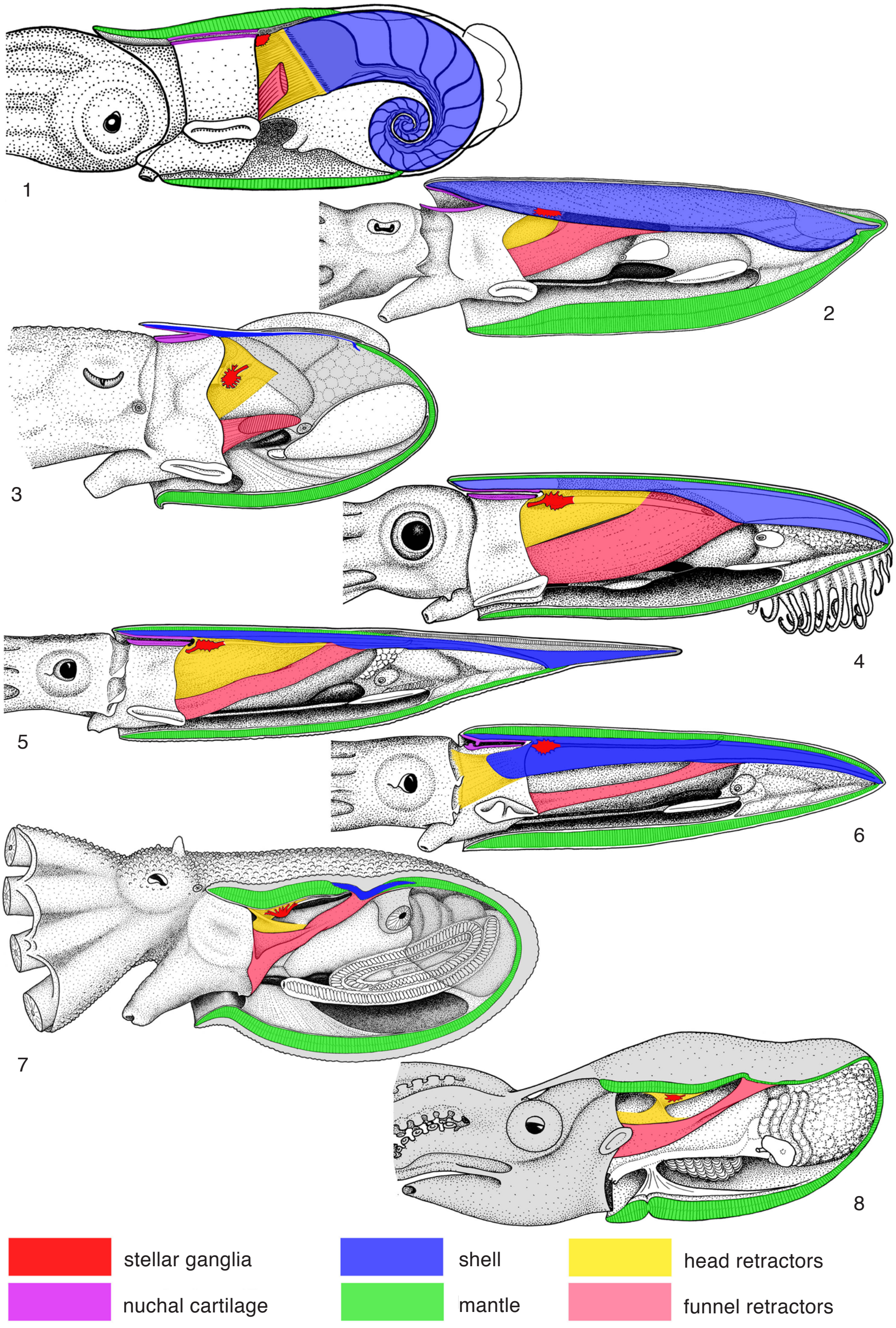

Fig. 3. For explanation, see facing page.

(1817) and Owen (1879). Remarkably, this Bauplan is conserved among those forms with a highly reduced or vestigial shell and in those taxa that completely lack an internal shell. Overall, the evolution of the shell among the Coleoidea has proceeded in close coordination with identifiable aspects of the body musculature. Therefore, the attachment sites of specific muscles to the shell represent an informative set of homologous markers of the shell across the divergent groups of coleoid cephalopods.

TYPES OF CONTACT BETWEEN MUSCLES AND THE SHELL

Another important criterion supporting the understanding of shell homology in the Coleoidea is the type of contact between the muscles and shell. The coleoid cephalopods are the only mollusks that display attachment of the muscles to the outer surface of the shell. Two evolutionary innovations allowed for this arrangement: (1) the formation of a closed epithelial shell sac completely surrounding the shell and (2) the development of the anterior projection of the dorsal wall of living chamber (proostracum). The shell sac appears to have arisen as a result of the fusion of edges of the mantle folds to completely enclose the shell (Naef, 1921–1923). Development of the epithelial shell sac that tightly encapsulates the shell provides for the muscle attachment to the outer walls of the shell sac at any place along entire surface of the shell, both inner (ventral) and outer (dorsal) (Bizikov, 2008).

Taking into consideration the potential for nearly unlimited sites of attachment, the diverse array of anatomical connections between the muscles and the shell in Coleoidea can be classified into two major types, primary and derived insertions. Primary insertions are those that were inherited from ectocochleate ancestors (Bizikov, 2008). These insertions represent attachment of the muscles to the inner (ventral) shell surface through the thin, membranous shell sac (primary shell sac). The attachment of head and funnel retractors to the inner side of the shell is a typical example of the primary insertions (Bizikov, 2008). Derived insertions include those that developed following the phylogenetic transition of the shell to a completely internal position. These are insertions of the muscular mantle and its derivates (fins) to the outer (dorsal) side of the shell through the secondary shell sac. The difference between the primary and secondary shell sac is that the latter is reinforced at the site of muscular insertion by a cartilage that develops from the walls of the shell sac.

Reduction of the shell in some coleoid lineages resulted in the transformation of primary insertions into derived ones. As the shell became further reduced, the zones of muscle attachment shifted from the inner surface of the shell towards its margins (e.g., funnel retractors in Vampyroteuthidae and Onychoteuthidae, head retractors in *Spirula*) or to the outer (dorsal) side of the shell (e.g., head retractors in Thysanoteuthidae, funnel retractors in Gonatidae), or in some taxa towards the inner surface of the mantle wall (e.g., funnel retractors in Sepiolida, Incirrina, Ommastrephidae). Displacement of the muscle attachment sites from the inner to outer surface of the shell resulted in their transformation from primary to derived type of insertions. The general evolutionary tendency in the Coleoidea is the gradual reduction of primary insertions

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Fig. 3. Anatomical relationship between the shell and the soft body in the major groups of extant Coleoidea; all specimens shown from the left side, with skin, muscular mantle, and gill removed to show the underlying internal anatomy; *1, Spirula* Linnaeus, 1758 in 1758–1759; *2, Sepia* Linnaeus, 1758 in 1758–1759; *3, Rossia* Owen, 1835; *4, Chtenopteryx* Appellöf, 1890; *5, Moroteuthis* Verrill, 1881 (=*Onykia* Lesueur, 1821, *sensu* Bolstad, 2010); *6, Thysanoteuthis* Troshel, 1857; *7, Octopus* Cuvier, 1797; *8, Argonauta* Linnaeus, 1758 in 1758–1759 (new).

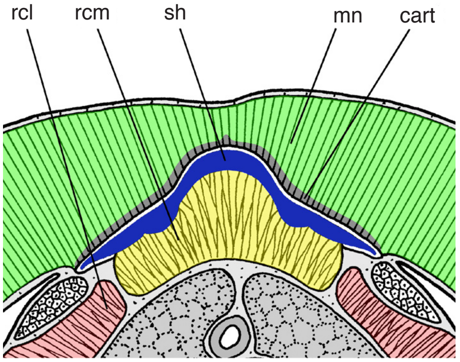

FIG. 4. Types of insertions between muscles and shell in *Loligo* sp.; cross section of dorsal part of the mantle (*mn*) behind the stellar ganglia; the median component of the cephalopodium (head) retractor (*rcm*) and lateral components of the cephalopodium retractors (*rcl*) attach directly to the inner side of the shell (*sh*) (primary insertion); the mantle attaches to outer side of the shell, through the shell sac (derived insertion), which is reinforced with cartilage (*cart*) (adapted from Bizikov, 2008).

and development of derived insertions. Among extant coleoids, primary insertions are best demonstrated in the Vampyroteuthidae, Sepiidae, Loliginidae, and in some mesopelagic squids with wide gladii (e.g., Ctenopterygidae, Enoploteuthidae, Pterygoteuthidae). Derived insertions are highly developed among such nektonic squids as the Ommastrephidae, Onychoteuthidae, and Gonatidae, as well as the Sepiolida and Spirulidae.

Among the extant Coleoidea, primary insertions are highly conservative in their structure. As a rule, they involve the simple attachment of muscles to the inner (ventral) shell surface via a primary membranous shell sac (Fig. 4). Derived insertions, on the other hand, are highly variable in structure and manner of muscle attachment. In general, derived insertions can be classified into three basic groups: (1) fixed insertions, the fixed attachment of muscles to the shell sac; (2) mobile sliding insertions: fins; and (3) mobile locking insertions: locking cartilages.

Fixed insertions are the most common type of derived insertions among the Coleoidea. In the most simple form, the muscles attach directly to the shell sac with no, or only minimal, cartilage reinforcement (Fig. 5.1). This arrangement, in which the mantle attaches to the dorsal side of the gladius, is found in the Loliginidae, Chtenopterygidae, and Thysanoteuthidae. In more derived examples, the attachment site is strengthened through cartilage and shell surfaces with interlocking surface typologies. These can include knobs or granules on the dorsal surface of the shell (Fig. 5.2); longitudinal ribs and furrows (Fig. 5.3); rigid ribs of varying profiles (Fig. 5.4); deep slits along thickened margins of the shell (Fig. 5.5); longitudinal grooves formed by proostracum with varying profiles and depths (Fig. 5.6); winglike, dorsolateral folds of the outer shell layer (Fig. 5.7); and spiral coiling of the posterior part of the gladius (Fig. 5.8).

In taxa exhibiting a mobile sliding insertion (coleoid fins), the development of fin basal cartilages and epithelial basal pockets allowed the fins bases to glide over the shell sac or mantle (Fig. 6.1). Fine control of fin position is regulated by the fin elevator and depressor muscles. Ontogenetically, the basal epithelial pockets first appear as lateral branches of the shell sac and subsequently separate from it (NAEF, 1928; BANDEL & BOLETZKY, 1979). It would appear that the ancestral fins initially were located over the conus flags. As part of the process of shell reduction and/or as a result of submersion of the shell within the mantle, the fins bases shifted to the mantle (Sepiolidae, Loliginidae, Thysanoteuthidae; Fig. 6.2). In some squid families (e.g., Ommastrephidae, Gonatidae, and Onychoteuthidae), narrowing of the posterior part of the gladius induces fusion of the fins cartilages into single axial cartilage. The paired basal pockets fused into single epithelial pocket, the elevator muscles disappeared, and the depressor muscles transitioned to adjust the position of the fins along the horizontal plane (Fig. 6.3). The complete reduction of basal pockets and rigid attachment of the fins to the shell has evolved independently in multiple squid taxa (e.g., Chiroteuthidae and Cranchiidae; Fig. 6.4) and is correlated with the development

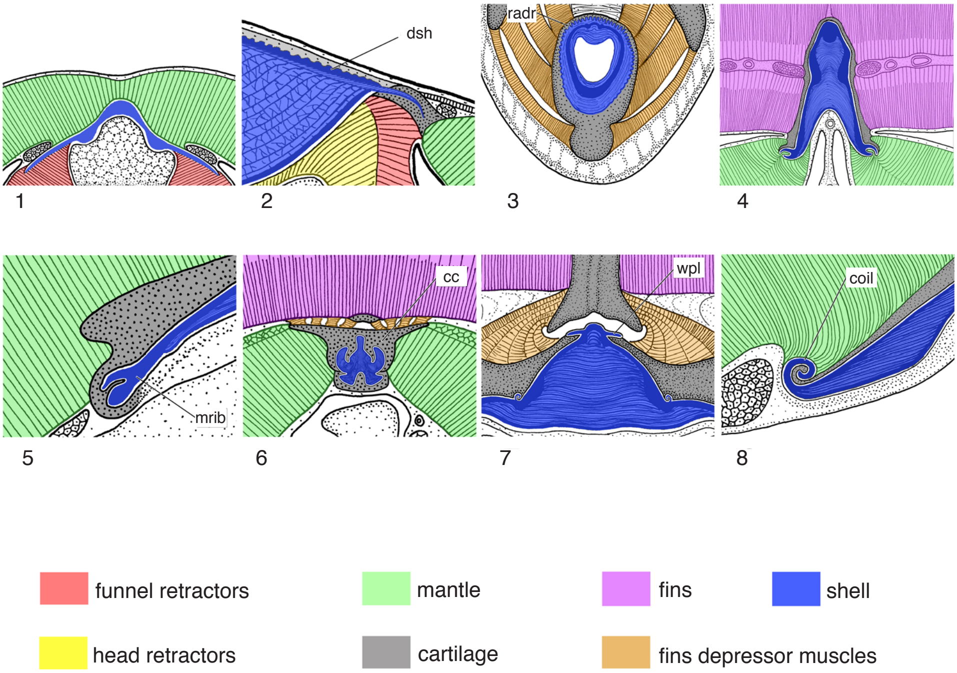

FIG. 5. Variability of derived fixed insertions between the muscles and shell in the Coleoidea; *1,* simple attachment of muscles to the shell sac; shell surface at site of attachment is smooth (*Loligo* LAMARCK, 1798); *2,* reinforcement of the shell sac with layer of cartilaginous tissue; development of surface relief on the shell (*Sepia* LINNAEUS, 1758 in 1758–1759); *3,* cartilaginous cover over the shell (conus) connects to the conus by longitudinal complimentary ribs and furrows (*Todarodes* STEENSTRUP, 1880); *4,* attachment of muscles to supporting element (median keel) in posterior part of gladius (*Lycoteuthis* PFEFFER, 1900); *5,* attachment of mantle muscles (mantle cartilage) to deep slits along marginal ribs of gladius (*Moroteuthis* VERRILL, 1881; =*Onykia* LESUEUR, 1821, *sensu* BOLSTAD, 2010); *6,* anchoring of mantle cartilage in deep longitudinal grooves in gladius (stem in the gladius in Ommastrephidae); *7,* anchoring of mantle cartilage in slits formed by winglike processes in posterior part of the gladius (*Berryteuthis* NAEF, 1921 in 1921–1923; *8,* connection of the mantle cartilage with longitudinal spiral coiling in the gladius margins (*Berryteuthis*); *cc,* cartilaginous cover of gladius; *coil,* longitudinal spiral coiling of gladius margin; *dsh,* dorsal shield; *mrib,* marginal rib; *radr,* radial ribs; *wpl,* lateral winglike plates of the alveolus (adapted from Bizikov, 2008).

of large fins associated with a comparatively slender gladius. Among the cirrate octopods a similar reduction is correlated with the development of the unique cirrate fins that facilitate the distinctive locomotion called underwater flight swimming (SEIBEL, THUESSEN, & CHILDRESS, 1998; BIZIKOV, 2004).

Mobile locking cartilages represent another variation of derived insertions. Typically, coleoids have three mobile locking insertions: a single nuchal cartilage (Fig. 7.2) and a pair of funnel-locking cartilages (Fig. 7.3). Mobile locking insertions serve to attach soft-body complexes (head, funnel), rather than individual muscles. The nuchal cartilage is the only example of derived insertion situated on the inner (ventral) side of the shell (Fig. 7.2). This arrangement provides for the fixed orientation of the head position relative to the mantle, an essential prerequisite for locomotion by jetting. The nuchal cartilage is present in most of the extant Decabrachia and is highly conserved in structure.

Analysis of derived insertions in Coleoidea demonstrates that the most distinctive feature of these insertions is the presence of cartilage reinforcement at the site of insertion. Notably, the degree of cartilage development in derived contacts is directly

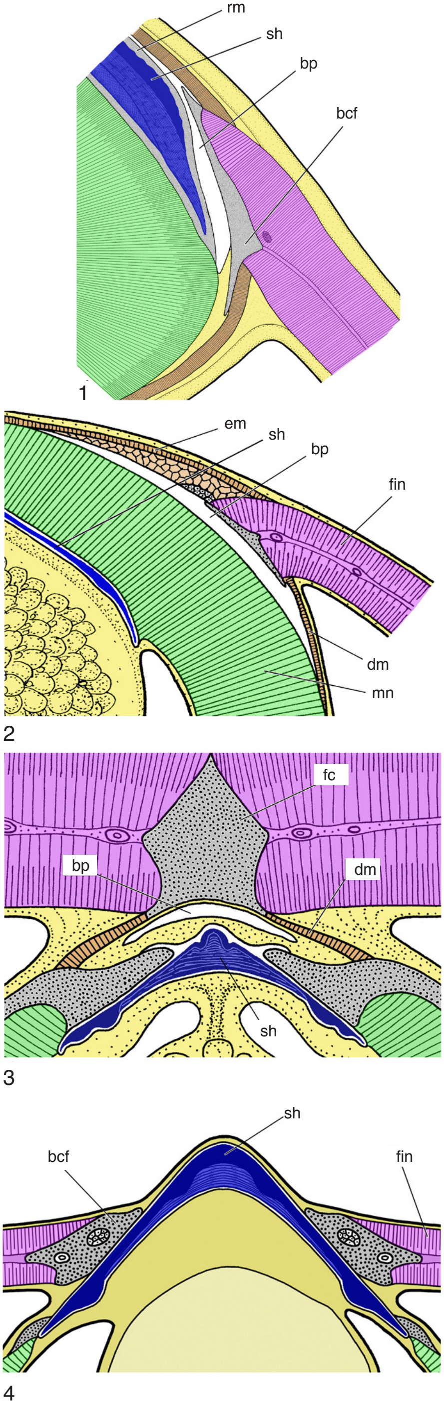

FIG. 6. *For explanation, see adjacent column.*

proportional to the level of locomotory activity. The fastest swimmers among extant coleoids, members of the oceanic squid families Ommastrephidae, Lycoteuthidae and some Onychoteuthidae, have the most highly derived and complex cartilages. In these groups, at the level of fins where the body sustains the greatest force loading during maneuvering at high speeds, these cartilages contribute to a single gladius-cartilage complex that in cross section is similar to the vertebra of primitive fishes (Fig. 8).

MORPHOLOGICAL CLASSIFICATION OF THE MODERN GLADIUS

Based on their composition, morphology, development of their component parts, and relationship with the soft body, shells in extant Coleoidea have been classified into twelve distinct types (BIZIKOV, 2008): spirulid, sepiid, sepiolid, myopsid, thysanoteuthid, vampyroteuthid, cirrate, incirrate, onychoteuthid, ommastrephid, chiroteuthid and cranchiid (Fig. 9). These twelve types are based on characteristic features of the shell and the relationship of the shell with soft-body structures. Comparisons of larval stages (Fig. 10) show that the characteristic features of the shell are clearly recognizable as early as the hatchling stage in most of the twelve primary anatomical types. In three types, the vampyroteuthid, myopsid, and

FIG. 6. Various forms of muscle insertions in Coleoidea; *1,* mobile (sliding) insertion of the fins to the dorsal surface of the gladius through basal pockets (derivatives of the shell sac); *2,* mobile (sliding) insertion of the fins to the mantle through basal pockets (*Loligo* LAMARCK, 1798); *3,* mobile (sliding) insertion of the axial cartilage of the fins to the gladius through single basal pocket (*Moroteuthis* VERRILL, 1881; =*Onykia* LESUEUR, 1821, *sensu* BOLSTAD, 2010); *4,* secondary rigid insertion of the fins to the shell sac as a result of reduction of the basal pockets (*Galiteuthis* JOUBIN, 1898); *bcf,* basal cartilage of fins; *bp,* basal pockets of fins; *dm,* depressor muscle; *em,* elevator muscle; *fc,* fin cartilage; *fin,* fins; *mn,* mantle; *rm,* cartilaginous reinforcement of the shell sac; *sh,* shell (adapted from Bizikov, 2008).

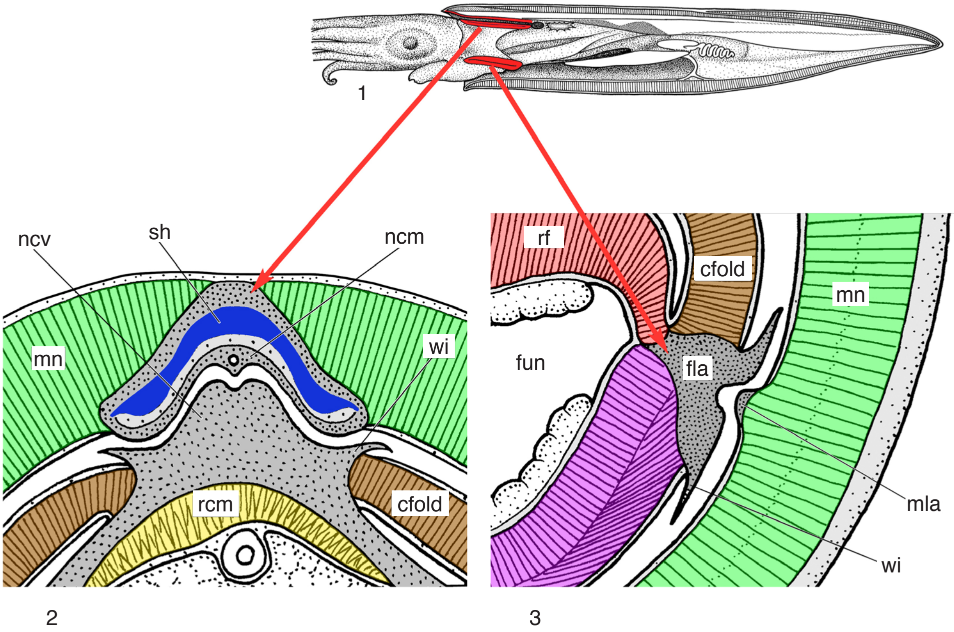

FIG. 7. Mobile locking insertions in squids (Loliginidae); *1,* lateral view of squid (with mantle removed from left side) showing position of locking apparati; *2,* cross section through the nuchal mantle–head-locking apparatus; *3,* cross section illustrating the structure of mantle–funnel-locking apparatus; *cfold,* collar folds; *fla,* close bond of the funnel; *fun,* funnel; *mla,* closer bond of the mantle; *mn,* mantle; *ncm,* nuchal locking cartilage (mantle component); *ncv,* nuchal locking cartilage (visceral component); *rcm,* medial component of the cephalopodium (head) retractor; *rf,* funnel retractor; *sh,* shell; *wi,* elastic margins of the locking cartilage (adapted from Bizikov, 2008).

onychoteuthid, the gladii of hatchlings are morphologically similar and subsequently acquire the characteristic features of the adult type during post-hatchling development.

The following descriptions include only the nonmineralized (phragmocone-less) gladius types. The mineralized (phragmocone-bearing) shells of the Spirulida (Fig. 9.1, Fig. 10.1) and Sepiida (Fig. 9.2, Fig. 10.2) are considered in another section (see *Treatise Online,* Chapter 8, Shell Morphology).

SEPIOLOID GLADIUS

This type of the gladius is found in the Sepiolida KEFERSTEIN, 1866 in 1862–1866, the so-called bobtail squids (Fig. 9.3). The gladius is narrow, rodlike, thickened anteriorly, and gradually tapering posteriorly. It is markedly shorter than the mantle length (i.e., the gladius does not extend to the posterior terminus of the mantle) and is absent in some taxa. The gladius consists of the pro-ostracum and a modified conus. The latter is transformed into an unfolded, flat vane at the posterior terminus of the gladius. The pro-ostracum is well developed. The gladius comprises only two shell layers, a middle and inner layer. The outer (rostrum-forming) shell layer is absent. The middle layer is composed of dense chitin and forms the pro-ostracum and conus. The inner layer is composed of less dense, hydrated chitin. The center of shell growth is located at the point of convergence of the paired asymptotes. The pro-ostracum consists of the rachis and a pair of lateral plates. The rachis is narrow, with a long anterior free part and two thick ribs along the lateral margins. The lateral plates are lanceolate; the rostrum is absent. The conus is unfolded into a flat, narrow plate with an apical angle of about 180°. The lateral walls of the conus are reduced

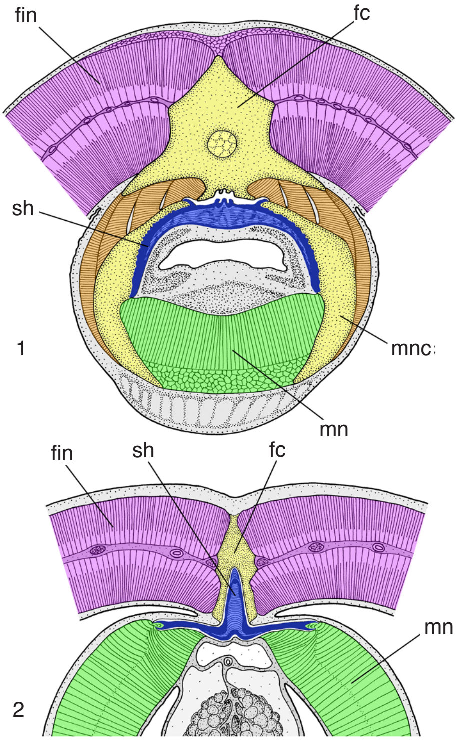

Fig. 8. Cross sections of the oceanic squids *Todarodes* Steenstrup, 1880 (*1*), and *Lycoteuthis* Pfeffer, 1900 (*2*), showing vertebra-like shape of the shell-cartilage complex; *fc,* fins cartilage; *fin,* fins; *mn,* mantle; *mnc,* mantle cartilage; *sh,* shell (gladius) (adapted from Bizikov, 2008).

to narrow vanes along the pro-ostracum and gradually taper anteriorly. The ventral wall of the conus is reflected backward, lying in the same plane as the pro-ostracum but growing in the opposite (posterior) direction. As a result, the shell apex occupies a subterminal position. The gladius is covered dorsally and partially ventrally by a thick, cartilaginous sheath formed by the shell sac. At the time of hatching, the gladius already exhibits all characteristic features associated with the adult type (Fig. 10.3).

LOLIGINOID GLADIUS

This type of gladius is found in the families Loliginidae, Australiteuthidae, Pickfordiateuthidae, Chtenopterygidae, and Bathyteuthidae (Fig. 9.4). The gladius is chitinous, feather-shaped, and subequal in length to the mantle. The gladius consists mainly of the pro-ostracum and its greatest width is located at about or posterior to the midpoint of its length. The conus and rostrum are highly reduced or absent. The gladius is composed of three shell layers. The core consists of the middle (chitinous) shell layer that forms the pro-ostracum and conus. The inner layer is made up of a low-density, hydrated form of chitin that covers the entire ventral (inner) surface in the posterior half of the gladius. The outer shell layer is composed of a low-density, hydrated chitin. The center of shell growth is located at the posterior apex of the gladius. The pro-ostracum consists of three longitudinal elements, the rachis and two paired vanes. The rachis is narrow, with a short anterior free portion. The vanes are wide and long. The typical conus is reduced to a tiny cuplike structure, completely lacking septa. Dorsolateral fields of the conus form well-developed, long, thickened plates, situated laterally from the lateral plates. The rostrum is reduced to a microscopic, thin-walled, cuplike alveolus surrounding the apical part of the conus. In one representative, *Alloteuthis* Wülker, 1920, the rostrum is represented as a minute spine on the posterior apex of the gladius (Naef, 1921–1923; Alexeev, 1989). At the time of hatching, the morphology of the gladius differs from that of the adults. It consists of the rachis with long anterior free part, wide vanes undifferentiated into lateral plates and conus flags, a wide shallow conus, and a minute rostrum (Fig. 10.4).

VAMPYROMORPH GLADIUS

A single living species, *Vampyroteuthis infernalis* Chun, 1903, exhibits this type of gladius. The shell forms a wide, chitinous gladius that is subequal to the mantle in length and widest near the midpoint of its length. The gladius consists of the pro-ostracum, conus, and rostrum. The pro-ostracum is the most-developed part of the gladius, with the conus and rostrum highly reduced. The gladius comprises three shell layers: the dense, chitinous

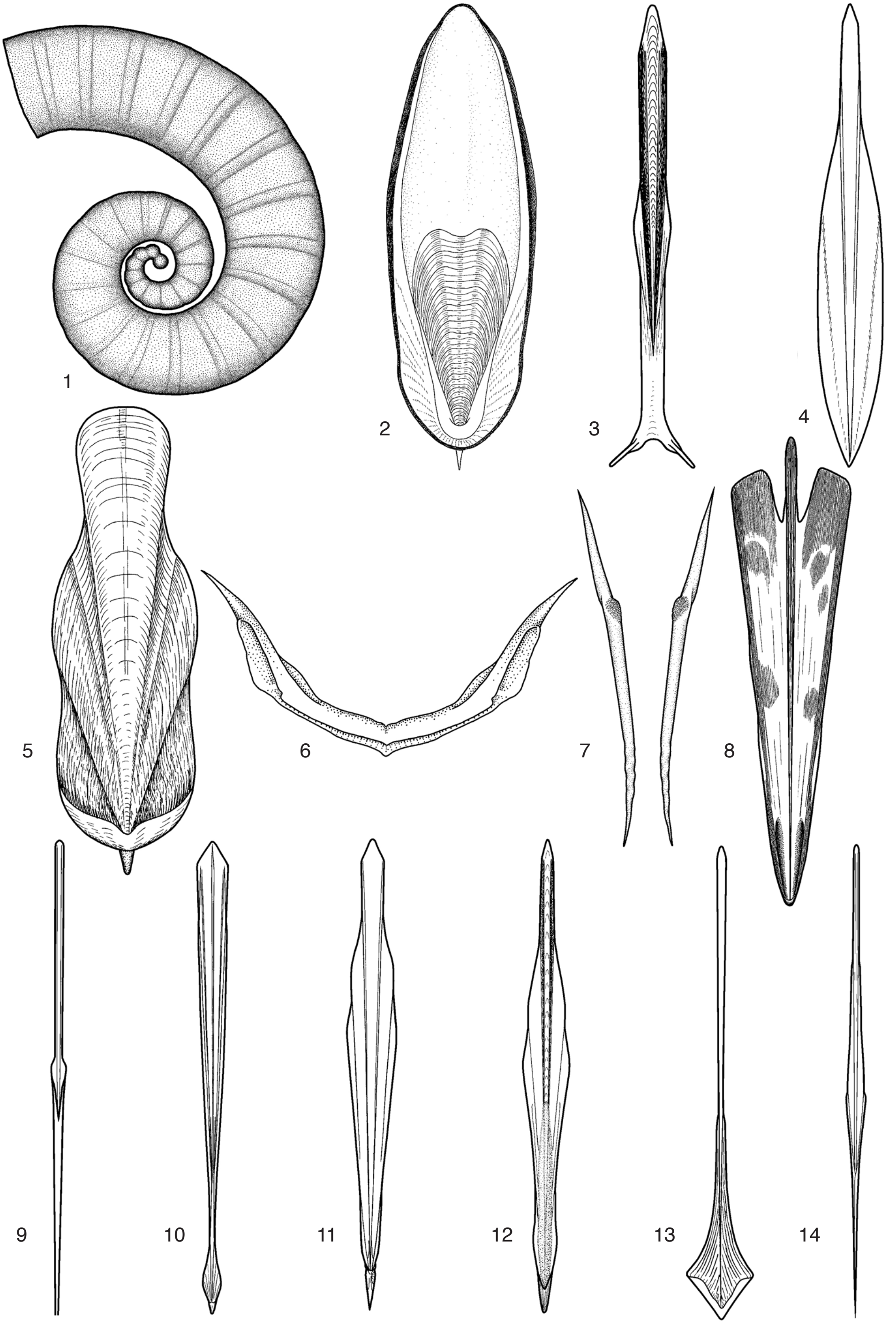

FIG. 9. Types of shell morphology in extant Coleoidea (adult stage); *1,* Spiruloid; *2,* Sepioid; *3,* Sepioloid; *4,* Loliginoid; *5,* Vampyromorph; *6,* Cirrate; *7,* Incirrate; *8,* Thysanoteuthoid; *9,* Chiroteuthoid; *10,* Ommastrephoid; *11,* Onychoteuthoid (with rostrum); *12,* Onychoteuthoid (without rostrum); *13,* Cranchioid (without tail); *14,* Cranchioid (with tail) (adapted from Bizikov, 2008).

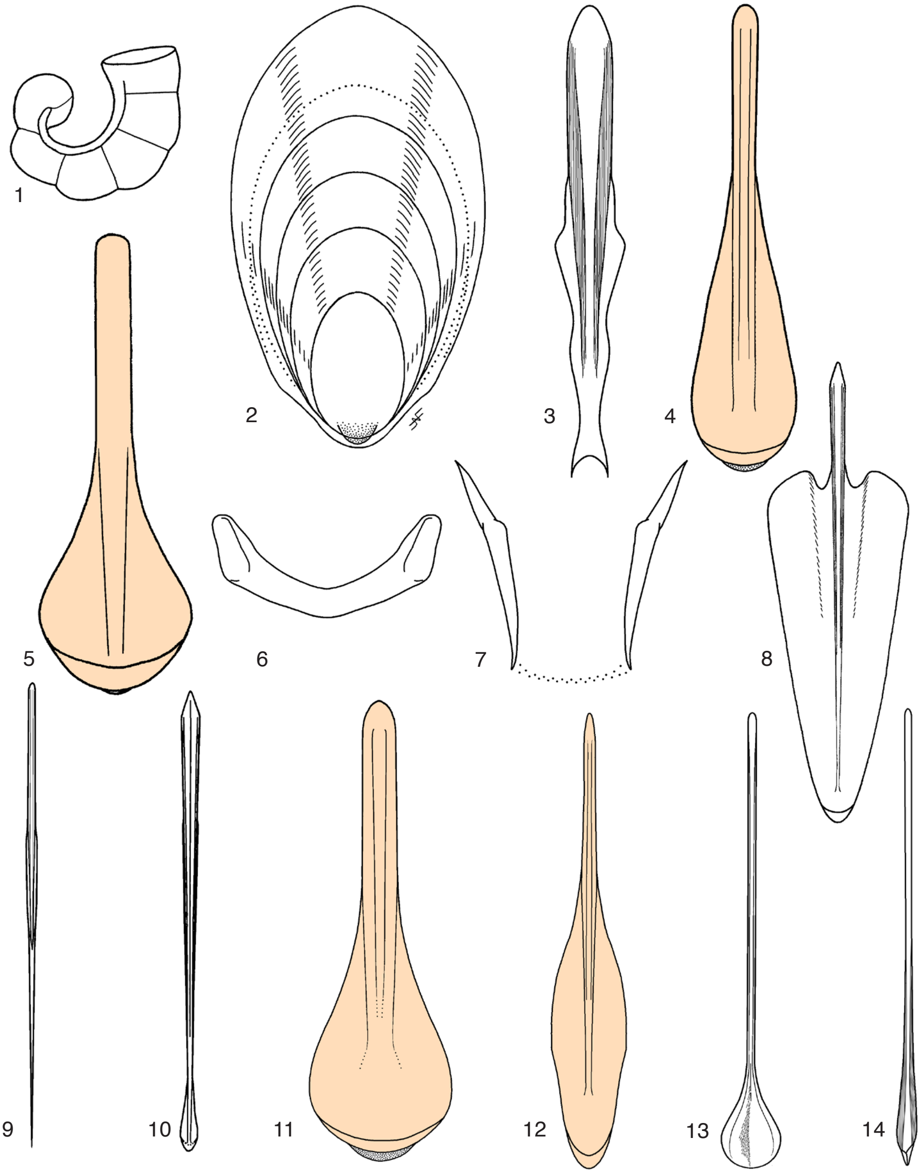

FIG. 10. Types of shell morphology in extant Coleoidea (paralarval stage); *1,* Spiruloid; *2,* Sepioid; *3,* Sepioloid; *4,* Loliginoid; *5,* Vampyromorph; *6,* Cirrate; *7,* Incirrate; *8,* Thysanoteuthoid; *9,* Chiroteuthoid; *10,* Ommastrephoid; *11,* Onychoteuthoid (with rostrum); *12,* Onychoteuthoid (without rostrum); *13,* Cranchioid (without tail); *14,* Cranchioid (with tail); note similar shell types in larval stage, marked by colored shading (adapted from Bizikov, 2008).

middle layer at the core, which forms the pro-ostracum and conus, and the inner and outer layers made up of a low-density, hydrated form of chitin. The center of shell growth is located at posterior apex of the conus (BIZIKOV, 1996, 2004). The pro-ostracum consists of five longitudinal elements: the median plate (rachis), paired lateral plates, and paired wings. The median plate (rachis) is wide, with a blunt anterior margin, and forms the longest part of the pro-ostracum. The anterior free part of the rachis is short. Lateral plates of the pro-ostracum are narrower than the wings. The conus is cup-shaped, short and wide, lacking septa. Its outer contour makes a blunt angle between 110° and 120°. The conus flags are well developed. The rostrum is reduced to a small spine, which is slightly compressed laterally, located at the apex of the conus. Pickford (1949) reported that the rostrum may be absent in some specimens (Fig. 9.5). The morphology of the hatchling gladius differs from that of the adults. It consists of a relatively narrow rachis with a long anterior free part, wide vanes, wide and shallow conus, and a minute rostrum (Fig. 10.5).

CIRRATE GLADIUS

This gladius type occurs in octopods of the Cirrina Grimpe, 1916 (Fig. 9.6). The cirrate gladius comprises a thick, cartilage-like, U- or saddle-shaped chitinous structure that is located transversally in a subterminal position and embedded within the dorsal side of the mantle. Because the gladius in cirrates provides support for fins, it is often referred to as the fin support (Aldred, Nixon, & Young, 1983). The gladius is considerably shorter than the mantle and appears to consist of a highly derived pro-ostracum and conus (Bizikov, 2004). It has a single shell layer that consists of a low-density, hydrated form of chitin. Based on its microstructure, this layer appears to correspond to the inner shell layer of ancestral coleoids. The gladius grows by deposition of concentric accretions. The center of gladius growth, which corresponds to the point of greatest thickness, is located midway along its length. The pro-ostracum is reduced to a transverse plate with widened lateral extensions (wings). Structural elements of the pro-ostracum are indistinct. A conus and rostrum are absent. The gladius in paralarvae is similar in morphology to that of the adult (Fig. 10.6).

INCIRRATE GLADIUS

This type occurs in octopods of the Incirrina Grimpe, 1916, in which the gladius is reduced to a pair of laterally displaced stylets, each of which is surrounded by paired shell sacs (Fig. 9.7). The stylets are substantially shorter than the mantle and are absent in some taxa. The stylets are thin, cartilage-like rods with pointed ends imbedded in the dorsolateral side of the mantle musculature at an acute angle to longitudinal axis. Each stylet is bent to form an obtuse angle with the apex directed inside the mantle. As evidenced by the muscle attachments, the apex of the bend and anterior shoulder of the stylets could be homologues of the horns and distal parts of the lateral wings in the cirrate gladius. The posterior shoulders, which are embedded in the mantle, appear to be homologous to the lateral wings and median saddle in the cirrate gladius. As with cirrate gladii, the stylets in the incirrate gladii are formed from a single shell layer that appears to correspond to the inner shell layer of other coleoids and consists of a low-density hydrated chitin. The stylets grow by deposition of concentric accretions with the center of growth (initial shell) at the apex of the angle. A pro-ostracum, conus, and rostrum are absent. Cartilage-like tissue in the walls of the shell sac is either weakly developed (in most benthic species) or entirely absent (in some pelagic species). Calcified stylets are known from one taxon, *Scaeurgus* Troschel, 1857 (Toll, personal observation, 2012). The stylets of paralarvae are morphologically similar to those of the adults (Fig. 10.7).

THYSANOTEUTHOID GLADIUS

This type of gladius occurs in a single living representative, *Thysanoteuthis rhombus* Troschel, 1857 (Fig. 9.8) and is morphologically distinct among the teuthoids. It is a spear-like plate that is pointed posteriorly and gradually widens anteriorly. The gladius consists mainly of the pro-ostracum, with a minute, cup-shaped conus at the posterior end and no rostrum. The gladius is formed by the middle and inner shell layers; the outer layer is absent. The middle layer is dense and chitinous layer and comprises the pro-ostracum and conus and is more developed than the inner layer, which is reduced to an indistinct thickening along the posterior third of the gladius. The center of gladius growth is located at the posterior apex of the conus. The pro-ostracum consists of seven longitudinal elements: the median plate (rachis), paired hyperbolic plates, paired lateral plates, and paired wings. The anterior part of the pro-ostracum in *Thysanoteuthis* is unique among extant Coleoids: its free lateral plates project anteriorly, almost reaching the anterior margin of the rachis. The median plate (rachis) is narrow, with three, rigid longitudinal ribs and a short anterior free portion. The hyperbolic plates are narrow and thin, situated laterally from the rachis, and the lateral plates are thick and wide, with subquadrangular lobes that project anteriorly. The wings are narrow, thickened plates with splayed margins and are situated in the posterior half of the gladius. The conus is cup-shaped, short, and wide and lacks septa; the conus flags are indistinct. The gladius in hatchlings shows all of the characteristic features of the adult type, including the overall shape, elements of the pro-ostracum, and conus (Fig. 10.7).

CHIROTEUTHOID GLADIUS

This type occurs in the deep-water planktonic or semiplanktonic families—the Chiroteuthidae, Mastigoteuthidae, Joubiniteuthidae, Grimalditeuthidae, and Batoteuthidae—as well as in the giant finned, deep-water squids of the Magnapinnidae (Vecchione & Young, 1998) (Fig. 9.9). The gladius is needle shaped and equal in length to the mantle and consists of a pro-ostracum and conus, which are subequal in length. It is formed by two shell layers, the middle and inner. The outer layer is absent. The middle layer consists of a firm form of chitin; the inner layer is more hydrated and lower in density. The middle layer is highly developed, forming the pro-ostracum and conus. The inner layer is limited to lining the inner walls of the conus. The center of gladius growth is situated in posterior apex of the conus. The pro-ostracum is long and narrow, consisting mainly of the rachis. If present, the lateral plates are narrow, very thin, and lanceolate. The conus is long, narrow, and needlelike. In some representatives, the conus contains irregular, transverse vestigial septa in its posterior end (Chun, 1910; Arkhipkin, Bizikov, & Fuchs, 2012). The conus length is 33% to 50% of the gladius length and is widest, 2.5% to 4.0% of the gladius length, at the aperture. The apical angle ranges from 1° to 10°, but it is usually 3° to 4°. A rostrum is absent. The gladius in hatchlings shows all of the characteristic features of the type (Fig. 10.9).

OMMASTREPHOID GLADIUS

This type of gladius is found in squids of family Ommastrephidae (Fig. 9.10). The gladius is a narrow, swordlike plate that is subequal in length to the mantle. It consists of a pro-ostracum, conus, and rostrum. The pro-ostracum is the main part of the gladius. The conus is small, with rhomboidal flags. The rostrum is small, barely macroscopic in adults. The gladius is formed from the three shell layers: middle, inner and outer layer. The middle layer is the most developed, consisting of a dense form of chitin, and comprises the pro-ostracum and conus. The inner layer, also a form of dense chitin, is located ventrally along the posterior portion of the gladius. The outer shell layer consists of a lower-density, hydrated form of chitin and forms a cuplike sheath over the outer surface of the conus. The center of gladius growth is located at posterior apex of the conus. The pro-ostracum consists of the median plate (rachis) and paired lateral plates. The rachis represents the main part of the pro-ostracum and is significantly strengthened by the presence of ribs, one median and a pair of marginal rigid ribs. The lateral plates form paired, highly developed, narrow, thickened, rigid lateral ribs adjacent to the rachis. The conus is short and round or slightly compressed laterally when viewed in cross section. The conus is 1% to 5% of the gladius length. Apical conus angles range from 18° to 56°. The apical end of the conus contains transverse vestigial septa, apparently representing the ancestral phragmocone (Arkhipkin, Bizikov, & Fuchs , 2012). The rostrum is reduced to a minute, chitinous spine that extends from a cap-like alveola over the conus. The gladius in hatchlings shows all the characteristic features of the type (Fig. 10.10).

ONYCHOTEUTHOID GLADIUS

Squids with this type of gladius comprise a diverse group of 13 families. The onychoteuthoid-type gladius can be further divided into two subgroups: rostrum-bearing (Onychoteuthidae, Pholidoteuthidae, Lycoteuthidae, and Ancistrocheiridae) and rostrum absent (Architeuthidae, Neoteuthidae, Octopoteuthidae, Psychroteuthidae, Histioteuthidae, Gonatidae, Enoploteuthidae, Pyroteuthidae and Lepidoteuthidae). The gladius length is equal to or slightly less than the mantle length. The gladius consists of a pro-ostracum and conus, with or without a rostrum, depending on the subgroup (Fig. 9.11–9.12). The gladius typically is formed by the middle, inner, and outer shell layers. The middle layer, made up of firm chitin, is the most developed and contributes to the pro-ostracum and conus. The inner and outer layers consist of a lower-density, hydrated form of chitin. The inner layer is located along the posterior portion of the gladius on the ventral surface of pro-ostracum and on the inner lining of the conus. The outer shell layer is located on the outer surface of the conus and comprises the rostrum. The center of gladius growth is located at the posterior apex of the conus. The pro-ostracum typically consists of five longitudinal elements: a single median plate (rachis), paired lateral plates, and paired wings. The anterior free part of the rachis is short. The lateral plates are long and variable in shape. The wings are typically well developed and are the widest part of the gladius. The conus is short and relatively wide, though absent in some taxa. The apical angle ranges from 15° to 30°. The conus flags are long and sometimes broad, contributing to the posterior (second) maximum of the gladius width. In some taxa, the apical portion of the conus contains vestigial transverse septa, apparently representing the ancestral phragmocone (Arkhipkin, Bizikov, & Fuchs, 2012). The rostrum (in rostrum-bearing forms) consists of a conical spine, located on the apical end of the conus. The basal portion of the rostrum forms a cuplike sheath, the alveolus, over the outer conus surface. The surface texture of rostrum is typically smooth; the alveolus typically displays radial striae. The gladius in hatchlings differs from that of adults and consists of the rachis with a long anterior free part; wide, nondifferentiated lateral vanes; and a wide, shallow conus with a rudimentary rostrum (Fig. 10.11–10.12).

CRANCHIOID GLADIUS

This type of gladius occurs in the squids of the family Cranchiidae (Fig. 9.13–9.14). The gladius is narrow and equal in length to the mantle. It consists of a pro-ostracum and conus. The gladius is formed by the middle shell layer, which is firm and chitinous, and the inner layer, which consists of a lower-density hydrated chitin. The middle layer comprises the majority of the pro-ostracum and conus. The inner layer lines the ventral surface of the pro-ostracum and the concavity of the conus. The center of gladius growth is located at the posterior apex. The pro-ostracum is narrow, typically consisting of the rachis and lateral plates. The rachis is narrow and rodlike, with an extensive anterior free part. The lateral plates are narrow and thin, though absent in some taxa. The conus is short and wide, with an apical angle ranging from 60° to 90°. The outer surface of the conus is smooth; conus flags are long. In the subfamily Taoniinae, a true conus is absent, and the paired conus flags are rolled ventrally to form a long and narrow, unfused needle-shaped structure, the pseudocone. A rostrum is absent. The gladius in hatchlings forms a narrow rod with spoon-like expansion at the posterior end. It consists primarily of the rachis with a long, anterior free portion (Fig. 10.13–10.14).

MORPHOLOGICAL VARIABILITY OF THE MODERN GLADIUS AND ITS TAXONOMIC SIGNIFICANCE

A comparison of the ten, nonmineralized morphological gladius types described above with the existing taxonomy of the groups demonstrated that most higher-level taxa—sepiolids, myopsid squids, vampyroteuthids, cirrates and incirrates—have a uniquely characteristic shell type. Oegopsid squids (Oegopsida) represent the sole exception, with at least six morphologically distinct types of gladii found across this group, each displaying the unique features associated with its type during the larval stage of development. Further, two oegopsid families, the Chtenopterygidae and Bathyteuthidae, possess gladii that exhibit morphological features similar to those of the myopsids.

The gladii of hatchling cirrates, incirrates, sepiolids, thysanoteuthids, ommastrephids, and chiroteuthids display all of the characteristic features of the respective adults, essentially resembling miniature copies of the adult structure. The gladii of hatchling vampyroteuthids, loliginids, and onychoteuthids are similar to one another and differ considerably from those of the respective adults (Fig. 10.4–10.5, 10.11–10.12). Their pro-ostracum consists mainly of the rachis with a long anterior free part. Lateral elements of pro-ostracum are represented by wide lateral vanes located along the posterior portion of the gladius. The vanes are not differentiated into lateral plates and wings. The posterior end of the gladius consists of a wide cup-shaped conus with a rudimentary apical rostrum. Conus fields are not delimited from the lateral vane of pro-ostracum. At the time of hatching, the gladii of the cranchiids, including the so-called tail-less and long-tailed forms, have a similar structure to each other, which is similar to the gladii of the vampyroteuthid, loliginid, and onychoteuthid types. In all groups where adults have gladii with two pairs of lateral elements (lateral plates and wings), hatchlings have gladii with a single pair of elements. Therefore, differentiation of the unified vane into the lateral plates and wings occurs during post-larval development.

The presence of a common, original Bauplan of the morphology in the coleoid pro-ostracum suggests the existence of common ancestor, indicative of monophyly of the pro-ostracum-bearing Coleoidea (Naef, 1921–1923). Conversely, the presence of six morphologically different types of gladii within the Oegopsida, all of them already distinct in hatchlings, suggests a polyphyletic origin of taxa within the suborder Oegopsida as currently defined (Bizikov, 2008). A general tendency of reduction of the gladius can be traced in all major groups of extant Coleoidea, culminating in the complete loss of the gladius in some incirrates, sepiolids, and idiosepiids.

STRUCTURAL HOMOLOGY OF THE SHELL

The amazing variability in structure and morphology of the shell in extant Coleoidea created insuperable difficulties in previous homological comparisons of the shell among different groups of Coleoidea (Naef, 1921–1923; Donovan & Toll, 1988; Toll, 1998; Nesis, 1982–1987; Khromov, 1990). However, a more robust analysis is possible if the anatomical relationship of the shell to the soft parts of organism are considered in addition to the morphology of the shell itself. As demonstrated above (Fig. 3), the soft-body structures of extant Coleoidea, especially their muscular system, is more highly conservative than the shell. As all the muscles in the locomotory system of coleoids make contacts with the shell either directly or indirectly, an understanding of shell structural homologies can be inferred by direct comparison of the position and types of the corresponding muscle contacts, the mantle, fins, head, and funnel retractors. Among the other soft-body parts, a key for the analysis of homologies is the position of the stellate ganglia (Bizikov, 2008).

Based on the overall correlation between the shell and soft-body structures in Coleoidea, Bizikov (2008) carried out a homological comparison of the shell in different groups. The criteria listed below were used in this comparison:

1. Nuchal cartilage (when present) always corresponds to the anterior part of the rachis.
2. Median segments of the head retractors always attach within the rachis, posteriorly from the nuchal cartilage.
3. Lateral segments of the head retractors always attach along the anterior margins of the gladius lateral plates, laterally from the rachis.
4. Funnel retractors (when they attach to the gladius) always attach to the anterolateral margins of the lateral plates, posteriorly and laterally from the lateral segments of the head retractors. If the funnel retractors and lateral segments of the head retractors are fused posteriorly (as in Loliginidae, Chtenopterygidae, Bathyteuthidae, and some Lycoteuthidae), their attachment sites on the gladius lateral plates are not subdivided. If the funnel retractors and the lateral segments of the head retractors are not fused, their attachment sites are usually separated and form two pairs of elements of the gladius pro-ostracum: lateral plates (attachment sites of the lateral segments of head retractors) and wings (attachment sites of the funnel retractors).
5. Stellate ganglia in most Coleoidea are located on each side of the gladius at the level of anterior margins of the lateral plates.
6. The mantle can adhere to the pro-ostracum either along its margins or to its dorsal side. The ventroposterior wall of the mantle always attaches to the margins of the conus and its dorsolateral fields, either from the inner or outer surface.
7. The fins bases in the groups with separate, paired fins are always situated over the conus flags.
8. Shell function is also important in homological analysis. Hydrostatic and protective functions of the shell have been reduced in most lineages of Coleoidea while skeletal function, on the contrary, has increased (Zuev, 1965). In lineages where the shell has been transformed into a gladius, skeletal role became the principal function of the shell. In these lineages the shell evolved mainly as an internal skeleton providing support for developing locomotory apparatus of coleoids: mantle-funnel complex and fins.

Each group of muscles has its specific attachment site on the shell. During growth, muscles attachment sites increase in size and gradually shift along the growing shell leaving on it a mark in the shape of a sector. It is this mechanism—growth of the musculature and the soft body parts—that determines radial plane of the pro-ostracum structure in all coleoids typically consisting of rachis, lateral plates and wings radiating from the shell apex.

HOMOLOGIES IN THE GLADII OF OEGOPSIDA

The gladii of the Oegopsida are highly variable in shape and structure across the many taxa. In some families, structural homologies are readily apparent, while in others the determination of true homologies can be controversial (Toll, 1982, 1998; Bizikov, 1996). In families with the onychoteuthoid gladius, such as Onychoteuthidae, Gonatidae, Enoploteuthidae, and Psychroteuthidae, homologies of the gladius parts are easy to interpret. Typically, the pro-ostracum in onychoteuthoid gladii is separated into five distinct longitudinal elements: the median plate (rachis) serving for supporting nuchal cartilage and attachment of the median component of the head retractors; the paired lateral plates serving for attachment of the lateral components of the head retractors; and the paired wings serving

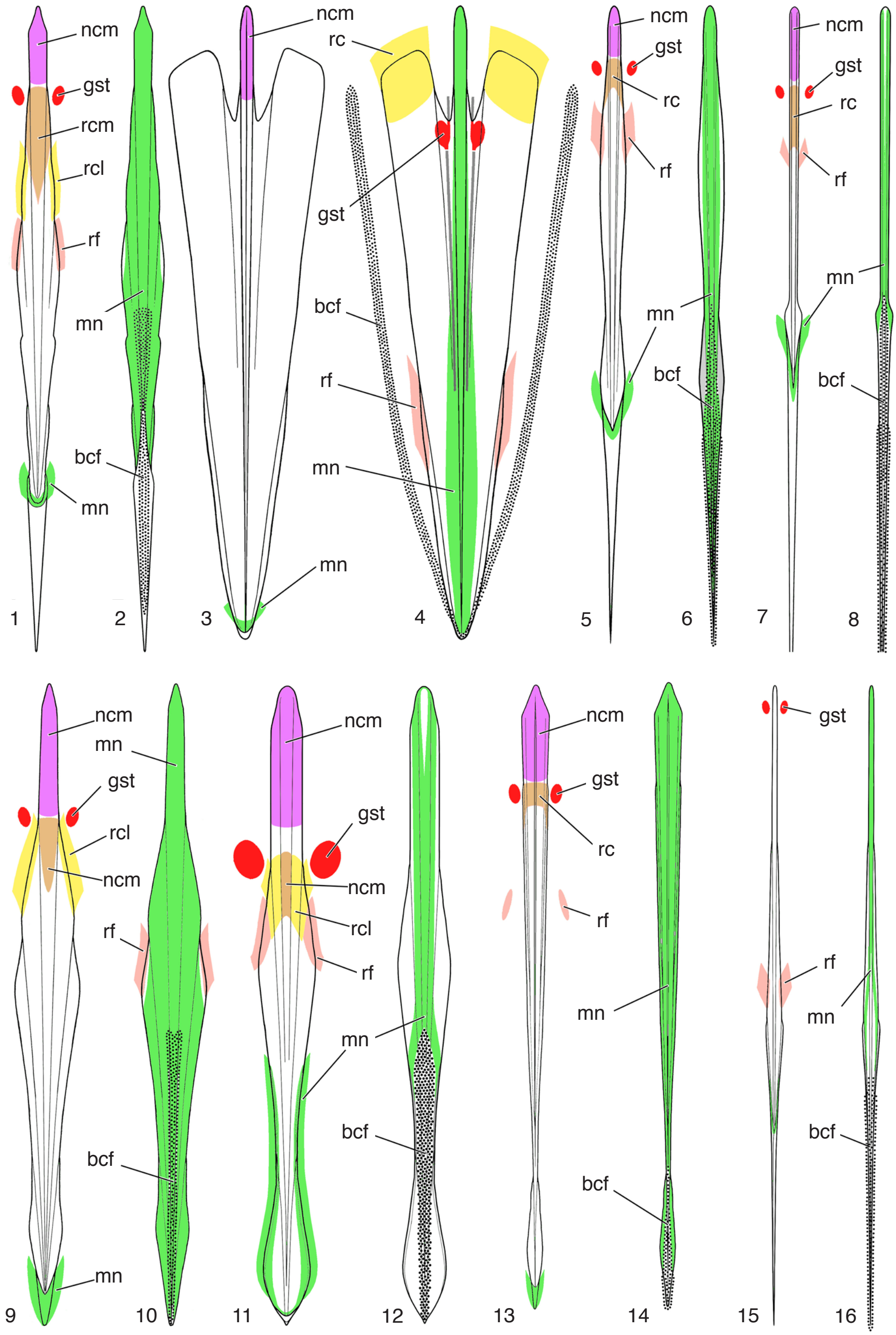

FIG. 11. *For explanation, see facing page.*

for attachment of the funnel retractors (Fig. 11.1–11.2, 11.9–11.12).

In the gladius of Thysanoteuthidae (Fig. 11.3–11.4), the unusual wide lateral vanes projecting anteriorly under the collar folds were termed in different ways, and their homology with structural parts of the other oegopsid gladii has never been confirmed (NAEF, 1921–1923; NESIS, 1982–1987; TOLL, 1988). As reflected by the muscle attachment, the lateral vanes in the thysanoteuthid gladius represent modified lateral plates. In *Thysanoteuthis* the wings are small and limited to the posterior half of the gladius, and the unusual, paired hyperbolar zones of the pro-ostracum do not appear to serve a supportive function but instead mark the locations from which the pallial nerves exit the visceral sac to the dorsal side of the gladius where they join the stellar ganglia (Fig. 11.4). Another unique feature of the *Thysanoteuthis* is that it projects inside the mantle cavity, thereby partly enveloping the visceral sac. The gills attach to the mantle wall outside from the gladius.

NAEF (1921–1923) interpreted the sword-like gladius of the Ommastrephidae (Fig. 11.13–11.14) as consisting primarily of the rachis and conus. However, thorough examination of ommastrephid gladii using serial cross-sectioning revealed the presence of paired lateral plates, a vestigial rostrum, and transverse cup-like septa in the conus (TOLL, 1990; BIZIKOV, 1996; ARKHIPKIN, BIZIKOV, & FUCHS, 2012). The paired lateral plates in ommastrephoid gladii are narrow, thickened longitudinal ribs located laterally to the rachis. Stellar ganglia mark the level of the anterior margins of the lateral plates. Wings are absent in ommastrephids, and the funnel retractors attach to the inner mantle wall, apart from the gladius. In families with chiroteuthoid gladius, such as Chiroteuthidae and Mastigoteuthidae, the pro-ostracum, as identified by the muscular attachment, consists of the rachis serving for the support of the nuchal cartilage and attachment of the head retractors, and the lateral plates serving for attachment of the funnel retractors (Fig. 11.7–11.8).

HOMOLOGIES IN THE GLADII OF VAMPYROPODA

The gladii of the Octopoda present the greatest difficulties for homological comparison with those of other Coleoidea. In extant octopods the gladius is so greatly reduced that no structural elements typical for coleoid gladius can be identified. NAEF (1921–1923) stated that the gladius in octopods consists mainly of the remnants of pro-ostracum and conus. HAAS (2002), based principally on paleontological data, suggested that the gladius in Cirrina is homologous to the conus flags—also termed wings by HAAS (2002) and lateral fields by FUCHS & DONOVAN (see *Treatise Online,* Part M, Chapter 9)—and the conus of fossil vampyromorphs.

Analysis of the muscle attachments in octopod gladius allows for a more detailed homological comparison (Fig. 12). The attachment of the mantle, retractors, and fins indicate that the gladius in cirrate octopods is a vestige of the paired lateral elements of the pro-ostracum and conus of the vampyromorph gladius. The median part of the cirrate gladius (saddle) corresponds to the median plate (rachis) of pro-ostracum. The attachment of the head retractors to the lateral wings and funnel retractors to the horns in the cirrate gladius suggests

FIG. 11. Ventral and dorsal views of muscle-shell attachments in extant squid families; *1–2,* Onychoteuthidae; *3–4,* Thysanoteuthidae; *5–6,* Mastigoteuthidae; *7–8,* Chiroteuthidae; *9–10,* Gonatidae; *11–12,* Lycoteuthidae; *13–14,* Ommastrephidae; 1*5–16,* Cranchiidae; *bcf,* position of basal cartilages of fins; *gst,* stellar ganglia; *mn,* mantle; *ncm,* nuchal cartilage; *rc,* cephalopodium (head) retractors; *rcl,* lateral component of cephalopodium (head) retractors; *rcm,* medial component of cephalopodium (head) retractors; *rf,* funnel retractors (adapted from Bizikov, 2008).

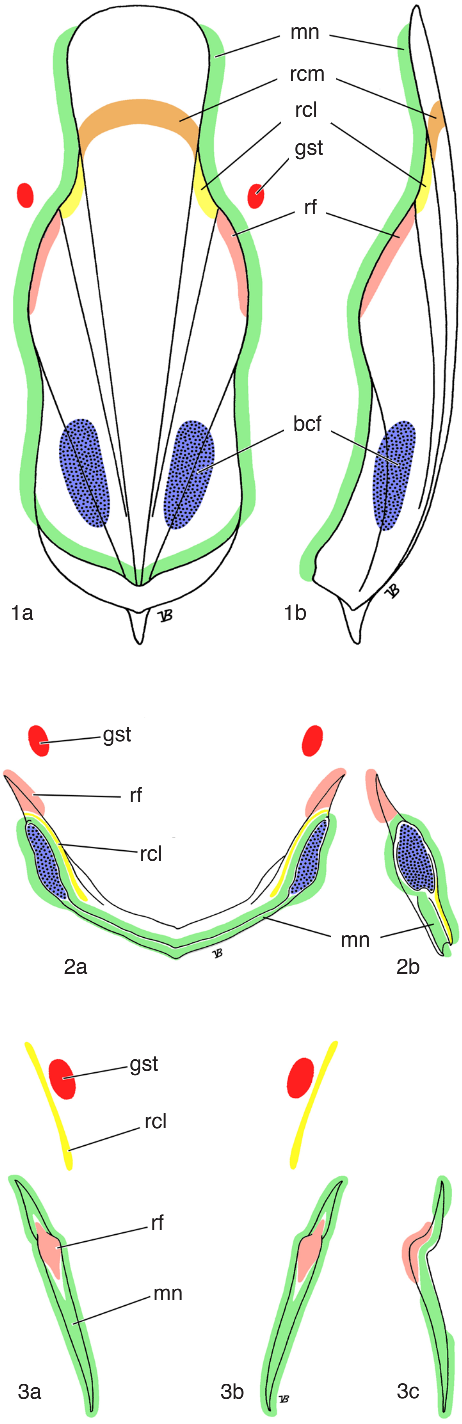

Fig. 12. *For explanation, see adjacent column.*

homology of these elements to the lateral plates and wings of the pro-ostracum, respectively. Paired rods, or stylets, in incirrate octopods correspond anatomically to the lateral parts of the gladius in primitive Cirrina (Fig. 12.3). The anterior portion of the stylets in Incirrina (anterior shoulder and the apex of the angular bend) represents the vestige of the outer parts of the lateral plates of pro-ostracum. The posterior shoulder of the stylets appears to correspond to the lateral wings and horns of cirrate gladius and to the conus flags in teuthoid gladius.

HOMOLOGIES IN THE LOLIGINOID GLADIUS

The tripartite pro-ostracum of the loliginoid gladius consists of the median plate (rachis), flanked by wide feather-like lateral vanes (Fig. 13.3–13.6). The rachis serves to support the nuchal cartilage and the attachment of the median component of the head retractors. The lateral vanes serve as attachments for the lateral components of the head retractors and the funnel retractors. A characteristic feature of the muscle attachment in the loliginoid gladius is that the lateral components of the head and funnel retractors are fused posteriorly and have a common (merged) attachment to the lateral vanes of the pro-ostracum (Fig. 13.3,5). This pattern of retractor attachments is found in all loliginid squids, as well as in the oegopsid families Bathyteuthidae and Ctenopter-

Fig. 12. Attachments of main muscles to the shell in Vampyropoda; *1a–b, Vampyroteuthis* Chun, 1903, ventral view with anterior end at the top (*1a*) and lateral view from left side with dorsal side on the right (*1b*); *2a–b, Opisthoteuthis* Verrill, 1883, dorsal view with anterior end at the top (*2a*) and lateral view from left dorsal side (*2b*); *3a–c, Octopus* Cuvier, 1797, ventral view with anterior end at the top (*1a*) and lateral view from left side with dorsal side on the right (*1b*); *bcf,* position of basal cartilages of the fins; *gst,* stellar ganglia; *mn,* mantle; *rcl,* lateral component of the cephalopodium (head) retractors; *rcm,* medial component of the cephalopodium (head) retractors; *rf,* funnel retractors (adapted from Bizikov, 2004).

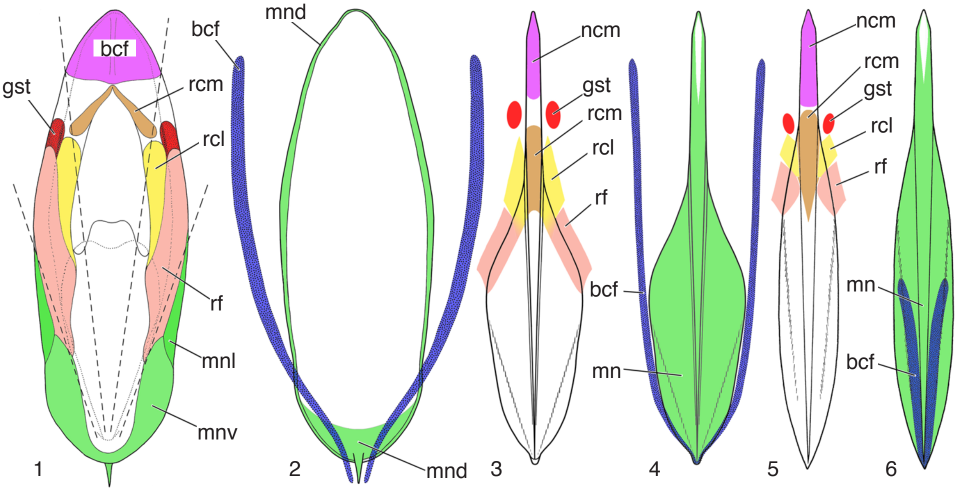

Fig. 13. Attachment of muscles to the shell; *1–2, Sepia* Linnaeus, 1758 in 1758–1759, ventral (*1*) and dorsal (*2*) views; *3–4, Chtenopteryx* Appellöf, 1890, ventral (*3*) and dorsal (*4*) views; *5–6, Loligo* Lamarck, 1798, ventral (*5*) and dorsal (*6*) views; zones of muscle attachment indicated by different colors; *bcf,* position of basal cartilages of the fins; *gst,* stellar ganglia; *mn,* mantle; *mnd,* dorsal mantle; *mnl,* lateral mantle; *mnv,* ventral mantle; *ncm,* nuchal cartilage; *rcl,* lateral component of the cephalopodium (head) retractors; *rcm,* medial component of the cephalopodium (head) retractors; *rf,* funnel retractors (adapted from Bizikov, 2008).

ygidae, which also have a loliginoid-type gladius. Homological comparison of loliginoid, onychoteuthoid, and thysanoteuthoid gladii shows that the lateral vanes in the loliginoid gladius correspond to the lateral plates and wings in the onychoteuthoid and thysanoteuthoid gladii. The presence of single lateral vanes could represent the primitive (plesiomorphic) condition in the coleoid pro-ostracum. The separation of the attachment sites of the head and funnel retractors and the corresponding differentiation of the single lateral vanes into lateral plates and wing represents the apomorphic condition.

Surprisingly, the loliginoid pattern of muscle attachment to the shell has a striking resemblance to the attachment of muscles in the cuttlebone of sepiids (Bizikov, 2008). Homological interpretation of the structural parts of the sepiid shell remains controversial. The sepion, the thick, calcified, porous cuttlebone of sepiids, has been commonly interpreted as a derivative of the phragmocone with a greatly reduced ventral part and completely reduced pro-ostracum (Naef, 1921–1923; Haas 2003). According to this interpretation, the chitinous dorsal shield that underlies dorsally the phragmocone layer, represents the dorsal wall of conotheca. However, according to Naef (1921–1923), the retractor muscles that attach to the pro-ostracum in all coleoids, in sepiids attach to the ventral surface of porous calcified layer representing the phragmocone. Khromov (1987) was the first to suggest that dorsal shield in sepiid cuttlebone corresponds to the pro-ostracum covered ventrally by modified phragmocone. He analyzed sepions that had undergone decalcification (by exposure to hydrochloric acid) and found that dissolution of the septal phragmocone exposed the structure of the dorsal shield, which, like the pro-ostracum of other coleoids, has a radial structure and consists of a wide median plate and paired lateral vanes separated by asymptotic lines.

Further confirmation that the dorsal shield of the sepiid cuttlebone is homologous with the pro-ostracum resulted from an analysis of muscular attachment to the cuttlebone (Bizikov, 2008). As demonstrated by the muscle attachment (Fig. 13.1–13.2), the median plate of the dorsal shield in sepiids supports the nuchal cartilage and serves for attachment of the median component of the head retractors. Thus, it clearly corresponds to the rachis in the typical coleoid pro-ostracum. The tripartite structure of the sepiid dorsal plate, in particular, is similar to the tripartite pro-ostracum of the loliginoid gladius. The lateral vanes of the sepiid dorsal shield provide attachment to the lateral components of the head retractors and the funnel retractors. In Sepiida, the head retractors and the lateral components of funnel retractors are fused in their posterior parts, in the same manner as in squids with a loliginoid gladius. The comparison of muscle attachment among the Sepiida and the families Loliginidae, Bathyteuthidae, and Chtenopterygidae shows that all these groups have the same general pattern of muscle attachment and corresponding pro-ostracum structure (Fig. 13), which differ from other groups of squids and Vampyropoda.

MUSCLE ATTACHMENTS IN THE *SPIRULA* SHELL

The presence of a phragmocone in *Spirula* shells traditionally supported comparisons of *Spirula* with the chambered shells of nautilids, ammonites, and belemnites (Owen, 1879; Appellöf, 1893). Moreover, the absence of a pro-ostracum in the shell of *Spirula* hampered comparison with the shells of other coleoids. However, such a comparison is possible if the relationship of the shell to soft-tissue components is considered (Fig. 14). The muscular attachment to the shell in *Spirula* is highly derived. Indeed, there are no primary muscular insertions in *Spirula,* and all insertions are derived: the muscles, including the head retractors, attach to the shell by means of a thick cartilage reinforcement of the shell sac (Bizikov, 2008). As the shell grows in its diagnostic spiral pattern, the sites of muscles attachment are constantly shifting along the shell surface. Therefore, as the body grows, the shell in *Spirula* is slowly rotating within (Bruun, 1943). The mantle in *Spirula* attaches to the shell in a unique manner, along its dorsolateral walls, which leaves the median part of the shell free (Fig. 14.2). Retractor attachment is also highly derived. Medial and lateral components of the head retractors are fused into a single circular muscle that attaches along the margins of the shell aperture. The funnel retractors attach to the mantle walls bilaterally from the shell. The shell aperture in *Spirula* is evenly circular, lacking any dorsal projection (pro-ostracum). However, the presence of the nuchal cartilage and the position of the stellate ganglia in *Spirula* suggest derivation from an ancestor with a well-developed pro-ostracum. The position of the fins bases, as well as the mantle attachment in *Spirula* is consistent with its apparent homology with the phragmocone of cuttlefishes and is indicative of a homology with the conus of squids.

EVOLUTIONARY DEVELOPMENTS OF THE LOCOMOTORY APPARATUS

The only extant representative of ectocochleate cephalopods, *Nautilus,* has a single means of locomotion—jetting—with two modes, slow and fast (Bizikov, 2002). In the slow-jetting mode, thrust is generated as a side effect of respiration, by means of undulating movements of the collar folds. In the fast-jetting mode, the thrust is generated by rapid, piston-like movement of the head inside the living chamber resulting from contraction of the primary locomotory muscles in *Nautilus*, the head retractors (Fig. 15.1). The funnel retractors in *Nautilus* are comparatively weak and reduced in size; in fossil Nautiloidea the funnel retractors could be attached to the shell, ventrally from the head retractors (Mutvei, 1964; Kröger & Mutvei, 2005).

In Coleoidea, the slow-jetting mode by means of undulation of the collar folds was lost, and the mechanism of the fast-jetting mode changed radically: the head became

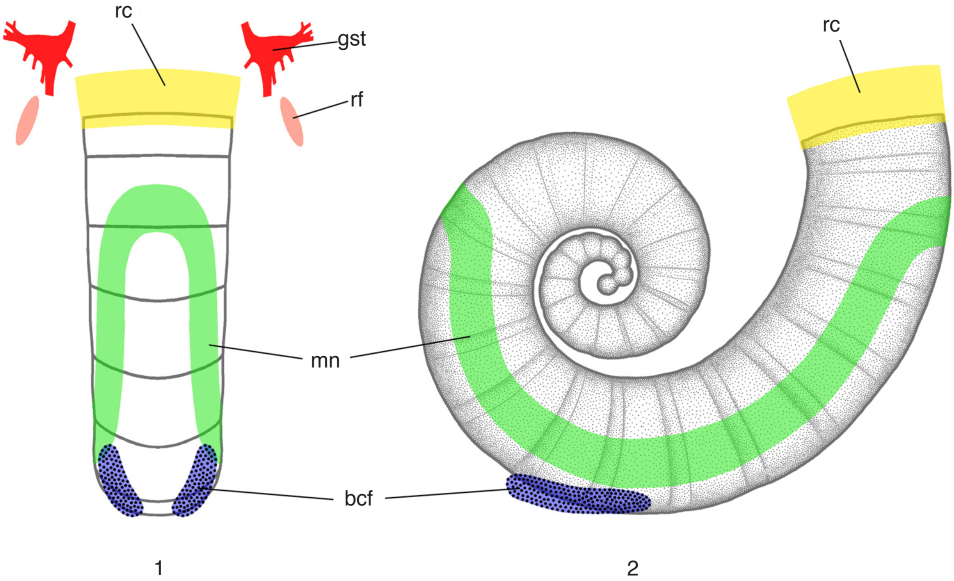

Fig. 14. Attachment of muscles to the shell in *Spirula* LINNAEUS, 1758 in 1758–1759; *1,* dorsal view of the shell (anterior end is at the top); *2,* lateral view (dorsal side is on the right); zones of muscle attachment are marked by different colors; *bcf,* position of basal cartilages of the fins; *gst,* stellar ganglia; *mn,* mantle; *rc,* cephalopodium (head) retractors; *rf,* funnel retractors (adapted from Bizikov, 2004).

fixed by connection with the nuchal cartilage and thrust is generated by contraction of the muscular mantle (Fig. 15.2). The attachment of the gills along the mantle walls by special ligaments allows continuous respiration during fast jetting; it also resolves a functional conflict between the respiratory and locomotory systems and makes the continuous jetting swimming possible (BIZIKOV, 2002). Some Coleoidea, however, acquired an additional means of locomotion, swimming by fin undulation. As a result of this transformation, the head retractors in Coleoidea lost their locomotory function and became reduced to a thin, muscular envelope around the visceral sac. In contrast, the funnel retractors became strong and powerful to control the funnel's position under the increased loads associated with fast jetting. In general, the main locomotory muscles in coleoids are those differentiated from the primary mantle fold, the muscular mantle and fins.

The use of the mantle for generating jetting thrust in Coleoidea required the presence of the pro-ostracum, the anterior projection of the shell, to support the mantle. The earliest Coleoidea are believed to lack the pro-ostracum (JELETZKY, 1966). The first coleoid groups to evolve a definitive pro-ostracum are Phragmoteuthida and Belemnitida (JELETZKY, 1966).

There are two alternative views on the origin of pro-ostracum. Some authors interpreted the pro-ostracum as a dorsal remnant of the body chamber, which evolved as a reduction of lateral and ventral walls of the body chamber in ancient coleoids (NAEF, 1922; JELETZKY, 1966; TOLL, 1998). Other investigators pointed to the differences in the ultrastructure of the coleoid pro-ostracum and conotheca, arguing that the pro-ostracum represents a novel morphological feature of coleoids that evolved independently from the living chamber (DOGUZHAEVA, MUTVEI, & WEITSCHAT, 2003). The former hypothesis seems to be more likely, as in all extant coleoids the pro-ostracum is formed by the same two layers (middle and inner) that form the conus and its flags (BIZIKOV, 2002). The fact that retractor muscles typically

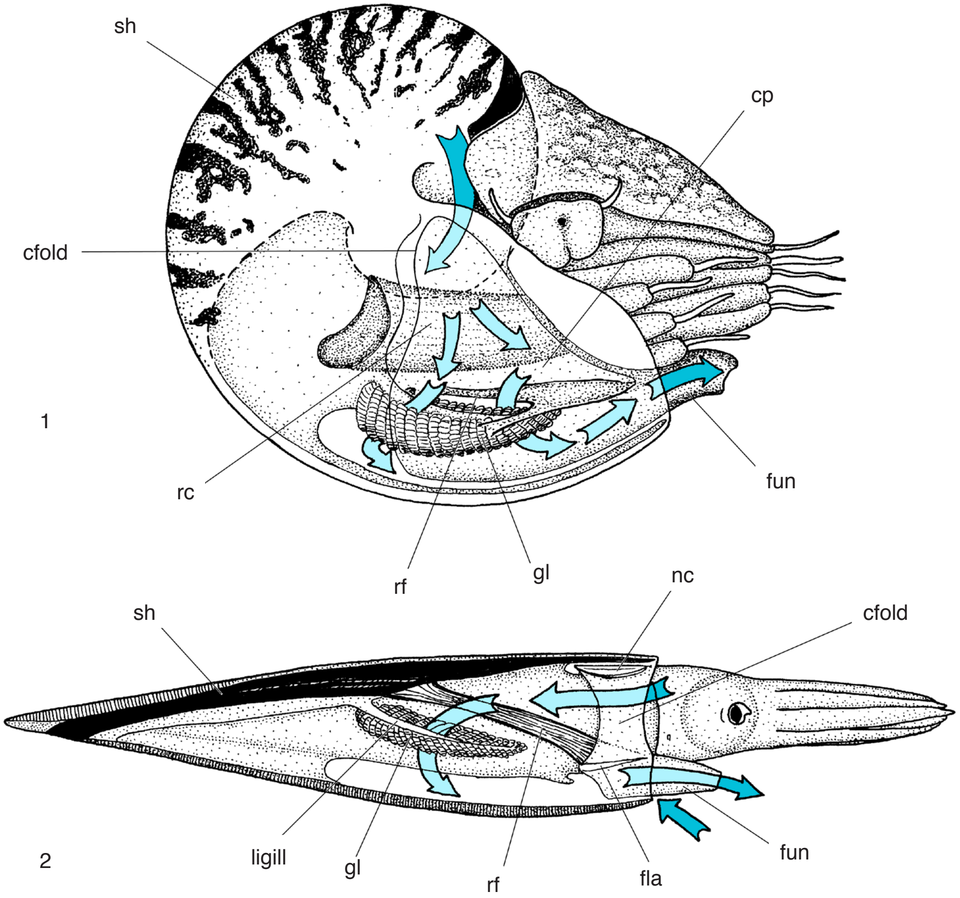

FIG. 15. Comparison of swimming and breathing mechanisms; arrows show the flow of water during breathing and swimming; *cfold,* collar folds; *cp,* collar pockets; *fla,* closer bond of the funnel; *fun,* funnel; *gl,* gills; *ligill,* ligament connecting gills to the lateral mantle wall; *nc,* nuchal cartilage; *rc,* cephalopodium (head) retractors; *rf,* funnel retractors; *sh,* shell; *1, Nautilus* LINNAEUS, 1758 in 1758–1759 (adapted from Wells, 1988); *2,* squids (adapted from Naef, 1921–1923).

attach to the pro-ostracum, and this attachment represents primary insertion, is another strong evidence that the pro-ostracum evolved through the reduction of the living chamber.

It is beyond any reasonable doubt, however, that the development of pro-ostracum was accompanied by the reduction of the living chamber. The phragmocone also decreased in size. As a result of overgrowth of the shell by the mantle, a new shell layer (the outer layer) appeared on the former outer surface of the shell. This layer was already present in Paleozoic coleoids with no pro-ostracum (DOGUZHAEVA, MAPES, & MUTVEI, 2002).

The calcification of the shell in Coleoidea is functionally related to the presence of a gas-filled phragmocone. It is commonly assumed that the mechanism of pumping fluid out of the cameral phragmocone in fossil phragmocone-bearing coleoids was basically the same as in recent *Nautilus* LINNAEUS, 1758 in 1758–1759, *Sepia,* and *Spirula* (DENTON & GILPIN-BROWN, 1973). Hence, the gas pressure inside the phragmocone in fossil coleoids was most probably roughly equivalent to that in extant phragmocone-bearing forms: about 0.7 atmospheres. Had the phragmocone been decalcified, at such a low internal pressure, it would not have been capable of withstanding the ambient water pressure, even at a depth of several meters, let alone lower depths. Thus, calcification of the shell in cephalopods represents a strict requirement for functioning as a gas-fluid hydrostatic apparatus.

On the other hand, an internal skeleton, if not segmented as in the Vertebrata, must be flexible, elastic, and light. Apparently, decalcification of the coleoid shell occurred rather quickly in geologic time (BIZIKOV, 2008). Among Holocene Coleoidea, a calcified shell is always associated with a phragmocone—with the exception of the incirrate genus *Scaeurgus,* in which calcification of the stylets is almost certainly a secondary derivation resulting from a uncalcified plesiomorphic condition. Belemnitids provide one of the most vivid examples of functionally conditioned decalcification of the shell: their hydrostatic apparatus (the phragmocone and its counterweight, the rostrum) were calcified, while their support structure, the pro-ostracum, was mainly chitinous (NAEF, 1922; JELETZKY, 1966, DOGUZHAEVA, MAPES, & MUTVEI, 2002).

The trend in gladius reduction that lead to its complete loss can be traced in all major groups of Coleoidea. Final loss of the gladius usually occurred in specialized benthic forms (some Octopodoidea, Idiosepiidae) and planktonic forms (Argonautoidea, Bolitaenoidea, and Cranchiidae). The absence of the gladius typically was associated with the reduction or loss of the ability to swim by jetting but was never associated with significant alterations in the general Bauplan.

In squid ancestors, the reduction of the phragmocone likely occurred prior to the shell decalcification (ARKHIPKIN, BIZIKOV, & FUCHS, 2012). Having lost the air-filled phragmocone, ancestors of extant squids exploited an evolutionary opportunity to radiate to deeper waters.

The presence of a decalcified shell, the gladius, in the sepiolids (Sepiolidae), incirrate octopods (again, with singular exception of *Scaeurgus*), and teuthoids, as well as the remarkable morphological variability of the gladius among extant taxa indicates that the modern gladius developed repeatedly and independently in different coleoid clades. In fact, coleoids developed the gladius each time decalcification of the shell provided an adaptive opportunity. As the growth of the shell in coleoids always proceeds through bio-crystallization of carbonate material within an organic (chitinous) matrix (BANDEL & BOLETZKY, 1979), the cessation of carbonate deposition always held out the potential for anatomical and morphological divergence of resulting chitinous skeletal structure: the gladius. Evolutionary adaptation of the gladius involved transformation of the shell into a supporting skeletal structure and diversification toward more active and maneuverable squid-like forms. The grouping known as the squids represents a convergent set, rather than a distinct systematic taxon. Therefore, phragmocone-lacking coleoids, currently included into the order Teuthida NAEF, 1916, represent a polyphyletic taxon (BIZIKOV, 2008). Numerous morphological and molecular data support this view (e.g., CARLINI & GRAVES, 1999; CARLINI, REECE, & GRAVES, 2000; LINDGREN, GIRIBET, & NISHIGUCHI, 2004).

CONVERGENCE IN EVOLUTION OF LOCOMOTORY AND SKELETAL SYSTEMS BETWEEN COLEOIDS AND FISHES

A comparison of the evolution of the internal skeleton and locomotory system in coleoid cephalopods and primitive Vertebrata (armored, jawless, fish-like fossil vertebrate groups) showed that the principal morpho-functional solutions realized in evolution of locomotory system in coleoids mimicked those previously demonstrated by the primitive Vertebrata (BIZIKOV, 2008). However, in coleoids these solutions were realized on a significantly different (molluscan) Bauplan. The parallels between coleoids and primitive, armored, jawless ancestors of fishes is manifested as follows (BIZIKOV, 2008):

1. Both coleoids and primitive vertebrates developed an internal, longitudinal skeletal element that is comparable with the body in size: the gladius and notochord, respectively.
2. In both groups the cartilage skeleton developed around a longitudinal support element to strengthen attachment of the muscles, and special cartilages developed to protect the central nervous system.
3. On the basis of a longitudinal support element surrounded by cartilage skeleton, new locomotory organs developed that used an undulatory means of locomotion: muscular fins in coleoids and tail and long fins in primitive fish.
4. Development of an internal skeleton in both coleoids and primitive, fishlike, jawless vertebrates was accompanied by the reduction of an external skeleton: in cephalopods it occurred through derivation of an internal shell from an external one; in primitive Vertebrata it was achieved through the reduction of extensive dermal armor that existed in primitive ostracoderms (e.g., Pteraspidomorphi and Galeaspida).

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