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COMPARATIVE MORPHOLOGICAL STUDY OF SOME TELLINIDAE FROM THAILAND (BIVALVIA: TELLINOIDEA)

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***ABSTRACT.* –** A comparative study of seven species of Tellinidae, collected at Kungkrabaen Bay, Gulf of Thailand, is presented. The species are *Serratina capsoides* (Lamarck, 1818), *Moerella* cf. *nitens* (Deshayes, 1854), *Cadella* cf. *semen* (Hanley, 1845), *Pinguitellina* cf. *pinguis* (Hanley, 1844), *Elpidollina* sp., and *Tellinides timorensis* (Lamarck, 1818) of the subfamily Tellininae, and *Macomona* sp. of the subfamily Macominae. With the objective of performing the study in a comparative and testable scenario, a phylogenetic analysis was carried out based on 43 morphological characters (94 states). A single cladogram was obtained as follows: (*Serratina capsoides* (*Tellinides timorensis* (*Pinguitellina* cf. *pinguis* (*Cadella* cf. *semen* (*Moerella* cf. *nitens* (*Elpidollina* sp. – *Macomona* sp.))))))). A semelid and a solenid were operationally analyzed as part of the ingroup; polarisation was based on a plicatulid. In this analysis, Tellinoidea and Tellinidae were monophyletic, supported by 19 and 9 synapomorphies, respectively. Tellininae was paraphyletic. Good and significant morphological differences were found for all taxa, including at the species level. Some structures are reported for the first time, such as pseudogills, insertion of the pedal protractor dividing the anterior adductor muscle, and a circular muscle surrounding part of the anterior adductor muscle.

***KEYWORDS.* –** Tellininae, Macominae, morphology, anatomy, phylogeny, systematics.

INTRODUCTION

Members of the family Tellinidae are typically characterised by rapid burrowing and by pretty, usually pink-pigmented, flattened shells. The outer surface is normally opaque, but in some species can be glossy. Sculpture is typically commarginal, with delicate undulations and growth lines, but some species possess radial or oblique striations with more elevated commarginal scales. Representatives of the tellinids occur in all oceans, latitudes, and depths, but they are more common in tropical and shallow waters. They occur mostly in the open sea, but some estuarine species also exist. As far as is known, tellinids only occur on soft bottoms (sand or mud) and lack a byssus (Holme, 1961).

Despite the diversity and ecological importance of the tellinids, there is almost unanimity among malacologists that the taxonomy of the family is chaotic. The systematics of the family is almost, if not completely, based on conchological characters, which have proven to be uninformative to resolve the issues. Taxonomic definition at all levels, from family to species, is problematic.

During the International Marine Bivalve Workshop at Kungkrabaen Bay, Chantaburi, Thailand, the idea arose of incorporating anatomy to possibly identify additional characters that could help to resolve the taxonomic problems of Tellinidae. The aim of this investigation is to test the strength of studying anatomy for tellinid systematics. For this propose, a comparative discussion of the morphological characters is provided. A phylogenetic analysis is provided, but no intention of phylogenetic inference is suggested in so small a sample of a highly diverse group. The intention is only to enhance the character discussion using the testable, falsifiable platform provided by phylogenetic methodology.

MATERIALS AND METHODS

The specimens were collected during the fieldwork period at the workshop. They were maintained alive in seawater for a number of days for live dissection. Following this, all specimens were fixed in 70% ethanol for further studies.

Dissections were made under a stereomicroscope, with specimens immersed in fixative or seawater. Dissection techniques were standard. Digital photographs of all major steps in each dissection were taken. All drawings were obtained with the aid of a camera lucida. Presented measurements were obtained from selected specimens, normally those dissected (these specimens are labeled as such in the collection); the measurements are (anteroposterior) length, (dorsoventral) height, and (latero-lateral) width, all in mm.

The description of the first and most abundant species, *Serratina capsoides*, is the most complete. For the remaining species, the description is comparative and more focused on distinctions. The same approach is given in the figures.

Type specimens examined from the collection of The Natural History Museum (BMNH), London, U. K., were as follows: *Tellina nitens* Deshayes, 1854, holotype/syntype, BMNH 20060798, 19.01 by 11.25 mm; *T. semen* Hanley, 1845b, 4 possible syntypes (2 specimens and 2 valves), BMNH 20060797, largest specimen 12.10 by 8.05 mm; *T. pinguis* Hanley, 1844a, types not found – the photographed specimen was the measured holotype/syntype of *T. naovaecaledonia* Baird, 1873, BMNH 20060801, 8.5 by 6.85 mm; *T. cygnus* Hanley, 1844b, probable holotype/syntype, BMNH 1874.12.11.373, 13.57 by 9.62 mm; *T. australis* Deshayes, 1854, types not found – the examined specimen was from the non-type BMNH collection.

The comparative biology part of this paper is presented as a phylogenetic (cladistic) analysis, which is the most practical and testable method. However, no intention is suggested to consider this analysis as "the phylogeny of the tellinids". Nevertheless, it is expected that the putative phylogenetic relationships among the species will remain even with the addition of more species and that some taxonomic inferences can already be made. The analysis was performed with the aid of the program Tree Gardener (Ramos, 1997; under a few modifications for Windows XP), which is basically an interface for the program Hennig86 (Farris, 1988). The algorithm used was "ie." Two species were used as outgroups to root the cladogram: *Plicatulostrea onca* Simone & Amaral, 2008 (Plicatulidae; see description in this volume) and *Solen curtus* Des Moulins, 1832 (Solenidae; L. Simone, unpubl. data). Another two species were outgroups, but they were operationally analyzed as part of the ingroup; these are *Semele sinensis* Adams, 1853, and *S. carnicolor* (Hanley, 1845a) (Semelidae). This measure is for testing the monophyly of the tellinids; conversely, the indices are shared with these semelids. In the Discussion of Characters, a short descriptive sentence is given for each character, followed by plesiomorphic and apomorphic states and conditions in the most parsimonious hypothesis; a list of taxa is usually given only for those bearing the apomorphic states. The consistency index (CI) and the retention index (RI) are given last, expressed as percentages. Several other characters were considered but excluded from this analysis because their states were overlapping or purely autapomorphic. However, some autapomorphic states were retained; this measure is based on interest in the character state or to test its importance.

SYSTEMATICS

Serratina capsoides (Lamarck, 1818)

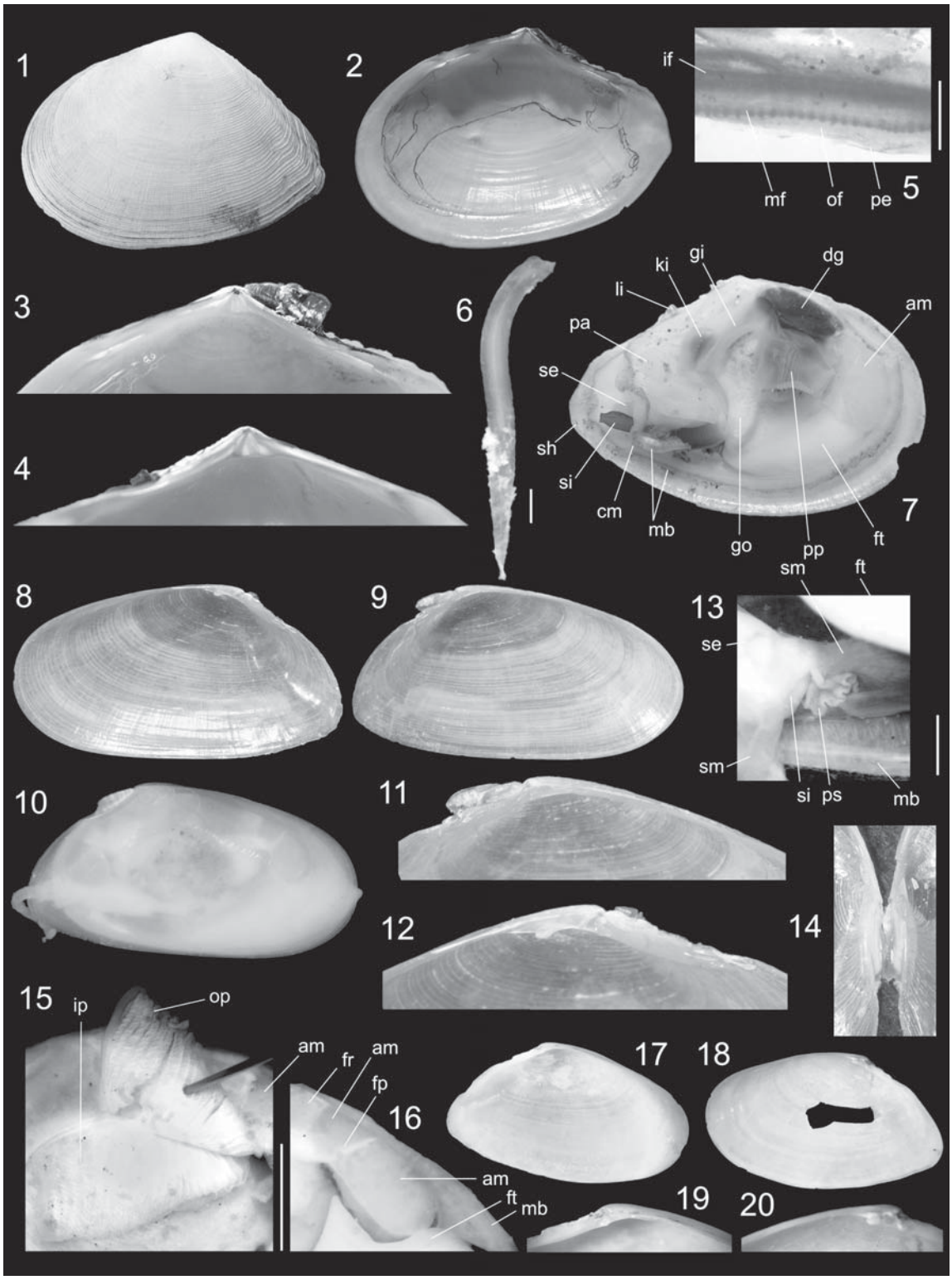
(Figs. 1–7, 74–82)

Tellina capsoides Lamarck, 1818: 149; Küster & Römer, 1841: 48–49, pl. 14, figs. 1–3; Sowerby, 1867: pl. 33, fig. 183.
Tellina (*Serratina*) *capsoides*: Robba et al., 2002: 97, pl. 14, fig. 3.
Serratina capsoides: Rosenberg, 2006.
For additional synonymy, see Robba et al., 2002: 97.

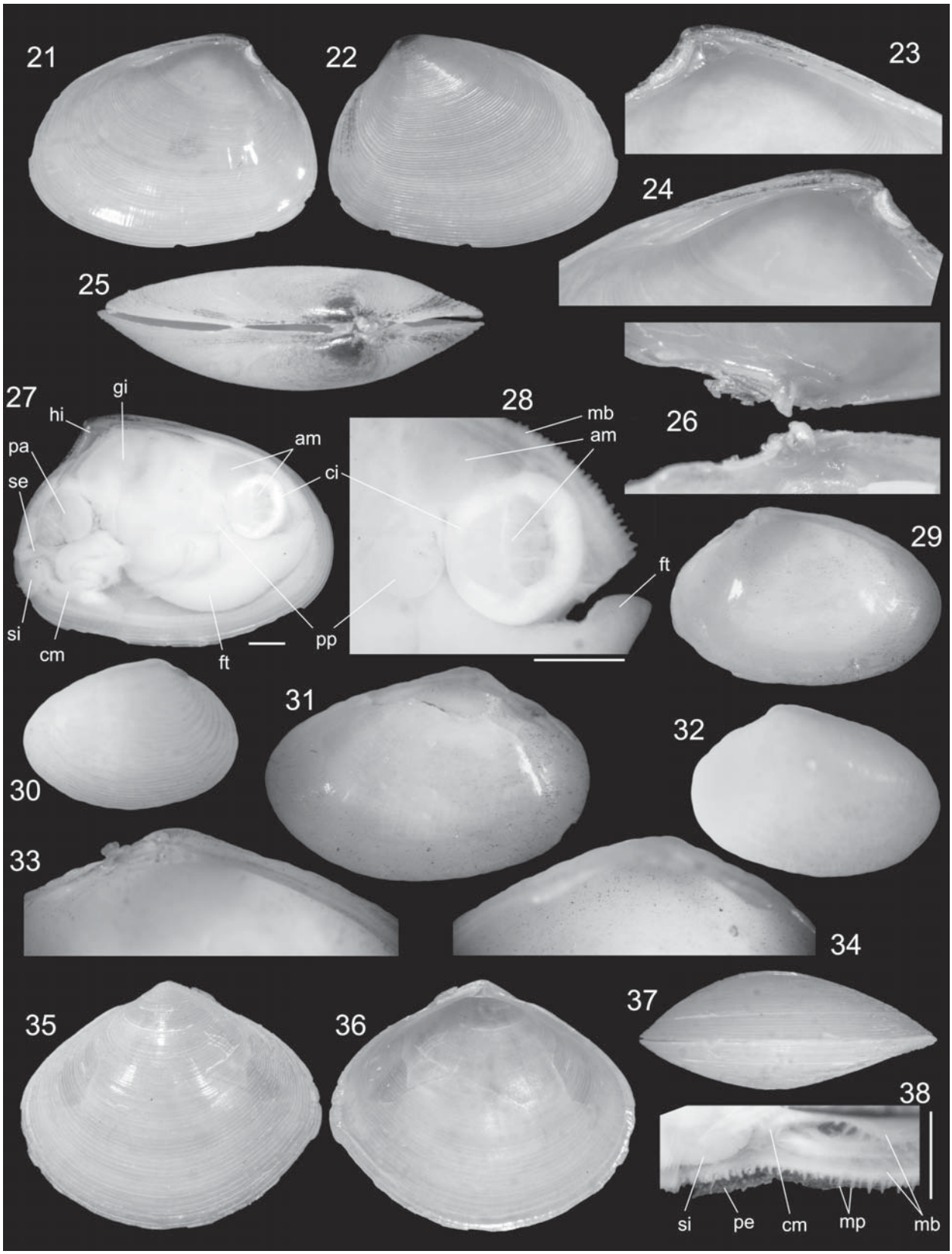
Material examined. – All Thailand, Chantaburi (Gulf of Thailand), Kungkrabaen Bay, 12°35.16'N–12°35.31'N 101°54.40'E–101°54.29'E, sta. KKB-03/04, "middle of bay station", coll. Simone & Wilkinson, Aug.2005; 52 ex. (MZSP 62352); 5 ex. (MZSP 62330); 5 ex. (MZSP 55034).

Description. – Shell (Figs. 1–4, 7, 74): Outline somewhat circular (dorsoventral height ca. 70% of anteroposterior length); laterally flattened (width ca. one-quarter of length); walls relatively thick, weakly curved to right; left valve slightly more concave than right valve. Colour whitish to pale green. Umbones bluntly pointed, at approximately mid-valve or somewhat posterior. Anterior edge amply rounded, continuous with anterior edge of umbo. Ventral edge rounded. Posterior edge straight, as posterior continuation of umbo, with narrow slope (Fig. 1), and low, wide carina along lateral edges of slope. Transition between posterior and ventral edges marked by rounded edge, more weakly rounded than umbo. Sculpture uniformly commarginal, with low scales somewhat longer on posterior region, particularly on posterior slope (Fig. 1), four or five per mm; each scale separated from neighboring scales by space equivalent to four to five times its width. Very delicate radial furrows detectable in interspaces between scales, of width and concentration equivalent to those of commarginal sculpture; stronger on anterior and mid regions. Inner surface whitish, glossy (Figs. 2–4). Cardinal teeth restricted to infraumbonal region, consisting of three teeth disposed divergently; anterior teeth somewhat longer (Figs. 2–4). Pair of almost symmetrical lateral teeth, anteroposteriorly elongated, running parallel and at short distance from dorsal shell edge, each approximately midway between umbo and posterior or anterior end. Ligament external, larger from umbo to mid region of posterior shell edge. Muscle scars very shallow (Fig. 2). Scar of anterior adductor muscle elliptical, dorsoventrally elongated, with dorsal and ventral ends pointed, occupying ca. one-fifteenth of inner valve surface, located at short distance surrounding anterior edge. Scar of posterior adductor muscle ca. two-thirds size of anterior scar. Ventral region of pallial sinus somewhat pointed posteriorly. Pallial sinus wide, forming arch ca. half size of valve, running close to, but at some distance from anterior adductor muscle scar (Fig. 2). Scar of cruciform muscle located in pallial line parallel to mantle edge, directly below posterior adductor muscle, at posteroventral end of pallial sinus.

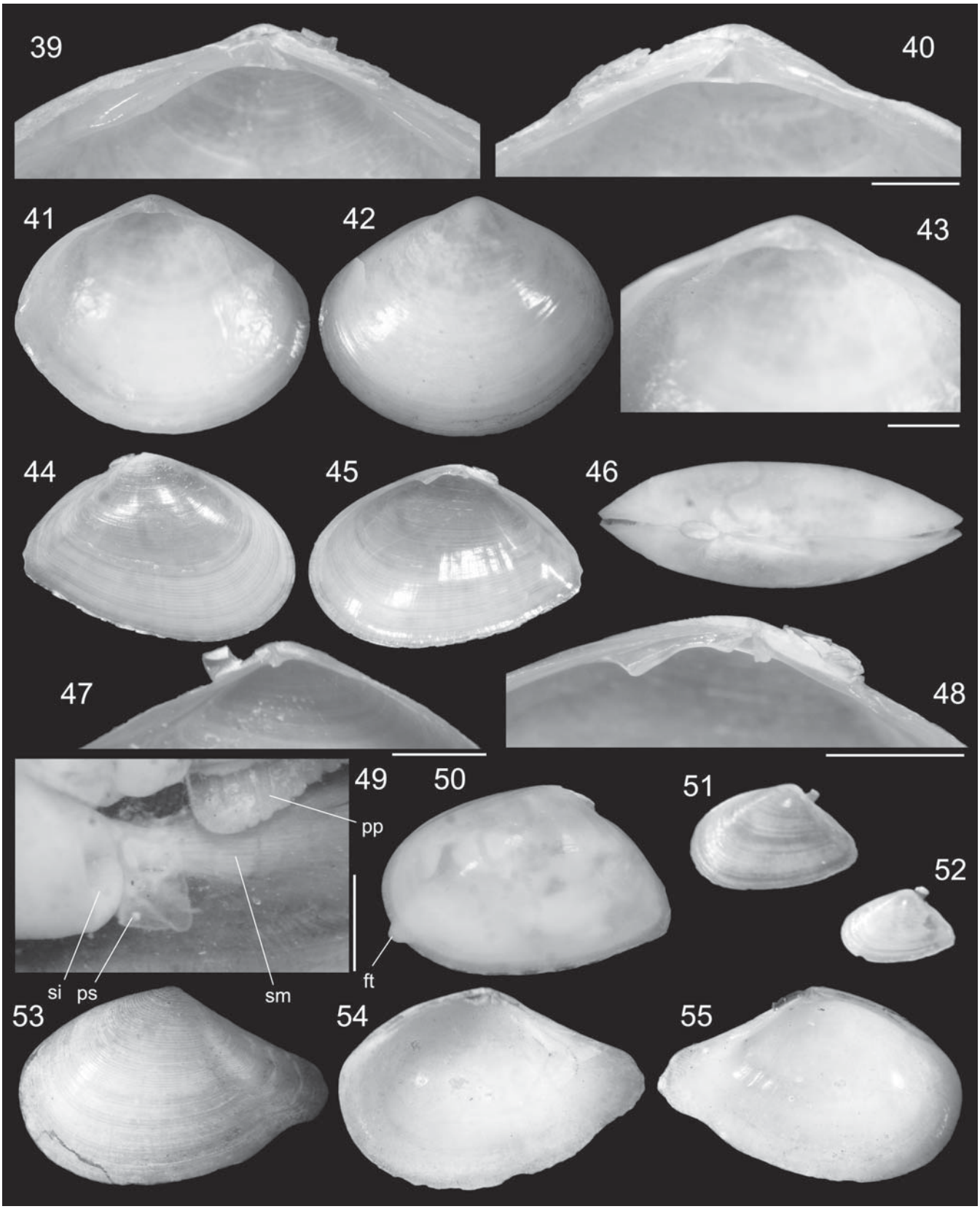
Main muscle system (Figs. 7, 74, 80): Anterior adductor muscle elliptical in cross section, dorsoventrally elongated, situated obliquely, parallel to and at short distance from shell



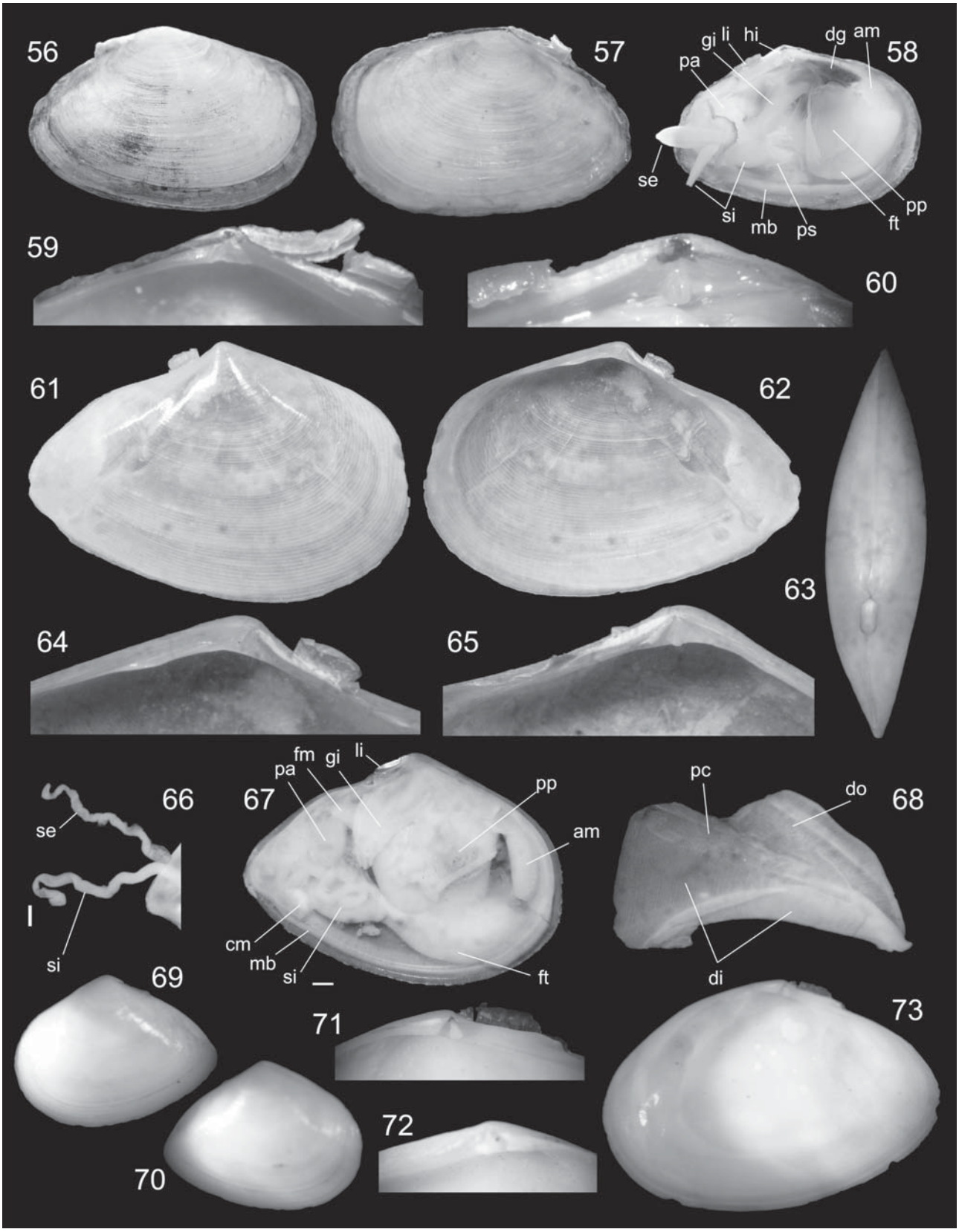
Figs. 1–20. Shells and anatomical aspects: 1–7, *Serratina capsoides* (MZSP 62353, length 32.5 mm): 1, left valve, external view; 2, right valve, interior view, muscle scars artificially emphasised with pencil; 3, hinge, right valve; 4, hinge, left valve; 5, detail of mantle border in mid region of ventral side, interior view; 6, crystalline style, isolated, gastric end uppermost; 7, whole right view, right valve and part of right lobe removed. 8–16, *Moerella* cf. *nitens* (MZSP 62347, length 9.7 mm): 8, right valve, interior view; 9, left valve, interior view; 10, whole right view, some structures seen by transparency; 11, hinge, left valve; 12, hinge, right valve; 13, detail of siphonal base showing pseudogill, left mantle lobe, interior view, right portion of siphonal retractor muscle deflected; 14, hinge, both valves connected but opened, ventral view; 15, right palp and adjacent region, right view, interior hemipalp deflected; 16, anterior adductor muscle and adjacent region, right view. 17–20, *Moerella nitens*, type specimen (BMNH 20060798, length 19 mm): 17, left valve, interior view; 18, right valve, interior view; 19, hinge, left valve; 20, hinge, right valve. am, anterior adductor muscle; cm, cruciform muscle; dg, digestive diverticula; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; gi, gill; go, gonad; if, inner fold of mantle border; ip, inner hemipalp; ki, kidney; li, ligament; mb, mantle border; mf, middle fold of mantle border; of, outer fold of mantle border; op, outer hemipalp; pa, posterior adductor muscle; pe, periostracum; pp, palp; ps, pseudogill; se, excurrent siphon; sh, shell; si, incurrent siphon; sm, siphonal retractor muscle. Scale bars = 1 mm.



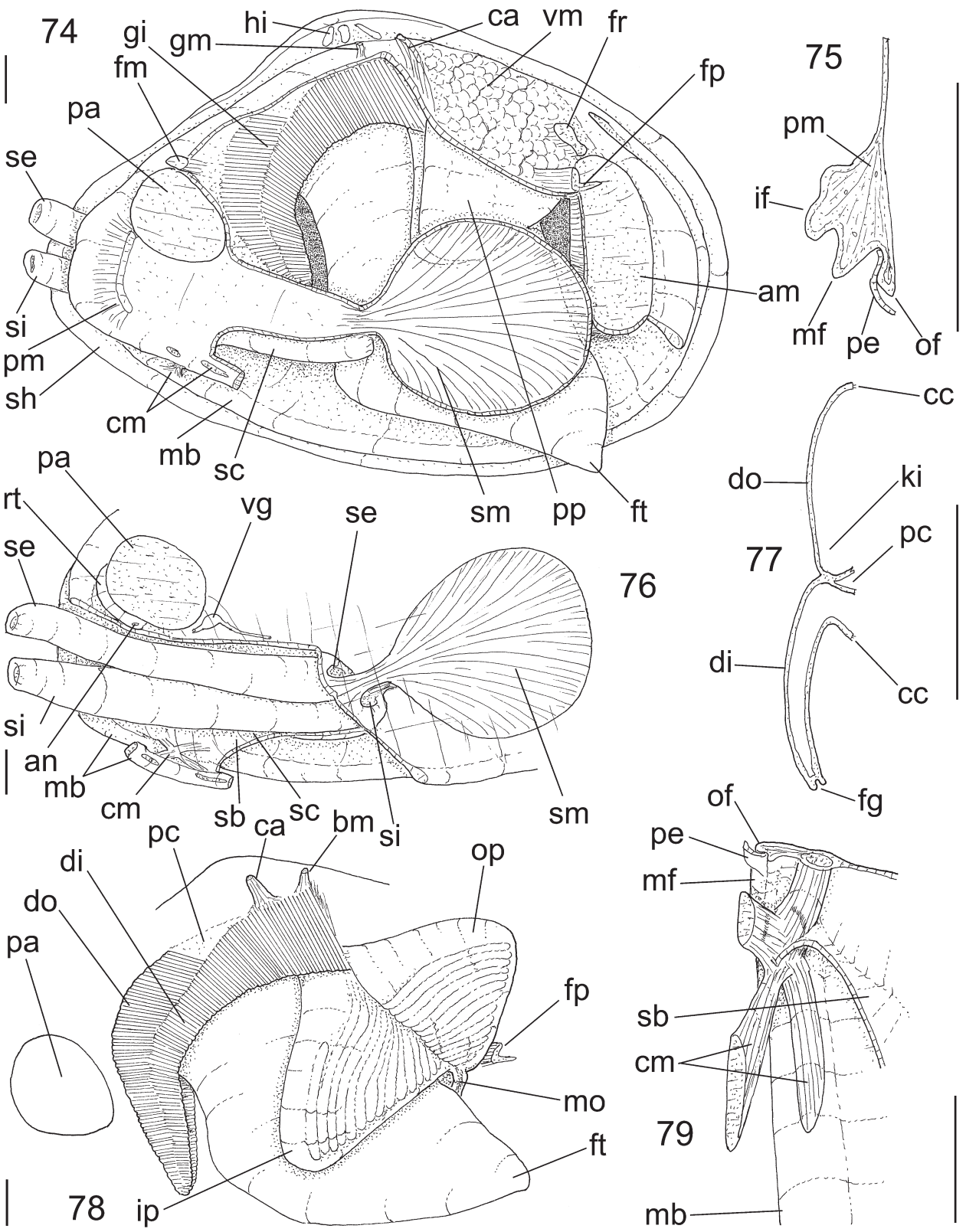
Figs. 21–38. Shells and anatomical aspects: 21–28, *Cadella* cf. *semen* (MZSP 62346, length 9.0 mm): 21, right valve, interior view; 22, same, exterior view; 23, hinge, left valve; 24, hinge, right valve; 25, articulated dorsal view; 26, hinge of both valves, ventral view; 27, whole right view, right valve and part of right mantle lobe removed; 28, region of anterior adductor muscle, right view, part of adjacent mantle lobe removed. 29–34, *Tellina semen*, syntypes (BMNH 20060797, length of largest specimen 12.1 mm): 29, left valve, interior view; 30-31, whole left views; 32, whole right view; 33, hinge, left view; 34, hinge, right valve. 35–38, *Pinguitellina pinguis* (MZSP 62345, length 9.1 mm): 35, left valve, exterior view; 36, same, interior view; 37, articulated ventral view; 38, detail of ventral region of mantle border, in siphonal base, mantle border weakly deflected, shell removed. am, anterior adductor muscle; ci, circular muscle fibers of anterior adductor muscle; cm, cruciform muscle; ft, foot; gi, gill; hi, hinge; mb, mantle border; mp, mantle papillae; pa, posterior adductor muscle; pe, periostracum; pp, palp; se, excurrent siphon; si, incurrent siphon. Scale bars = 1 mm.



Figs. 39–55. Shells and anatomical aspects: 39–43, *Pinguitellina pinguis* (MZSP 62345, length 5.3 mm): 39, hinge, right valve; 40, hinge, left valve. 41–43, possible type specimen (see text), left valve; 41, interior view; 42, exterior view; 43, hinge. 44–52, *Elpidollina* sp. (MZSP 62351, length 8.4 mm): 44, right valve, exterior view; 45, same, interior view; 46, articulated dorsal view; 47, hinge, left view; 48, hinge, right valve; 49, region of base of siphon, right view; 50, whole left view, some structures seen by transparency; 51, left valve of another specimen (length 12.0 mm); 52, same (length 7.8 mm). 53–55, *Pinguimacoma cygnus*, type specimen (BMNH 1874.12.11.373, length 13.6 mm): 53, left valve, exterior view; 54, right valve, interior view; 55, left valve, interior view. ft, foot; pp, palp; ps, pseudogill; si, incurrent siphon; sm, siphonal retractor muscle. Scale bars = 1 mm.



Figs. 56–73. Shells and anatomical aspects: 56–60, *Tellinides timorensis* (MZSP 62343, length 18.3 mm): 56, right valve, exterior view; 57, same, interior view; 58, whole right view, right valve and part of right mantle lobe removed. 59, hinge, right valve; 60, hinge, left valve. 61–68, *Macomona* sp. (MZSP 62342, length 14.1 mm): 61, right valve, exterior view; 62, same, interior view; 63, whole dorsal view; 64, hinge, right valve; 65, hinge, left valve; 66, detail of uncoiled siphons; 67, whole right view, right valve and part of right mantle lobe removed; 68, isolated right gill, interior view. 69–73, *Macomona australis* (BMNH, see text): 69, whole left view; 70, whole right view; 71, hinge, right valve; 72, hinge, left view; 73, right valve, interior view. am, anterior adductor muscle; cm, cruciform muscle; dg, digestive diverticula; di, inner demibranch; do, outer demibranch; fm, posterior pedal retractor muscle; ft, foot; gi, gill; hi, hinge; li, ligament; mb, mantle border; pa, posterior adductor muscle; pc, pericardium; pp, palp; ps, pseudogill; se, excurrent siphon; si, incurrent siphon. Scale bar = 1 mm.



Figs. 74–79. *Serratina capsoides* anatomy: 74, Whole right view, right valve and part of mantle lobe removed; 75, mantle border, transverse section at mid level of ventral region; 76, detail of posteroventral region, right view, mantle portion of siphonal chamber partially removed; 77, gill, transverse section in mid region; 78, pallial structures, right view, topology of some adjacent structures also shown; 79, detail of cruciform muscle, right view, some portions of mantle removed. am, anterior adductor muscle; an, anus; bm, branchial muscle; ca, cardinal muscle; cc, ciliary connection; cm, cruciform muscle; di, inner demibranch; do, outer demibranch; fg, gill food groove; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; gi, gill; gm, gill retractor muscle; hi, hinge; if, inner fold of mantle border; ip, inner hemipalp; ki, kidney; mb, mantle border; mf, middle fold of mantle border; mo, mouth; of, outer fold of mantle border; op, outer hemipalp; pa, posterior adductor muscle; pc, pericardium; pe, periostracum; pm, pallial muscles; pp, palp; rt, rectum; sb, siphonal membrane; sc, siphonal chamber; se, excurrent siphon; sh, shell; si, incurrent siphon; sm, siphonal retractor muscle; vg, visceral ganglia; vm, visceral mass. Scale bars = 2 mm.

edge; area equivalent to one-twentieth of shell area. Posterior adductor muscle somewhat triangular in cross section, located in posterior region opposed to and at same level as anterior adductor muscle; occupying ca. half of anterior adductor muscle area; inferior region wider than superior region. Two anterior pairs of pedal muscles. Pair of pedal protractor muscles disposed anteroposteriorly; originating just dorsal to anterior adductor muscle, closer to its anterodorsal edge; area ca. one-twentieth of latter muscle; running towards posterior, splaying like a fan in mid and ventral regions of visceral sac lateral walls, thicker ventrally; some fibers also inserting along intersection of both hemipalps. Pair of anterior pedal retractor muscles disposed dorsoventrally, slightly thicker than protractor muscles, originating just dorsal and slightly posterior to anterolateral muscle origin, running ventrally and slightly posterior between both anterolateral muscles, splaying onto anterior surface of visceral sac and foot, becoming thicker, bulging inside visceral cavity. Pair of posterior pedal retractor muscles of size equivalent to anterior pedal retractor muscles, originating just dorsal to posterior adductor muscle, running towards anterior, initially at some distance from each other, gradually becoming close and running attached into integument, splaying along posterior and ventral region of visceral sac and foot, bulging in visceral cavity. Cardinal muscle slender (Figs. 74, 80, ca); originating in mid region of umbonal cavity, in area ca. one-twentieth of posterior adductor muscle; running ventrally, splaying along thin visceral sac dorsolateral region. Pair of branchial muscles of size equivalent to cardinal muscle (Fig. 74, gm), originating in medial region of umbonal cavity, running along intersection of inner and outer demibranchs, becoming gradually thinner as near gill posterior ends. Pair of siphonal retractor muscles originating in pallial sinus, with fibers directed commarginally towards lateral side of intersection of incurrent and excurrent siphons (Figs. 74, 76); after this, running along both siphons, splaying along their walls as thin longitudinal layer of muscles. Cruciform muscle with total length slightly shorter than posterior adductor muscle (Figs. 74, 76, cm); located close to ventral shell edge at same horizontal level as posterior adductor muscle; anterior branches ca. twice as long and more obliquely disposed than posterior branches (Fig. 79); posterior branches each possessing conspicuous transverse furrow on its base restricted to dorsal surface.

Foot and byssus (Figs. 7, 74, 78, 80): Foot flattened, of ca. one-third shell volume when retracted; distal tip pointed. Byssus absent.

Mantle (Figs. 5, 7, 74–76, 79): External regions of mantle edge pigmented pale brown. Mantle edge trifolded (Fig. 75); outer fold flattened, ca. half width of shell thickness; periostracum attached to inner surface of outer fold (Figs. 5, 75, pe); middle and inner folds similar to each other, with same height and ca. twice thickness of outer fold. Mantle edges mostly free from each other, except close to siphonal chamber (Figs. 74, 76, 79). Middle fold almost smooth, with very small, low, uniformly distributed papillae (Fig. 5). Incurrent and excurrent siphons totally separated from each other, except at their base (Fig. 76); incurrent siphon somewhat thicker and longer than excurrent siphon; excurrent siphon normally pigmented brown (Fig. 7, si), incurrent siphon lacking pigment (Fig. 7, se). Inner surface of siphons simple, smooth. Siphonal tips simple, lacking papillae. Siphonal chamber composed of inner mantle edge fold, thin, semitransparent (Figs. 7, 76), occupying ca. one-quarter of shell volume; both siphons can be totally retracted inside this chamber; with two apertures: posterior siphonal aperture and posterodorsal branchial aperture (covered by gill, gill connected to membrane by cilia; Fig. 76). Pair of retractor muscles of lateral walls of siphonal chamber as single bundle (Fig. 74, pm) running along distance equivalent to one-tenth of total length of valves; running directly towards posterior, with divergent fibers immersed in mantle. Cruciform muscle as described above, at anteroventral end of siphonal chamber. Mantle inner folds fused along posterior surface of anterior branches of cruciform muscle, like a septum (Figs. 76, 79).

Pallial cavity (Figs. 7, 74, 78): Transverse area equivalent to four-fifths of that of valve, excluding both adductor muscles and narrow portion of visceral mass extending from anterior adductor muscle to umbonal region. Palps somewhat triangular (Figs. 7, 74, 78, pp); each hemipalp similarly sized, of ca. one-eighth of valve area. Intersection of hemipalps attached to visceral mass at its anterodorsal edge, at distance from anterodorsal valve edge equivalent to one-third of dorsoventral valve height, with part of anterolateral pedal retractor muscle running along this intersection. Outer surface of palps smooth. Inner surface (Figs. 7, 78) possessing transverse, dorsoventral folds; posterior one-eighth of inner surface smooth, lacking folds. Each palp fold with rounded ventral end, at short distance from hemipalp ventral end, with narrow smooth margin; folds gradually disappearing close to intersection between hemipalps; in this intersection, oblique, very narrow furrow appearing as continuation of each fold, turning posteriorly. Palp narrowing towards anterior. Gill (Figs. 7, 74, 78, gi) slightly smaller than each hemipalp in area, of ca. half of total shell length; height ca. one-fifth of that of shell in anterior region, gradually narrowing towards posterior. Outer demibranch positioned dorsal to inner demibranch (Fig. 77); anterior end sharply pointed, located posterior to that of inner demibranch, ca. one-quarter of total inner demibranch length; outer demibranch middle portion wider, occupying ca. half of total gill width; gradually decreasing posteriorly. Outer demibranch with single lamella covering adjacent region of visceral mass and pericardium (Fig. 77); dorsal edge connected by row of cilia surrounding dorsal edge of pallial cavity (cc); ventral edge connected to inner demibranch, also to ctenidial vein and auricle; posterior third connected laterally to anterodorsal wall of siphonal chamber aperture. Inner demibranch positioned ventral to outer demibranch, comprising entire gill in its anterior third; possessing descending and ascending branches covering visceral mass; outer connection of tissue with outer demibranch and pericardial structures; inner connection of row of cilia in visceral sac, running at short distance ventral to outer connection; food groove along ventral edge of inner demibranch (Fig. 77, fg); posterior half of inner demibranch connected medially by tissue with its pair. Gill muscle as described above.

Visceral mass (Figs. 80, 82): Visceral sac occupying ca. two-thirds of total visceral mass-foot; flattened laterally, longer dorsoventrally, somewhat triangular. Anterior and posterior walls relatively compressed by pedal retractor muscles. Anterodorsal third filled by dark brown digestive diverticula, remaining filled by pale cream gonad. Stomach-style sac running vertically along mid portion of visceral mass.

Circulatory and excretory systems (Figs. 80, 82): Pericardial structures lying in dorsal region of visceral mass, from umbonal cavity to posterodorsal surface of posterior adductor muscle; anteroposteriorly long, occupying ca. one-sixth of total visceral volume. Pair of auricles anteroposteriorly long, connected to anterior and middle thirds of gill; wall thin, transparent. Ventricle surrounding ca. 80% of intestine passing through pericardium; connecting to auricles in mid region of its lateral walls, narrow, anteroposteriorly long. Kidneys brown, solid, elongated, located in posteroventral quarter of pericardium, additionally externally surrounding both posterior retractor muscles of foot to posterior surface of posterior adductor muscle. Nephropores anteroposteriorly elongated, each located in anterior region of kidney (Fig. 82, ne), in suprabranchial chamber of inner demibranch.

Digestive system (Figs. 80, 81): Palps as described above. Mouth with relatively thick lips (Fig. 78), internally smooth, lacking folds. Oesophagus long and narrow, dorsoventrally flattened; anterior end contacting dorsal end of anterior adductor muscle, running directly dorsal and posteriorly a distance equivalent to half of anterior adductor muscle length, immersed in digestive diverticula, somewhat displaced to right; inner surface with longitudinal, narrow, low folds. Stomach oval, anteroposteriorly long, located anterior to umbones, of ca. half of visceral sac length and one-quarter of its height; pair of ducts of digestive diverticula located ventrally, on each side of oesophageal insertion, both turned anteriorly; single glandular diverticulum on right-posterior region of gastric dorsal surface, connected to stomach by narrow duct, gradually expanding, becoming lobed, balloon-like, hollow. Dorsal hood (sd) shallow, not extruding exteriorly on stomach, as small chamber dorsal to and left of transverse fold. Well-developed transverse muscles aligned between glandular diverticulum and adjacent gastric wall. Internal gastric surface (Fig. 81) mostly smooth (no clear sorting area visible), with gastric shield occupying ca. half of surface, thin, transparent, covering most of left-dorsal side, with anterior expansions to dorsal hood and to left duct of digestive diverticula; transverse fold wide and relatively tall, lying obliquely dorsal to oesophageal aperture, with both ends of this fold as anterior border of each duct of digestive diverticula; aperture to digestive diverticula a single pair, relatively wide, located on both sides of area ventral to oesophageal aperture; right duct of digestive diverticula protected externally by expansion of transverse fold, and another, as continuation of transverse fold, running ventrally to style sac; left duct of digestive diverticula protected internally by bifurcation of transverse fold; posterior branch of this bifurcation of ca. half width of anterior branch; transition between gastric chamber and style sac-intestine marked by transverse, narrow fold almost completely surrounding orifice of style sac, except for portion of intestinal origin, in this region, both ends of transverse fold becoming, within a short distance, broader, abruptly curving perpendicularly, running along style sac as pair of parallel folds separating style sac from intestine; this pair of longitudinal folds placed along right surface. Digestive diverticula as described above. Style sac straight, situated dorsoventrally, narrowing gradually to ventral end of visceral sac; style (Fig. 6) well-developed, protruding inside gastric chamber, occupying half of volume of chamber. Intestine narrow, becoming free from style sac terminally; performing several short loops, more concentrated in mid and dorsal levels of stomach (as shown in Fig. 80); estimated intestinal length ca. three times that of style sac; fecal pellets distinguishable in first loops at mid level of stomach, where intestine becomes slightly broader. Terminal intestinal set of loops covering posterodorsal region of stomach and glandular diverticulum; last loop passing through pericardium and ventricle (Fig. 82), after this, traversing dorsal and posterior surfaces of posterior adductor muscle along median line. Anus simple, sessile, on ventral surface of posterior adductor muscle, in chamber at base of excurrent siphon.

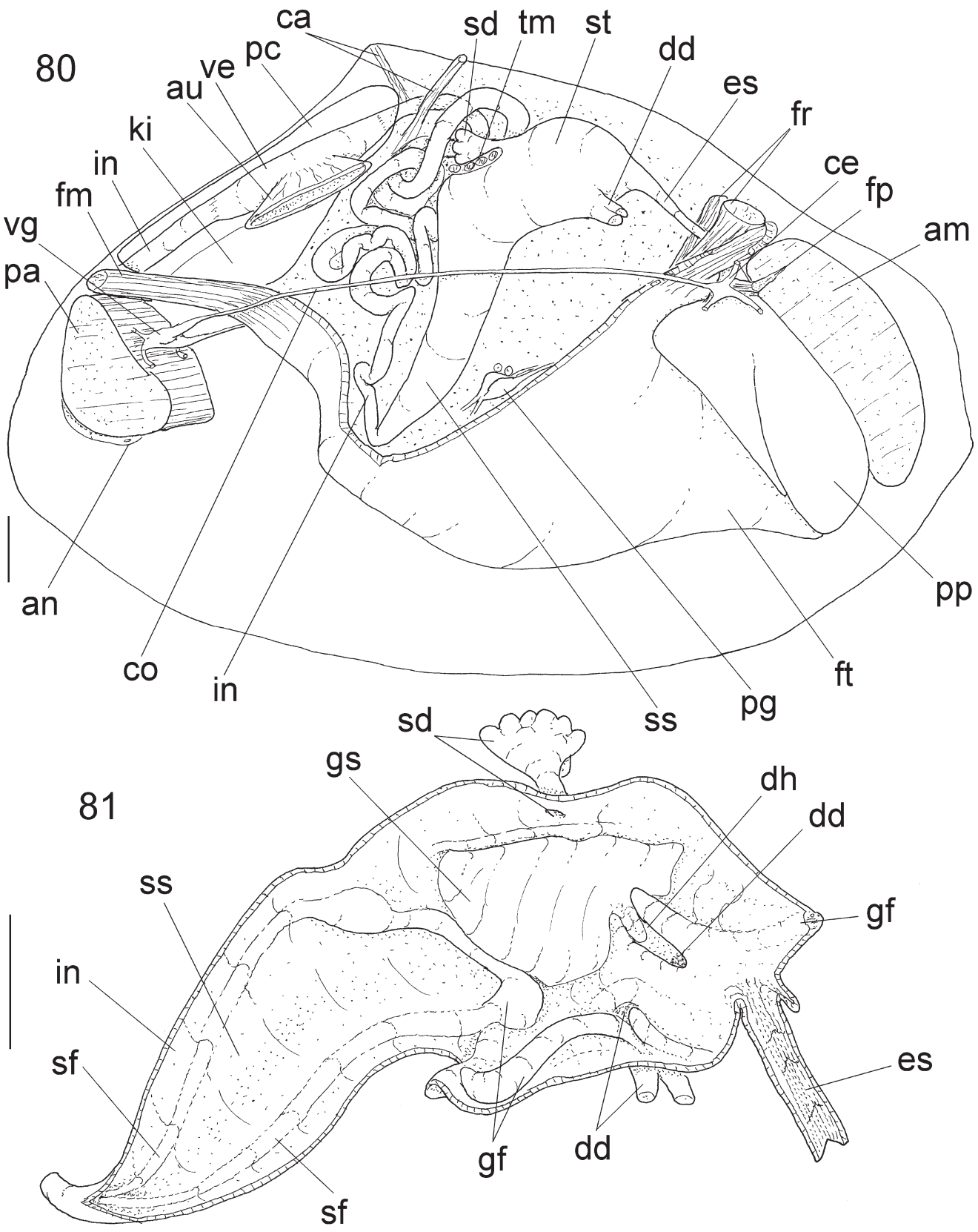
Genital system (Fig. 82): Gonad as described above. Pair of genital ducts receiving branches from several gonadal acini along their length in posterior region of visceral sac, running dorsoventrally. Genital pores simple, each located at short distance from nephropore, slightly anterior and ventral to latter.

Central nervous system (Fig. 80): Cerebral ganglia of approximately same cross-sectional area as oesophagus, located very laterally, between protractor muscle of foot and posterodorsal end of anterior adductor muscle, protected by thin layer of pallial membrane; cerebral commissure long, almost as long as adductor muscle width. Pair of pedal ganglia located very close to each other, approximately midway between cerebral ganglia and ventral end of visceral cavity, contacting anterior wall of cavity (anterior retractor muscles of foot); volume of each pedal ganglion ca. 1.5 of that of cerebral ganglion. Pair of statocysts on mid region of dorsal surface of each pedal ganglion; approximate volume ca. one-eighth of that of pedal ganglion. Cerebropedal connective very narrow, running through anterior pedal retractor musculature. Pair of visceral ganglia located close to each other on mid region of anterior surface of posterior adductor muscle (Figs. 76, 80, 82); volume of each visceral ganglion ca. twice that of cerebral ganglion; cerebrovisceral connective long, of ca. twice thickness of cerebropedal connective; each visceral ganglion elongated anteroposteriorly, with two pairs of larger anterior nerves, one of them running dorsally, and another pair, of ca. three times dorsal nerve thickness, running to siphonal bases.

Measurements. – MZSP 62352 (#1): 33.4 × 24.5 × 10.2 mm.

Distribution. – Australia (Queensland) to South Africa.

Habitat. – Muddy bottoms, shallow water; burying to ca. 5 cm below sediment surface.



Figs. 80–81. *Serratina capsoides* anatomy: 80, Topology of visceral structures, central nervous system and main muscles, right view, palps deflected; 81, stomach, right view, longitudinally sectioned to expose interior surface. am, anterior adductor muscle; an, anus; au, auricle; ca, cardinal muscle; ce, cerebral ganglion; co, cerebrovisceral connective; dd, ducts of digestive diverticula; dh, dorsal hood; es, oesophagus; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; gf, gastric fold; gs, gastric shield; in, intestine; ki, kidney; pa, posterior adductor muscle; pc, pericardium; pg, pedal ganglia; pp, palp; sd, stomach diverticulum; sf, fold separating intestine from style sac; ss, style sac; st, stomach; tm, transverse muscles of visceral sac; ve, ventricle; vg, visceral ganglia. Scale bars = 2 mm.

***Moerella* cf. *nitens* (Deshayes, 1854)**
(Figs. 9–16, 83–92)

Tellina (Moerella) nitens: Robba et al., 2002: 95, pl. 13, figs. 10a, b.
For additional synonymy, see Robba et al., 2002: 95.

***Material examined.* –** 13 ex. (MZSP 62347), Thailand, Chantaburi (Gulf of Thailand), Chao Lao Beach, oceanside near pier with fishing nets, 12°32.578'N 101°57.831'E, sta. KKB-15, coll. Simone & Wilkinson, Aug.2005.

***Description.* –** Shell (Figs. 8–12, 14): Outline anteroposteriorly elongated (dorsoventral height ca. half anteroposterior length); laterally flattened (width ca. one-quarter of length); walls thin, semitranslucent (Figs. 8–10); valves symmetrical. Colour white to pale pink. Umbones blunt, approximately between middle and posterior thirds of valves. Anterior edge rounded, continuing from somewhat horizontal anterior edge of umbo. Ventral edge almost straight. Posterior edge rounded, as posterior continuation of umbo, with gradual slope, without carina. Transition between posterior and ventral edges marked by rounded edge, more weakly rounded than umbo. Sculpture of uniform, commarginal, low undulations and growth lines (Fig. 10), ca. 11 per mm; each undulation separated from neighboring undulations by space equivalent to its width. No radial sculpture. Ligament of ca. one-sixth of shell length (Figs. 8–12, 83). Inner surface whitish, glossy (Figs. 8–9). Cardinal teeth restricted to infraumbonal region, comprising three teeth disposed divergently (Figs. 11–14); posterior teeth somewhat longer and more horizontally disposed; anterior teeth of left valve located close to each other and almost vertical. Lateral teeth low and narrow, anteroposteriorly elongated, located just posterior to ligament (Fig. 12). Muscle scars very shallow. Scar of anterior adductor muscle elliptical, dorsoventrally longer, with pointed dorsal end, occupying ca. one-tenth of inner valve surface, located at short distance surrounding anterior edge. Scar of posterior adductor muscle slightly more ventral, of approximately same size as anterior scar. Pallial line rounded posteriorly. Pallial sinus wide, forming arch of ca. half size of valve, running close to but at some distance from anterior adductor muscle scar. Scar of cruciform muscle ventral to posterior adductor muscle.

Main muscle system (Figs. 16, 83, 85): Anterior adductor muscle area equivalent to one-tenth of shell area. Posterior adductor muscle rounded in cross section, at somewhat more ventral level than anterior adductor muscle (dorsal surface at approximate mid level of anterior adductor muscle); occupying ca. three-quarters of anterior adductor muscle area. Pair of pedal protractor muscles originating in area ca. one-tenth of anterior adductor muscle; some fibers also

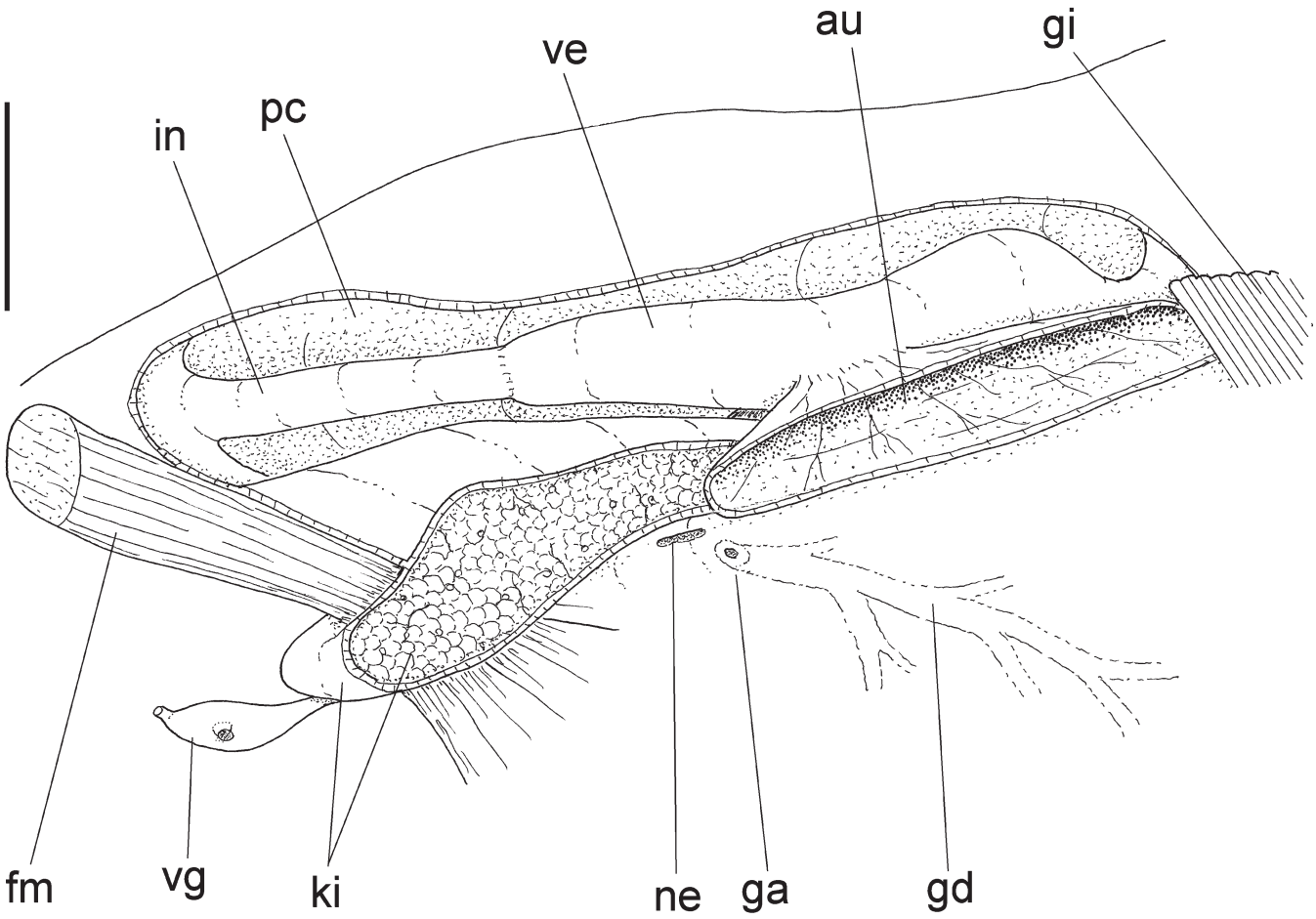
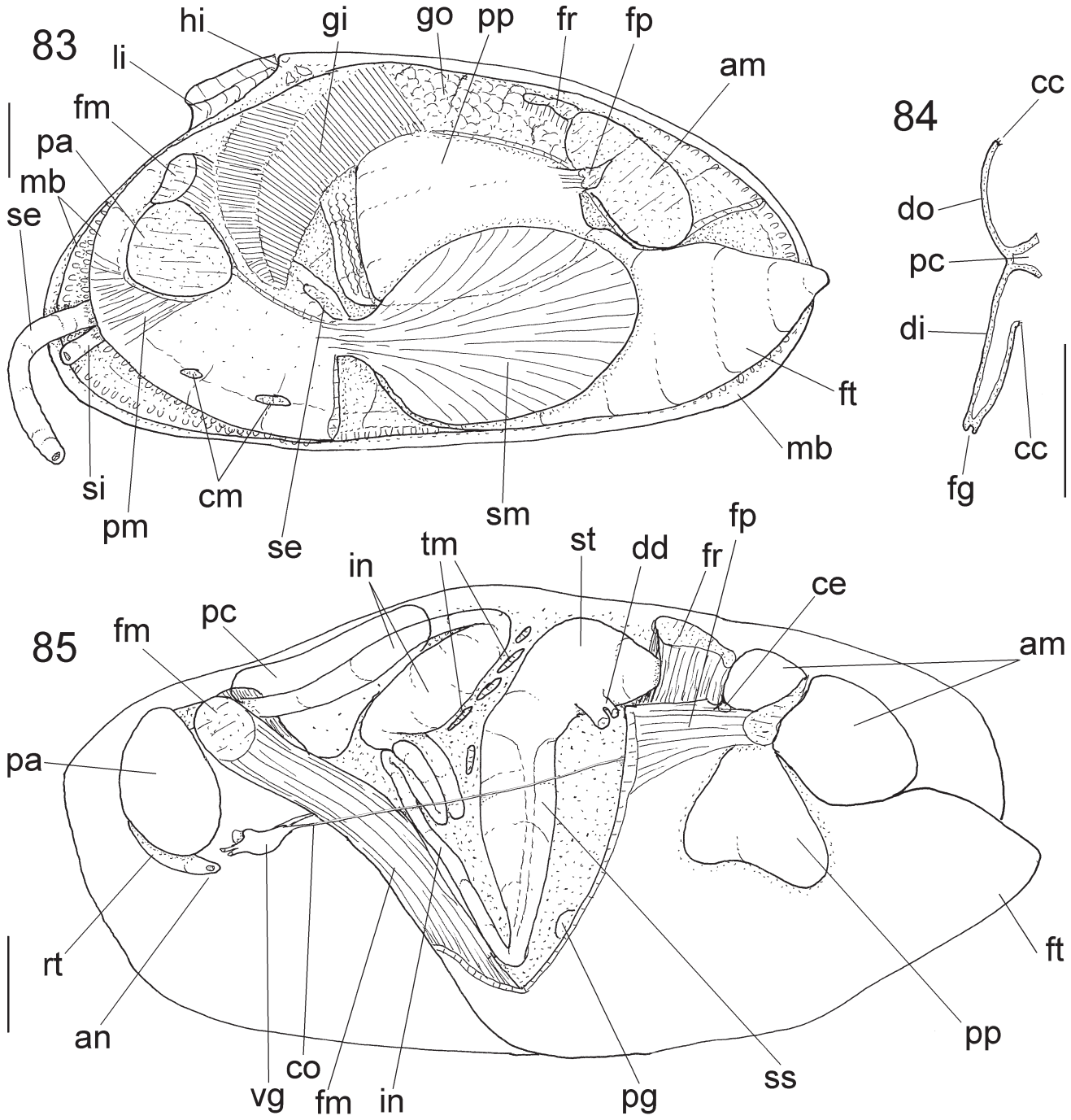


Fig. 82. *Serratina capsoides* anatomy; detail of renopericardial region and some adjacent structures, right view, gill and right wall of kidney removed, gonoducts seen by transparency. au, auricle; fm, posterior pedal retractor muscle; ga, genital aperture; gd, genital duct; gi, gill; in, intestine; ki, kidney; ne, nephropore; pc, pericardium; ve, ventricle; vg, visceral ganglia. Scale bar = 2 mm.

inserting along intersection of hemipalps; origin of protractor muscles with a narrow projection completely dividing anterior adductor muscle between its middle and dorsal thirds. Pair of anterior pedal retractor muscles originating just dorsal to anterior adductor muscle. Pair of posterior pedal retractor muscles ca. 60% of size of anterior pedal retractor muscles. No cardinal muscle. Pair of branchial muscles very small, almost undetectable. Cruciform muscle with total length equivalent to that of posterior adductor muscle, located posterior to horizontal level of posterior adductor muscle; posterior branches lacking transverse furrows on their bases.



Figs. 83–85. *Moerella* cf. *nitens* anatomy: 83, Whole right view, right valve and part of mantle lobe removed; 84, gill, transverse section in its mid region; 85, topology of visceral structures, central nervous system, and main muscles, right view, palps deflected. am, anterior adductor muscle; an, anus; cc, ciliary connection; ce, cerebral ganglion; cm, cruciform muscle; co, cerebrovisceral connective; dd, ducts of digestive diverticula; di, inner demibranch; do, outer demibranch; fg, gill food groove; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; gi, gill; go, gonad; hi, hinge; in, intestine; li, ligament; mb, mantle border; pa, posterior adductor muscle; pc, pericardium; pg, pedal ganglia; pp, palp; rt, rectum; se, excurrent siphon; si, incurrent siphon; sm, siphonal retractor muscle; ss, style sac; st, stomach; tm, transverse muscles of visceral sac; vg, visceral ganglia. Scale bars = 1 mm.

Foot (Figs. 83, 85): Foot flattened, of ca. one-third of shell volume when retracted; distal tip pointed.

Mantle (Figs. 83, 86): External regions of mantle edge lacking pigment (Fig. 16). Mantle edge middle and inner folds of similar height (ca. six times shell wall thickness); middle fold almost as thick as shell wall and ca. twice inner fold thickness; inner fold at some distance from middle fold (distance equivalent to half of their height). Middle fold with a series of small, narrow, uniformly distributed papillae (Fig. 86); each papilla cylindrical, with rounded tip, separated from next by space equivalent to its width. Incurrent siphon of ca. same thickness and ca. 30% longer than excurrent siphon, lacking pigment. Siphonal tips simple, lacking papillae. Pair of retractor muscles of lateral walls of siphonal chamber with single main, dorsal bundle. Pseudogill as described below.

Pallial cavity (Figs. 15, 83, 86): Palps somewhat rectangular; each hemipalp of ca. one-fifth of valve area. Length of intersection of hemipalps equivalent to one-third of dorsoventral valve height. Outer hemipalp of ca. three-quarters of inner hemipalp length (posterior edge shorter than that of inner hemipalp). Inner surface folds relatively wide; smooth area surrounding entire hemipalp free edge, of area equivalent to those of each inner fold. Each palp fold comprising several, successive transverse, secondary folds in mid and posterior regions (Figs. 15, 87); folds of anterior region simple. Gill slightly smaller than each hemipalp in area, ca. one-eighth of valve area; length ca. one-third of total shell length; height ca. one-fifth of that of shell in anterior region. Outer demibranch anterior end oblique, at approximate mid level of inner demibranch (leaving region of visceral surface anterior to it exposed) (Fig. 83). Inner demibranch inner lamella ca. three-quarters of outer lamella size; food groove along ventral edge of inner demibranch (Fig. 84). Pseudogill single (Fig. 86, ps), on left side of incurrent siphonal base; formed as wide, thin flap, situated anteroposteriorly, parallel to mantle edge, with approximately half inside siphon; size ca. twice siphonal cross section.

Visceral mass (Figs. 85, 88): Anterodorsal third filled by greenish pale brown digestive diverticula; remaining filled by pale cream gonad. Stomach-style sac running vertically along mid portion of visceral mass.

Circulatory and excretory systems (Fig. 88): Pericardial structures occupying ca. one-sixth of total visceral volume (Fig. 85). Pair of auricles anteroposteriorly long, connected to middle third of gill. Ventricular connection to auricles in anterior region of its lateral walls. Kidneys white. Nephropores rounded, each on anterior region of kidney.

Digestive system (Fig. 85): Palps as described above. Oesophagus of approximately same length as anterior adductor muscle and ca. half its width, dorsoventrally flattened; inner surface smooth. Stomach lacking dorsal glandular diverticulum. Well-developed transverse muscles aligned between posterior gastric wall and adjacent intestinal loop (preceding pericardium). Internal gastric surface (Fig. 89) with relatively tall transverse fold, restricted to anterior region in front of oesophageal aperture; left duct of digestive diverticula protected externally by expansion of transverse fold. Intestine performing four or five tight, short loops in region adjacent to origin of style sac in stomach, with another very wide loop dorsally, preceding pericardium; estimated intestinal length ca. twice that of style sac.

Genital system (Fig. 88): Gonad as described above. Genital pores simple, each on low, sessile papilla at short distance from nephropore, slightly anterior and ventral to latter.

Central nervous system (Figs. 85, 90-92): Cerebral ganglia (Fig. 90) of approximately one-quarter the cross section of oesophagus. Pair of pedal ganglia (Fig. 92) located very close to each other, totally fused along median line, located on inferior third of visceral cavity anterior surface; volume of both pedal ganglia ca. 1.5 times that of both cerebral ganglia. Pair of visceral ganglia (Fig. 91) located at short distance from posteroventral surface of posterior adductor muscle; volume of each visceral ganglion ca. twice that of one cerebral ganglion; each visceral ganglion elongated anteroposteriorly, with three pairs of large anterior nerves.

Measurements. – MZSP 62347 (#1): 11.1 × 6.0 × 2.2; (#2): 12.5 × 6.4 × 2.8 mm.

Distribution. – Japan to Persian Gulf.

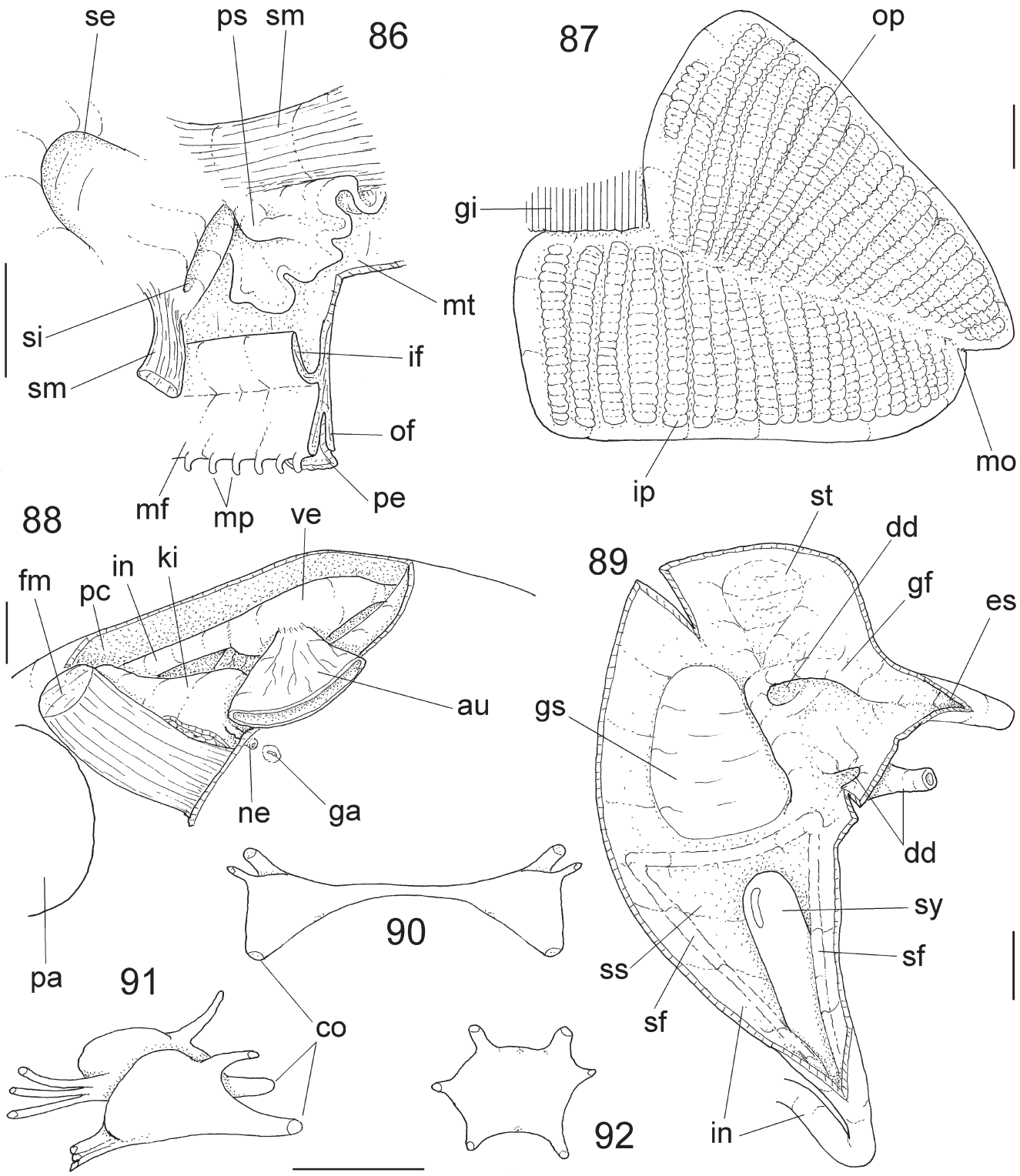
Habitat. – Muddy bottoms, in shallow water.

Remarks. – The examined samples have certain shell similarities with the type specimens of *Moerella nitens* (Deshayes, 1854) (Figs. 17–20), however, some small differences are detectable, precluding a secure identification. The Thai samples are slightly more elongated anteroposteriorly (compare Figs. 8–9 with 17–18). The umbo is somewhat displaced posteriorly in Thai samples (between middle and posterior thirds), whereas the type specimens have the umbo almost central. The ventral edge is almost straight in the Thai samples, whereas it is clearly convex in the types. The hinge is almost identical (compare Figs. 11–12 with 19–20); the Thai sample has a slightly narrower hinge, and the anterior lateral tooth of the right valve is positioned slightly farther away from the cardinal teeth than is interpreted in the type specimens (Figs. 12, 20). In the present concept, these differences are considered as variation, however, a completely secure identification is dependent on further studies. The samples also resemble *Tellina caseus* Sowerby, 1867; however, the Thai samples have a more rounded posterior region and a less pointed umbo.

Cadella cf. *semen* Hanley, 1845b

(Figs. 21–28, 93–101)

Tellina semen Hanley, 1845b: 164.
Tellina (*Cadella*) *semen*: Robba et al., 2002: 93, pl. 13, fig. 6.
For additional synonymy, see Robba et al., 2002: 93.



Figs. 86–92. *Moerella* cf. *nitens* anatomy: 86, detail of base of incurrent siphon showing pseudogill, right and slightly dorsal view, some parts of mantle lobes removed; 87, right palp, right view, exterior hemipalp deflected, adjacent region of gill also shown; 88, detail of renopericardial region and some adjacent structures, right view, gill and right wall of kidney removed; 89, stomach, right view, longitudinally sectioned to expose interior surface, crystalline style shown in place; 90, cerebral ganglia, anterior view; 91, visceral ganglia, right and slightly posterior view; 92, pedal ganglia, posterior view. au, auricle; co, cerebrovisceral connective; dd, ducts of digestive diverticula; es, oesophagus; fm, posterior pedal retractor muscle; ga, genital aperture; gf, gastric fold; gi, gill; gs, gastric shield; if, inner fold of mantle border; in, intestine; ip, inner hemipalp; ki, kidney; mf, middle fold of mantle border; mo, mouth; mp, mantle papillae; mt, mantle; ne, nephropore; of, outer fold of mantle border; op, outer hemipalp; pa, posterior adductor muscle; pc, pericardium; pe, periostracum; ps, pseudogill; se, excurrent siphon; sf, fold separating intestine from style sac; si, incurrent siphon; sm, siphonal retractor muscle; ss, style sac; st, stomach; sy, crystalline style; ve, ventricle. Scale bars = 0.5 mm.

***Material examined.* –** 16 ex. (MZSP 62346), Thailand, Chantaburi (Gulf of Thailand), Chao Lao Beach, oceanside near pier with fishing nets, 12°32.578'N 101°57.831'E, sta. KKB-15, coll. Simone & Wilkinson, Aug.2005.

***Description.* –** Shell (Figs. 21–26): Outline somewhat rounded (dorsoventral height ca. 70% of anteroposterior length) (Figs. 21, 22); laterally flattened (width ca. 30% of length); walls relatively thick; valves weakly asymmetrical, with right valve more weakly planar than left valve (Fig. 25). Colour pure white; brown spot of periostracum on umbones, disappearing gradually towards periphery. Umbones pointed (Figs. 23, 24), somewhat projecting, approximately between middle and posterior thirds. Anterior edge rounded, ample, continuing from somewhat horizontal anterior edge of umbo. Ventral edge rounded. Posterior edge rounded, as posterior continuation of umbo, with gradual slope; without carina. Transition between posterior and ventral edges marked by rounded edge, slightly more rounded than umbo and sharper than anterior edge. Sculpture of uniform, commarginal, well-marked undulations (Fig. 22), ca. 9 per mm; each undulation separated from neighboring undulations by space equivalent to its width. No radial sculpture. Ligament of ca. one-twelfth shell length, located posterior to umbo (Figs. 25, 26). Inner surface glossy, whitish; pink in umbonal cavity. Cardinal teeth restricted to infraumbonal region (Figs. 23–26), comprising two teeth disposed divergently, anterior right tooth ca. three times taller than others. Pair of lateral teeth low and narrow, anteroposteriorly elongated; anterior tooth in mid region between umbo and anterior end; posterior tooth in dorsal third of posterior edge, just posterior to ligament (Figs. 21, 24). Muscle scars very shallow. Scar of anterior adductor muscle elliptical, dorsoventrally longer, with dorsal end pointed, occupying ca. one-tenth of inner valve surface, located at short distance surrounding anterior edge. Scar of posterior adductor muscle with ventral edge at level of anterior scar, of ca. half size of anterior scar. Pallial sinus narrower than that in preceding species, forming arch of ca. one-quarter size of valve, well separated from anterior adductor muscle scar. Scar of cruciform muscle ventral and slightly anterior to posterior adductor muscle.

Main muscle system (Figs. 27, 28, 93, 95): Anterior adductor muscle area equivalent to one-tenth of shell area, clearly divided into two similarly sized regions; ventral region totally surrounded by circular fibers of ca. half of ventral region thickness (Figs. 27, 28, 93, ci); dorsal region slightly larger than ventral region and somewhat triangular. Posterior adductor muscle rounded in cross section, located more ventral than anterior adductor muscle (ventral surface at approximately same level as that of anterior adductor muscle); occupying ca. half of anterior adductor muscle area. Pair of pedal protractor muscles very small, thin, originating in imperceptible area at mid level of anterior adductor muscle posterior edge. Pair of anterior pedal retractor muscles originating just dorsal to anterior adductor muscle; approximate size of origin ca. one-twentieth of anterior adductor muscle. Pair of posterior pedal retractor muscles of approximately same size as anterior pedal retractor muscles. No cardinal muscle. Pair of branchial muscles very small, almost undetectable. Cruciform muscle of total length equivalent to that of posterior adductor muscle; located posterior to horizontal level of posterior adductor muscle; posterior branches lacking transverse furrows on their bases.

Foot (Figs. 27, 93, 95): Flattened, of ca. one-quarter of shell volume when retracted; distal tip pointed.

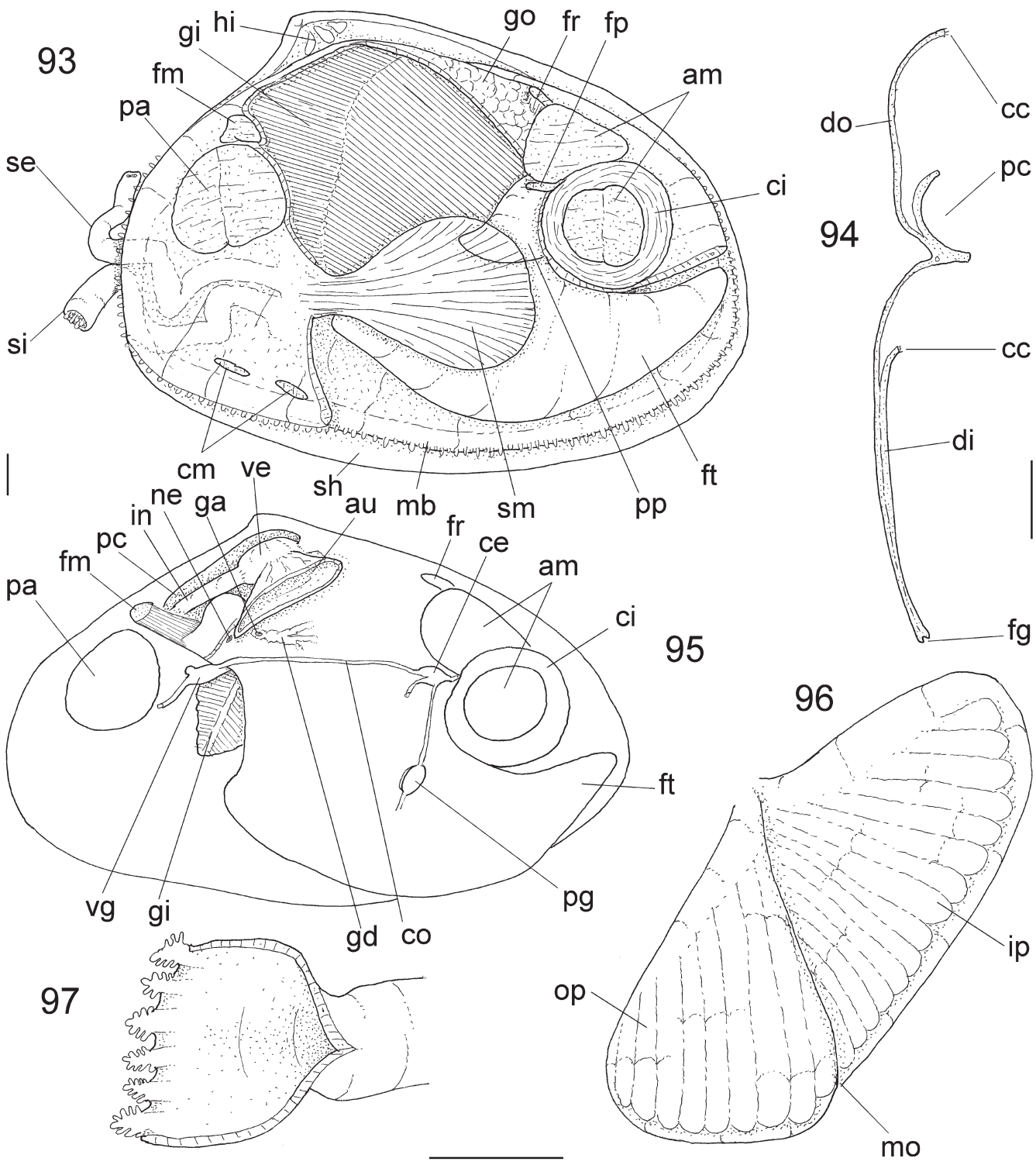
Mantle (Figs. 27, 28, 93, 100): Folds of mantle edge (Fig. 100) of similar height (ca. three times shell thickness), almost half as thick as shell wall; inner fold located at some distance from middle fold (distance equivalent to half of their height). Middle fold with series of small, narrow, uniformly distributed papillae (Figs. 28, 100), normally disposed as intercalated longer and shorter papilla (shorter of ca. half length of longer papilla); each papilla cylindrical, with rounded tip, separated from others by space equivalent to its width. Incurrent siphon of approximately same thickness and length as excurrent siphon (Figs. 27, 93), lacking pigment; series of six papillae on edge of incurrent siphon, each with three pairs of secondary papillae on each side (Fig. 97). Pair of retractor muscles of lateral walls of siphonal chamber with single main, dorsal bundle. No pseudogill.

Pallial cavity (Figs. 27, 93): Palps somewhat triangular; each hemipalp of ca. one-twentieth of valve area. Length of intersection of hemipalps equivalent to one-twelfth of dorsoventral valve height (Figs. 28, 93). Inner surface (Fig. 96) with relatively wide folds; smooth area surrounding entire hemipalp free edge, dorsally wider (ca. one-quarter of palp width), ventrally very narrow. Each fold of palp wide, of barely one-fifth of palp width. Gill of eight times palp area, ca. one-quarter of valve area, of ca. half of total shell length; height ca. one-third of that of shell in anterior region (Figs. 27, 93). Outer demibranch of ca. half of inner demibranch width, at approximately same level as inner demibranch anterior end (Fig. 94). Inner demibranch inner lamella ca. three-quarters of size of outer lamella; food groove along ventral edge of inner demibranch (Fig. 94).

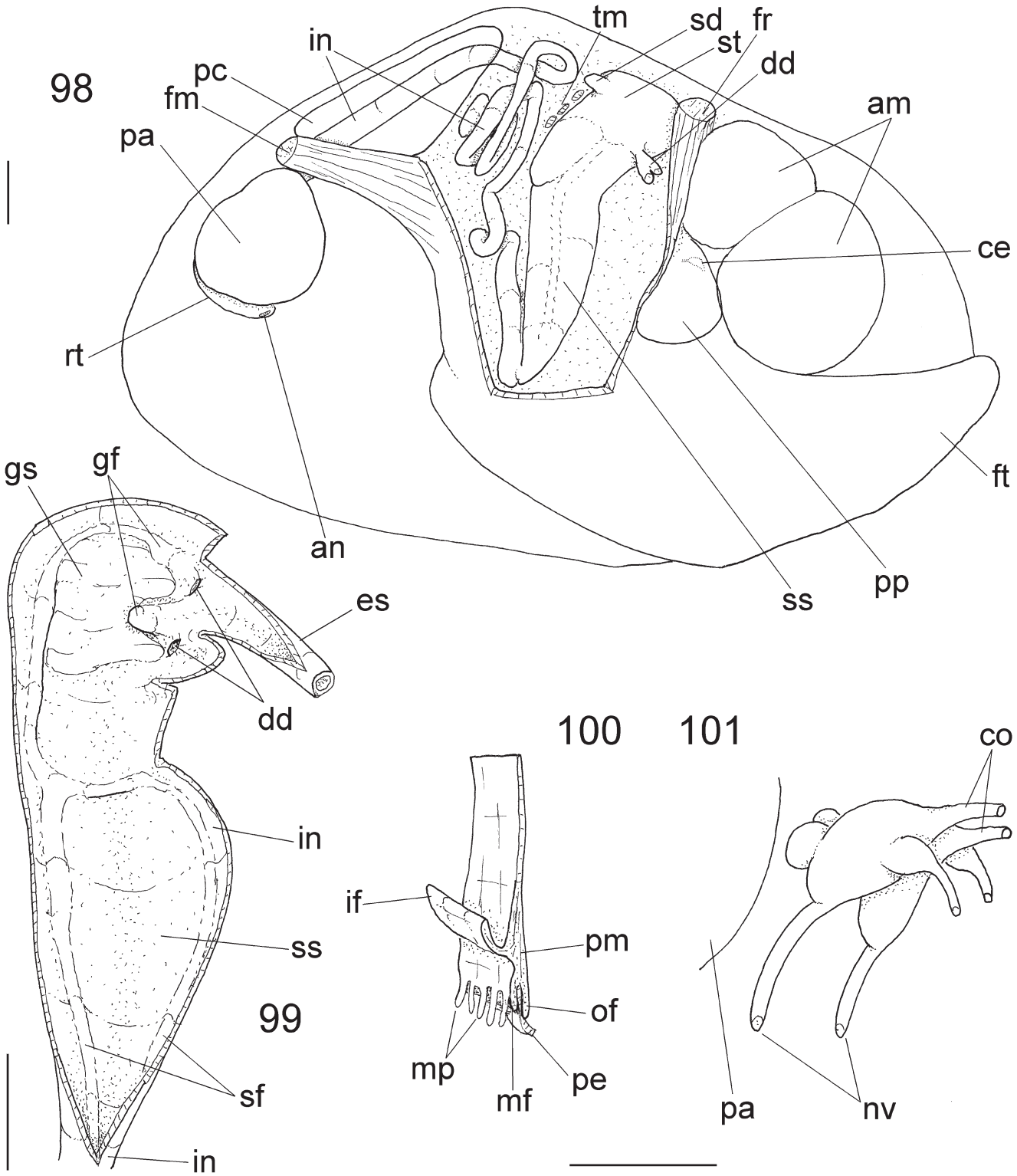
Visceral mass (Figs. 95, 98): Anterodorsal third filled by dark greenish-brown digestive diverticula; remaining filled by pale cream gonad. Stomach-style sac running vertically along mid portion of visceral mass.

Circulatory and excretory systems (Fig. 95): Pericardial structures occupying ca. one-fifth of total visceral volume (Fig. 98). Pair of auricles connected to middle third of gill. Ventricular connection to auricles in anterior region of its lateral walls. Kidneys white. Nephropores rounded, each in mid region of kidney surface exposed to suprabranchial chamber.

Digestive system (Fig. 98): Palps as described above. Oesophagus of ca. half the length of anterior adductor muscle and ca. one-third its width, dorsoventrally flattened; inner surface smooth. Stomach with short, dorsal glandular diverticulum (ca. one-twentieth its size) on posterodorsal right side. Well-developed transverse muscles (tm) aligned



Figs. 93–97. *Cadella* cf. *semen* anatomy: 93, Whole right view, right valve and part of mantle lobe removed; 94, gill, transverse section in mid region; 95, topology of renopericardial structures and central nervous system, right view, topology of other structures also shown; 96, right palp, right view, outer hemipalp deflected; 97, incurrent siphon, detail of its tip partially sectioned longitudinally. am, anterior adductor muscle; au, auricle; cc, ciliary connection; ce, cerebral ganglion; ci, circular muscle fibers of anterior adductor muscle; cm, cruciform muscle; co, cerebrovisceral connective; di, inner demibranch; do, outer demibranch; fg, gill food groove; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; ga, genital aperture; gd, genital duct; gi, gill; go, gonad; hi, hinge; in, intestine; ip, inner hemipalp; mb, mantle border; mo, mouth; ne, nephropore; op, outer hemipalp; pa, posterior adductor muscle; pc, pericardium; pg, pedal ganglia; pp, palp; se, excurrent siphon; sh, shell; si, incurrent siphon; sm, siphonal retractor muscle; ve, ventricle; vg, visceral ganglia. Scale bars = 0.5 mm.



Figs. 98–101. *Cadella* cf. *semen* anatomy: 98, Topology of visceral structures and main muscles, right view, palps deflected; 99, stomach, right view, longitudinally sectioned to expose interior surface; 100, mantle border, transverse section at mid level of ventral region; 101, visceral ganglia, right and slightly anterior view, topology of adjacent structure also shown. am, anterior adductor muscle; an, anus; ce, cerebral ganglion; co, cerebrovisceral connective; dd, ducts of digestive diverticula; es, oesophagus; fm, posterior pedal retractor muscle; fr, anterior pedal retractor muscle; ft, foot; gf, gastric fold; gs, gastric shield; if, inner fold of mantle border; in, intestine; mf, middle fold of mantle border; mp, mantle papillae; nv, nerve; of, outer fold of mantle border; pa, posterior adductor muscle; pc, pericardium; pe, periostracum; pm, pallial muscles; pp, palp; rt, rectum; sd, stomach diverticulum; sf, fold separating intestine from style sac; ss, style sac; st, stomach; tm, transverse muscles of visceral sac. Scale bars = 0.5 mm.

between posterior gastric wall and adjacent intestinal loop (preceding pericardium). Internal gastric surface (Fig. 99) with relatively low transverse fold, restricted to anterior region, in front of oesophageal aperture; left duct of digestive diverticula protected externally by expansion of transverse fold. Intestine forming single, small loop at mid level of style sac, additionally four or five tight, short loops dorsal to level of origin of style sac on stomach; estimated intestinal length ca. three times that of style sac.

Genital system (Fig. 95): Gonad as described above. Genital duct short as result of convergence of two secondary (dorsal and ventral) ducts. Genital pores simple, each at short distance from nephropore, slightly anterior to latter.

Central nervous system (Fig. 95): Cerebral ganglia of ca. half size of cross section of oesophagus. Pair of pedal ganglia located very close to each other, located on inferior third of visceral cavity anterior surface; volume of each pedal ganglion ca. same as that of one cerebral ganglion. Pair of visceral ganglia at short distance from posteroventral surface of posterior adductor muscle; volume of each visceral ganglion ca. 1.5 times that of both cerebral ganglia; each visceral ganglion elongated anteroposteriorly, with pair of large anterior nerves and a pair of secondary protuberances on posterodorsal surfaces of ganglia (Fig. 101).

Measurements. – MZSP 62346: 8.8 × 7.3 mm.

Distribution. – Japan to South Africa.

Habitat. – Sandy bottoms, in shallow water.

Remarks. – There are similarities between the samples collected in Thailand and the type specimens of *Cadella semen* (Figs. 29–34) (see also Sowerby, 1867: fig. 232). However, some differences are found that preclude a precise identification. The main difference is in the posterior region, which is shorter and more abrupt in the Thai samples but longer and more rounded in the types (compare Figs. 21–22 with 29–32). Another difference is the sculpture, which is somewhat stronger in the posterior regions of the types (Figs. 30) than in the Thai samples (Fig. 22). The umbo is also slightly more pointed in the Thai samples (Figs. 23, 24) than those of the types (Figs. 33, 34). The hinge is similar, however, the anterior lateral tooth of the right valve appears to be longer in the Thai specimens (Figs. 21, 24) than in the types (Fig. 34). Despite these differences, the samples have been considered conspecific pending further studies. A similar shell shape is also found in the Australian *Psammacoma retrorsa* (Sowerby, 1867); however, the Thai samples possess lateral teeth and have more posterior umbones.

Pinguitellina cf. *pinguis* (Hanley, 1844a)
(Figs. 35–43, 102–111)

Tellina pinguis: Sowerby, 1867: pl. 31, fig. 172.
Tellina (*Pinguitellina*) *pinguis*: Robba et al., 2002: 97, pl. 14, fig. 1.
For additional synonymy, see Robba et al., 2002: 97.

Material examined. – All Thailand, Chantaburi (Gulf of Thailand), Kungkrabaen Bay, 12°35.16'N 101°54.40'E, sta. KKB-03, "middle of bay station," coll. Simone & Wilkinson, Aug.2005; 1 ex. (MZSP 62348); 5 ex. (MZSP 62345).

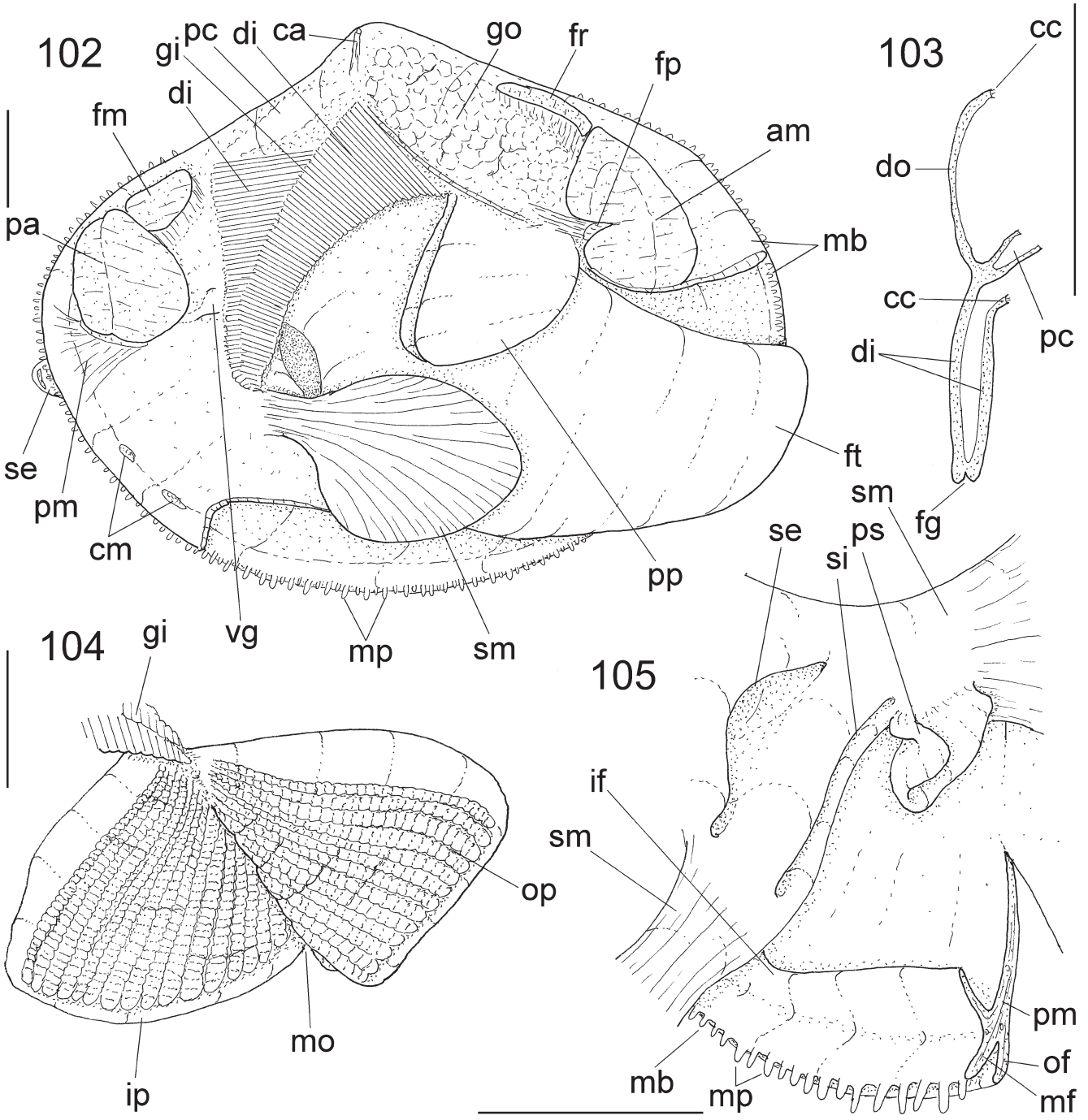
Description. – Shell (Figs. 35–37, 39–43): Outline somewhat rounded (dorsoventral height ca. 70% of anteroposterior length); laterally tumid (width ca. 45% of length); walls thin; valves weakly asymmetrical, with right valve more weakly planar than left valve (Fig. 37). Colour pure white, with beige remains of periostracum on dorsal edge, diminishing gradually. Umbones pointed, somewhat projecting, located approximately at center. Anterior and posterior edges rounded, ample, in continuation from umbo, similar to one another (posterior end slightly more pointed). Ventral edge rounded. Sculpture uniform, commarginal, weakly striated (Figs. 35, 42), with ca. eight striations per mm; each striation separated from neighbouring striations by space equivalent to four times its width. No radial sculpture. Ligament of ca. one-seventeenth of shell length, located posterior to umbo. Inner surface glossy, whitish. Cardinal teeth (Figs. 39, 40, 43) restricted to infraumbonal region, comprising two teeth disposed divergently, similarly sized. Right valve with pair of symmetrical lateral teeth, low and narrow, anteroposteriorly elongated (ca. one-tenth of shell length), each in dorsal third of region between umbo and anterior or posterior ends. Muscle scars very shallow (Figs. 36, 41). Scar of anterior adductor muscle elliptical, dorsoventrally longer, dorsally pointed, occupying ca. one-tenth of inner valve surface at distance equivalent to its width from anterior edge. Scar of posterior adductor muscle with ventral edge at same level as that of anterior scar, slightly smaller than anterior scar. Pallial sinus performing arch of ca. one-third size of valve, well separated from anterior adductor muscle scar (separation ca. same width of anterior adductor muscle). Scar of cruciform muscle ventral and slightly anterior to posterior adductor muscle.

Main muscle system (Figs. 102, 106): Anterior adductor muscle area equivalent to one-tenth of shell area; divided into two regions; anterior and dorsal region of ca. half of width of posterior region; dorsal half slightly larger than ventral half and somewhat triangular. Posterior adductor muscle elliptical in cross section, located at same level as anterior adductor muscle; slightly smaller than anterior adductor muscle area. Pair of pedal protractor muscles very small, thin, originating at mid level of anterior adductor muscle posterior edge, in area equivalent to one-fifteenth of that of adductor muscle; penetration into anterior adductor muscle posterior side approximately at center, with narrow projection penetrating ca. one-quarter of adductor muscle (anteroposterior) width. Pair of anterior pedal retractor muscles originating just dorsal to anterior adductor muscle; approximate size of origin ca. one-quarter of anterior adductor muscle; a portion of these muscles surrounding dorsal edge of adductor muscle. Pair of posterior pedal retractor muscles ca. same size as anterior pedal retractor muscles. Cardinal muscle narrow, relatively long, originating in center of umbonal cavity. Pair of branchial muscles very small, almost undetectable. Cruciform muscle of total length equivalent to

that of posterior adductor muscle, located slightly posterior to horizontal level of posterior adductor muscle; posterior branches lacking transverse furrows on their bases.

Foot (Fig. 102): Flattened, of ca. one-quarter of shell volume when retracted; distal tip pointed.

Mantle (Figs. 38, 102, 105): Folds of mantle edge of similar height (ca. three times shell wall thickness), almost half as thick as shell wall; inner fold originating with middle fold. Middle fold with series of small, narrow, similarly sized, uniformly distributed papillae (Fig. 38); each papilla cylindrical, with rounded tip, separated from neighboring



Figs. 102–105. *Pinguitellina* cf. *pinguis* anatomy: 102, Whole right view, right valve and part of mantle lobe removed; 103, gill, transverse section in mid region; 104, right palp, right view, exterior hemipalp deflected; 105, detail of base of both siphons and adjacent region of left mantle lobe, right siphonal retractor muscle deflected, mantle artificially sectioned, gill cilial connection removed. am, anterior adductor muscle; ca, cardinal muscle; cc, ciliary connection; cm, cruciform muscle; di, inner demibranch; do, outer demibranch; fg, gill food groove; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; gi, gill; go, gonad; if, inner fold of mantle border; ip, inner hemipalp; mb, mantle border; mf, middle fold of mantle border; mo, mouth; mp, mantle papillae; of, outer fold of mantle border; op, outer hemipalp; pa, posterior adductor muscle; pc, pericardium; pm, pallial muscles; pp, palp; ps, pseudogill; se, excurrent siphon; si, incurrent siphon; sm, siphonal retractor muscle; vg, visceral ganglia. Scale bars = 1 mm.

papillae by space equivalent to its width; length of each papilla ca. half that of fold. Incurrent siphon of approximately same thickness and length of excurrent siphon, lacking pigment and papillae. Pair of retractor muscles of lateral walls of siphonal chamber with single, dorsal main bundle (Fig. 102, pm). Pseudogill (Fig. 105, ps) small, flat, at left base of incurrent siphon, just where its left retractor muscle begins running in valve; size equivalent to 1.5 times height of mantle folds.

Pallial cavity (Figs. 102, 105): Palps rounded; each hemipalp of length ca. one-ninth of valve area. Length of intersection of hemipalps equivalent to one-quarter of dorsoventral valve height. Inner surface (Fig. 104) with narrow folds; smooth area surrounding entire hemipalp free edge, dorsally wider (ca. one-quarter of palp width), ventrally very narrow; posterior smooth edge relatively wide (ca. one-eighth of palp length). Each fold of palp wide, with ca. 20 folds in each hemipalp, comprising a series of transverse secondary folds (Fig. 104). Gill approximately as large as palp, ca. one-eighth of valve area, of ca. half of total shell length; height ca. one-fifth of that of shell in anterior region. Outer demibranch of ca. three-quarters of inner demibranch width, located somewhat posterior to inner demibranch anterior end (Fig. 103). Inner demibranch inner lamella approximately as long as outer lamella; food groove along ventral edge of inner demibranch (Fig. 103).

Visceral mass (Figs. 106, 108): Anterodorsal third filled by beige digestive diverticula; remaining filled by pale cream gonad. Stomach-style sac running vertically along mid portion of visceral mass.

Circulatory and excretory systems (Fig. 108): Pericardial structures occupying ca. one-fifth of total visceral volume (Fig. 106). Pair of auricles connected to middle and anterior thirds of gill. Ventricular connection to auricles in mid region of its lateral walls. Kidneys white. Nephropores rounded, each on posterior region of kidney surface exposed to suprabranchial chamber, preceded by urinary canal of ca. one-third of kidney height.

Digestive system (Fig. 106): Palps as described above. Oesophagus of ca. half length of anterior adductor muscle and ca. one-third its width, dorsoventrally flattened; inner surface smooth. Stomach lacking dorsal glandular diverticulum, occupying ca. one-fifth of visceral volume. Dorsal hood on left gastric surface, narrow, of ca. half of gastric length; tip pointed; inner surface smooth. No special transverse muscles detected. Internal gastric surface (Fig. 107) with relatively tall transverse fold (of ca. one-third of gastric width), restricted to anterior region in front of oesophageal aperture; left and right ducts of digestive diverticula protected externally by expansions of transverse fold; dorsal hood aperture at short distance dorsal to left duct of digestive diverticula. Intestine performing long loop to mid level of style sac, additionally ca. 10 tight, short loops just ventral to level of origin of style sac in stomach; intestine gradually becoming wider and thin-walled from mid region of these loops to rectum; containing sandy material; estimated intestinal length ca. three times that of style sac.

Genital system: Gonad as described above. No genital duct detected. Genital pores simple (Fig. 108, ga), each slit-like, at short distance from nephropore, slightly anterior to latter.

Central nervous system (Figs. 106, 109–111): Cerebral ganglia (Fig. 110) of ca. half size of cross section of oesophagus. Pair of pedal ganglia (Fig. 109) very close to one another on mid part of visceral cavity anterior surface, volume of each pedal ganglion approximately same as one cerebral ganglion. Pair of visceral ganglia (Fig. 111) at short distance anterior to posteroventral surface of posterior adductor muscle; volume of each visceral ganglion ca. 1.5 that of one cerebral ganglion; each visceral ganglion anteroposteriorly elongated, with pair of large anterior nerves and a pair of secondary protuberances on anterodorsal surface of posterior ganglionic region.

Measurements. – MZSP 62348 (#1): 9.1 × 7.6 × 4.7 mm; (#2): 9.1 × 7.4 × 3.8 mm.

Distribution. – Japan to Red Sea.

Habitat. – Muddy bottoms, in shallow water.

Remarks.– Examination of the type specimens of *Pinguitellina pinguis* (Figs. 41–43) confirmed the identification. Despite some small differences, both samples appear to belong to the same species. The Thai samples have thinner shell walls, but the remaining shell characters appear the same. Sometimes this species is illustrated with a posterior low carina (e.g., Sowerby, 1867: fig. 172); this feature was not found in the Thai samples.

Elpidollina sp.

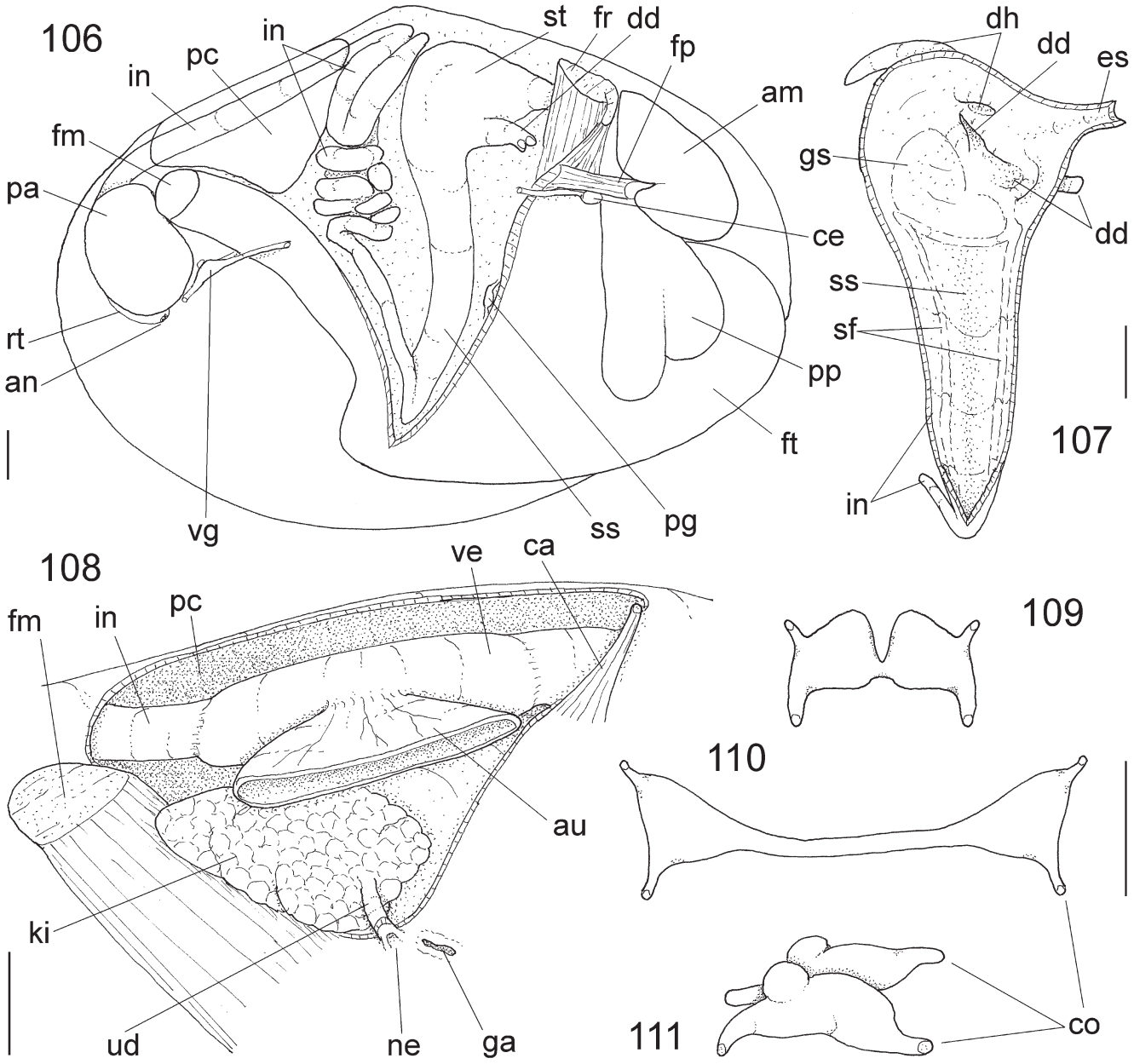
(Figs. 44–52, 112–123)

Material examined. – 3 ex., 3 shells (MZSP 62351), Thailand, Chantaburi (Gulf of Thailand), Kungkrabaen Bay, 12°34.42'N 101°54.25'E, sta. KKB-01, "boardwalk location," mud surrounding mangrove fringe, coll., Simone & Wilkinson, Aug.2005.

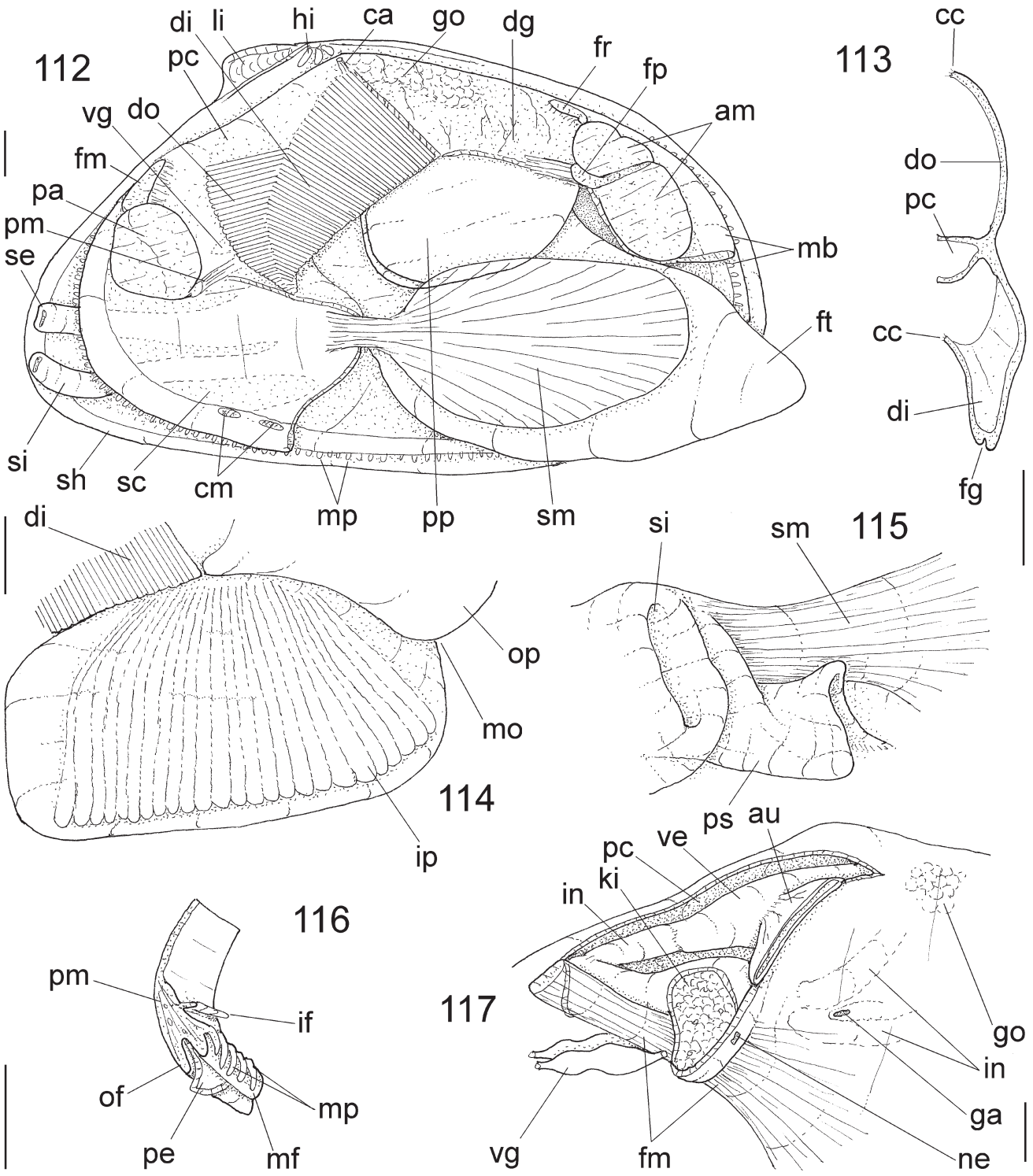
Description. – Shell (Figs. 44–48, 50–52): Outline somewhat elongated (dorsoventral height ca. 68% of anteroposterior length); laterally flattened (width ca. 34% of length); walls thin, translucent (Fig. 50); valves weakly asymmetrical, with right valve slightly more planar than left valve (Fig. 46). Colour pure white. Umbones blunt, weakly projecting, located approximately in center. Anterior edge rounded, ample, in continuation from umbo. Posterior edge roundly triangular, subrostrate; dorsal edge almost straight (Figs. 51, 52) to somewhat convex (Figs. 44, 45). Ventral edge widely rounded. Sculpture absent; surface smooth, glossy, except for growth lines. Ligament of ca. one-seventh of shell length, located posterior to umbo. Inner surface glossy, whitish. Cardinal teeth restricted to infraumbonal region (Figs. 47, 48), comprising two similarly sized teeth disposed largely divergently in right valve; single, central tooth in left valve. Right valve with single, anterior lateral tooth (Figs. 45, 48), relatively tall, narrow and triangular, anteroposteriorly

elongated (ca. one-tenth of shell length), located at short distance from cardinal teeth. Scar of anterior adductor muscle elliptical, dorsoventrally longer, with dorsal end pointed, occupying ca. one-fifteenth of inner valve surface at distance equivalent to half of its width from anterior edge. Scar of posterior adductor muscle with ventral edge at same level as that of anterior adductor scar, of ca. three-quarters of anterior scar area. Pallial sinus forming arch of ca. one-third size of valve, well separated from anterior adductor muscle scar (separation of approximately same width as anterior adductor muscle). Scar of cruciform muscle totally anterior to vertical level of posterior adductor muscle.

Main muscle system (Figs. 112, 118): Anterior adductor muscle area equivalent to one-fifteenth of shell area; division unclear; dorsal third of same width as ventral two-thirds and barely triangular. Posterior adductor muscle elliptical in cross section, located at same level as anterior adductor muscle; of ca. two-thirds of anterior adductor muscle area. Pair of pedal protractor muscles very small, thin, originating



Figs. 106–111. *Pinguitellina* cf. *pinguis* anatomy: 106, Topology of visceral structures, central nervous system, and main muscles, right view, palps deflected; 107, stomach, right view, longitudinally sectioned to expose interior surface; 108, detail of renopericardial region and some adjacent structures, right view, with gill, right wall of kidney, and pericardium removed; 109, pedal ganglia, posterior view; 110, cerebral ganglia, anterior view; 111, visceral ganglia, right and slightly anterior view. am, anterior adductor muscle; an, anus; au, auricle; ca, cardinal muscle; ce, cerebral ganglion; co, cerebrovisceral connective; dd, ducts of digestive diverticula; dh, dorsal hood; es, oesophagus; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; ga, genital aperture; gs, gastric shield; in, intestine; ki, kidney; ne, nephropore; pa, posterior adductor muscle; pc, pericardium; pg, pedal ganglia; pp, palp; rt, rectum; sf, fold separating intestine from style sac; ss, style sac; st, stomach; ud, urinary duct; ve, ventricle; vg, visceral ganglia. Scale bars = 0.5 mm.



Figs. 112–117. *Elpidollina* sp. anatomy: 112, Whole right view, right valve and part of mantle lobe removed; 113, gill, transverse section in mid region; 114, right palp, right view, exterior hemipalp deflected; 115, detail of base of both siphons and adjacent region of left mantle lobe, right siphonal retractor muscle deflected; 116, mantle border, transverse section at mid level of ventral region; 117, detail of renopericardial region and some adjacent structures, right view, gill and right wall of kidney removed, gonoduct and other visceral structures seen by transparency. am, anterior adductor muscle; au, auricle; ca, cardinal muscle; cc, ciliary connection; cm, cruciform muscle; dg, digestive diverticula; di, inner demibranch; do, outer demibranch; fg, gill food groove; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; ga, genital aperture; go, gonad; hi, hinge; if, inner fold of mantle border; in, intestine; ip, inner hemipalp; ki, kidney; li, ligament; mb, mantle border; mf, middle fold of mantle border; mo, mouth; mp, mantle papillae; ne, nephropore; of, outer fold of mantle border; op, outer hemipalp; pa, posterior adductor muscle; pc, pericardium; pe, periostracum; pm, pallial muscles; pp, palp; ps, pseudogill; sc, siphonal chamber; se, excurrent siphon; sh, shell; si, incurrent siphon; sm, siphonal retractor muscle; ve, ventricle; vg, visceral ganglia. Scale bars = 0.5 mm.

at mid level of anterior adductor muscle posterior edge, of area equivalent to one-twentieth of that of adductor muscle; penetration in anterior adductor muscle posterior side over almost its entire width. Pair of anterior pedal retractor muscles originating just dorsal to anterior adductor muscle, somewhat L-shaped; approximate size of origin ca. one-quarter of anterior adductor muscle, with narrow portion of these muscles surrounding dorsal edge of adductor muscle. Pair of posterior pedal retractor muscles of approximately same size as anterior pedal retractor muscles. Cardinal muscle narrow, short, originating in mid region of umbonal cavity. Cruciform muscle of total length equivalent to that of posterior adductor muscle, totally posterior to horizontal level of posterior adductor muscle; posterior branches lacking transverse furrows on their bases.

Foot (Figs. 112, 118): Flattened, of ca. one-third of shell volume when retracted; distal tip pointed.

Mantle (Fig. 112): Outer and middle folds of mantle edge of similar height (ca. three times shell wall thickness; Fig. 116); almost half as thick as shell wall; inner fold ca. half of height and thickness of remaining folds, originating slightly more internally (distance equivalent to middle fold height). Middle fold with series of small, narrow, similarly sized, uniformly distributed papillae (Figs. 112, 116), located on inner side (not terminally); each papilla separated from others by space equivalent to double its width; length of each papilla approximately same as fold length. Incurrent siphon of approximately same thickness and length as excurrent siphon, lacking papillae. Pair of retractor muscles of lateral walls of siphonal chamber with two bundles, with dorsal bundle wider. Pair of narrow pallial muscle from dorsal region of incurrent siphon, surrounding ventral edge of posterior adductor muscle, splaying over mantle region ventral to adductor muscle. Pseudogill (Figs. 49, 115, ps) wide, flat, located anteroposteriorly at left base of incurrent siphon, just where its left retractor muscle bears running in valve; size equivalent to three times mantle fold height.

Pallial cavity (Fig. 112): Palps rounded; each hemipalp of ca. one-ninth of valve area. Length of intersection of hemipalps equivalent to one-quarter of dorsoventral valve height. Inner surface (Figs. 49, 114) with narrow folds; smooth area surrounding entire hemipalp free edge, dorsally wider (ca. one-eighth of palp width), ventrally very narrow, with posterior smooth edge relatively wide (ca. one-eighth of palp length). Each fold of palp narrow; ca. 22 folds on each hemipalp. Gill approximately as large as palp, ca. one-eighth of valve area, of ca. half of total shell length; height ca. one-fifth of that of shell in anterior region. Outer demibranch approximately as wide as inner demibranch (Fig. 113), located posterior to inner demibranch anterior end (anterior end of outer demibranch approximately in mid region of inner demibranch). Inner demibranch inner lamella ca. three-quarters of size of outer lamella, connected by transverse septum (Fig. 113, di); food groove along ventral edge of inner demibranch (Fig. 113, fg).

Visceral mass (Figs. 117–118): Anterodorsal third filled by greenish beige digestive diverticula; remaining filled by pale cream gonad. Stomach-style sac running vertically along mid portion of visceral mass.

Circulatory and excretory systems (Fig. 117): Pericardial structures occupying ca. one-sixth of total visceral volume (Fig. 118). Pair of auricles connected to middle third of gill. Ventricular connection to auricles oblique, located in mid region of its lateral walls. Kidneys white, occupying ca. one-fifth of renopericardial volume. Nephropores very small, each slit-like, in mid region of renal side exposed to suprabranchial chamber.

Digestive system (Fig. 118): Palps as described above. Oesophagus of ca. half length of anterior adductor muscle and ca. one-third its width, dorsoventrally flattened, at some distance from anterior adductor muscle; inner surface smooth. Stomach occupying ca. one-sixth of visceral volume. Gastric dorsal glandular diverticulum long, slender, of length approximately same as stomach; inserted in right side of posterodorsal gastric wall; base narrow, widening gradually, wider in subterminal region; tip rounded; inner surface smooth. Dorsal hood on left-dorsal gastric surface, as low diverticulum directed anteriorly; inner surface smooth. Transverse muscles narrow, aligned between posterior gastric wall and adjacent intestinal loops posterior to it; folds ca. five or six in number (Fig. 118, tm). Internal gastric surface (Fig. 120) with relatively tall transverse fold (ca. one-quarter of gastric width), restricted to anterior region, ventral to oesophageal aperture; left and right ducts of digestive diverticula protected externally by expansions of transverse fold; satellite fold just ventral to transverse fold, similar to the latter but lower and narrower; both folds producing a furrow connecting apertures of both ducts of digestive diverticula; dorsal hood aperture at short distance dorsal to left duct of digestive diverticula, opening into longitudinal, narrow furrow, continuous with furrow ventral to transverse fold; aperture of gastric dorsal glandular diverticulum small, at end of low, narrow, longitudinal furrow along gastric dorsal surface in direction of oesophagus. Intestine forming long loop to mid level of style sac (Figs. 118, 119), then ca. five tight, short loops also at mid level of style sac, then another set of three or four loops just posterior to gastric chamber, the last set of loops with wider and thinner walls; estimated intestinal length ca. four times that of style sac.

Genital system (Fig. 117): Gonad as described above. Genital duct directed anteroposteriorly, preceding pore. Genital pores simple, each slit-like, ventral to terminal set of intestinal loops, at considerable distance from nephropore (ca. half of pericardial length), at same level anterior to that.

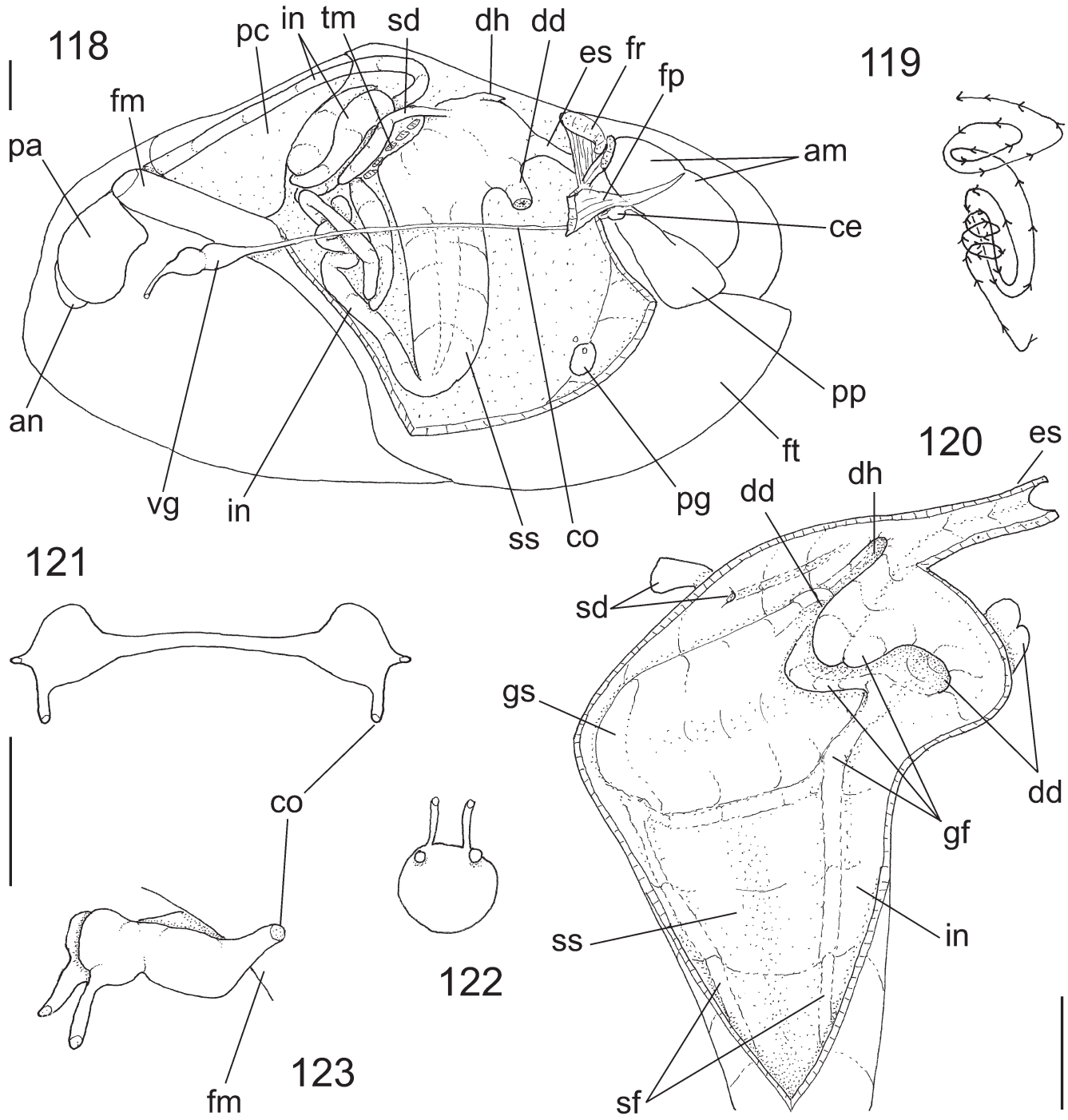
Central nervous system (Figs. 118, 121–123): Cerebral ganglia (Fig. 121) of ca. half size of cross section of oesophagus. Pair of pedal ganglia (Fig. 122) fused medially, located in mid part of visceral cavity anterior surface, volume of each pedal ganglion ca. three-quarters of one cerebral ganglion. Pair of statocysts on anterodorsal side of pedal ganglia; volume ca. one-twentieth of that of ganglia (Figs. 118, 122). Pair of visceral ganglia (Fig. 123) at considerable distance

anterior to posterodorsal surface of posterior adductor muscle (approximately same as muscle width); volume of each visceral ganglion ca. twice that of one cerebral ganglion; each visceral ganglion elongated anteroposteriorly, with pair of larger anterior nerves and pair of secondary protuberances on anterodorsal end of posterior ganglionic region.

Measurements. – MZSP 62351 (#1): 9.4 × 6.5 × 3.2 mm; (#2): 8.5 × 5.9 × 2.8 mm.

Distribution. – New Caledonia to China Sea.

Habitat. – Muddy bottoms, in shallow water.



Figs. 118–123. *Elpidollina* sp. anatomy: 118, Topology of visceral structures, central nervous system, and main muscles, right view, palps deflected; 119, schematic representation of intestinal loops in situ (same position as preceding figure); 120, stomach, right view, longitudinally sectioned to expose interior surface; 121, cerebral ganglia, anterior view; 122, pedal ganglia, posterior view; 123, visceral ganglia, right view. am, anterior adductor muscle; an, anus; ce, cerebral ganglion; co, cerebrovisceral connective; dd, ducts of digestive diverticula; dh, dorsal hood; es, oesophagus; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; gf, gastric fold; gs, gastric shield; in, intestine; pa, posterior adductor muscle; pc, pericardium; pg, pedal ganglia; pp, palp; sd, stomach diverticulum; sf, fold separating intestine from style sac; ss, style sac; tm, transverse muscles of visceral sac; vg, visceral ganglia. Scale bars = 0.5 mm.

***Remarks.* –** Because of superficial similarity, the studied lot was initially identified as *Pinguimacoma cygnus* (Hanley, 1844b: 144). However, by examining the type specimen (Figs. 53–55), it was possible to note that *P. cygnus* has a heavy, thick-walled shell, stronger commarginal sculpture, a sharper posterior region, a wide radial furrow at the mid level of the posterior region, and a different hinge. On the other hand, the Thai samples have close similarity to *Elpidollina decumbens* (Carpenter, 1865). This is the type species, by original designation, of the genus *Elpidollina* Olsson, 1961. The similarities include thin-walled shells, a subtrigonal shape, and the shell somewhat inflated. Moreover, the hinge is the main diagnostic feature; it has a very large anterior lateral tooth in the right valve (Figs. 45, 48) and small lateral teeth in the remaining regions (including the left valve) (Fig. 47). A strong anterior lateral tooth in the right valve is also found in the genus *Angulus* Mühlfeld, 1811. However, the species of this genus have a shell more thick-walled and strongly sculptured than the specimens examined here. Additionally, they usually have lateral teeth well developed. The Thai samples also resemble *Moerella iridescens* (Benson, 1842) from China. They differ by a more rounded posterior region, by the tip of posterior region more dorsally displaced, and by greater thinness of shell walls. Their outline also looks like the northern Pacific *Heteromacoma nasuta* (Conrad, 1837) (see Higo, Callomon & Goto, 1999), from which they differ by having thinner walls, a glossy outer surface, and by the presence of an anterior lateral hinge tooth.

Tellinides timorensis (Lamarck, 1818)
(Figs. 56–60, 124–133)

Tellina Timorensis: Küster & Römer, 1841: 166–168, pl. 34, figs. 4–6; Sowerby, 1866: pl. 4, fig. 14.
Tellina (*Tellinides*) *timorensis*: Robba et al., 2002: 97–98, pl. 14, figs. 5a–b.
For additional synonymy, see Robba et al., 2002: 97–98.

***Material examined.* –** 1 ex. (MZSP 62343), Thailand, Chantaburi (Gulf of Thailand), Kungkrabaen Bay, 12°35.31'N 101°54.29'E, sta. KKB-04, coll. Simone, Aug.2005.

***Description.* –** Shell (Figs. 56–60): Outline somewhat elongated (dorsoventral height ca. 65% of anteroposterior length), subrectangular; laterally flattened (width ca. 31% of length); walls relatively thick. Colour pink close to umbo, gradually becoming white closer to borders. Periostracum relatively thick, mainly close to margins, brown, velvet-like. Umbo blunt, low, located approximately at valve center (Figs. 56–58, 124). Anterior and posterior edges rounded, ample, in continuation from umbo; posterior edge slightly more pointed. Ventral edge widely rounded. Sculpture absent; surface smooth, opaque, with relatively strong growth lines. Ligament ca. 22% of shell length. Cardinal teeth comprising two similarly sized teeth disposed divergently in right valve (Figs. 59, 60); single, central, tall tooth in left valve. Right valve with single, low, anterior lateral tooth, anteroposteriorly elongated (ca. one-seventh of shell length), located midway between cardinal teeth and anterior edge. Scar of anterior adductor muscle elliptical (Fig. 57), almost round, weakly dorsoventrally longer, with blunt dorsal end, occupying ca. one-fifteenth of inner valve surface, located at a distance equivalent to half of its width from anterior edge. Scar of posterior adductor muscle with ventral edge at same level as that of anterior scar, area ca. three-quarters of that of anterior adductor scar. Pallial sinus forming arch of ca. one-third of valve area, running close to anterior adductor muscle scar. Scar of cruciform muscle at vertical level of posterior adductor muscle, slightly displaced anteriorly.

Main muscle system (Figs. 58, 124, 128): Anterior adductor muscle area equivalent to one-fifteenth of shell area; divided into two areas: anterior area forming arch of ca. three-quarters of total muscle volume, posterior area restricted to middle and central regions. Posterior adductor muscle elliptical in cross section, located at same level as anterior adductor muscle; of ca. two-thirds of anterior adductor muscle area; division transverse, approximately in middle. Pair of pedal protractor muscles very small, thin, originating between middle and dorsal thirds of anterior adductor muscle posterior edge, in area equivalent to one thirtieth of that of adductor muscle; penetration into anterior adductor muscle posterior side half its width. Pair of anterior pedal retractor muscles originating just dorsal to anterior adductor muscle, somewhat L-shaped; approximate size of origin ca. one-eighth of anterior adductor muscle; origin divided into two similarly sized bundles. Pair of posterior pedal retractor muscles of ca. twice the size of anterior pedal retractor muscles. Cardinal muscle relatively wide, short, originating in mid region of umbonal cavity. Cruciform muscle with total length equivalent to three-quarters of posterior adductor muscle, located at same horizontal level as posterior adductor muscle; posterior branches lacking transverse furrows on their bases.

Foot (Figs. 58, 124): Flattened, of ca. one-third of shell volume when retracted; distal tip pointed.

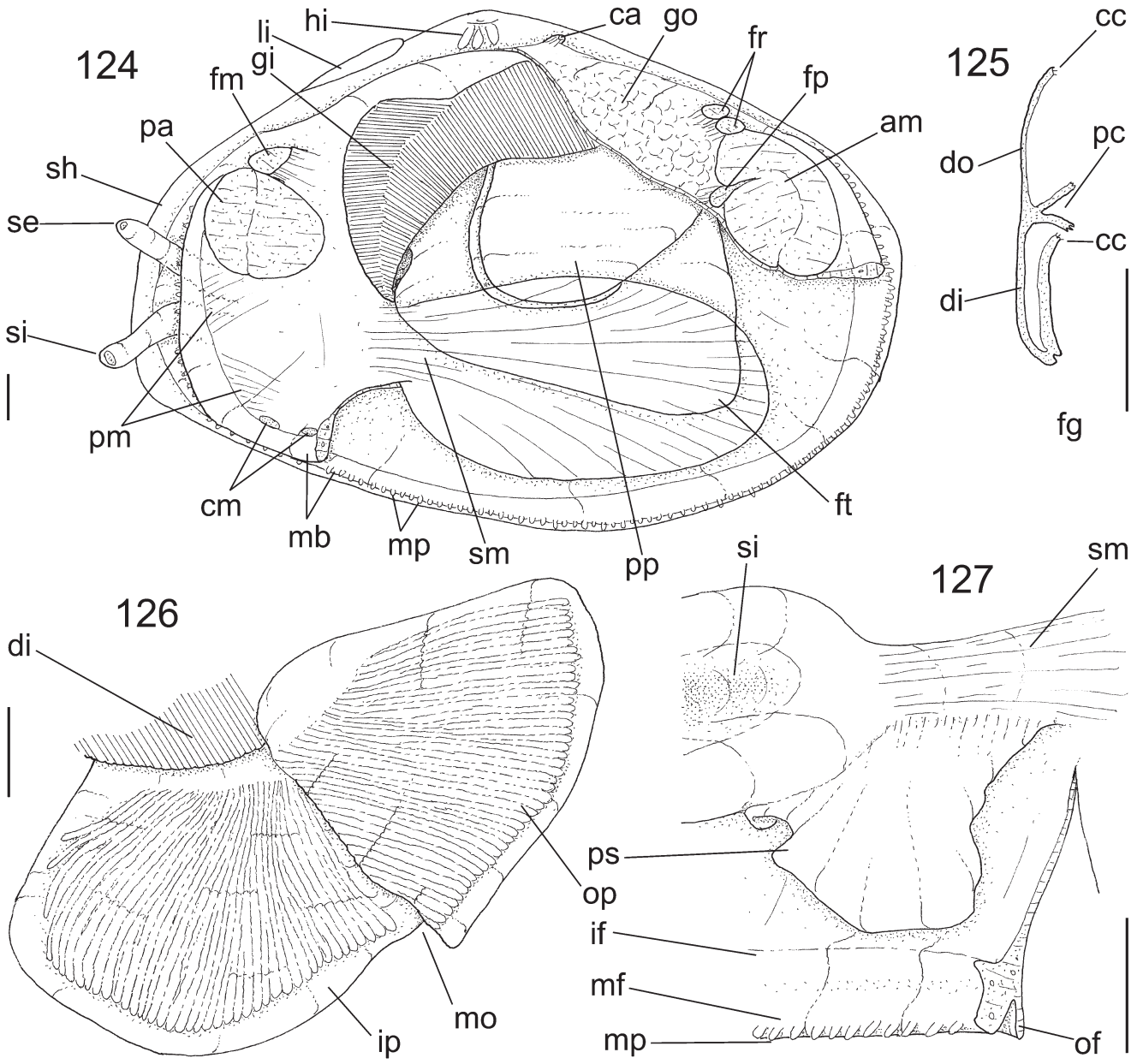
Mantle (Figs. 58, 124): Outer and middle folds of mantle edge of similar height (ca. three times shell wall thickness) (Fig. 127); outer fold almost one-third as thick as shell wall; middle fold approximately as thick as shell wall; inner fold relatively low, ca. one-third of height of remaining folds, base wide, originating as appendix of middle fold base. Middle fold with series of small, narrow, similarly sized, uniformly distributed papillae (Fig. 127); each papilla separated from others by space equivalent to double its width; length of each papilla ca. half of fold height. Incurrent siphon of approximately same thickness and length as excurrent siphon, lacking papillae (Fig. 58). Pair of retractor muscles of lateral walls of siphonal chamber with two similarly sized bundles (Fig. 124, pm). Pseudogill wide, flat, located anteroposteriorly in left base of incurrent siphon, just where left retractor muscle begins running in valve (Fig. 127, ps); size equivalent to posterior adductor muscle width.

Pallial cavity (Figs. 58, 124): Palps rounded; each hemipalp of ca. one-eighth of valve area. Length of intersection of hemipalps equivalent to one-quarter of dorsoventral valve height. Inner surface (Fig. 126) with narrow folds; smooth area surrounding entire hemipalp free edge, dorsally slightly

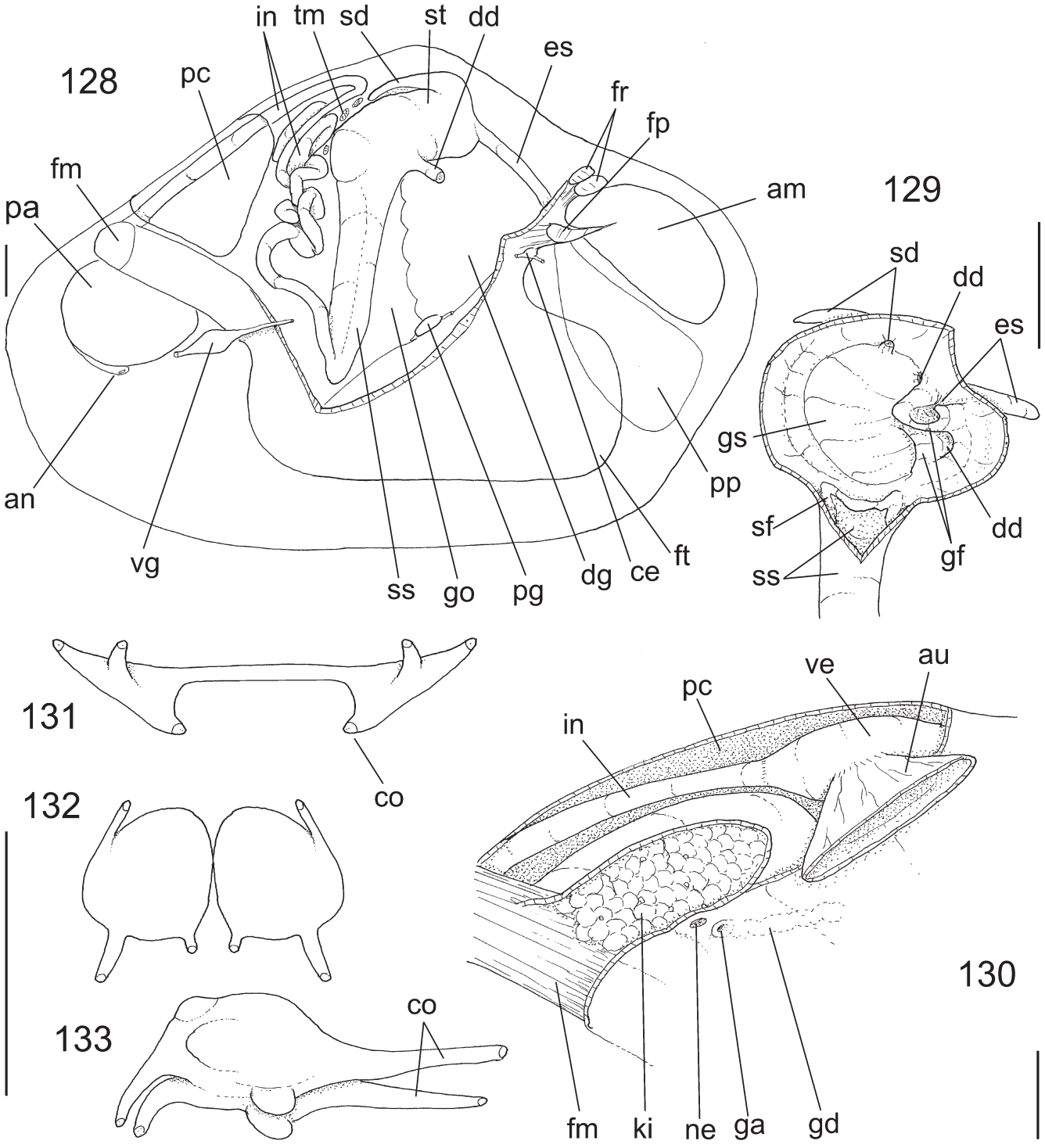
wider (ca. one-eighth of palp width), ventrally and posteriorly narrow (ca. one-twentieth of palp length). Folds of palp narrow, ca. 35 on each hemipalp. Gill approximately as large as palp, ca. one-eighth of valve area, of ca. half of total shell length; height ca. one-fifth of that of shell in anterior region. Outer demibranch approximately as wide as inner demibranch (Fig. 125), located posterior to inner demibranch anterior end (anterior end of outer demibranch between middle and anterior thirds of inner demibranch). Inner demibranch inner lamella approximately as tall as outer lamella; food groove along ventral edge of inner demibranch (Fig. 125, fg).

Visceral mass (Figs. 128, 130): Anterodorsal third filled by pale beige digestive diverticula; remaining filled by pale cream gonad. Stomach-style sac running vertically along middle portion of visceral mass.

Circulatory and excretory systems (Fig. 130): Pericardial structures occupying ca. one-fifth of total visceral volume (Fig. 128). Pair of auricles connected to middle third of gill. Ventricular connection to auricles in mid region of its lateral walls. Kidneys white, occupying ca. one-quarter of renopericardial volume. Nephropores very small, each a slit



Figs. 124–127. *Tellinides timorensis* anatomy: 124, Whole right view, right valve and part of mantle lobe removed; 125, gill, transverse section in mid region; 126, right palp, right view, exterior hemipalp deflected, adjacent portion of gill also shown; 127, detail of base of siphons and adjacent region of left mantle lobe, right siphonal retractor muscle deflected. am, anterior adductor muscle; ca, cardinal muscle; cc, ciliary connection; cm, cruciform muscle; di, inner demibranch; do, outer demibranch; fg, gill food groove; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; gi, gill; go, gonad; hi, hinge; if, inner fold of mantle border; ip, inner hemipalp; li, ligament; mb, mantle border; mf, middle fold of mantle border; mo, mouth; mp, mantle papillae; of, outer fold of mantle border; op, outer hemipalp; pa, posterior adductor muscle; pc, pericardium; pm, pallial muscles; pp, palp; ps, pseudogill; se, excurrent siphon; sh, shell; si, incurrent siphon; sm, siphonal retractor muscle. Scale bars = 1 mm.



Figs. 128–133. *Tellinides timorensis* anatomy: 128, Topology of visceral structures, central nervous system, and main muscles, right view, palps deflected; 129, stomach, right view, longitudinally sectioned to expose interior surface; 130, detail of renopericardial region and some adjacent structures, right view, gill and right wall of kidney removed, gonoduct seen by transparency; 131, cerebral ganglia, ventral view; 132, pedal ganglia, posterior view; 133, visceral ganglia, right view. am, anterior adductor muscle; an, anus; au, auricle; ce, cerebral ganglion; co, cerebrovisceral connective; dd, ducts of digestive diverticula; dg, digestive diverticula; es, oesophagus; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; ga, genital aperture; gd, genital duct; gf,` gastric fold; go, gonad; gs, gastric shield; in, intestine; ki, kidney; ne, nephropore; pa, posterior adductor muscle; pc, pericardium; pg, pedal ganglia; pp, palp; sd, stomach diverticulum; sf, fold separating intestine from style sac; ss, style sac; st, stomach; tm, transverse muscles of visceral sac; ve, ventricle; vg, visceral ganglia. Scale bars = 1 mm.

in posterior region of renal side exposed in suprabranchial chamber.

Digestive system (Fig. 128): Palps as described above. Oesophagus of approximately same length as anterior adductor muscle and ca. one-third its width, somewhat cylindrical, running at some distance away from adductor muscle, slightly closer at its anterior end. Stomach occupying ca. one-fifth of visceral volume. Gastric dorsal glandular diverticulum long, slender, length ca. half that of stomach; inserted in right side of posterodorsal gastric wall; widening gradually along its length; tip pointed; inner surface smooth. Dorsal hood on left-dorsal gastric surface, low, directed posteriorly; inner surface smooth. Transverse muscles narrow, aligned between posterior gastric wall and adjacent intestinal loops posterior to it (Fig. 128, tm), ca. three or four in number. Internal gastric surface (Fig. 129) with transverse fold relatively low (ca. one-eighth of gastric width), expanding to lateral regions protecting oesophageal aperture; left and right ducts of digestive diverticula protected externally by ventral expansions of transverse fold; satellite fold just ventral to transverse fold, similar to latter but lower and narrower, restricted to right duct of digestive diverticula; dorsal hood aperture narrow, located at short distance dorsal and posterior to left duct of digestive diverticula; secondary longitudinal folds relatively low, narrow (ca. half of transverse fold width), surrounding gastric shield (Fig. 129). Intestine forming long loop to mid level of style sac; after this, ca. five tight, short loops also at mid level of style sac, after and dorsal to this another set of three or four longer loops just posterior to gastric chamber, last set of loops of intestine with wider and thinner walls; estimated intestinal length ca. three times that of style sac.

Genital system (Fig. 130): Gonad as described above. Genital duct directed anteroposteriorly edging pericardium, at great distance preceding genital pore (ca. one-third of visceral cavity anteroposterior length). Genital pores simple, each slit-like, very close and at same level anterior and slightly ventral to nephropore.

Central nervous system (Figs. 128, 131–133): Cerebral ganglia (Fig. 131) of ca. half size of cross section of oesophagus. Pair of pedal ganglia (Fig. 132) very close to each other (commissure extremely short), located in mid part of visceral cavity anterior surface; volume of each pedal ganglion ca. 1.5 times that of one cerebral ganglion. Pair of visceral ganglia (Fig. 133) just anterior from posteroventral surface of posterior adductor muscle; volume of each visceral ganglion ca. three times that of one cerebral ganglion; each visceral ganglion oval, elongated anteroposteriorly, with pair of larger anterior nerves and two pairs of secondary protuberances at anterodorsal end of posterior ganglionic region, on mid region of ventral ganglionic surface.

Measurements. – MZSP 62343 (#1): 18.3 × 12.6 × 5.6 mm.

Distribution. – Japan to Red Sea.

Habitat. – Muddy bottoms in mangrove hummocks, in shallow water.

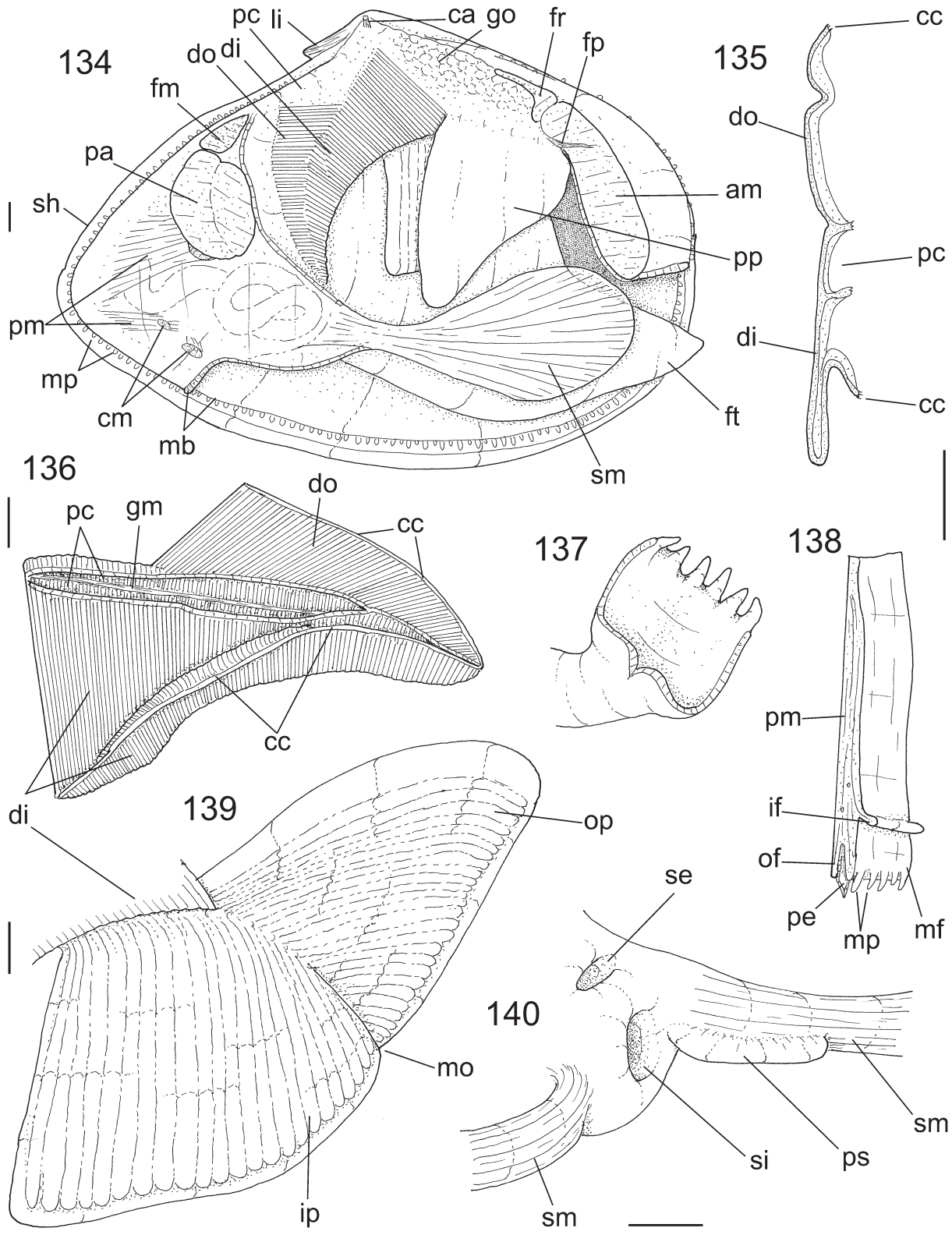
Macomona sp.

(Figs. 61–68, 134–146)

Material examined. – 2 ex. (MZSP 62342), Thailand, Chantaburi (Gulf of Thailand), Kungkrabaen Bay, Chao Lao Beach, oceanside near pier with fishing nets, 12°32.578'N 101°57.831'E, sta. KKB-15, coll. Simone, Aug.2005.

Description. – Shell (Figs. 61–65): Outline somewhat elongated (dorsoventral height ca. 70% of anteroposterior length), oval; laterally flattened (width ca. 32% of length); walls thin. Colour pure white, translucent. Periostracum undetectable. Umbones pointed, wide, projecting, located approximately at center. Anterior edge rounded, ample, in continuation from umbo; posterior edge pointed, triangular, subrostrate, slightly flexed to right (Fig. 63). Ventral edge widely rounded. General sculpture of uniform commarginal undulations (Fig. 61); surface glossy, with relatively strong growth lines; pair of low, wide, divergent furrows on posterior slope. Ligament of ca. 14% of shell length. Cardinal teeth (Figs. 64, 65) comprising two similarly sized teeth disposed divergently on both valves (posterior teeth slightly longer and more horizontal). Right valve with single, low, anterior lateral tooth, anteroposteriorly elongated (ca. one-tenth of shell length), close to cardinal teeth. Posterior lateral tooth of right valve very small (ca. 7% of shell length), located midway between umbo and posterior end, just posterior to ligament. Scar of anterior adductor muscle oval, dorsoventrally longer, with pointed dorsal end, occupying ca. one-fifteenth of inner valve surface, located at a distance equivalent to half of width from anterior edge. Scar of posterior adductor muscle (Fig. 62) with ventral edge at same level as that of anterior adductor scar, area ca. three-quarters of that of anterior scar. Pallial sinus forming arch of ca. half size of valve, running close to anterior adductor muscle scar. Scar of cruciform muscle at vertical level of posterior adductor muscle, displaced slightly posteriorly.

Main muscle system (Figs. 67, 134, 141): Anterior adductor muscle area equivalent to one-fifteenth of shell area, dorsoventrally elongated (dorsoventral height ca. three times anteroposterior length) (Figs. 67, 134), divided dorsoventrally into two similarly sized areas; dorsal end pointed; ventral end rounded. Posterior adductor muscle elliptical in cross section, located at same ventral level as anterior adductor muscle; of ca. two-thirds of anterior adductor muscle area, slightly wider; division transverse, approximately in middle. Pair of pedal protractor muscles very small, thin, originating between dorsal and subsequent ventral quarter of anterior adductor muscle posterior edge, area equivalent to one thirtieth of that of adductor muscle; penetration into anterior adductor muscle posterior side over approximately its entire width. Pair of anterior pedal retractor muscles originating just dorsal to anterior adductor muscle, somewhat L-shaped; approximate size of origin ca. one-eighth of anterior adductor muscle; origin arched (concavity posterior), with ventral



Figs. 134–140. *Macomona* sp. anatomy: 134, Whole right view, right valve and part of mantle lobe removed; 135, gill, transverse section in mid region; 136, isolated gill, whole interior view; 137, incurrent siphon, detail of tip, partly sectioned longitudinally; 138, mantle border, transverse section at mid level of ventral region; 139, right palp, right view, exterior hemipalp deflected, adjacent portion of gill also shown; 140, detail of base of siphons, right siphonal retractor muscle deflected. am, anterior adductor muscle; ca, cardinal muscle; cc, ciliary connection; cm, cruciform muscle; di, inner demibranch; do, outer demibranch; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; gm, gill retractor muscle; go, gonad; if, inner fold of mantle border; ip, inner hemipalp; li, ligament; mb, mantle border; mf, middle fold of mantle border; mo, mouth; mp, mantle papillae; of, outer fold of mantle border; op, outer hemipalp; pa, posterior adductor muscle; pc, pericardium; pe, periostracum; pm, pallial muscles; pp, palp; ps, pseudogill; se, excurrent siphon; sh, shell; si, incurrent siphon; sm, siphonal retractor muscle. Scale bars = 0.5 mm.

region three times wider. Pair of posterior pedal retractor muscles as large as anterior pedal retractor muscles. Cardinal muscle very narrow, short, originating in mid region of umbonal cavity. Cruciform muscle of total length equivalent to three-quarters of posterior adductor muscle, located at same horizontal level as posterior adductor muscle, displaced somewhat posteriorly; posterior branches lacking transverse furrows on their bases.

Foot (Figs. 67, 134): Flattened, of ca. one-quarter of shell volume when retracted.

Mantle (Figs. 67, 134): Three folds of mantle edge (Fig. 138) of similar height (ca. three times shell wall thickness) and thickness (ca. one-third of shell wall thickness). Middle fold with series of small, narrow, similarly sized, uniformly distributed papillae (Fig. 138); each papilla separated from others by space equivalent to its width; length of each papilla ca. one-third of fold height. Inner fold weakly displaced internally. Both siphons similarly sized, narrow, very long (1.5 times longer than shell length in retracted condition) (Figs. 66–67), withdrawing inside siphonal chamber by means of intense coiling (Figs. 67, 134, si). Incurrent siphon with six short, uniform, narrow papillae on distal edge (Fig. 137); each papilla somewhat triangular, with pointed tip, separated from others by space equivalent to its width. Pair of retractor muscles of lateral walls of siphonal chamber with two bundles (Fig. 134, pm); dorsal bundle wider, with thicker muscular region at ventral edge, inserting at base of posterior adductor muscle. Pseudogill (Fig. 140) wide, flat, low, located anteroposteriorly in left base of incurrent siphon, just where left retractor muscle begins running in valve; length equivalent to half of posterior adductor muscle width, height ca. one-quarter of posterior adductor muscle width.

Pallial cavity (Figs. 67, 134): Palps triangular; each hemipalp of ca. one-sixth of valve area. Length of intersection of hemipalps equivalent to one-third of dorsoventral valve height. Outer hemipalp ca. one-quarter shorter than inner hemipalp length. Inner surface (Fig. 139) with relatively wide folds; smooth area surrounding entire hemipalp free edge of relatively uniformly width (ca. one-twelfth of palp width); ca. 20 folds on inner hemipalp, 17 on outer hemipalp. Gill approximately as large as palp, ca. one-eighth of valve area, of ca. half of total shell length; height ca. one-seventh of that of shell in anterior region. Outer demibranch a little wider than inner demibranch, located posterior to inner demibranch anterior end (anterior end of outer demibranch between middle and anterior thirds of inner demibranch) (Figs. 68, 135, 136). Inner demibranch inner lamella approximately as tall as outer lamella; no detectable food groove along ventral edge of inner demibranch. Inner insertions of gill as in Figs. 68 and 136.

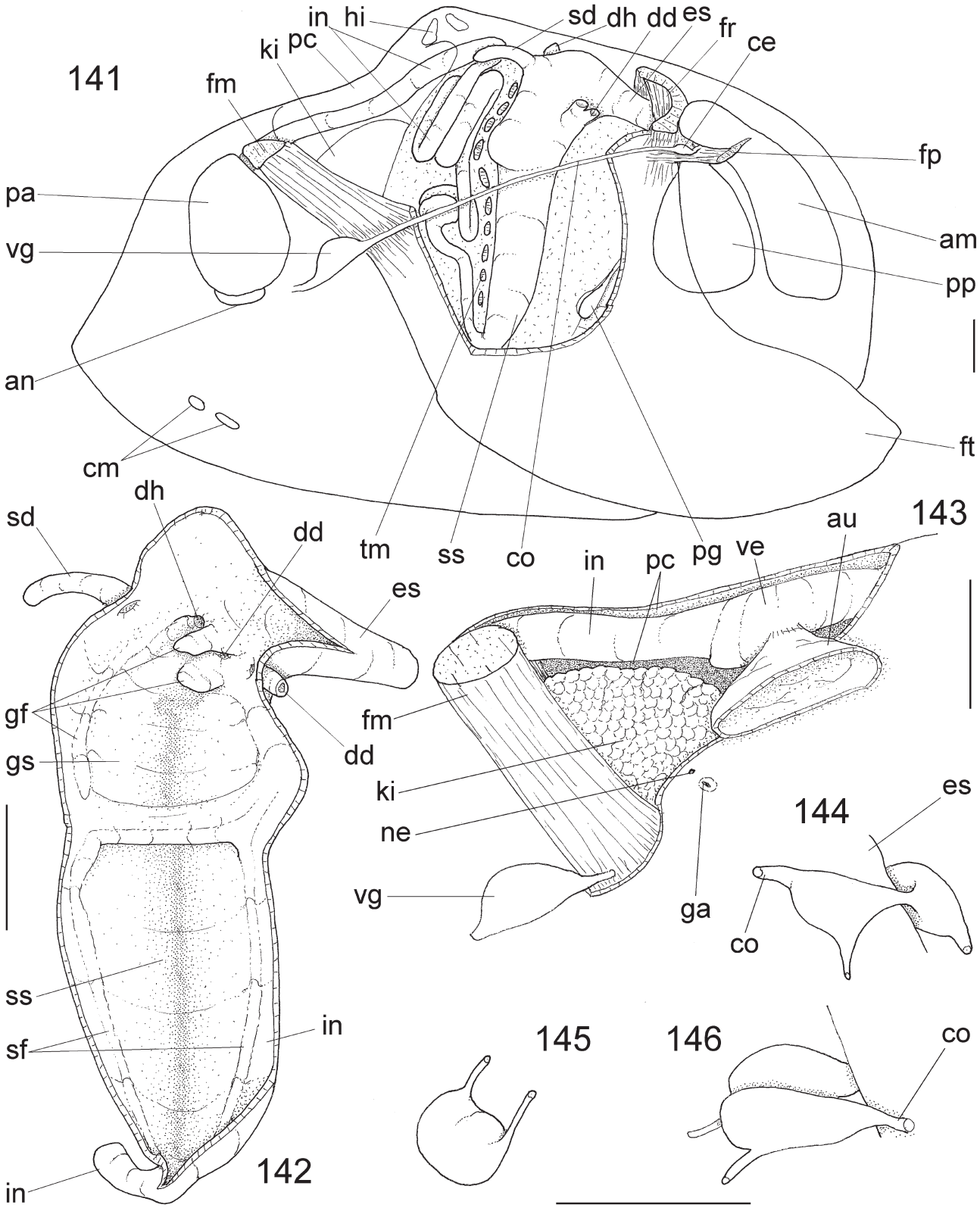
Visceral mass (Figs. 141, 143): Anterodorsal third filled by pale beige digestive diverticula; remaining filled by white gonad. Stomach-style sac running vertically along entire middle portion of visceral mass.

Circulatory and excretory systems (Fig. 143): Pericardial structures occupying ca. one-quarter of total visceral volume (Fig. 141). Pair of auricles connected to middle third of gill. Ventricular connection to auricles in mid region of its lateral walls. Kidneys white, occupying ca. one-quarter of renopericardial volume. Nephropores very small, each in mid region of renal side exposed in suprabranchial chamber.

Digestive system (Fig. 141): Palps as described above. Oesophagus of approximately same length as anterior adductor muscle and ca. half its width, somewhat cylindrical, running at some distance away from adductor muscle except at anterior end. Stomach occupying ca. one-fifth of visceral volume. Gastric dorsal glandular diverticulum long, slender, of length ca. half that of stomach, inserted on right side of posterodorsal gastric wall, of uniform width along its length; inner surface smooth; tip rounded, projecting posteriorly as arch covering intestinal loops. Dorsal hood on left-dorsal gastric surface, low, pointed, directed to left; inner surface smooth. Transverse muscles narrow, aligned between posterior gastric wall and adjacent intestinal loops posterior to it, also distributed along posterior wall of style sac (Fig. 141, tm); folds ca. 10 in number. Internal gastric surface (Fig. 142) with transverse fold relatively low (ca. one-eighth of gastric width), short, restricted to ventral side of oesophageal aperture; left and right ducts of digestive diverticula free from transverse fold; satellite fold just ventral to transverse fold, similar to latter in size and characters; dorsal hood aperture narrow, located at short distance dorsal and posterior to left duct of digestive diverticula, at end of wide longitudinal furrow partially covered by projection of gastric shield; secondary longitudinal fold relatively low, narrow (ca. half width of transverse fold) surrounding posterior edge of gastric shield (Fig. 142). Intestine forming loop to mid level of style sac; after this, ca. three tight, short loops also at mid level of style sac, after and at some distance dorsal to this, another set of three or four longer loops just posterior to gastric chamber, last set of loops with wider, thinner walls; estimated intestinal length ca. four times that of style sac.

Genital system – Gonad as described above. No genital duct detected. Genital pores simple, each slit-like, surrounded by sphincter, located very close to nephropore, at same level anterior and slightly ventral to latter (Fig. 143).

Central nervous system (Figs. 141, 144-146): Cerebral ganglia (Fig. 144) of ca. half size of cross section of oesophagus, located slightly closer to median line, with short cerebral commissure (of approximately same length as ganglia). Pair of pedal ganglia (Fig. 145) fused (no detectable commissure), located between middle and ventral thirds of visceral cavity anterior surface; volume of each pedal ganglion approximately same as one cerebral ganglion. Pair of visceral ganglia (Fig. 146) just anterior to posteroventral surface of posterior adductor muscle; volume of each visceral ganglion ca. 1.5 times that of one cerebral ganglion; each visceral ganglion oval, elongated anteroposteriorly, with pair of large anterior nerves inserted ventrally, without detectable protuberances.



Figs. 141–146. *Macomona* sp. anatomy: 141, Topology of visceral structures, central nervous system, and main muscles, right view, palps deflected; 142, stomach, right view, longitudinally sectioned to expose interior surface; 143, detail of renopericardial region and some adjacent structures, right view, gill and right wall of kidney removed; 144, cerebral ganglia, right and slightly anterior view; 145, pedal ganglia, posterior and slightly right view; 146, visceral ganglia, right and slightly dorsal view. am, anterior adductor muscle; an, anus; au, auricle; ce, cerebral ganglion; cm, cruciform muscle; co, cerebrovisceral connective; dd, ducts of digestive diverticula; dh, dorsal hood; es, oesophagus; fm, posterior pedal retractor muscle; fp, pedal protractor muscle; fr, anterior pedal retractor muscle; ft, foot; ga, genital aperture; gf, gastric fold; gs, gastric shield; hi, hinge; in, intestine; ki, kidney; ne, nephropore; pa, posterior adductor muscle; pc, pericardium; pg, pedal ganglia; pp, palp; sd, stomach diverticulum; sf, fold separating intestine from style sac; ss, style sac; tm, transverse muscles of visceral sac; ve, ventricle; vg, visceral ganglia. Scale bars = 1 mm.

Measurements. – MZSP 62342 (#1): 14.1 × 10.4 × 4.3 mm.

Habitat. – Muddy sand bottoms, in shallow water.

Remarks–The Thai samples were initially identified as *Macomona australis* (Deshayes, 1854). However, after examination of the type specimens (Figs. 69–73), some important differences have arisen. *Macomona* sp. differs from *M. australis* in having thinner, translucent shell walls, the umbones and posterior region slightly more sharply pointed (Figs. 61, 62), and a different hinge arrangement; in the right valve (compare Figs. 64 and 71) *M.* sp. has a better developed anterior lateral tooth and lacks a nymph; in the left valve (compare Figs. 65 and 72) *M.* sp. has a weak anterior lateral tooth, narrower cardinal teeth, and lacks a nymph.

Attribution to the genus *Macomona* Finlay, 1927 (type species *Tellina liliana* Iredale, 1915, by original designation) is based on the compressed appearance, with the posterior region somewhat pointed and twisted (Fig. 63), and on the presence of anterior lateral teeth in the hinge (Keen, 1969).

DISCUSSION OF CHARACTERS

This section is organised as a phylogenetic analysis, however, as stated in the Introduction, there us no intention to undertake a phylogeny of the Tellinidae. The goal is to perform this discussion in a testable scenario. In some cases, if the list of taxa is referred to as "all," the character is included in both the ingroup and the semelids.

Shell

1. Shell form: 0 = somewhat cylindrical (*Solen*); 1 = laterally flattened (width less than one-quarter of length) (remaining) (CI 100; RI 100). Because the tellinids are rapid diggers, the shell must be flattened, in a form of an axe. Certainly this conformation is more adequate to penetrate into unconsolidated substrata (Trueman et al., 1966). The same can be extended to the semelids, psammobiids, and donacids, the other constituent families of the Tellinoidea.

2. Shell surface: 0 = opaque; 1 = glossy (*Moerella* cf. *nitens, Cadella* cf. *semen, Pinguitellina* cf. *pinguis, Elpidollina* sp., *Macomona* sp.) (CI 100; RI 100).

3. Shell wall thickness: 0 = thick; 1 = thin, translucent (*Moerella* cf. *nitens, Cadella* cf. *semen, Pinguitellina* cf. *pinguis, Elpidollina* sp., *Macomona* sp.) (CI 100; RI 100). According to the resulting cladogram, evolution of the tellinids resulted in a lighter shell with a glossy outer surface. This is explored in characters 2 and 3. There is also a perceptible trend towards reduction of body size, because the more basal species are of larger proportions, ca. 40 mm, whereas the others are ca. 10 mm. This character (size), however, was not used because of the difficulty in stating standards.

4. Shell valves: 0 = symmetrical (*Moerella* cf. *nitens, Semele, Solen*); 1 = asymmetrical (remaining) (CI 50; RI 50). Asymmetry of bivalves is normally related to a position in the substratum different from perpendicular. However, as far as has been observed in fieldwork, all tellinids and semelids lie perpendicularly positioned in relation to the bottom surface. Nonetheless, asymmetry in the tellinoideans (Figs. 25, 37, 46, 63) appears to be widespread.

5. Periostracum: 0 = relatively well developed; 1 = weak, only present in region close to umbo (*Cadella* cf. *semen, Pinguitellina* cf. *pinguis*); 2 = absent (*Moerella* cf. *nitens, Elpidollina* sp., *Macomona* sp.) (CI 100; RI 100; not additive).

6. Sculpture (commarginal and radial): 0 = present (*Serratina capsoides, Semele, Solen*); 1 = absent (remaining) (CI 100; RI 100).

7. Cardinal teeth: 0 = different in both valves (*Tellinides timorensis, Semele, Solen*); 1 = somewhat similar (remaining) (CI 50; RI 50). Of course the similarity in both valves takes into consideration that each tooth encases in a socket. Despite this, the appearance of the hinge is similar in both valves. It is equally parsimonious to consider state 1 as a synapomorphy of node 2, with a reversal in *Tellinides timorensis*, or as convergence between *Serratina capsoides* and node 4. The first hypothesis is shown in Fig. 147.

8. Anterior lateral tooth in right valve: 0 = close to umbo; 1 = at long distance from umbo (*Cadella* cf. *semen, Tellinides timorensis*); 2 = absent (*Serratina capsoides*) (CI 66; RI 0; not additive). The resulting cladogram shows that state 1 of this character is homoplastic, whereas state 2 is, in this assemblage, an autapomorphy of *Serratina capsoides*.

9. Posterior lateral tooth in right valve: 0 = present; 1 = absent (*Serratina capsoides, Elpidollina* sp., *Tellinides timorensis*) (CI 33; RI 0). The presence of lateral teeth is of particular importance in Tellinidae systematics, because it defines the subfamily Tellininae, whereas their absence defines the subfamily Macominae (Keen, 1969; Coan et al., 2000). However, based on morphology, the subfamily Tellininae is at least paraphyletic (it could be polyphyletic) as shown the resulting cladogram. On the other hand, many kinds of arrangement between both extremes can be observed, with intermediate species possessing lateral teeth in a single valve or single side (Figs. 3, 12, 24, 34, 39, 48).

In character 9, it is equally parsimonious to consider state 1 as a mere convergence among the three species, as well as a synapomorphy at node 2, with a reversal at node 4 and reappearance in *Elpidollina* sp. The second hypothesis is shown in Fig. 147.

The ligament is very conservative in all examined species. A single difference was found in the outgroup *Semele*; the semelids differ from the remaining tellinoideans by the internal component of the ligament (Trueman, 1949, 1953). An opisthodetic, parivicular ligament has been considered characteristic of the Tellinoidea (Trueman, 1966).

Main muscles

10. Adductor muscles: 0 = similarly sized; 1 = anterior muscle at least one-third larger (*Serratina capsoides, Moerella* cf. *nitens, Cadella* cf. *semen, Elpidollina* sp., *Macomona* sp., *Semele*) (CI 33; RI 0). It is equally parsimonious to consider state 1 as synapomorphy of node 5, with convergence in *Semele* and *Serratina capsoides*, or a synapomorphy of node 1, with a reversal at node 3 and reappearance at node 5. The second optimisation is shown in Fig. 147.

11. Shape of anterior adductor muscle: 0 = weakly elliptical, almost rounded (*Solen*); 1 = dorsoventrally longer (remaining) (CI 100; RI 100). The anterior adductor muscle has two additional modifications explored in characters 10 and 11. This appears to be an increase of this muscle (e.g. Figs. 58, 67), rather than a reduction of the posterior adductor muscle. Asymmetry of the two adductor muscles is normally due to increase of the posterior and reduction of the anterior, which even disappears in monomyarian taxa. This gradation is clear in some families, such as Mytilidae, which encompasses many kinds of adductor muscle shapes (Yonge, 1955; Simone & Gonçalves, 2006). However in tellinoideans, the contrary trend appears: an increment of the anterior adductor muscle.

12. Pedal protractor muscles: 0 = on ventral side of anterior adductor muscle (*Solen*); 1 = on dorsal side of anterior adductor muscle (remaining) (CI 100; RI 100).

13. Origin of pedal protractor muscles: 0 = separated from anterior adductor muscle (*Solen*); 1 = dividing anterior adductor muscle into two regions (remaining) (CI 100; RI 100).

14. Level of insertion of pedal protractors into anterior adductor muscle: 0 = not related; 1 = between dorsal and middle thirds (*Serratina capsoides, Moerella* cf. *nitens, Elpidollina* sp., *Tellinides timorensis, Macomona* sp.); 2 = in mid region (*Cadella* cf. *semen, Pinguitellina* cf. *pinguis, Semele*) (CI 50; RI 0; not additive). Although the states of this character are treated as not additive, the placement of the states in the cladogram shows that state 2 appeared at the base of the cladogram (node 1). State 1 is convergent among the mentioned species, including node 6. This makes sense, because the plesiomorphic state is having the pedal protractors close to the ventral region of the anterior adductor muscle; its position in the mid level of that adductor (state 2) (e.g., Figs. 93, 102) appears to be intermediate between the basal state and the more dorsally positioned origin of the muscle (state 1) (e.g., Figs. 16, 74, 83).

15. Degree of separation of anterior adductor muscle by pedal protractors: 0 = not separated; 1 = partial (*Serratina capsoides, Pinguitellina* cf. *pinguis, Tellinides timorensis, Semele*); 2 = total (*Moerella* cf. *nitens, Cadella* cf. *semen, Elpidollina* sp., *Macomona* sp.) (CI 100; RI 100; not additive). Although treated as not additive, the states of this character revealed that they can be considered ordered, because state 1 appeared at node 1 and state 2 at node 5. This optimisation shows that the probable evolution of the origin of the pedal protractors is in the direction of dividing the anterior adductor muscle completely.

Beyond the increase of the anterior adductor muscle, another evolutionary trend in the tellinids and semelids is the further modification of the pedal protractors, explored in characters 12–15. Basally, this pair of muscles penetrates the posterior surface of the anterior adductor muscle (Fig. 16). This infiltration tends to divide the adductor muscle, from partially to completely, into two pieces. This evolutionary scenario has its apogee in *Cadella* cf. *semen*, in which the anterior adductor is completely separated into two similarly sized pieces (Figs. 27–28, 93); the ventral portion is additionally surrounded by a thick layer of circular muscles (ci). This is a surprising discovery, because such functional inferences are difficult to predict. It is a quite possible that this circular muscle is a synapomorphy of a special branch of the family, if confirmed in other species.

The division of the anterior adductor muscle by the pedal protractors could be another notable synapomorphy of the superfamily Tellinoidea. This character occurs in tellinids and semelids; the character has yet to be researched in psammobiids and donacids.

16. Origin of anterior pedal retractor muscles: 0 = circular; 1 = L-shaped, partially surrounding dorsal edge of anterior adductor muscle (*Pinguitellina* cf. *pinguis, Elpidollina* sp., *Macomona* sp., *Semele*) (CI 33; RI 33). In the case of *Tellinides timorensis*, the origin of this pair of muscles is duplicated (Fig. 124). This was not included as another state of this character because it is an autapomorphy. The strange shape of the origin of the anterior pedal retractors represented by state 1 resulted as a synapomorphy of node 7, and was convergent with the state in *Semele* and *P.* cf. *pinguis*.

Foot

17. Shape: 0 = rounded, weakly flattened (*Solen*); 1 = pointed, greatly flattened (remaining) (CI 100; RI 100).

18. Byssus in adult form: 0 = present (*Solen*); 1 = absent (remaining) (CI 100; RI 100). The foot of the tellinoideans is adapted to rapid excavation. The form of the foot (e.g., Figs. 7, 27, 58, 67), explored in character 17, and the absence of the byssus in adult forms (character 18), are clear adaptations for this behavior.

Mantle

19. Incurrent and excurrent siphons: 0 = connected with each other (*Solen*); 1 = totally free from each other (remaining) (CI 100; RI 100). Separation of the incurrent and excurrent siphons is a long-known character of tellinoideans (Yonge, 1949).

20. Middle fold of mantle edge: 0 = barely smooth (*Serratina capsoides, Solen*); 1 = evidently papillate (remaining) (CI 50; RI 0). The presence of papillae on the middle fold of

the mantle edge (Figs. 28, 38, 116) is a common feature of burrowing bivalves. This attribute is an adaptation for reducing the entrance of sand and other particles into the pallial cavity. Another adaptation for that reduction is fusion of the middle folds of the mantle lobes. This, however, was not found in any of the examined tellinoideans, except in the region preceding the siphons.

Although the appearance of mantle edge papillae (state 1) is optimised in Fig. 147 at the node 1, with a reversal (reduction) in *Serratina capsoides* (Fig. 5), it is equally parsimonious to optimise this as convergence between *Semele* and node 3.

Details of the tissue organisation of the mantle edge of a tellinid were provided by Barón & Ciocco (1997).

21. Inner fold of mantle edge: 0 = close to other two folds; 1 = at some distance from other two folds (*Moerella* cf. *nitens, Cadella* cf. *semen, Elpidollina* sp., *Macomona* sp., *Semele*) (CI 50; RI 66). State 1 is clear, because the distance of the inner fold is larger than the height of each fold (Figs. 86, 100, 116). In state 0, on the other hand, the origin of this fold is close to the origin of the other two folds.

22. Incurrent siphon, distal tip: 0 = lacking papillae; 1 = with six papillae (*Cadella* cf. *semen, Macomona* sp., *Semele*) (CI 33; RI 0). Although siphonal papillae are a conspicuous feature (Figs. 97, 137), the result indicated mere convergence among the three species. In the other examined species, the tip of the incurrent siphon is completely smooth, as in other tellinids (Barón & Ciocco, 1998).

23. Siphonal retractor muscles: 0 = free from anterior adductor muscle; 1 = close to anterior adductor muscle (*Serratina capsoides, Pinguitellina* cf. *pinguis, Tellinides timorensis*); 2 = reaching anterior adductor muscle (*Moerella* cf. *nitens, Cadella* cf. *semen, Elpidollina* sp., *Macomona* sp.) (CI 100; RI 100; not additive). The three states of this character are optimised as unordered, but based on the resultant cladogram, state 1 appeared at node 2, and state 2 at node 5. This shows a strong possibility that they are ordered as an evolutionary trend to amplify the origin of these siphonal retractor muscles. Furthermore, nothing changes (index and resulting topology) if the character is treated as ordered. The scar left by these muscles on the shell, called the pallial sinus, and its relation to the anterior adductor muscle scar, is commonly used in species diagnoses (e.g., Oinomikado, 1934; Coan et al., 2000).

24. Muscular arrangement of lateral walls of siphonal chamber: 0 = radial (*Serratina capsoides, Solen*); 1 = in two (dorsal and ventral) bundles (remaining) (CI 50; RI 0). This muscular arrangement is derived from the pallial muscles (Figs. 74, 83, 102, 124, pm), as well as the siphonal retractor muscles. Its function is to retract the mantle portions that surround the siphonal chamber. Fig. 147 shows optimisation of state 1 of this character as a synapomorphy of node 1, with a reversal in *Serratina capsoides*. However, it is equally parsimonious to optimise this as a convergence of *Semele* and node 3.

Other secondary muscles appear in the siphonal chamber in some species, as, e.g. *Elpidollina* sp. (Fig. 112, pm). However, those muscles were not coded because of autapomorphic results.

25. Dorsal bundle of muscular arrangement of lateral walls of siphonal chamber: 0 = uniform; 1 = ventral edge thicker (*Elpidollina* sp., *Macomona* sp.) (CI 100; RI 100).

26. Cruciform muscle: 0 = absent (*Solen*); 1 = present (all) (CI 100; RI 100).

27. Cruciform muscle allocation in relation to vertical level of posterior adductor muscle: 0 = absent; 1 = anterior to it (*Moerella* cf. *nitens, Cadella* cf. *semen, Pinguitellina* cf. *pinguis, Elpidollina* sp., *Tellinides timorensis, Semele*); 2 = just ventral to it (*Serratina capsoides*); 3 = posterior to it (*Macomona* sp.) (not additive) (CI 100; RI 100). The cruciform muscle (Fig. 79) is another long-known feature of the tellinoideans (Ihering, 1900; Graham, 1934). It is a sensory organ (Frenkiel, 1979; Frenkiel & Moueza, 1985) and an accessory of the adductor muscles, located at the ventral edge of the valves, in the ventral side of the incurrent siphonal base. Its sensitivity is possibly provided by an internal sensory channel, usually found inside each branch (Yonge, 1949; Barón & Ciocco, 1997). The cruciform muscle usually produces a pair of small and rounded scars in each valve (Fig. 2), indicating its position. The relative position of the cruciform muscle in relation to the vertical level of the posterior adductor muscle is taken based on a horizontal virtual axis of the hinge. Character 27 is based on this. Based on the obtained cladogram, state 1 appears to be a synapomorphy of node 1, with the other two states as autapomorphies.

Further modification of the musculature in the region of cruciform muscle has been found in a member of Macominae (Arruda & Domaneschi, 2005), as an accessory adductor muscle.

Pallial structures

28. Gill area: 0 = larger than three-quarters of valve area (*Semele, Solen*); 1 = almost half of valve area (remaining) (CI 100; RI 100).

29. Relative positions of demibranchs: 0 = both demibranchs side by side (*Solen*); 1 = outer demibranch positioned dorsal to inner demibranch (remaining) (CI 100; RI 100).

30. Gill food groove along edge of inner demibranch: 0 = absent (*Macomona* sp.); 1 = present (remaining) (CI 50; RI 0). State 1 resulted as a synapomorphy of node 1, being, however, reversed in *Macomona* sp. The species of tellinids examined here do not have the gill profile discussed by Pohlo (1983: fig. 1), in which a food groove is not shown on the inner demibranch.

The gills of the examined tellinids are relatively small compared to those of other filter-feeding bivalves. This

feature and the bizarre position of the demibranchs are explored in characters 28–30 are apparently common for every member of the family (Figs. 77, 84, 94, 103, 113, 125, 135). *Macomona* sp., however, is the single species that has no detectable food groove on the ventral edge of the inner demibranch (Fig. 135). Details of the gill filaments were provided by Barón & Ciocco (1997: figs. 14–15) for *Tellina petitiana* d'Orbigny, 1846, which also lacks food groove on the inner demibranch.

It is possible to deduce that the small size of the tellinioidean gill could be compensated by a higher velocity of filtration. This is indicated by the obligatory water flow through the gill from the infrabranchial to suprabranchial chambers at the base of the siphons. However, despite these modified features and the eulamellibranch condition of the tellinoidean gills, the examined specimens show no tissue connections of the gills with neighboring structures. They are connected with the visceral sac and mantle by means of ciliated strips (Figs. 68, 136, cc). The single tissue connection of the gills is between inner and outer demibranchs, with the pericardium (Fig. 136, pc). Tellinoideans have been considered as deposit feeders by some authors (e.g., Pohlo, 1983). For a discussion of the ciliary currents of some tellinoidean gills, see Graham (1937).

31. Pseudogill at left proximal base of incurrent siphon; 0 = absent; 1 = present (*Moerella* cf. *nitens, Pinguitellina* cf. *pinguis, Elpidollina* sp.*, Tellinides timorensis, Macomona* sp.) (CI 50; RI 66). The tall fold at the left base of the incurrent siphon in the above-listed species, positioned parallel to the mantle border, has been here called a pseudogill (Figs. 49, 86, 105, 115, 127, 140). The functional name is based on similar structures in that region in other bivalves, e.g., lucinids (Taylor & Glover, 2000; Glover & Taylor, 2001; as mantle gills). But, in those cases, the pseudogills are paired. The tellinid pseudogill is very similar among the species that possess it. This is a possible adaptation to the relatively small gill, although the species that lack the pseudogill have comparably sized gills. On the other hand, it is possible that the pseudogill has another function, which awaits further studies.

Something similar to pseudogills has been described for *Macoma biota* Arruda & Domaneschi, 2005, called a siphonal organ. Different from the pseudogills described here, the siphonal organs are relatively large, paired and symmetrical (Arruda & Domaneschi, 2005: fig. 7), however, the structure appears to be located in a place equivalent place to that of the pseudogills. On the other hand, *M. constricta* (Bruguiére, 1792), which occurs sympatrically with *M. biota*, apparently possesses a pseudogill (Narchi, 2003; as unilateral siphonal organ).

The pseudogill resulted as a synapomorphy of node 3, with a reversal in *Cadella* cf. *semen*.

32. Palp size relative to gill: 0 = conspicuously smaller (*Cadella* cf. *semen, Semele, Solen*); 1 = of equal size or larger (remaining) (CI 50; RI 50). The relative increase in size of the palps resulted as a synapomorphy of the tellinids (node 2), with a notable reversal in *C.* cf. *semen*. It is found in other tellinids (e.g., *Tellina petitiana* by Ciocco & Barón, 1998: fig. 3). However, some tellinids with small-sized palps have been reported in the literature [e.g., *T. crassa* (Pennant, 1777) by Graham, 1937].

33. Relative size of hemipalps: 0 = similarly sized; 1 = outer hemipalp ca. one-third shorter than inner hemipalp (*Pinguitellina* cf. *pinguis, Macomona* sp.) (CI 50; RI 0). State 1 (Figs. 104, 134) resulted as convergent autapomorphies of the two species.

The features of the palps, explored in characters 32 and 33, are indicative of further modifications of these structures towards larger proportions. This is in notable contrast with the trend towards reduction of the gill. Complementary studies are necessary to postulate why the palps are so large in such species.

Digestive system

34. Position of oesophagus: 0 = edging the anterior adductor muscle posterior surface (*Semele, Solen*); 1 = free from anterior adductor muscle, except in region close to mouth (remaining) (CI 100; RI 100). The position of the oesophagus in most bivalves is close to the posterior surface of the anterior adductor muscle. Its origin is in the mouth, which normally is positioned close to the ventral region of that adductor muscle. The oesophagus then runs dorsally, closely surrounding this adductor muscle posterior surface, along the median line. However, in the examined tellinids, this feature is modified. The mouth is positioned close to the posterodorsal region of the adductor muscle posterior surface, and the oesophagus runs towards the posterior, away from the adductor muscle (Figs. 80, 85, 98, 106, 118, 128, 141, es).

35. Stomach dorsal hood: 0 = present; 1 = absent (*Moerella* cf. *nitens, Cadella* cf. *semen, Tellinides timorensis*) (CI 33; RI 0). The presence of the dorsal hood is considered plesiomorphic because it is present in most bivalves. It is a relatively long, pointed diverticulum positioned at the left side of the stomach (e.g., Fig. 118, dh). The function normally is for further sorting of food particles inside the gastric chamber. In the case of the examined tellinids, the dorsal hood is smooth internally, lacking any detectable folds or special sorting areas. State 1 can be optimised as convergence between *T. timorensis* and node 5, with an additional reversal at node 7. This possibility is shown in Fig. 147. However, it could be merely convergent autapomorphies of the three species.

36. Stomach dorsal glandular diverticulum on right-dorsal side: 0 = absent; 1 = present (*Serratina capsoides, Cadella* cf. *semen, Elpidollina* sp., *Tellinides timorensis, Macomona* sp., *Semele*) (CI 33; RI 0).

37. Stomach glandular diverticulum form: 0 = balloon-like; 1 = elongated (*Cadella* cf. *semen, Elpidollina* sp.*, Tellinides timorensis, Macomona* sp.) [? in *Moerella* cf.

nitens, Pinguitellina cf. *pinguis*] (CI 100; RI 100). Besides the dorsal hood, the stomach of most examined species also possesses an additional diverticulum (characters 36–37), which sometimes is very long and as wide as the intestine (Fig. 118, sd). This diverticulum is also present in donacids (Simone & Dougherty, 2004) and appears to be another synapomorphy of the tellinoideans. In some cases, as in donacids and semelids, this diverticulum is in the form of a small balloon (Figs. 80–81). This condition is considered plesiomorphic in character 37, with the elongated form considered apomorphic. The gastric diverticulum is smooth inside, lacking any special folds or glands.

38. Stomach transverse fold at base of oesophageal insertion: 0 = absent; 1 = present (*Cadella* cf. *semen, Pinguitellina* cf. *pinguis, Elpidollina* sp., *Tellinides timorensis, Macomona* sp., *Semele*) (CI 33; RI 0).

39. Gastric transverse fold surrounding aperture of digestive diverticulum: 0 = absent; 1 = present (*Pinguitellina* cf. *pinguis, Elpidollina* sp., *Tellinides timorensis*) (CI 33; RI 0). The characters of the inner folds of the stomach (characters 38–39) are here based on dissections of living and fixed specimens. Comparisons showed that no special differences were noticed after fixation. In the optimisation shown in Fig. 147, state 1 is a synapomorphy of node 3, with a reversal at node 5, and the state reappearing in *E.* sp. However, another optimisation is possible, as mere convergent autapomorphies of the three species.

40. Muscles aligned between posterior side of stomach and adjacent intestinal loops: 0 = absent (*Semele, Solen*); 1 = present (remaining) (CI 100; RI 100). Transverse muscles passing though the visceral glands are common in the visceral mass of bivalves. They run from left to right possibly as muscular reinforcement for foot movement. They surround the digestive tubes, passing only through glands (gonad and digestive). However, these muscles are almost imperceptible. In the case of the species examined here, the transverse muscles are enlarged, especially those in the region separating the stomach and the style sac from the adjacent intestinal loops (Figs. 80, 85, 98, 118, 128, 141, tm). This is a noteworthy modified condition.

41. Intestinal coiling: 0 = some wide loops (*Solen*); 1 = several loops separated into two conjuncts (one ventral, another dorsal, preceding pericardium) (remaining); 2 = reunited in mid level of style sac (*Semele*) (CI 100; RI 100; not additive). The normal condition of the intestinal loops inside the visceral sac of bivalves is wide, ample coils. The ingroup species possess a tightly coiled intestine, normally (in case of tellinids) in two conjuncts (Figs. 80, 85, 98, 106, 118, 128, 141, in). The ventral set of coils is normally of a narrower portion of the intestine, whereas the dorsal set is composed of wider, thinner-walled coils with sand-like content. This arrangement is apparently absent in *Tellina petitiana* (see Ciocco & Barón, 1998).

Central nervous system

42. Pedal ganglia: 0 = separated from each other; 1 = fused (*Moerella* cf. *nitens, Elpidollina* sp., *Macomona* sp., *Semele*) (CI 50; RI 66). The pedal ganglia are normally close to each other in most bivalves, along the median line. A very short commissure is always perceptible in those cases. However, in the above-mentioned species, this condition is further modified, as both ganglia are medially fused with each other, appearing like a single ganglion (Figs. 92, 122, 145). The fusion of the pedal ganglia is a notable synapomorphy supporting node 6. However, there is a noteworthy convergence in *Semele*.

43. Visceral ganglia dorsal protuberance: 0 = absent; 1 = present (*Cadella* cf. *semen, Pinguitellina* cf. *pinguis, Elpidollina* sp., *Tellinides timorensis, Semele*) (CI 66; RI 33). The pair of visceral ganglia is normally the largest in the bivalve nervous system. In the above-listed species, there is an additional modification in the form of protuberances. These do not appear to be additional ganglia, because no visible nerves originate from them (Figs. 101, 111, 123, 133).

A more detailed description of a central nervous system was provided by Lammens (1969) for *Macoma baltica*, and Barón & Ciocco (1998) for *Tellina petitiana*, both of which provided data on nerves and histological aspects. The species examined here are mostly similar. *T. petitiana*, in particular, also has a long commissure between the cerebral ganglia, and fusion of the pedal ganglia along medial line; on the other hand, no protuberances were found on the visceral ganglia.

DISCUSSION OF THE CLADOGRAM

Despite the number of analyzed species here being very small in relation to the Tellinidae total biodiversity, the phylogenetic analysis performed here allows some conceptual inferences, which cannot be changed even with the addition of many species. However, as stated above, the present analysis was not intended to be "the phylogeny of the Tellinidae," but only a way of performing a comparative analysis in a testable scenario.

The following discussion is based on Figs. 147–148, which represent the most parsimonious cladogram, based on the matrix of characters (Table 1).

Tellinidae appears to be a monophyletic taxon (node 2), supported by nine synapomorphies (when compared with a semelid). The more interesting synapomorphies are the asymmetry of the valves (character 4), the similarity of the hinge in both valves (7), the tendency of the retractor muscles of the siphons to be positioned deeper, close to the anterior adductor muscle (23), the tendency for reduction of the gill area (28), the increment of the palps (32), the oesophagus placed away from the anterior adductor muscle (34), the development of the transverse muscles in the visceral sac (40), and the different fashion of intestinal coiling (41).

Table 1. Matrix of characters and their states of the ingroup and one outgroup (last row).

Taxa	Character states								
		1		2		3		4	
	12345	67890	12345	67890	12345	67890	12345	67890	123
Serratina capsoides	10010	01211	11111	01110	00100	12111	01010	10001	100
Moerella cf. *nitens*	11102	11001	11112	01111	10210	11111	11011	0?001	110
Cadella cf. *semen*	11111	11101	11122	01111	11210	11111	00011	11101	101
Pinguitellina cf. *pinguis*	11111	11000	11121	11111	00110	11111	11110	0?111	101
Elpidollina sp.	11112	11011	11112	11111	10211	11111	11010	11111	111
Tellinides timorens	10010	10110	11111	01111	00110	11111	11011	11111	101
Macomona sp.	11112	11001	11112	11111	11211	13110	11110	11101	110
Semele sinensis	10000	00001	11121	11111	11010	11011	00000	10100	211
Solen curtus	00000	00000	00000	00000	00000	00000	00000	00000	000

Node 3 unites the tellinids except *Serratina capsoides*, and has as its main synapomorphies the absence of radial sculpture (character 6), the pseudogill (31) (that is reversed in *Cadella*), the elongation of the stomach diverticulum (37), and augmentation of the transverse fold of the stomach inner surface (39).

Node 4 bears the ingroup species allocated after *Tellinides timorensis*, supported by four synapomorphies. The more important are the glossy outer shell surface (character 2), a tendency for the shell be thin and fragile (3), and the reduction of the periostracum (5).

Node 5 unites the taxa after *Pinguitellina* cf. *pinguis*, supported by six synapomorphies. The more important are the anterior adductor muscle split into two sections by the pedal protractor muscles (character 15), the pair of siphonal retractor muscles reaching the anterior adductor muscle (23), and loss of the dorsal hood of the stomach (35).

Node 6 is a set of *Moerella, Elpidollina* and *Macomona*, supported by three synapomorphies: reduction of the periostracum (character 5), the pedal protractor originating from mid level of the anterior adductor muscle (14), and fusion of the pedal ganglia.

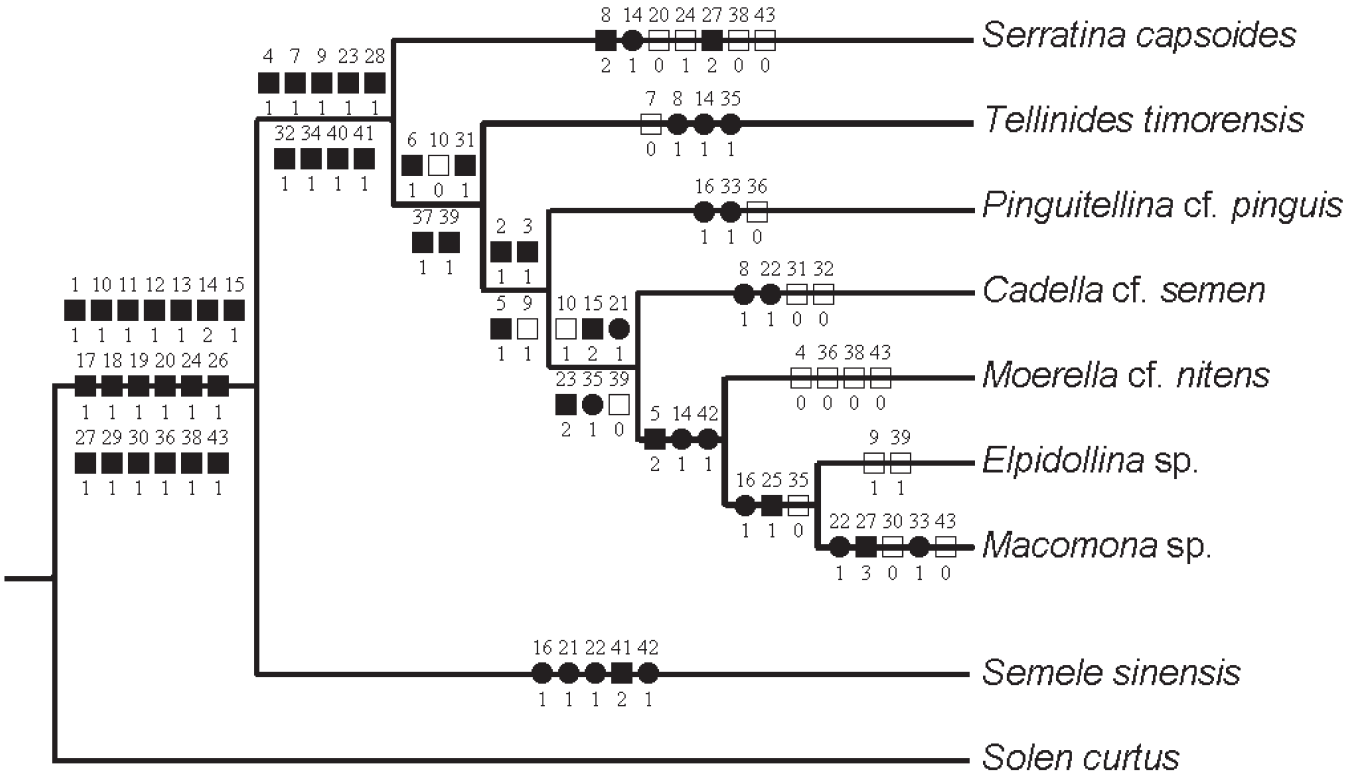


Fig. 147. Most parsimonious cladogram of the ingroup, with allocation of two outgroups (*Semele*, *Solen*). Characters supporting each node are represented by symbols; the number above the line is the character number; the number below the line is the character state. Dark square = nonhomoplastic synapomorphy; dark circle = convergence; white square = reversal. Length 83; CI 61; RI 51.

Node 7, supported by three synapomorphies, bears *Elpidollina* and *Macomona*. The L-shaped origin of the anterior pedal retractor muscles (character 16), and increment of the central bundle of the pallial muscles placed on the lateral walls of siphonal chamber (25) are the more important synapomorphies.

Because *Serratina, Tellinides, Pinguitellina, Cadella, Moerella*, and *Elpidollina* are genera of Tellininae, whereas *Macomona* is a genus of Macominae, it is possible to infer from this result that the subfamily Tellininae is not monophyletic. It is at least paraphyletic according to the resultant cladogram. Nothing can be inferred with respect to the subfamily Macominae, because only a single species was studied herein.

If polarisation is performed on the eulamellibranch *Solen* and the filibranch *Plicatulostrea* (as stated above), a series of synapomorphies appear supporting a branch with the tellinids and the semelids (node 1). This node is supported by 19 synapomorphies, with the more important being the flattened shell (character 1), the enlargement of the anterior adductor muscle (10–11), the modification of the pedal protractor muscles infiltrating the posterior region of anterior adductor muscle (12–15), the axe-shaped, triangular foot (17), the almost total separation of the incurrent siphon from the excurrent siphon (19), the papillated middle fold of mantle border (20), the cruciform muscle (26–27), the modifications and the position of the demibranchs (29–30), the glandular diverticulum of the right-dorsal region of stomach (36), and the dorsal protuberance of the visceral ganglia (43). Several of these synapomorphies are found in other tellinoideans, such as donacids and psammobiids, and can be considered as synapomorphies supporting Tellinoidea. Based on the literature, only a few of them are presently considered. Amplification of the set of tellinoidean synapomorphies depends on a wider sample, including more species and members of all tellinoidean families.

CONCLUSIONS

1. An analysis of anatomy bears sufficient data for a comparative analysis, implicating both systematics and phylogeny.
2. Despite the presently analyzed sample being small, some phylogenetic inferences are possible, such as the non-monophyletic nature of the Tellininae and the possible monophyly of Tellinidae and Tellinoidea.

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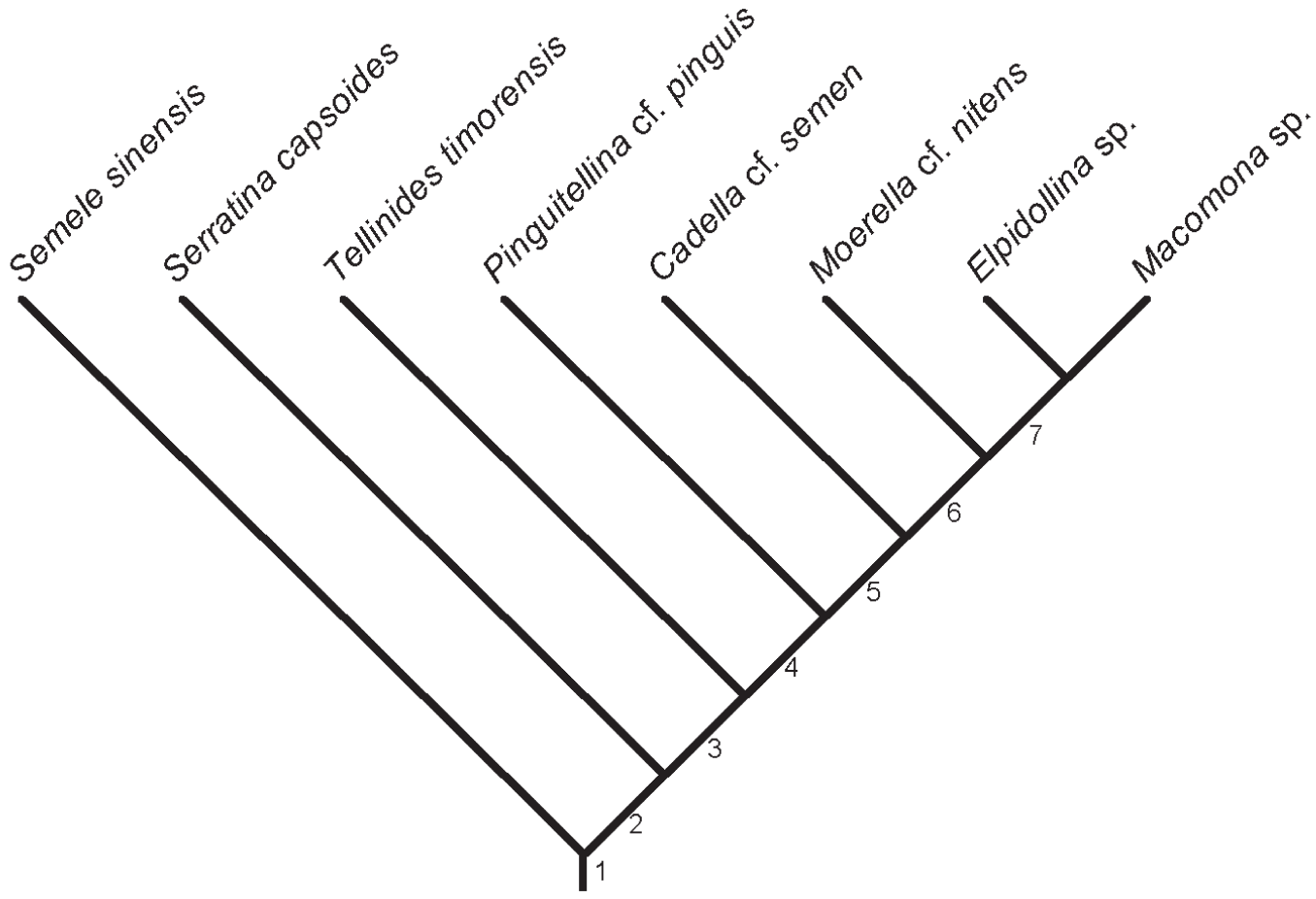

Fig. 148. Most parsimonious cladogram of the ingroup. Numbered nodes are discussed in the text. Length 83; CI 61; RI 51.

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THAI ABSTRACT

รายงานวิจัยเรื่องนี้เป็นการเปรียบเทียบลักษณะของหอยสองฝาวงศ์เทลไลนิดีย์ 7 ชนิดจากอ่าวคุ้งกระเบน ในอ่าวไทย หอยสองฝาทั้ง 7 ชนิดดังกล่าวคือ *Serratina capsoides* (Lamarck, 1818), *Moerella* cf. *nitens* (Deshayes, 1854), *Cadella* cf. *semen* (Hanley, 1844), *Pinguitellina pinguis* (Hanley, 1844), *Elpidollina* sp., และ *Tellinides timorensis* (Lamarck, 1818) ในวงศ์ย่อย เทลไลนินีย์ และ *Macomona* sp. ในวงศ์ย่อย มาโคมินีย์ ผู้วิจัยมีวัตถุประสงค์ในการเปรียบเทียบความสำคัญระหว่างชนิดโดยทำการวิเคราะห์ทาง phylogenetic โดยพิจารณาผ่านการวิเคราะห์ลักษณะทางสัณฐานวิทยา 43 ลักษณะ (94 สถานะ) โดยให้ผลการวิเคราะห์ที่สามารถนำเสนอในลักษณะ cladogram ดังรายละเอียดคือ (*Serratina capsoides* (*Tellinides timorensis* (*Pinguitellina* cf. *pinguis* (*Cadella* cf. *semen* (*Moerella* cf. *nitens* (*Elpidollina* sp.-*Macomona* sp.)))))) หอยซีมีลิดและโซไลนิดถูกนำมาวิเคราะห์ร่วมเป็นส่วนหนึ่งของ ingroup ส่วน polarization อยู่บนพื้นฐานของลักษณะจำเพาะของหอยสองฝาพลิคาทูลิดชนิดหนึ่ง ในการวิเคราะห์ครั้งนี้พบว่าเทลลินอยเดียและวงศ์เทลไลนิดีย์มีลักษณะ monophyletic ซึ่งมีข้อมูลสนับสนุนจาก synapomorphies จำนวน 19 และ 9 ลักษณะตามลำดับ ส่วนหอยสองฝาวงศ์เทลไลนิดีย์มีลักษณะ paraphyletic ผู้วิจัยพบว่ามีลักษณะทางสัณฐานวิทยาที่แตกต่างอย่างเห็นได้ชัดในทุก taxa ลงไปจนถึงระดับชนิด (species) โดยมีโครงสร้างบางชนิดที่ไม่เคย มีการรายงานมาก่อน ได้แก่เหงือกเทียม (pseudogills) ลักษณะของกล้ามเนื้อ pedal protractor ที่แทรกเข้าไปในกล้ามเนื้อยึดเปลือก มัดหน้า (anterior adductor muscle) รวมทั้งกล้ามเนื้อทรงกลม ที่ล้อมรอบส่วนหนึ่งของกล้ามเนื้อยึดเปลือกมัดหน้า

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