Out of Australia: *Belloliva* (Neogastropoda: Olividae) in the Coral Sea and New Caledonia

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Abstract: The genus *Belloliva* (Gastropoda: Olividae) consists of small (<15 mm) operculate species and was hitherto thought to be essentially confined to coastal waters of southern and eastern Australia. We report a small radiation from deep water (100-1000 m) in the Coral Sea and New Caledonia, consisting essentially of undescribed species. The new genus *Calyptoliva*, which differs from *Belloliva* by the absence of a mantle filament and the presence of a mantle lobe, is also represented in the same area by new species. Based on correlation with shell characters, we suggest that the olivid mantle lobe is responsible for secreting the primary spire callus that overlies the suture, rather than producing the columellar callus as was previously believed (Marcus and Marcus 1959). *Belloliva* and *Calyptoliva* combine a suite of shell, radular, and anatomical characters that is shared with either the Olivinae or the Ancillariinae. This raises the question of the distinctiveness of the two classically recognized subfamilies within the family Olividae. All species have paucispiral protoconchs with inferred limited larval dispersal, and many have extremely narrow distributions, sometimes endemic to a single guyot, or they show discrete geographical differentiation. New species: *Belloliva iota* sp. nov., *Belloliva alaos* sp. nov., *Belloliva amblys* sp. nov., *Calyptoliva tatyanae* sp. nov.

Key words: Anatomy, classification, new species, endemism

The neogastropod family Olividae stands out as a minor component in offshore and deep-water molluscan faunas. Only 15 species have been recorded worldwide from depths below 400 m, all belonging to subfamily Ancillariinae (Kantor and Bouchet 1999), with only four of these (belonging to genera Amalda, Ancilla, and Baryspira) reaching below 1000 m. Ongoing exploration of deep-water benthos in the South West Pacific confirms this unspectacular diversification of Olividae in the local molluscan fauna (Kilburn and Bouchet 1988, Bouchet and Kilburn 1991), although species of Amalda can be locally common on seamounts of the Norfolk Ridge (Y. Kantor and P. Bouchet pers. obs.). The discrete radiation of species from the Coral Sea and New Caledonia described in the present paper is thus remarkable because of its magnitude: 11 species, 8 of which reach or normally occur below 400 meters, and all of them undescribed. Six species are placed in the genus Belloliva Iredale in Peile, 1922, and three in the new genus Calyptoliva.

The genus *Belloliva* Iredale in Peile, 1922 was established for *Olivella brazieri* Angas, 1877, and a second species from Australian coastal waters, *Olivella pardalis* A. Adams and Angas, 1864, was also originally included in the genus. Peile (1922: 18) highlighted that the two species "have a tricuspid rachidian, similar to that of *Oliva* but with minute additional cusp outside each of the lateral cusps;" this was the basis for the establishment of *Belloliva*. Since Peile (1922), no anatomical data nor additional data on radulae have been published, and the genus has remained little known. Based on radular morphology, Olsson (1956) allocated *Belloliva* to the subfamily Olivinae, whereas Wilson (1994) without any discussion included the genus in the subfamily Olivellinae, an opinion that was followed by Tursch and Greifeneder (2001). Currently, *Belloliva* includes four Australian coastal species; a fifth one from the Caribbean has also controversially been referred to it (see Discussion below).

In the present paper, we redefine *Belloliva* based on the anatomy of the Australian species, including the type species; we describe the Coral Sea and New Caledonian species attributable to it; we describe the new genus *Calyptoliva* that superficially resembles *Belloliva*; and finally we discuss the position of *Belloliva* in the family Olividae.

MATERIAL AND METHODS

The present paper is based on the extensive material collected by recent expeditions exploring the Coral Sea and New Caledonia area (Richer de Forges 1990, 1993, Richer de Forges and Chevillon 1996) and housed in Muséum national d'Histoire naturelle, Paris (MNHN). The material is not individually catalogued but is unambiguously referred to by the acronym of the cruise (e.g., MUSORSTOM 4, BATHUS

1) and the station number. In lists of material examined, "lv" refers to live-taken specimens and "dd" to empty shells.

The following standard shell measurements were made: shell length (SL); last whorl length (BWL); aperture length (AL); shell width (SW). For the purposes of species discrimination, we used a number of protoconch and teleoconch measurements following those defined and described in detail by Tursch and Germain (1985, 1986), and demonstrated by us to be operational (Bouchet and Kantor 2004). The method used for counting protoconch whorls or measuring protoconch is usually not specified in the literature, making comparisons difficult. We counted protoconch whorls from the origin of the suture (Fig. 1B). The number of protoconch and teleoconch whorls was counted with an accuracy of 0.125 whorl.

Because measurements taken from camera lucida drawings are more accurate than those made directly on the shell with the aid of an ocular micrometer, protoconchs were drawn in standard position, i.e., with the protoconchteleoconch transition facing the observer (Fig. 1), and measurements were made from the drawings. Instead of protoconch diameter, we used "D1" which equals protoconch diameter + 0.25 of the first teleoconch whorl. "PRE" represents the exposed height of the protoconch and is referred to in the text as protoconch elevation. "TL1" is the diameter of the first 1.25 teleoconch whorls (this measurement can easily be done on the drawings of "standard" protoconch position). Measurements "TL2" and "TL3" are defined on Fig. 1A.

Radulae were studied with scanning electron microscopy (SEM). After being cleaned in diluted bleach, air-dried,



We studied histology of some organs of *Belloliva* (anterior foregut and mantle). The tissues were dehydrated and embedded in paraffin and serially sectioned at 10 μ m. Sections were stained with Masson's triple stain.

The terminology of the shell base of oliviform gastropods has not yet been fully standardized and is sometimes "taxonomy-dependent" (e.g., "ancillid band" and "ancillid groove"). We follow Tursch and Greifeneder (2001), who discussed the terminology used in descriptions of olivid genera and suggested homologies. The shell base of Belloliva is rather simplified in comparison with other olivid genera. The anterior band (Fig. 2B) is usually covered with inconspicuous axial striations. It is elevated over the surface of the remaining part of the last whorl (cloak, Fig. 2A) and delimited by a rather sharp step (sometimes referred to as "groove," or "ancillid groove": see Kilburn 1977). The plication plate (Fig. 2C) in turn is raised over both the cloak and the anterior band. It can be divided (by the posterior limit of the anterior band, or ancillid groove) into parietal plate and anterior plating. The parietal plate is a slightly thickened area, actually formed by the parietal callus. Its surface can differ from the cloak, being very finely shagreened. The anterior plating is sharply delimited from the anterior band on the ventral shell surface, but this border becomes more obscured on the lowest part of the shell. The plication plate can be smooth, but usually has several plicae on the anterior plating and a few on the parietal plate.



RESULTS

Olividae Latreille, 1825 Belloliva Iredale in Peile, 1922

Type species

Olivella brazieri Angas, 1877 (original designation).

Remarks

Four Australian species have traditionally been included in *Belloliva* (Kaicher 1987, Wilson 1994) (for more details see Discussion). Here we describe in details the anatomy of the type species, *Belloliva brazieri*, and provide comparative remarks on the second studied Australian species, *Belloliva leucozona*.





Figure 2. Terminology used in shell descriptions, with emphasis on the shell base.

Belloliva brazieri (Angas, 1877) (Figs. 3, 4A-D, 32A-B)

Olivella brazieri Angas 1877: 172, pl. 26, fig. 6.

Type material

Not traced.

Type locality

Newcastle Beach, New South Wales, Australia.

Material examined

Australia, New South Wales, 2 km E of Long Bay, Sydney, 33°58.8'S, 151°17.0'E, 66 m, AMS C388726. Dissected specimen male: SL 12.9, BWL 9.75, AL 7.4 mm, SW 4.8 mm. After dissection, the radula was removed and the anterior foregut was serially sectioned.

Anatomy

General morphology.—Body consisting of nearly 5 whorls, mantle cavity spanning about 0.5 whorl, nephridium more than 0.3 whorls, digestive gland about 1.25 whorls, testis about 3 upper whorls (Fig. 3A-B). Nephridium with transparent walls, excretory lamellae very distinct in posterior part and more closely spaced anteriorly, 15 in total. Ne-

phridial gland narrow. Anterior lobe of digestive gland small, spanning about 0.3 whorls and separated from posterior lobe by the stomach, which is oriented obliquely with regard to columellar axis (Fig. 3A). Posterior lobe spanning slightly less than one whorl, occupying the entire width of the whorl immediately posterior to the stomach and more posteriorly has the shape of narrow band occupying the upper part of the whorl above testis. Foot thick, metapodium broadly triangular-oval, propodium small in comparison with crescent shaped propodium typical for Olividae, subdivided longitudinally on the ventral surface (Fig. 3C) and separated from metapodium by thin but distinct furrow on both the dorsal and ventral sides. Parapodia of medium size. Operculum completely transparent, yellowish, very thin, elongate-oval. Operculum attached along narrow oval area (about 0.5 of operculum width) to opercular pad. In its posterior third, part of the opercular pad is free from the dorsal side of the foot, forming a tongue-like projection. Head rather large, with two separate vertical flaps (Fig. 3C, tn) separated by a long, deep furrow. No eyes.

Mantle cavity (Fig. 3F).—Mantle edge even and slightly thickened. Mantle thin, osphradium, ctenidium, and hypobranchial gland visible by transparency. Siphon with thick and contracted walls, long, extending considerably beyond



Figure 3. Anatomy of *Belloliva brazieri* (Angas, 1877). A, B, Dorsal and ventral views, respectively, of the body removed from the shell. C, Head-foot, antero-dorsal view, mantle removed. D, E, Right and left views, respectively, of the anterior foregut. F, Mantle complex. Abbreviations: ag, anal (rectal) gland; aldg, anterior lobe of digestive gland; bm, buccal mass; cme, cut mantle edge; ct, ctenidium; gL, gland of Leiblein; hg, hypobranchial gland; lsg, left salivary gland; mf, mantle filament; ne, nephridium; nr, circumesophageal nerve ring; odr, odontophoral retractor; oe, esophagus; op, operculum; os, osphradium; p, penis; par, parapodium; pldg, posterior lobe of digestive gland; pr, proboscis; prp, propodium; prr, proboscis retractor; re, rectum; rsg, right salivary gland; s, siphon; sl, sole of the foot; st, stomach; te, testis; tn, cephalic tentacles; vL, valve of Leiblein; vs, seminal vesicle.

mantle edge. Ctenidium large, occupying about 0.8 of mantle length, consisting of simple triangular lamellae. Osphradium as wide as ctenidium and 0.75 of its length, symmetrical. Mantle filament (Fig. 3A, F, mf), rather short when contracted. Mantle lobe and anterior mantle tentacles absent. Hypobranchial gland very distinct, narrow, brown, lacking folds. Rectum narrow, very thin in posterior third, gradually narrowing towards the anal opening. Rectal gland distinctly visible through the mantle wall as a narrow red sinuose line (Fig. 3A, ag), extending along most of rectum length.

Alimentary system (Fig. 3D-E).-Rhynchostome asymmetrical, situated below the right head flap. Proboscis short in contracted state (1.4 mm, or 0.19 AL), occupying nearly the entire rhynchocoel length, rhynchodeum semitransparent. Proboscis walls and rhynchodeum very thin, about 30 µm (7% of proboscis diameter), covered by cuticularized cuboidal epithelium in histological section. Walls with a very thin outer layer of circular muscle fibers and an inner layer of longitudinal fibers, constituting about half of the wall thickness. Mouth opening very broad compared to proboscis diameter. Buccal tube long (about 0.3 of proboscis length) and broad, lined with thick cuticle, leading to buccal cavity. Radular diverticulum long and narrow, extending at least 0.5 of proboscis length. Odontophoral retractor large, flattened (Fig. 3D, odr), extending posteriorly from the proboscis, running anteriorly along ventral side of rhynchodeum and bypassing the nerve ring, following to the ventral side of cephalic hemocoel, its edges thickened, the muscle itself being rather thin and transparent. Esophagus rather broad posterior to proboscis and forming a very short loop. Several very thin retractor muscles attached to the rhynchodeum (wall of the proboscis sheath) in its mid-length. Odontophore protruding significantly behind the proboscis edge. Radular sac nearly as long as odontophore. Radula (Fig. 4A-D) comprising about 80 teeth rows, membrane width about 120 µm (0.93% SL, 1.62% AL). Rachidian tooth with 3 main cusps, central cusp about 1.5 times narrower and shorter than the lateral cusps, and an additional small but distinct cusp abutting each side of the main lateral cusps. Small and shallow depressions on dorsal side of main lateral cusps, corresponding to cusps of preceding row. Anterior profile of the rachidian slightly concave. Lateral sides of basal plate gradually embedded into the membrane without distinct border. Lateral teeth (Fig. 4D) with subrectangular base and long, curved, hook-like cusp. Valve of Leiblein large, pyriform, well demarcated from the esophagus, with ciliary cone. Esophagus very narrow immediately posterior to the valve and passing through the nerve ring. Circumesophageal nerve ring comparatively very large, nearly as long as retracted proboscis. Posterior esophagus (posterior to the opening of the duct of the gland of Leiblein) significantly widening as approaching the stomach. Gland of Leiblein large, colorless in preserved condition, bulky anteriorly, and tapering posteriorly, opening into esophagus by very short and constricted duct close to the nerve ring. Gland of Leiblein with broad internal cavity, separated by tall and rather narrow folds. Salivary glands medium-sized, separate, loose, ramified-tubular, typical for Olivoidea (Fig. 3D-E, rsg, lsg). Wall of each tube composed of a single layer of large, irregularly angular, glandular cells with granulated cytoplasm, at least some of them ciliated. Glands situated on both sides of posterior part of rhynchodeum and anterior esophagus and tightly attached to them by connective tissue fibers. Salivary ducts rather thick, passing into the tubules of the salivary glands without obvious border. Ducts fused with the walls of esophagus at posterior end of proboscis. Accessory salivary glands absent. Stomach badly damaged while extracting the body, but in general appearance similar to that of Belloliva leucozona (see below).

Reproductive system.—Testis large, occupying 3 upper whorls, situated ventral to the digestive gland in the anterior part, contrary to other neogastropods. Seminal vesicle poorly differentiated from the testis, consisting of few loops and situated at the lower part of the whorl, in close proximity to the stomach. Within the mantle cavity, seminal duct and prostate gland forming several large tight loops and then extending to the base of the penis. Penis as long as the mantle cavity, of even diameter along its length, tip rounded, without seminal papilla.

> Belloliva leucozona (A. Adams and Angas, 1864) (Figs. 4E-H, 5, 32C-D)

Olivella leucozona A. Adams and Angas 1864: 422, pl. 37, fig. 23.

Type material

Four syntypes BMNH 1870.10.26.93.

Type locality

Port Jackson, New South Wales, Australia, 6 fathoms (11 m).

Material examined

Australia, New South Wales, 2.3 km E of Malabar, 33°59.5'S, 151°16.8'E, 66-73 m, AMS C330373. Dissected specimen, male: SL 12.25, BWL 8.89, AL 7.13, SW 4.38; after dissection, mantle serially sectioned.

Anatomy

Body morphology (Fig. 5A-B) is similar to that of *Belloliva brazieri*, except that testis spans 3.5 whorls instead of 3 in *B. brazieri*. Nephridium has less pronounced excretory lamellae, 9 in total as seen through nephridial wall.

Mantle cavity.—Mantle cavity in all details similar to that of *Belloliva brazieri*. The main difference is the absence



Figure 4. Scanning electron micrographs of the radulae of *Belloliva brazieri* (A-D) and *Belloliva leucozona* (E-H). A, E, Dorsal view of the central part of the radular membrane. B, F, Enlarged rachidian teeth. C, G, Left lateral view of the rachidian teeth. D, H, Left lateral view of the lateral teeth. Scale bars = $10 \mu m$.



Figure 5. Anatomy of Belloliva leucozona (A. Adams and Angas, 1864). A, B, Ventral and dorsal views, respectively, of the body removed from the shell. C, Head-foot, dorsal view, mantle and visceral mass removed. D, E, Left and right views, respectively, of the anterior foregut. F, External view of the stomach and part of the visceral mass. G, Posterior whorl of the visceral mass, view from inside, whorls slightly uncoiled, nephridium removed. Abbreviations: aldg, anterior lobe of digestive gland; aoe, anterior esophagus; att, attachment of the opercular pad to the operculum; bm, buccal mass; cm, columellar muscle; cme, cut mantle edge; ct, ctenidium; gL, gland of Leiblein; hg, hypobranchial gland; int, intestine; mf, mantle filament; ne, nephridium; nr, circumesophageal nerve ring; odr, odontophoral retractor; op, operculum; os, osphradium; p, penis; par, parapodium; pldg, posterior lobe of digestive gland; poe, posterior esophagus; pr, proboscis; prp, propodium; rs, radular sac; s, siphon; sem.d, seminal duct; sg, salivary gland; sl, sole of the foot; st, stomach; te, testis; tn, cephalic tentacles; vL, valve of Leiblein; vs, seminal vesicle.

of the rectal gland. Filament channel on upper shell whorls occluded with solid debris and obviously filament is not able to extend further than about last 2.5 whorls. Mantle filament (serially sectioned) composed mostly of muscular elements, both longitudinal and helical, with few connective tissue cells. Innervation poor. Alimentary system.—Anatomy of the alimentary system is similar to *Belloliva brazieri*. The minor differences include: shorter proboscis in contracted state (0.85 mm, or 0.12 AL) (Fig. 5D, E, pr); odontophore and radular sac strongly protruding posterior to the proboscis (Fig. 5E, bm, rs); radular sac slightly longer than odontophore; relatively larger and more rounded valve of Leiblein (Fig. 5D, vL); position of the valve more anterior to the circumesophageal nerve ring; larger fused salivary glands (Fig. 5D, E, sg), situated posteriorly to the retracted proboscis and surrounding anterior esophagus and valve of Leiblein; more coiled gland of Leiblein (Fig. 5D, E, gL).

Radula (Fig. 4E-H) comprised of about 80 teeth rows, membrane width about 130 μ m (1.1% SL, 1.82% AL). Anterior profile of rachidian straight.

Reproductive system. Seminal vesicle situated at the ventral border between gonad and posterior lobe of digestive gland, comprising a very thickened, wide, short vesicle, and the much narrower duct (Fig. 5G, vs). Seminal duct entering the mantle cavity where it forms numerous very wide loops on the right side of the mantle cavity and continuing to the base of the penis (Fig. 5C, sem.d), nearly straight within penis.

Belloliva alaos Kantor and Bouchet sp. nov. (Figs. 6, 7, 8A-C, 9)

Type material

Holotype (Moll 9469) and 4 paratypes (Moll 9470) in MNHN.

Material examined

North of New Caledonia. MUSORSTOM 4, st. DW156, 18°54'S, 163°19'E, 525 m (2 dd); st. DW159, 18°46'S,



Figure 6. Belloliva alaos sp. nov. A-C, Holotype. D, E, Paratype (st. DW918, SL 12.1 mm). F, G, Paratype (st. DW918, SL 8.2 mm). H, St. DW916, SL 7.2 mm. All shells illustrated at the same scale.

163°16'E, 585 m (11 dd); st. DW160, 18°42'S, 163°13'E, 668 m (5 dd, 1 lv [anatomy and radula]). BATHUS 4, st. DW914, 18°49'S, 163°15'E, 600-616 m (1 dd); st. DW916, 18°53'S, 163°20'E, 518-570 m (1 dd); st. DW917, 18°47'S, 163°14'E, 397-400 m (27 dd); st. DW918, 18°49'S, 163°16'E, 613-647 m (22 dd—holotype and 4 paratypes); st. DW919, 18°50'S, 163°17'E, 610-660 m (1 dd).

Type locality

North of New Caledonia, 18°49'S, 163°16'E, 613-647 m (BATHUS 4, st. DW918).

Description (holotype)

Shell solid, glossy, oval (BWL/SL = 0.76, AL/SL = 0.60, D/SL = 0.46), with moderately wide aperture and elevated, somewhat turreted spire, consisting of about 1.0 protoconch and almost 3 teleoconch whorls. Protoconch large, evenly rounded, diameter 1650 μ m, exposed height 1140 μ m, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Profile of whorls evenly rounded, with very obtuse shoulder. Filament channel completely open. Aperture lanceolate-oval, gradually narrowing abapically. Outer lip slightly convex, nearly straight in most adapical part, straight in middle portion and evenly rounded abapically. Parietal plate narrow, slightly thickened, anterior plating having one inconspicuous plica. Color uniformly white, upper teleoconch whorls and protoconch translucent.

Dimensions (holotype): SL 10.8 mm, SW 5.0 mm, BWL 8.2 mm, AL 6.5 mm. Largest specimen (paratype): SL 12.1 mm, SW 5.3 mm, BWL 8.6 mm, AL 6.5 mm.

Anatomy

The anatomy of the single live-taken female (SL 11.7 mm, BWL 9.6 mm, AL 7.5 mm, SW 6.0 mm) has been studied (Fig. 7). Body in alcohol uniformly pale yellow, lacking pigmentation.

General morphology.-Body consisting of nearly 4 whorls, mantle cavity spanning about 0.5 whorls, nephridium 0.3 whorls, digestive gland about 1 whorl. Ovary occupying upper 2 whorls of the visceral hump, its border with posterior digestive gland forming a wavy line across the whorl. Nephridium with transparent walls, with 8 main excretory lamellae (Fig. 7B, ne). Nephridial gland narrow, with nearly smooth walls (Fig. 7B, ng). Anterior digestive gland small, spanning about 0.25 whorls and completely separated from posterior one by obliquely situated stomach (Fig. 7A, C). Foot thick, strongly contracted during fixation, folded transversely, metapodium broadly triangular-oval, propodium small in comparison to metapodium, typically crescent-shaped, subdivided longitudinally (Fig. 7C). Operculum transparent, very thin, elongate, constricted in adapical part, and slightly thickened along low inner edge. Operculum attached to opercular pad along long narrow area (less than 0.3 of operculum width) (Fig. 7B, att). About 1/5 of most posterior part of the pad detached from dorsal surface of the foot, forming a tongue-like extension. Head weakly distinguished from the body, with two separate small vertical flaps (Fig. 7C, tn). No eyes.

Mantle cavity.---Mantle edge even. Mantle thin, and osphradium and ctenidium are seen through it. Siphon short, rather thin-walled, slightly extending beyond mantle edge, with smooth edges. Osphradium bipectinate, nearly symmetrical, with very narrow axis, very broad, slightly exceeding the maximal width of large, deeply pendant ctenidium (Fig. 7G, os). The inner row of osphradial lamellae overhang the ctenidium; when viewing the mantle from the inside, the osphradial maximal width appears to be 1.5 the ctenidial width. The length of osphradium nearly equals the length of ctenidium. Ctenidium occupies nearly entire mantle length, formed of very tall triangular lamellae. Hypobranchial gland moderately glandular, although not forming distinct folds (Fig. 7G, hg). Mantle filament not long, with folded walls, indicating significant state of contraction. Posterior mantle tentacle and mantle lobe absent. Female pallial gonoduct large, swollen. Bursa copulatrix rather large, long, subcylindrical. Female genital opening situated close to anus.

Alimentary system.-Rhynchostome asymmetrical, situated below the right tentacle. Proboscis short in contracted state (about 1.7 mm, or 0.3 AL) (Fig. 7D, E, pr), thin (about 0.5 mm in diameter), occupying nearly the entire rhynchocoel length. Rhynchodeum (Fig. 7E, rnh) thin-walled, semitransparent. Proboscis wall very thin, about 20 µm (4% of the proboscis diameter), lined with low cuboidal epithelium (12 µm), underlain by single layers of circular and longitudinal muscle fibers (8 µm thick overall). Mouth opening rather wide. Muscular buccal tube, not less than 0.5 of proboscis length, leading from mouth to buccal cavity. Wall of buccal tube, in contrast to proboscis wall, thick, about 130 µm in total, lined with thick cuticle (20 µm) and cubical epithelium (12 µm), and underlain by very thick layer of circular muscles (about 90 µm). Proboscis lumen filled with oval cells with slightly granular cytoplasm. Several very thin retractor muscles attached to median part of rhynchodeum (wall of the proboscis sheath) when proboscis is retracted. From posterior to the proboscis, esophagus rather narrow and forming a long loop when proboscis is retracted. Large odontophoral retractor leaving proboscis from the posterior, extending anteriorly along ventral side of rhynchodeum and bypassing the nerve ring, attached to ventral side of cephalic hemocoel (Fig. 7E, odr). Radula (Fig. 8A-C) about 145 µm wide (1.24% SL, 1.93% AL), consisting of 70 rows of teeth. Rachidian with 3 main cusps, central cusp having the same width as the lateral and about 1.5 times shorter than the lateral cusps, and a secondary, very small, indistinct cusp on



Figure 7. Anatomy of *Belloliva alaos* sp. nov. A, B, Ventral and dorsal views, respectively, of the body removed from the shell. C, Head-foot, dorsal view, mantle and visceral mass removed. D, E, Right and left views, respectively, of the anterior foregut. F, External view of the stomach and part of the visceral mass. G, Mantle complex. Abbreviations: ag, anal (rectal) gland; aldg, anterior lobe of digestive gland; aoe, anterior esophagus; att, attachment of the opercular pad to the operculum; bc, bursa copulatrix; cm, columellar muscle; cme, cut mantle edge; ct, ctenidium; gL, gland of Leiblein; hg, hypobranchial gland; lsg, left salivary gland; mf, mantle filament; ne, nephridium; ng, nephridial gland; nr, circumesophageal nerve ring; odr, odontophoral retractor; op, operculum; os, osphradium; ov, ovary; par, parapodium; per, pericardium; pg, pallial gonoduct; pldg, posterior lobe of digestive gland; pma, posterior mixing area; poe, posterior esophagus; pr, proboscis; prp, propodium; prr, proboscis retractor; re, rectum; rnh, rhynchodeum (=proboscis sheath); rsg, right salivary gland; s, siphon; st, stomach; tn, cephalic tentacles; vL, valve of Leiblein.

each side of the main lateral cusps; secondary cusps most visible on lateral view of the rachidians (Fig. 8C, indicated by black arrows). Rachidians rather widely spaced, cusps not abutting the next teeth. Anterior profile of the rachidian slightly convex, nearly straight. Lateral sides of the basal plate gradually embedded in the membrane without distinct border. Lateral teeth with subtriangular bases and long, curved, hook-like cusps. Valve of Leiblein large, pyriform, well distinguished from esophagus, which becomes very narrow immediately after the valve and passes through the nerve ring. Circumesophageal nerve ring comparatively very large, with enlarged pedal and buccal ganglia. Posterior esophagus significantly widening posteriorly towards the stomach. Gland of Leiblein large, very light brown, tubular, and coiled, bulky anteriorly, opening into esophagus by very narrow constricted duct abutting the nerve ring posteriorly. Salivary glands medium-sized, ramified-tubular, left one slightly smaller than right, situated on either side of esophagus and nearly fused around valve of Leiblein, in retracted position of proboscis situated mostly on right side of rhynchodeum, rather loose in appearance with several blind tubules extending from the main part of the gland. Salivary ducts poorly differentiated from the glands, appearing like short extensions of the tubules. They enter the esophageal wall anterior to the valve of Leiblein and pass towards their openings the lateral folds of esophagus. Accessory salivary glands absent. Stomach large, with very long posterior mixing area (Fig. 7F, pma) that spans more than 0.5 whorl. Stomach anatomy not investigated due to poor fixation. Rectal gland a simple, blind, rather long tube (Fig. 7G, ag), colorless.

Distribution

North of New Caledonia, shells in 400-668 m, alive in 668 m.

Remarks

Belloliva alaos sp. nov. is conchologically most similar to Belloliva apoma sp. nov., and they could easily be mistaken as variations of one another unless their anatomy is examined. However, *B. alaos* is distinguished by its significantly larger adult size, 12.1 versus 7.6 mm, and its slightly larger protoconch (Fig. 9). Anatomically, *B. alaos* is readily distinguished by the presence of a large operculum and the absence of eyes. The radulae also differ markedly in the shape of the rachidian: in *B. alaos*, the basal plate of the rachidian is shorter than in *B. apoma* and the anterior profile is nearly straight; in *B. apoma*, the basal plate is longer and the anterior profile, which coincides with the anterior edge of the basal plate, is clearly convex. In addition, in *B. apoma* the central cusp is relatively much narrower and shorter than in *B. alaos*.

Etymology

From the Greek alaos, blind.

Belloliva apoma Kantor and Bouchet sp.nov. (Figs. 8D-F, 9, 10)

Type material

Holotype (Moll 9471) and 3 paratypes (Moll 9472) in MNHN.

Material examined

North of New Caledonia. BATHUS 4, st. DW923, 18°52'S, 163°24'E, 470-502 m (15 dd) (co-occurring with *Belloliva exquisita* and *Belloliva simplex*); st. DW929, 18°52'S, 163°23'E, 502-516 m (7 dd, 2 lv [holotype with dried soft parts and 3 paratypes]). LAGON, st. 475, 18°36'S, 163°11'E, 415-460 m (16 dd). MUSORSTOM 4, st. DW197, 18°51'S, 163°21'E, 550 m (1 dd).

Type locality

North of New Caledonia, 18°52'S, 163°23'E, 502-516 m (BATHUS 4, st. DW929).

Description (holotype)

Shell solid, glossy, oval (BWL/SL = 0.80, AL/SL = 0.66, D/SL = 0.51), with moderately narrow aperture and elevated, somewhat turreted spire, consisting of approximately 0.5 protoconch and 2.5 teleoconch whorls. Protoconch large, evenly rounded, diameter 1330 µm, exposed height 770 µm, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Whorls moderately convex, evenly rounded, poorly shouldered. Filament channel completely open. Aperture lanceolate-oval, gradually narrowing adapically. Outer lip rather evenly convex in most adapical part, nearly straight in median part and evenly rounded abapically. Parietal plate narrow, very thin, anterior plating broadening in abapical part of aperture, appearing nearly smooth in front view, but several very weak oblique plicae visible when the shell is slightly rotated clockwise (Fig. 10D). Color uniformly off-white.

Dimensions (holotype): SL 6.8 mm, SW 3.5 mm, BWL 5.4 mm, AL 4.5 mm. Largest specimen (LAGON, st. 475): SL 7.6 mm, SW 3.9 mm, BWL 6.1 mm, AL 5.1 mm.

Eyes large. Operculum absent.

Radular width about 95 μ m (1.45% SL, 2.16% AL), consisting of about 55 rows of teeth. Rachidian with 3 main cusps, central cusp more than twice narrower than lateral and about 1.5 times shorter than the lateral cusps, and a very small, indistinct secondary cusp on each side of main lateral cusps (Fig. 8E, F indicated by arrow). Rachidians rather widely spaced, cusps not abutting the next teeth. Anterior profile of the rachidian clearly convex and coinciding with the anterior edge of the basal plate of the tooth. Lateral sides



Figure 8. Scanning electron micrographs of the radulae of *Belloliva alaos* sp. nov. (A-C) (MUSORSTOM 4, st. DW160) and *Belloliva apoma* sp. nov. (holotype) (D-F) (BATHUS 4, st. DW929). A, D, Dorsal view of the central portion of the radular ribbon. B, E, Enlarged rachidian tooth. C, F, Left lateral view of the radular ribbon. Arrows on C, E, F indicate secondary cusps of the rachidians. Scale bars = 50 μ m (A, D), 10 μ m (B, C, E, F).

of the basal plate gradually embedded in the membrane without distinct border. Lateral teeth are with subtriangular bases and long, curved, hook-like cusps.

Distribution

North of New Caledonia, shells in 460-550 m, alive in 502-516 m.

Remarks

Specimens of *Belloliva apoma* may be off-white or may have very faint yellow broad spiral bands (one subsutural and one on shell base above periphery), and/or inconspicuous yellowish-brown spots on the rim bordering the filament channel, and/or also inconspicuous zigzag axial lines on last whorl (Fig. 10H-I).



Figure 9. Morphometric comparison of protoconch dimensions of *Belloliva alaos* sp. nov. and *Belloliva apoma* sp. nov.

For comparison with *Belloliva alaos* sp. nov., see under that species.

Etymology

From the Greek *poma*, operculum, and prefix *a*-, without; used as a noun in apposition.

> Belloliva simplex (Pease, 1868) (Figs. 11, 12A-D)

Olivella (Callianax) simplex Pease 1868: 281-282, pl. 23, fig. 24.

Type material

Lectotype designated by Johnson (1994: 24), Academy of Natural Sciences of Philadelphia, ANSP 28969 (Fig. 11A-C).

Material examined

North of New Caledonia. BATHUS 4, st. DW923, 18°52'S, 163°24'E, 470-502 m (1 dd) (co-occurring with *Belloliva exquisita* and *Belloliva apoma*). East coast. LAGON, st. 830, 20°49'S, 165°19'E, 105-110 m (37 dd). BATHUS 1, st. DW692, 20°35'S, 164°59'E, 140-150 m (1 dd). West coast. BATHUS 4, st. DW887, 21°07'S, 164°28'E, 320-344 m (3 dd) (co-occurring with *B. exquisita*). EXPEDITION MON-TROUZIER, st. 1255, 20°43'S, 165°08'E, 11 m (3 lv); st. 1259, 20°44.6'S, 165°13.7'E, 15-35 m (2 lv, 4 dd); st. 1260, 20°44'S, 165°14'E, 49-59 m (1 dd); st. 1261, 20°46'-20°47'S, 164°15'-164°16.5'E, 45-65 m (1 lv); st. 1269, 20°35.1'S, 165°08'E, 15-20 m (22 lv, 6 dd); st. 1271, 20°52.7'S, 165°19.5'E, 5-25 m (3 dd); st. 1272, 20°49.5'S, 165°19.6'E, 10 m (10 lv); st. 1273, 20°50.4'S, 165°22.8'E, 20 m (4 dd, 10 lv); st. 1275, 20°49'S, 165°17'E, 50-62 m (2 dd); st. 1311,

20°40.4'S, 164°14.9'E, 10-60 m (9 lv) (co-occurring with *B. exquisita*); st. 1312, 20°40.4'S, 164°14.9'E, 26-40 m (2 dd, 1 lv) (co-occurring with *B. exquisita*); st. 1316, 20°40'S, 164°11.2'E, 12 m (1 lv, 1 dd); st. 1318, 20°41.4'S, 164°14.8'E, 20-30 m (17 lv [radula examined]); st. 1319, 20°44.7'S, 164°15.5'E, 15-20 m (4 lv); st. 1322, 20°45.2'S, 164°15.2'E, 53-71 m (1 dd) (co-occurring with *B. exquisita*); st. 1331, 20°40.6'S, 164°12.1'E, 55-57 m (4 dd) (co-occurring with *B. exquisita*).

Loyalty Islands, Lifou. LIFOU 2000, st. 1423, 20°54.0'S, 167°07.3'E, 12 m (2 dd); st. 1432, 20°53.5'S, 167°02.7'E, 12-32 m (7 dd); st. 1434, 20°52.5'S, 167°08.1'E, 5-20 m (13 dd); st. 1435, 20°55.2'S, 167°00.7'E, 5-30 m (3 dd); st. 1436, 20°55.5'S, 167°04.2'E, 10-20 m (14 dd); st. 1441, 20°46.4'S, 167°02.0'E, 20 m (1 lv, 5 dd); st. 1442, 20°46.4'S, 167°02.0'E, 47 m (1 dd); st. 1443, 20°53.8'S, 167°07.3'E, 48-52 m (3 dd); st. 1454, 20°56.65'S, 167°02.0'E, 15-18 m (1 lv); st. 1456, 20°49.3'S, 167°10.4'E, 25-30 m (7 dd); st. 1469, 20°54.2'S, 167°00.4'E, 70-130 m (1 dd).

Type locality

Paumotus Islands [Tuamotu Archipelago], French Polynesia.

Description

Shell very small, fragile, semitransparent, glossy, oval, with moderately wide aperture and rather low spire, consisting of about 0.75 protoconch and 1.75 teleoconch whorls. Protoconch large in comparison with the teleoconch, evenly rounded, diameter around 1000 μ m, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Profile of whorls evenly rounded, last whorl weakly shouldered. Filament channel completely open. Aperture lanceolate-oval, gradually narrowing abapically. Outer lip slightly thickened, almost straight adapically, evenly rounded abapically. Parietal plate narrow, slightly thickened, anterior plating much thicker, broadening on abapical part of aperture, without plicae, clearly concave in profile. Color uniformly off-white.

Dimensions: The lectotype, SL 4.2 mm, seems to be the largest specimen. The largest specimen at our disposal (LAGON, st. 830) has SL 3.8 mm, SW 1.9 mm, BWL 3.1 mm, AL 2.5 mm.

The morphology of one rehydrated female specimen from Koumac, New Caledonia (EXPEDITION MON-TROUZIER, st. 1318, SL 4.1, AL 2.5, BWL 3.2, SW 2.0 mm) was examined. Outer morphology similar to other studied species. Eyes large, mantle filament comparatively very short and thick, probably due to fixation. Radula (Fig. 12A-D) about 65 μ m wide (1.59% SL, 2.6% AL), consisting of 85 rows of teeth, including 5-6 nascent; width of rachidian approximately 25 μ m (38% of radular width). Rachidian narrowly spaced, cusps strongly abutting the next tooth, with



Figure 10. *Belloliva apoma* sp. nov. A-D, Holotype. E, Paratype (SL 7.0 mm). F, Paratype (SL 6.5 mm). G, LAGON, st. 475, SL 7.6 mm. H, I, LAGON, st. 475, SL 7.4 mm. All shells illustrated at the same scale except D.



Figure 11. *Belloliva simplex* (Peace, 187X). A-C, Lectotype, ANSP 28969, SL 4.2 mm (courtesy of P. Callomon, ANSP). D-G, New Caledonia, east coast, LAGON, st. 830, 105-110 m. D, (SL 3.6 mm). E, (SL 3.5 mm). F, (SL 3.6 mm). G, (SL 3.5 mm). H, Lifou, st. 1456 m, 25-30 m (SL 3.3 mm). I, New Caledonia, west coast, Expedition Montrouzier, st. 1273, 20 m (SL 3.2 mm). All shells illustrated at the same scale.

short lateral flaps, anterior edge straight, lateral sides of basal plate gradually embedded in membrane without distinct border; 3 main cusps, central cusp narrower and nearly twice as short as the lateral cusps, and a secondary, very small, indistinct cusp on each side of the main lateral cusps; secondary cusps most distinct in lateral view. Lateral teeth with broadened subtriangular bases and long, curved, hook-like cusps, and 2-3 very distinct denticles at the base of the cusp.



Figure 12. Scanning electron micrographs of the radulae of *Belloliva simplex* (A-D), New Caledonia, west coast, MONTROUZIER, st. 1318, 20-30 m (SL 4.1 mm), and *Belloliva iota* sp. nov. (E-F), Coral Sea, Lansdowne Bank, EBISCO, st. DW2631, 372-404 m (SL 7.2 mm). A, E, Dorsal view of the central part of the radular membrane. B, F, Enlarged rachidian teeth. C, D, Left lateral view of the rachidian teeth. Scale bars = $10 \mu m$.

Distribution

Earlier known from the Tuamotu Islands, Tonga (Thiele 1929 in 1929-1931), and Western Samoa (Thiele 1929 in 1929-1931; 2 specimens from "Upolu" Samoa—Museum für Naturkunde, Humboldt University Berlin, ZMB 18.304; M. Glaubrecht pers. comm.), now recorded from the Loyalty Islands (Lifou) and northern and western New Caledonia, live in 10-45 m, shells down to 110-470 m.

Remarks

The original description is very brief and the accompanying illustration is uninformative. However, the identity of the species is established by the name-bearing type, and is confirmed by our examination of topotypical material from Anaa, Tuamotu Islands, in the collection of Jean Tröndle (La Force, France). Thiele's illustration (1929 in 1929-1931: fig. 384) of a specimen from western Samoa agrees with this material.

Belloliva simplex differs from its congeners by its very small adult size. It superficially resembles juveniles of *Belloliva exquisita*, with which it co-occurs at several stations, and from which it is readily distinguished by its smaller protoconch (1000 μ m versus 1240-1580 μ m in *B. exquisita*) and by its smooth, arcuate columella. For comparison with *Belloliva iota* sp. nov., see under that species.

Belloliva iota Kantor and Bouchet sp. nov. (Figs. 12E-F, 13)

Type material

Holotype (Moll 9473) and 4 paratypes (Moll 9474) in MNHN.

Material examined

Coral Sea, Lansdowne Bank, MUSORSTOM 5, st. 388, 20°45'S, 160°54'E, 500-510 m (2 dd). EBISCO, st. DW2618, 20°06'S, 160°23'E, 280-304 m (2 dd; co-occurring with *Belloliva obeon* sp. nov.); st. DW2631, 21°03'S, 160°44'E, 372-404 m (4 lv); st. DW2639, 20°47'S, 161°01'E, 289-294 m (25 dd).

Type locality

Coral Sea, Lansdowne Bank, 20°47′S, 161°01′E, 289-294 m (EBISCO, st. DW2639).

Description (holotype)

Shell solid, glossy, elongate-oval (BWL/SL = 0.73, AL/SL = 0.59, D/SL = 0.46), with narrow aperture and elevated, somewhat turreted spire, consisting of approximately 0.5 protoconch and nearly 4 teleoconch whorls. Protoconch small, evenly rounded, diameter 820 µm, exposed height 580 µm, smooth, protoconch-teleoconch transition distinctly

marked by onset of filament channel. Whorls moderately convex, evenly rounded, shoulder not pronounced. Filament channel completely open. Aperture lanceolate-oval, gradually narrowing adapically. Outer lip thickened, evenly convex in most of adapical part, nearly straight in median part and evenly rounded abapically. Parietal plate narrow, thin, anterior plating broadening in abapical part of aperture and having 4 plicae, adapicalmost being very weak. Color uniformly off-white.

Dimensions (holotype): SL 5.6 mm, SW 2.6 mm, BWL 4.1 mm, AL 3.3 mm. Largest specimen (MUSORSTOM 5, st. 388): SL 7.6 mm, SW 3.6 mm, BWL 5.5 mm, AL 4.6 mm.

One male specimen (EBISCO, st. DW2631, SL 7.2 mm, AL 4.4 mm; Fig. 13G) was dissected. General morphology similar to other studied congeners. Cephalic flaps with relatively large eyes. Penis long, exceeding the length of the mantle cavity, of even diameter along its length and obtuse at the tip. Gland of Leiblein narrow, tubular, slightly coiled anteriorly and nearly straight posteriorly, grey, opening into esophagus without constricted duct. Radula (Fig. 12E-F) about 85 µm wide (1.18% SL, 1.93% AL), consisting of 60 rows of teeth, of which 12-13 nascent; width of rachidian approximately 23 µm (27% of radular width). Rachidians narrowly spaced, cusps abutting the next tooth, anterior edge straight, lateral sides of basal plate gradually embedded in membrane without distinct border. Rachidian with short lateral flaps, 3 main cusps, central cusp narrower and 1.5 times shorter than lateral cusps, and a secondary, very small, indistinct cusp on each side of the main lateral cusps. Lateral teeth with broadened subtriangular bases and long, curved, hook-like cusps.

Distribution

Coral Sea, Lansdowne Bank, alive in 372-404 m, shells in 294-500 m.

Remarks

Belloliva iota varies only little in the degree of development of the plicae on anterior plating, which are nevertheless never very conspicuous. One of the specimens from the type locality has 3 extremely faint yellow axial zigzag lines. Belloliva iota sp. nov. differs from most congeners by its small adult size. It superficially resembles juveniles of Belloliva exquisita, from which it is readily distinguished by its smaller protoconch (800 µm versus 1240-1580 µm in B. exquisita). Belloliva iota sp. nov. differs from Belloliva simplex by its larger shell with slightly smaller protoconch, by the plicae on the anterior plating, and by its relatively smaller radula, consisting of smaller number of rows, with the rachidian teeth having nearly subrectangular lateral flaps (Fig. 12F) versus subtriangular ones in B. simplex (Fig. 12B), and in the absence of denticles at the bases of the cusps on the lateral teeth.



Figure 13. *Belloliva iota* sp. nov. A-D, Holotype. D, Detail of columellar region. E, Paratype, SL 5.4 mm. F, Paratype, SL 5.5 mm. G, EBISCO, st. DW2631, SL 7.1 mm. H, MUSORSTOM 5, st. 388, SL 7.6 mm. All shells illustrated at the same scale except D.

Etymology

From the Greek *iota*: very small; used as a noun in apposition.

Belloliva ellenae Kantor and Bouchet sp. nov. (Figs. 14, 15, 16A-D)

Type material

Holotype (Moll 9475) in MNHN.

Material examined

Coral Sea, Chesterfield plateau: MUSORSTOM 5, st. 339, 19°53'S, 158°38'E, 380-395 m (2 dd); st. 361, 19°53'S, 158°38'E, 400 m (4 dd, 4 lv); st. 362, 19°53'S, 158°40'E, 410 m (5 dd); st. 379, 19°53'S, 158°40'E, 370-400 m (3 dd, 2 lv [holotype]). EBISCO, st. DW2596, 19°43'S, 158°37'E, 382-386 m (1 lv); st. DW2606, 19°36'S, 158°42'E, 442-443 m (3 lv, 3 dd); st. DW2607, 19°33'S, 158°40'E, 400-413 m



Figure 14. *Belloliva ellenae* sp. nov. A-D, Holotype. D, Detail of columellar region. E-H, MUSORSTOM 5, st. 361, SL 8.4 mm (E-F) and 8.6 mm (G-H). I, EBISCO, st. DW2596, intermediate between the "axially striped" and "pale" morphs, SL 6.5 mm. J-L, EBISCO, st. DW2610, "pale" morph, SL 8.8 mm (J) and 8.5 mm (K-L). All shells illustrated at the same scale except D.

(13 lv); st. DW2610, 19°34'S, 158°41'E, 486-494 m (39 lv, 13 dd).

Type locality

Coral Sea, Chesterfield plateau, 19°53'S, 158°40'E, 370-400 m (MUSORSTOM 5, st. 379).

Description (holotype)

Shell solid, glossy, oval-fusiform (BWL/SL = 0.80, AL/ SL = 0.65, D/SL = 0.49), with moderately wide aperture and elevated spire, width 49% of height, consisting of about 1.0 protoconch and 4.0 teleoconch whorls. Protoconch rather large, evenly rounded, diameter 1170 µm, exposed height 920 µm, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Profile of whorls nearly straight, very slightly concave below suture, evenly rounded below inconspicuous shoulder. Filament channel completely open. Aperture lanceolate, gradually narrowing towards its tip. Outer lip nearly straight in most adapical 0.3, evenly rounded in lower part. Parietal plate narrow and thin, anterior plating broadening in lower part of aperture and having 7 poorly developed plicae. Background color light yellow. Last whorl and last half of penultimate whorl with distinct, closely spaced, slightly wavy darker yellow axial color lines (27 on last whorl). Near adapical margin of anterior band, lines distinctly opisthocline and their coaslescence forming a distinct color band. First half of penultimate whorl with gradually fading axial lines, early teleoconch whorls with only faint and irregularly spaced spots. Anterior plating with distinct elongated brown spot.

Dimensions (holotype): SL 8.2 mm, SW 4.0 mm, BWL 6.6 mm, AL 5.3 mm. Largest specimen (st. 361): SL 8.8 mm, SW 4.6 mm, BWL 7.2 mm, AL 6.2 mm.

Distribution

Coral Sea, Chesterfield plateau, alive in 386-486 m.

Remarks

Two distinct forms of Belloliva ellenae sp. nov. can be recognized. The "axially striped" form (Fig. 14A-H) has 26-46 colored axial lines on the last whorl and a dark spot on the anterior plating. The plicae on the anterior plating vary from nearly completely absent to moderately strong. The "pale" form is similar in shell outline to the typical form, but differs in color: the background is ivory and instead of axial lines there are two narrow light-brown color bands, one at the adapical limit of the anterior band, the other one on the rim of the filament channel; there is no columellar spot. Specimens of this form also differ by their somewhat larger protoconch and first teleoconch whorl (average D1 = 1.51mm, range 1.45-1.56 mm in the "pale" form versus average D1 = 1.25 mm, range 1.17-1.29 mm in the "axially striped" form). The radulae (Fig. 16) and gross morphology are nearly identical in the two forms. The radula of a specimen of the "axially striped" form (MUSORSTOM 5, st. DW361,



Figure 15. Comparison of "pale" and "axially striped" forms of *Belloliva ellenae* sp. nov. Ordinate: protoconch diameter (D1, mm); abscissa: (left) diameter of first teleoconch whorl (TL1) and (right) protoconch elevation (PRE).



Figure 16. Scanning electron micrographs of the radulae of *Belloliva ellenae* sp. nov. (A-D) and *Belloliva dorcas* sp. nov. (E-F). A-B, "Axially striated" form (MUSORSTOM 5, st. DW361). C-D, "pale" form (EBISCO, st. DW2607). A, C, E, Dorsal view of the central part of the radular membrane, scale bars = $50 \ \mu\text{m}$. B, D, F, Enlarged rachidian teeth, scale bars = $10 \ \mu\text{m}$.

SL 8.6, AL 5.6 mm, male) was about 110 µm wide (1.27% of SL, 1.96% of AL) (Fig. 16A-B), consisting of 65 rows, of which 20 are nascent. Rachidians narrowly spaced, cusps abutting the previous tooth (Fig. 16B), anterior edge very slightly concave in its middle part and rounded at the edges. Lateral sides of basal plate gradually embedded into the membrane without distinct border. Rachidian with 3 broadly spaced main cusps, central cusp about 1.4 times shorter and much narrower than the lateral cusps, and one small, narrow, but distinct, additional cusp on each side of the main lateral cusps. Lateral teeth with subtriangular bases and long curved hook-like cusps bearing 1-2 small distinct denticles at their bases. The radula of the "pale" form (EBISCO, st. DW2607, SL 8.1, AL 5.4 mm, female) (Fig. 16C-D), was also about 110 µm broad (1.25% of SL, 1.96% of AL), consisting of 73 rows, of which 20 rows are nascent. Tooth shape was very similar to that of the "axially striped" form.

Both forms of Belloliva ellenae sp. nov. occur in a very limited area: the "axially striped" form was found at four stations that straddle only 3 km while the "pale" form was found at 3 stations spanning about 6 km, slightly to the north of the type locality. These two groups of stations are separated by 30 km. This distribution does not appear to be merely a sampling artifact, as hauls made during the EBI-SCO cruise at appropriate depths between the two areas were negative for Belloliva ellenae sp. nov., with the exception of a single specimen from a station (EBISCO, st. DW2596) situated right in the middle of the two clusters of stations. This specimen (Fig. 14I) is somewhat intermediate in coloration (axial lines are present but are very pale and the columellar spot is absent) and the dimensions of its protoconch and first teleoconch whorl are also intermediate (Fig. 15). This intermediate specimen from an intermediate locality is further evidence that the two forms are conspecific.

Belloliva ellenae sp. nov. is sympatric with Belloliva obeon sp. nov., Belloliva dorcas sp. nov., and Belloliva exquisita. It is readily distinguished from these, and from other congeners, by the combination of small adult size and color pattern (either of axial stripes and brown spot on anterior plating or of two narrow bands over ivory background).

Etymology

The species is named after our colleague Dr. Ellen E. Strong, curator at the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and companion of the two authors during several field seasons.

Belloliva obeon Kantor and Bouchet sp. nov. (Figs. 17, 18, 19, 20)

Type material

Holotype (Moll 9476) and 2 paratypes (Moll 9477) in MNHN.

Material examined

Coral Sea, Chesterfield Plateau, MUSORSTOM 5, st. 346, 19°40'S, 158°27'E, 245-252 m (3 dd [holotype and paratypes]); st. 388, 20°45'S, 160°54'E, 500-510 m (3 lv). EBISCO, st. DW2608, 19°33'S, 158°40'E, 393-396 m (5 dd, including 2 striped, co-occurring with *Belloliva dorcas* sp. nov.). Lansdowne Bank. CORAIL 2, st. DE16, 20°48'S, 160°56'E, 500 m (12 dd, 2 lv). EBISCO, st. DW2617, 20°06'S, 160°22'E, 427-505 m (8 dd, 1 lv striped); st. DW2618, 20°06'S, 160°23'E, 280-304 m (2 dd, striped; co-occurring with *Belloliva iota* sp. nov.); st. DW2619, 20°06'S, 160°23'E, 490-550 m (4 lv, striped); st. DW2625, 20°04.8'S, 160°20'E, 627-741 m (1 lv, striped); st. DW2629, 21°06'S, 160°46'E, 569-583 m (1 lv, 30 dd, striped).

Type locality

Coral Sea, Chesterfield Plateau, 19°40'S, 158°27'E, 245-252 m (MUSORSTOM 5, st. 346).

Description (holotype)

Shell medium-sized, solid, semitransparent in the central part of the last whorl, glossy, broadly oval (BWL/SL = 0.86, AL/SL = 0.70, D/SL = 0.52), with wide aperture and low spire, consisting of about 0.5 protoconch and 3.125 teleoconch whorls. Protoconch large, evenly rounded, diameter 1770 µm, exposed height 720 µm, smooth, protoconchteleoconch transition distinctly marked by onset of filament channel. Profile of whorls very slightly concave subsuturally, with rather distinct rounded shoulder. Filament channel completely open. Aperture elongate-oval, gradually narrowing and rounded abapically. Outer lip slightly thickened, the edge itself sharp, slightly concave in most adapical part, nearly straight along most of its length and evenly rounded abapically. Parietal plait very narrow, hardly thickened, anterior plating clearly concave in profile, broadened, bearing ten pronounced plicae, diminishing in size adapically. Color uniformly off-white.

Dimensions (holotype largest specimen): SL 14.3 mm, SW 10.1 mm, BWL 12.4 mm, AL 10.1 mm.

Anatomy

The anatomy of two specimens (MUSORSTOM 5, st. 388, Chesterfield Plateau, SL 13.8, BWL, 12.2, AL 9.8, SW 7.3 mm; EBISCO, st. DW2619, Lansdowne Bank, SL 9.0, BWL 7.9, AL 6.3, SW 5.0 mm) was examined.

General morphology.—The body of the first one was badly torn during extraction, but the external morphology is similar to that of *Belloliva alaos* sp. nov. Foot thick, strongly contracted during fixation, propodium bent ventrally. Metapodium very broad, triangular-oval. Propodium crescent-



Figure 17. *Belloliva obeon* sp. nov. A-D, Holotype. E, Paratype, SL 12.3 mm. F, Paratype, SL 12.6 mm. G-I, CORAIL2, st. DE16, SL 12.0 mm (G), 11.8 mm (H), and 11.3 mm (I). J-N, EBISCO, st. DW2629: "typical," SL 9.6 mm (J-K), transitional, SL 10.1 mm (L), and slender specimens, SL 10.2 mm (M) and 10.4 mm (N). All shells illustrated at the same scale except D.



Figure 18. Scanning electron micrographs of the radula of *Belloliva obeon* sp. nov. [A-C, Coral Sea, Chesterfield Plateau, MUSORSTOM 5, 500-510 m, st. 388 (SL 13.8 mm); D-F, Coral Sea, Lansdowne Bank, EBISCO, st. DW2619 (SL 9.0)]. A, D, Dorsal views of the central portion of the radular ribbon. B, E, Left lateral view of the radular ribbon. C, Dorsal view of the bending plane of the radular ribbon. E, Dorsal view of enlarged central teeth. Arrow on B indicates additional cusp on the rachidian. Scale bars = 50 μ m (A, C, D), 10 μ m (B, E, F).

shaped, subdivided longitudinally by deep furrow and delimited from metapodium by dorsal and ventral grooves. Parapodia rather short in contracted state. Operculum very large, extremely thin and transparent, attached to opercular disc by narrow oval zone along its left side (about 0.5 of operculum width) (Fig. 19A). About 1/5 of posteriormost part of pad detached from dorsal surface of foot, forming a tongue-like extension. Head well set off from the foot (Fig. 19A), with broadly separated, laterally compressed flaps with large eyes. Columellar muscle thick, splitting into 3 branches in its posterior part. *Mantle cavity.*—Mantle filament short. Anterior mantle tentacle and mantle lobe absent. Siphon long, narrow, and extending substantially beyond the evenly and slightly thickened mantle edge. Mantle itself very thin. Size and shape of osphradium and ctenidium very similar to those of *Belloliva alaos* sp. nov.

Alimentary system.—Organs of anterior foregut strongly contracted during fixation (Fig. 19B). Proboscis short with smooth walls. Salivary glands large, seemingly compact, fused around valve and posteriormost part of rhynchodeum, their structure ramified tubular, similar to that of *Belloliva*



Figure 19. Some details of the morphology of *Belloliva obeon* sp. nov. A, Head-foot, dorsal view, mantle and visceral mass removed. B, Right view of the anterior foregut. C, External view of the stomach and part of the visceral mass. Abbreviations: att, attachment of the opercular pad to the operculum; cm, columellar muscle; dgd, opening of the digestive gland into stomach; gL, gland of Leiblein; nr, circumesophageal nerve ring; odr, odontophoral retractor; op, operculum; opl, opercular lobe; p, penis; par, parapodium; pldg, posterior lobe of digestive gland; poe, posterior esophagus; pr, proboscis; prp, propodium; rnh, rhynchodeum (= proboscis sheath); rsg, right salivary gland; sem.d, seminal duct; st, stomach; tn, cephalic tentacle; vL, valve of Leiblein.

brazieri. Accessory salivary glands absent. Gland of Leiblein large, massive, not coiled, dark brownish-grey, opening by narrow duct into esophagus. Large odontophoral retractor muscle passing ventrally under very thin-walled rhynchodeum. Valve of Leiblein large, pyriform. Odontophore large, about 2/3 of proboscis length, deeply withdrawn, as in Amalda (Kantor 1991). Radular diverticulum strongly cuticularized. Radula about 170 µm wide (1.23% of SL, 1.73% of AL), consisting of 52 rows of teeth. Rachidian about 70 µm wide (41% of radular width) with 3 main cusps, central cusp about 1.6 times shorter and narrower than the lateral cusps, and one very small, indistinct additional cusp on each side of the main lateral cusps, best seen in lateral view (Fig. 18B, indicated by arrow). Rachidians rather narrowly spaced, cusps strongly bent in profile, the tips of the lateral cusps resting on the following teeth (Fig. 18B). Anterior profile of the rachidian nearly straight in middle part and rounded at the edges, coinciding with anterior edge of basal plate. Lateral sides of basal plate gradually embedded into the membrane without distinct border. Lateral teeth with subtriangular bases and long curved hook-like cusps. Only part of stomach retrieved, characterized by very long and very narrow posterior mixing area (Fig. 19C).

Reproductive system.—Penis very long, flattened, simple, tapering towards the tip. Seminal papilla absent.

The specimen from Lansdowne is similar in outer morphology. The stomach is slightly larger, with an even longer posterior mixing area. Proboscis length about 2 mm. Radula slightly more than half of proboscis length, about 120 μ m wide (1.33% of SL, 1.90% of AL), consisting of about 65 rows. Rachidian about 50 μ m wide (42% of radular width) with 3 main cusps, central cusp about 1.6 times shorter and narrower than the lateral cusps, and one small, but distinct additional cusp on each side of the main lateral cusps. Rachidians rather narrowly spaced, cusps abutting the previous tooth, but tips not resting on it (Fig. 18E) as in the specimen from Chesterfield Plateau (Fig. 18B).

Distribution

Coral Sea, Chesterfield Plateau and Lansdowne Bank (Fig. 20), alive in 500-627 m, shells from 252 m.

Remarks

Belloliva obeon sp. nov. is rather variable in terms of shell shape and coloration. The specimens from Chesterfield Plateau are mostly pure off-white (with the exception of one specimen from EBISCO st. DW2608 that has broad, light yellow, nearly axial stripes on the last part of the last whorl) and their shell shape is overall similar to the type material. On Lansdowne Bank, the species is more variable, especially in terms of shell shape. Some specimens are extremely similar to those from the Chesterfields, but most have moderately to strongly developed axial color stripes, sometimes extending over the whole shell, while the background color may differ from off white to light yellow. Slender specimens (e.g., Fig. 17N) resemble smaller specimens of Belloliva dorcas sp. nov. but a large sample (31 specimens) from EBISCO st. DW2629 (Fig. 17J-N) contains all transitions to "typical" broad specimens. Radular morphology is also similar between specimens from Chesterfield Plateau and Lansdowne Bank, although slight differences can be observed, especially in the shape of the cusps of the rachidian teeth, which are much more strongly bent in the specimen from Chesterfield (Fig. 18B) than in the specimen from Lansdowne (Fig. 18E). Such differences are smaller than differences with other similar species, especially Belloliva dorcas sp. nov. (Fig. 16E-F), and we consider them intraspecific.

The species superficially resembles *Belloliva alaos* sp. nov. from New Caledonia, differing in the well pronounced plication on the columellar plait, and in the presence of eyes. It also differs from all other species of *Belloliva* in its straight or sometimes slightly concave outer lip. For comparison with *Belloliva dorcas* sp. nov., see under that species.

Etymology

From the Greek for "egg;" used as a noun in apposition.

Belloliva dorcas Kantor and Bouchet sp. nov. (Figs. 16E-F, 20, 21, 22)

Type material

Holotype (Moll 9478) and 1 paratype (Moll 9479) in MNHN.

Material examined

Coral Sea. Bellona Plateau. MUSORSTOM 5, st. 328, 20°23'S, 158°44'E, 355-340 m (1 dd); st. 329, 20°23'S, 158°47'E, 320 m (1 dd); EBISCO, st. DW2564, 20°25'S, 158°41'E, 333-386 m (1 lv); st. DW2574, 20°20'S, 158°45'E, 358-374 m (1 lv, radula extracted, co-occurring with *Belloliva exquisita*). Chesterfield Plateau. MUSORSTOM 5, st. 347, 19°39'S, 158°28'E, 260 m (1 dd); st. 375, 19°52'S, 158°30'E, 300 m (3 dd [holotype and paratype]); CHALCAL 1984, st. D31, 19°33.5'S, 158°40'E, 393-396 m (1 dd, co-occurring with *Belloliva obeon* sp. nov.). Lansdowne Bank. MUSORSTOM 5, st. 389, 20°45'S, 160°54'E, 500 m (4 dd).

Type locality

Coral Sea, Chesterfield Plateau, 19°52'S, 158°30'E, 300 m (MUSORSTOM 5, st. 375).







Figure 21. *Belloliva dorcas* sp. nov. A-D, Holotype, MUSORSTOM 5, sta. 375, SL 13.6 mm. E, Bellona Plateau, EBISCO sta. DW2574 (SL 12.5 mm, radula studied). F, Chesterfield Plateau, MUSORSTOM 5, sta. 328, SL 11.1 mm. G, H, Specimens from Lansdowne Bank (MUSORSTOM 5, sta. 389). G, (SL 11.1 mm). H, (SL 10.6 mm). I-J, Cheesterfield Plateau. I, CHALCAL, st. D31 (SL 9.6 mm). J, Chesterfield Plateau, MUSORSTOM 5, sta. 347 (SL 11.0 mm). All shells illustrated at the same scale except D.

Description (holotype)

Shell large, solid, glossy, elongate-oval (BWL/SL = 0.78, AL/SL = 0.69, D/SL = 0.45), with moderately narrow aperture and elevated spire, consisting of about 0.75 protoconch

and 3 teleoconch whorls. Protoconch large, evenly rounded, diameter 1970 μ m, exposed height 1070 μ m, smooth, protoconch-teleoconch transition distinctly marked by onset of filament channel. Profile of whorls moderately convex,

evenly rounded. Filament channel completely open. Aperture lanceolate-oval, gradually tapering adapically. Outer lip slightly convex, nearly straight in adapical-most part, evenly rounded abapically. Parietal plate very narrow, not visible in strictly ventral view, very thin, anterior plating thickening and broadening in abapical part of aperture, bearing 6 weak plicae (Fig. 21D). Background color creamy yellow. Last and penultimate whorls (except anterior plating) covered by distinct, rather broad, and irregularly shaped zigzag brown lines, well pronounced on the anterior band. Rim of filament channel marked by row of irregularly spaced brown spots or dashes.

Dimensions (holotype): SL 13.6 mm, SW 6.1 mm, BWL 10.6 mm, AL 9.4 mm. Largest specimen (paratype): SL 14.0 mm, SW 6.3 mm, BWL 11.1 mm, AL 9.6 mm.

Anatomy

Part of the body was retrieved from one specimen (EBISCO sta. 2574, SL 12.5 mm, AL 8.5 mm - shell see Fig. 21E). External morphology very similar to that of Belloliva obeon, including the presence of eyes. Penis differing from that of B. obeon in being of nearly even diameter along its length, obtuse at the tip, and lacking the attenuated tip. Gland of Leiblein long, tubular, slightly coiled, with strong transverse folds visible through the gland wall. Radula (Fig. 16E-F) about 140 µm wide (1.12% of SL, 1.64% of AL), consisting of about 85 rows of teeth, including 6 nascent. Rachidians rather narrowly spaced, cusps strongly abutting previous teeth (Fig. 16F). Anterior edge of rachidian slightly convex and rounded at the edges. Lateral sides of basal plate gradually embedded into the membrane without distinct border. Rachidian about 68 µm wide (49% of radula width) with 3 main, closely spaced cusps and broad lateral flaps, central cusp about 1.3 times shorter and narrower than lateral cusps, and one small, but distinct, additional cusp on each side of main lateral cusps. Lateral teeth with subtriangular bases and long, curved, hook-like cusps.

Distribution

Coral Sea, northern Bellona Plateau, Chesterfield Plateau, and Lansdowne Bank (Fig. 20), alive in 358-374 m, shells from 230 m.

Remarks

Belloliva dorcas sp. nov. is variable in terms of shell shape and coloration. The holotype has the most pronounced zigzag lines; in other specimens, these are either rather inconspicuous (Fig. 21G) or completely absent, the shell then being nearly white with only a row of small light brown dots at the rim of the filament channel (Fig. 21F).

On the Chesterfield Plateau, *Belloliva dorcas* sp. nov. and *Belloliva obeon* sp. nov. are easily recognized on the basis of

Figure 22. Morphometric comparison of protoconch dimensions of *Belloliva dorcas* sp. nov. and different populations of *Belloliva exquisita* (Angas, 1871) from the Coral Sea.

shell shape, shell color, and radular morphology. In B. dorcas sp. nov., the shape of the rachidian is rather distinct in having much broader lateral flaps compared to B. obeon sp. nov. and the other species studied here. The radular membrane is also somewhat narrower in B. dorcas sp. nov. (1.12% of SL and 1.64% of AL versus 1.23-1.33% of SL, and 1.73%-1.90% of AL in B. obeon). Their co-occurrence at one station (EBISCO, st. DW2608) is additional evidence that they are distinct species and not variants. On Lansdowne Bank, the identity of a population that we attribute to Belloliva dorcas sp. nov. (Fig. 21G-H) is problematic and requires anatomical or molecular confirmation. Sympatric, but not syntopic, specimens of B. obeon sp. nov. (Fig. 17M-N), superficially ressemble it by their broad, rather straight, axial stripes (rather than the narrow, zigzag, chevron lines of *B. dorcas*); the characteristic row of irregularly spaced brown spots or dashes on the rim of the filament channel are another reason why we attribute this lot to B. dorcas.

Belloliva exquisita bears a rather strong resemblance to *Belloliva dorcas*, of which it superficially seems to be a diminutive form. The two species differ in protoconch morphometrics, with a significant gap in their diameters (Fig. 22). The two species are sympatric on the northern Bellona and Chesterfield Plateaus, and even syntopic at one station (EBISCO st. DW2574), thus leaving no doubt that two different species are involved.

The COI sequence was obtained for *Belloliva dorcas* (voucher specimen MNHN Moll 9484—Fig. 21E), GenBank accession no. DQ780463.



Etymology

From the Greek noun *dorcas*, designating a kind of gazelle, with reference to the elegant colour pattern; used as a noun in apposition.

Belloliva exquisita (Angas, 1871) (Figs. 22, 23, 24, 25, 26)

Olivella exquisuta Angas 1871: 13, pl. 1, fig. 2.

Type material

Holotype BMNH 1871.7.5.5 (Fig. 23A-C).

Material examined

Surprise Atoll: LAGON, st. 444, 18°15'S, 162°59'E, 300-350 m (1 dd); st. 502, 19°08'S, 163°30'E, 190 m (1 dd). PALEOSUPRISE, st. CP1391, 18°29.8'S, 163°02'E, 365 m (2 dd); st. CP1392, 18°29.8'S, 163°02.7'E, 370 m (1 dd).

North of New Caledonia: MUSORSTOM 4, st. DW142, 18°35'S, 163°10'E, 525 m (1 dd); st. DW149, 19°08'S, 163°23'E, 155 m (5 dd); st. DW150, 19°07'S, 163°22'E, 110 m (6 dd); st. DW151, 19°07'S, 163°22'E, 200 m (4 dd); st. DW162, 18°35'S, 163°10'E, 525 m (1 dd); st. DW164, 18°33'S, 163°13'E, 255 m (1 dd); st. DW184, 19°04'S, 163°27'E, 260 m (28 dd, 3 lv [1 specimen dissected]). BATHUS 4, st. DW923, 18°52'S, 163°24'E, 470-502 m (5 dd [co-occurring with *Belloliva simplex* and *Belloliva apoma*]); st. DW926, 18°57'S, 163°25'E, 325-330 m (1 dd); st. DW927, 18°56'S, 163°22'E, 444-452 m (1 dd); st. DW940, 19°00'S, 163°26'E, 305 m (4 dd, 1 lv); st. DW941, 19°02'S, 163°27'E, 270 m (1 dd); st. DW942, 19°04'S, 163°27'E, 264-270 m (11 dd).

New Caledonia proper: BATHUS 4, st. DW887, 21°07'S, 164°28'E, 320-344 m (2 dd [co-occurring with *Belloliva simplex*]). BATHUS 1, st. DW 688, 20°33'S, 165°00'E, 270-282 m (1 dd). West coast. EXPEDITION MONTROUZIER, st. 1304, 20°38.6'S, 164°13.2'E, 12-15 m (1 dd); st. 1311, 20°40.4'S, 164°14.9'E, 10-60 m (14 lv and dd) (co-occurring with *B. simplex*); st. 1312, 20°40.4'S, 164°14.9'E, 26-40 m (36 lv and dd) (co-occurring with *B. simplex*); st. 1312, 20°40.4'S, 164°14.9'E, 26-40 m (36 lv and dd) (co-occurring with *B. simplex*); st. 1319, 20°44.7'S, 164°15.5'E, 15-20 m (1 lv); st. 1321, 20°40.7'S, 164°14.9'E, 90-115 m (1 lv); st. 1322, 20°44.2'S, 164°15.2'E, 53-71 m (1 dd) (co-occurring with *B. simplex*); st. 1323, 20°40.9'S, 164°14.8'E, 82-120 m (4 dd); st. 1331, 20°40.0'-20°40.6'S, 164°11.2'-164°12.1'E, 55-57 m (4 lv) (co-occurring with *B. simplex*).

South of New Caledonia/Norfolk Ridge: MUSORSTOM 4, st. DW210, 22°44'S, 167°09'E, 340-345 m (1 dd, 1 lv). BIOCAL, st. DW41, 22°45'S, 167°12'E, 380-410 m (1 dd). BERYX 11, st. CH41, 23°39'S, 168°00'E, 230-360 m (1 dd). SMIB 5, st. DW79, 23°41'S, 168°01'E, 285 m (2 dd); st. DW80, 23°42'S, 168°00'E, 300 m (2 dd). East Jumeau Bank SMIB 8, st. DW170-172, 23°41'S, 168°00'-168°01'E, 230-290 m (4 dd); st. DW176, 23°42'S, 168°01'E, 283-290 m (1 dd); NORFOLK 1, st. DW1674, 23°40'S, 168°00'E, 245-253 m (1 dd). Antigonia Bank, NORFOLK 1, st. DW1712, 23°23'S, 168°02'E, 180-250 m (1 dd); st. DW1717, 23°23'S, 168°02'E, 250-312 m (1 dd). Banc P, NORFOLK 1, st. DW1723, 23°18'S, 168°15'E, 266-267 m (1 dd); st. DW1724, 23°17'S, 168°14'E, 200-291 m (1 dd); st. DW1726, 23°18'S, 168°15'E, 185-207 m (5 dd); st. DW1728, 23°19'S, 168°15'E, 207-276 m (4 dd).

Coral Sea, Capel Bank: MUSORSTOM 5, st. 256, 25°18'S, 159°53'E, 290-300 m (1 dd.); st. 258, 25°33'S, 159°46'E, 300 m (5 dd.), st. 263, 25°21'S, 159°46'E, 225-150 m (21 dd, 1 lv [radula and external morphology]); st. 265, 25°21'S, 159°45'E, 190-260 m (7 dd); st. 266, 25°20'S, 159°46′E, 240 m (3 dd, 2 lv); st. 270, 24°49′S, 159°34′E, 223 m (2 dd); st. 273, 24°43'S, 159°43'E, 290 m (3 dd); st. 274, 24°45'S, 159°41'E, 285 m (9 dd, 1 lv). Argo Bank: MUSOR-STOM 5, st. 298, 22°44'S, 159°22'E, 320 m (2 dd); st. 299, 22°48'S, 159°24'E, 360-390 m (1 dd). Nova Bank: MUSOR-STOM 5, st. 303, 22°12'S, 159°23'E, 332 m (1 dd). CHAL-CAL, st. D63, 22°11'S, 159°14'E, 305 m (4 dd). EBISCO, st. DW2522, 22°46'S, 159°21'E, 310-318 m (5 dd); st. DW2538, 22°20'S, 159°25'E, 318-323 m (5 dd). Kelso Bank: MUSOR-STOM 5, st. 277, 24°11'S, 159°35'E, 270 m (10 dd, 1 lv); st. 280, 24°10′S, 159°36′E, 270 m (1 dd). EBISCO, st. DW2509, 24°08'S, 159°35'E, 265 m (1 dd); st. DW2514, 24°06'S, 159°41'E, 295-310 m (1 dd); st. DW2515, 24°04'S, 159°41'E, 330-370 m (1 dd). Bellona Plateau: EBISCO, st. DW 2547, 21°06'S, 158°36'E, 356-438 m (1 dd); st. DW2574, 20°20'S, 158°45'E, 358-374 m (1 dd, co-occurring with Belloliva dorcas sp. nov.); Chesterfield Plateau: EBISCO, st. DW 2603, 19°36'S, 158°43'E, 570-568 m (8 dd).

Type locality

Coogee Bay, New South Wales, Australia.

Description

Shell solid, relatively thin, glossy, with moderately narrow aperture and elevated spire. Protoconch large, evenly rounded, diameter 1200-1600 μ m, smooth. Profile of whorls moderately convex, evenly rounded, very inconspicuously shouldered. Filament channel open. Aperture lanceolateoval, gradually tapering adapically. Outer lip slightly convex, nearly straight in most adapical part, evenly rounded abapically. Anterior plating bearing 5-7 rather weak, but distinct plicae.

Dimensions: largest specimen (Capel Bank, MUSORSTOM 5, st. 258) SL 12.5 mm, SW 5.2 mm, BWL 10.2 mm, AL 8.1 mm.

Distribution

Southeastern Australia, New South Wales, Queensland; Coral Sea guyots, New Caledonia including its continuation



Figure 23. *Belloliva exquisita* (Angas, 1871). A-C, Holotype, BMNH 1871.7.5.5 (SL 7.7 mm). D, Northern New Caledonia, MUSORSTOM 4, st. DW184 (SL 9.2 mm). E, Northern New Caledonia, MUSORSTOM 4, st. DW149, SL 6.4 mm. F, G, Northern New Caledonia, MUSORSTOM 4, st. DW149, SL 7.6 and 8.4 mm. H, Northern New Caledonia, PALEO-SURPRISE, st. DW1391, SL 6.7 mm. I, Koumac, western New Caledonia, st. 1311 (SL 6.5 mm). J, Southern New Caledonia, SMIB5, st. DW80 (SL 9.2 mm). K, Capel Bank, MUSORSTOM 5, st. 258 (SL 11.2 mm). L, Capel Bank, MUSORSTOM 5, st. 265, SL 8.9 mm. M, Kelso Bank, MUSORSTOM 5, st. 277 (SL 9.0 mm). N, Kelso Bank, MUSORSTOM 5, st. 277 (SL 8.7 mm). O, Bank Nova, CHALCAL, st. D63 (SL 8.8 mm). P, Argo Bank, MUSORSTOM 5, st. 299 (SL 9.8 mm). All shells illustrated at the same scale.



Figure 24. Scanning electron micrographs of the radula of *Belloliva exquisita* (Angas, 1871). A-D, Coral Sea, MUSORSTOM 5, sta. 263. E-H, Northern New Caledonia, MUSORSTOM 4, sta. DW 184. A, E, Dorsal view of the central part of the radular membrane. B, F, Enlarged rachidian teeth. C, G, Left and right lateral views of the rachidian teeth, respectively. D, H, Left and right lateral views of the lateral teeth, respectively. Scale bars = $10 \mu m$.

to Surprise Atoll in the North and Norfolk Ridge in the South, alive 26-345 m, shells in 12-525 m.

Remarks

We are treating *Belloliva exquisita* as a single, highly variable species, both in terms of geographical and bathymetric variation. Within-population variation concerns coloration, with very pale to practically white or semitransparent specimens not uncommon in all parts of the distribution.

Most populations from off the north, south and west coasts of New Caledonia, including Norfolk Ridge, are very similar and there is no doubt that they represent a single species. Conchologically specimens from these populations are most similar to those from New South Wales, including the holotype (Fig. 23A-C). These individuals are characterized by rather slender shells (D/SL 0.45, n = 6, range 0.43-0.46) with elevated spires (BWL/SL 0.77, n = 6, range 0.75-0.78), and a color pattern typically of narrow, irregular zigzag brown lines on a creamy yellow background, and two spiral rows of unevenly spaced, spirally elongated, brown spots, one on rim of filament channel, the other on whorl periphery. Coloration is more pronounced in southern populations (Fig. 23J), although pale to nearly white specimens are also found there, but in lesser proportion than in the northern populations (Fig. 23H).

A little more problematic is a series of populations from a rather narrow depth range (110-190 m) in a restricted area extending for about 13 km (MUSORSTOM 4, st. DW 149, 150, 151) that differ from the "typical" form in having a larger, much broader shell (average D/SL = 0.50, n = 6, range 0.49-0.51, Fig. 23F, G; versus D/SL = 0.45, n = 6, range 0.43-0.46 in "typical" form) and sharper and more numerous plicae on the anterior plating. At one station (MUSOR-STOM 4, st. DW 149) the broad and narrow (Fig. 23E) forms co-occur, which might indicate that they represent two different species. However, as only four empty shells were taken at that station, the evidence to treat them as two species is very weak and, in the absence of further data (radular morphology, anatomy), we prefer to hypothesize that the broad form represents a local variant of Belloliva exquisita. Ideally, this should be tested with molecular data.

Variation in the Coral Sea is more classically geographical, with each of the guyots having its own recognizable population, described below from south to north. However, the morphometries of specimens from different banks overlap and form a continuum with the "typical" form from New Caledonia (Fig. 25); we believe that this geographical variation reflects limited genetic exchange between banks, but not isolation.

Capel Bank (Fig. 23K, L). Shell to 12.5 mm in length, rather slender (D/SL 0.42, n = 7, range 0.39-0.46), with lower spire (BWL/SL 0.80, n = 7, range 0.77-0.81), usually

Argo Bank 1.5 D1, mm ova Bank Kelso Bank New Caledonia 1.0 0.8 PRE, mm 1.0 0.9 **Capel Bank** Argo Bank BWL/SL 0.8 Kelso Bank w Caledonia Nova Bank 0.4 0.5 D/SL

Figure 25. Morphometric comparisons of some protoconch and shell measurements of different populations of *Belloliva exquisita* (Angas, 1871) to illustrate the overlap of characters. Different populations are marked by different symbols.

pale, zigzag lines from very pale to absent, brown spots at channel rim present at least on parts of shell. Protoconch on average slightly larger (D1 = 1.37, n = 7, range 1.26-1.42) than in a "typical" form (D1 = 1.24, n = 6, range 1.21 \pm 1.30), although both forms overlap significantly (Fig. 25).

Kelso Bank (Fig. 23M, N). Shells to 9.0 mm in length, differing from previous in their broader, more oval shell (D/SL in average 0.46, n = 5, range 0.46-0.47) with shorter spire, generally light in background color, although with better pronounced brown zigzag lines. Protoconch dimensions slightly smaller than in specimens from Capel Bank, but overlapping with "typical" form.

Argo Bank (Fig. 23N). Shells more similar in shape to those from Capel Bank, but characterized by the largest protoconch dimensions. Coloration light, zigzag lines pale, but well defined.

Nova Bank (Fig. 23O). Shells to 11.6 mm, characterized by rather slender shells (D/SL in average 0.39, n = 4, range 0.38-0.40). Protoconch dimensions completely overlaping

with those from Capel Bank. Coloration light, some specimens with very pale zigzag lines.

Our material from Bellona and Chesterfield Plateaus is in rather poor condition and does not allow a detailed description, but is sufficient to record *Belloliva exquisita* in sympatry with *Belloliva dorcas* and to highlight the fact that the protoconch of these specimens is the smallest in all populations of *B. exquisita* examined (Fig. 22).

The anatomy of three specimens was examined, one from Capel Bank (MUSORSTOM 5, st. 263, SL 9.8, BWL 8.1, AL 6.2, SW 4.1), one from North of New Caledonia (MUSORSTOM 4, st. DW184, SL 9.4, BWL 7.2, AL 6.2, SW 4.2 mm), and one dried, rehydrated, specimen from Koumac (MONTROUZIER, st. 1312, SL 6.2, BWL 4.8, AL 4.3, SW 3.1 mm).

The specimen from the Coral Sea had the body strongly contracted, mantle cavity spanning about 0.5 whorls, nephridium 0.3 whorls, digestive gland with gonad about 3 whorls. Body in alcohol uniformly pale yellow, lacking pigmentation. Nephridium with transparent walls. Anterior lobe of digestive gland small, spanning about 0.3 whorls and completely separated from posterior lobe by stomach which is oriented obliquely with regard to columellar axis. Foot thick, strongly contracted during fixation, transversely folded, metapodium broadly triangular-oval, propodium small in comparison with metapodium, typically crescentshaped, subdivided longitudinally. Operculum transparent, very thin, elongate, constricted abapically, slightly thickened along low inner edge. Head well distinguished from the rest of the body, with two large vertical flaps, bearing large eyes.

Mantle cavity.—Mantle strongly contracted, edge straight and thickened. Mantle thin, osphradium and ctenidium showing through it. Siphon very thin-walled, slightly extending beyond mantle edge, with smooth edges. General arrangement and proportions of organs in the mantle complex similar to that of *Belloliva alaos*.

Alimentary system.-Anterior foregut very similar to that of Belloliva alaos. Salivary glands apparently ramifiedtubular. Accessory salivary glands absent. Radula consisting of about 75 rows of teeth, membrane width about 90 µm (0.92% SL, 1.45% AL). Rachidian with 3 main cusps, central cusp about twice as narrow and 1.5 times shorter than lateral cusps; an additional small but distinct cusp on each side of the main lateral cusps. Dorsal grooves on the main lateral cusps shallow and broad, best seen in lateral view (Figs. 24C, G). Anterior profile of rachidian nearly straight. Posterior edge of basal plate slightly convex. Sides of basal plate gradually embedded in the membrane without distinct border. Lateral teeth subtriangular with curved hook-like tips (Figs. 24D, H). Stomach large, spanning more than 0.5 whorl, with very long posterior mixing area. Stomach anatomy not examined in detail due to poor fixation. Rectal gland not found during dissection, probably obscured by thick mucous layer produced by hypobranchial gland.

Reproductive system.—Specimen a mature male, penis long, smooth, narrowing sharply towards its tip, similar to *Belloliva alaos*.

The external morphology of the two specimens from New Caledonia is very similar. Stomach similar in shape but much shorter. Digestive gland small, anterior spanning about 1/6 whorl, posterior about $\frac{1}{4}$ whorl. Upper 3 whorls occupied by testis. Seminal vesicle situated at lower corner of junction of digestive gland and testis, making several loops. Penis as long as mantle cavity, smooth, oval in section, ending in a small, nearly transparent, seminal papilla. Radula of both specimens identical and very similar to that of the Coral Sea specimen (Fig. 24E-H), differing only in the relatively broader, more triangular central cusp of the rachidian, as well as slightly wider radular membrane (membrane width 100 versus 95 μ m, i.e., 1.06% versus 1.53% of SL and 1.61% versus 2.20% of AL).

Calyptoliva Kantor and Bouchet gen. nov.

Diagnosis

Shell small, 7-15 mm, narrowly elongate-oval, with attenuated spire. Suture narrowly channeled, overlaid by thin primary callus. Protoconch paucispiral, consisting of about one whorl, smooth, evenly rounded, large, diameter 1300-1650 μ m, protoconch-teleoconch transition not clear. Aperture narrow, elongate. Parietal plate narrow, anterior plating smooth.

Foot with well developed parapodia and crescentshaped propodium. Operculum present. Mantle without filament, mantle lobe well developed. Head consisting of two separate vertical flaps, separated by furrow; eyes present or absent. Rhynchostome opening situated below the right flap. Proboscis short. Salivary glands paired, accessory salivary gland absent, valve of Leiblein large, gland of Leiblein narrow tubular, stomach with long posterior mixing area. Rachidian radular teeth with 3 main cusps, central cusp narrower and shorter, additional smaller cusp abutting each side of main lateral cusps. Lateral teeth with subtriangular bases and long curved hook-like cusps.

Type species

Calyptoliva bolis Kantor and Bouchet sp. nov.

Remarks

Calyptoliva gen. nov. bears a strong overall resemblance to *Belloliva*, both in protoconch and teleoconch shape, with similar soft body gross morphology and similar radula. *Calyptoliva* differs from *Belloliva* in the absence of open filament channel of the shell, and, correspondingly, of the



Figure 26. Distribution of different forms of Belloliva exquisita (Angas, 1871) in the Coral Sea and New Caledonia.

mantle filament; it also has a mantle lobe that is not present in *Belloliva*. The gland of Leiblein is massive in *Belloliva*, tubular in *Calyptoliva*. However, a specimen with corroded suture area (Fig. 27G) shows that a filament channel remains present below the callus.

The mophology of the suture requires special comments. In all but one specimen studied, the suture is concealed by a very thin callus, extending slightly adapically onto the preceding whorl, and there is no filament channel.

Etymology

From the Greek *kalypto*, meaning to cover, to conceal, referring to the concealed filament channel of the shell.

Calyptoliva bolis Kantor and Bouchet sp. nov. (Figs. 27A-C, 28, 29)

Type material

Holotype (Moll 9480) in MNHN.

Material examined

Coral Sea, Lansdowne-Fairway Bank, CORAIL 2, st. DE14, 21°01'S, 160°57'E, 650-660 m (1 dd). MUSORSTOM 5, st. 390, 21°01'S, 160°50'E, 745-825 m (1 lv).

Type locality

Coral Sea, Lansdowne-Fairway Bank, 21°01'S, 160°57'E, 650-660 m (CORAIL 2, st. DE14).

Description (holotype)

Shell solid, glossy, elongate-oval (BWL/SL = 0.71, AL/SL = 0.54, D/SL = 0.38), with narrow aperture and high spire, consisting of just over one protoconch and 3.75 teleoconch whorls. Protoconch large, low, evenly rounded, diameter 1650 µm, exposed height 780 µm, smooth, protoconchteleoconch transition indistinctly marked by the appearance of the callus overlapping the suture on teleoconch whorls. Profile of whorls moderately convex, evenly rounded. Suture shallowly impressed and overlain by very narrow and thin smooth callus, extending slightly adapically. Filament channel (seen by transparency through callus) narrow, closed by overlaid callus but not filled. Aperture narrow, gradually tapering adapically. Outer lip evenly and slightly convex. Parietal plate narrow, microshagreened, broadening and thickening in its abapical part prior to anterior band. Anterior plating without any plicae, similarly microshagreened except for most abapical part. Color very light yellow, anterior band white.

Dimensions (holotype largest specimen): SL 12.9 mm, SW 4.9 mm, BWL 9.2 mm, AL 7.0 mm.

Anatomy

General morphology.—Body only partially retrieved from shell, in alcohol uniformly off-white, lacking pigmentation. Mantle cavity spanning about 0.3 whorls, nephridium 0.25 whorls with transparent walls, with 8 low excretory lamellae. Anterior lobe of digestive gland small, spanning about ¹/₄ whorl and completely separated from posterior lobe by stomach, which is oriented obliquely with regard to columellar axis. Foot thick, strongly contracted, transversely folded, metapodium broadly oval, propodium small in comparison with metapodium, typically crescent-shaped, subdivided longitudinally. Operculum transparent, very thin, elongate, constricted in upper part, without pronounced growth lines. Head poorly distinguished from the rest of the body, with two small vertical flaps (Fig. 28C). No eyes.

Mantle cavity.—Mantle edge even, forming a long, rather muscular and thicker extension on the right side, terminating with a medium-sized posterior mantle lobe (Fig. 28B, E, ml). Mantle thin, osphradium and ctenidium showing through. Siphon short, thin-walled, slightly extending beyond mantle edge (Fig. 28E), with smooth edges. Osphradium bipectinate, broad, exceeding the width of the ctenidium and about 0.8 of its length. Osphradium nearly bilaterally symmetrical, with very narrow axis. Ctenidium occupying about 0.8 of mantle length, consisting of tall triangular lamellae, similar in shape and size along most of its length, except near mantle edge where ctenidium sharply narrows and lamellae become much lower. Hypobranchial gland moderately glandular, although not forming distinct folds. Mantle filament and posterior mantle tentacle absent.

Female pallial gonoduct large, swollen, not studied in detail due to poor fixation. Female genital opening situated close to anus.

Alimentary system.-Rhynchostome asymmetrical, situated below the right cephalic flap (Fig. 28C, rns). Organs of the anterior hemocoel very contracted, compact and situated nearly at right angle with regard to pedal axis. Proboscis short in contracted state (Fig. 28D, pr), about 1.2 mm in length (0.16 AL), thick (L/W approximately 2), occupying nearly the entire rhynchocoel length, rhynchodeum thinwalled, semi-transparent. Pair of thin retractor muscles attached to median part of the rhynchodeum (wall of proboscis sheath) in retracted condition. Large odontophoral retractor extends from proboscis posteriorly, then follows anteriorly along ventral side of rhynchodeum and, bypassing the nerve ring, attached to the ventral side of cephalic hemocoel. Esophagus, posterior to proboscis, rather broad and not forming a loop. Odontophore rather broad, occupying nearly entire volume of proboscis, about the same length as proboscis and not protruding from the rear of it. Subradular cartilages large, fused antero-ventrally by rather thin interconnection. Radular sac slightly longer than the odontophore. Radula (Fig. 29) consisting of about 45 rows of teeth, width of the membrane about 155 µm (1.23% SL, 2.02% AL). Rachidian with 3 main cusps, central cusp about three times as narrow and 1.5 times shorter than lateral cusps, and an additional very small, but distinct, cusp abutting outer side of main lateral cusps. Dorsal grooves on main lateral cusps shallow and broad, best seen in lateral view (Fig. 29C). Anterior profile of rachidian nearly straight, very slightly concave in the middle. Posterior edge of basal plate very slightly convex. Sides of basal plate gradually embedded in the membrane without distinct border. Lateral teeth subtriangular with curved hook-like tips (Fig. 29D). Valve of Leiblein very large, pyriform, well distinguished from



Figure 27. *Calyptoliva bolis* sp. nov. (A-C). A-B, Holotype, SL 12.9 mm. C, MUSORSTOM 5, st. 390, SL 12.6 mm. *Calyptoliva tatyanae* sp. nov. (D-G). D-E, Holotype, SL 13.1 mm. F, Paratype, SL 12.8 mm. G, Upper whorls of paratype, SL 13.0 mm, illustrating the open filament channel, covered by the callus; the areas with intact callus are indicated by white arrows. *Calyptoliva amblys* sp. nov. (H-J). H-I, Holotype, SL 9.3 mm. J, Paratype, SL 9.2 mm.



Figure 28. Morphology of *Calyptoliva bolis* sp. nov. (for shell see Fig. 26D). A, B, Dorsal and ventral views of the body removed from the shell, respectively. C, Head-foot, anterior view, mantle and visceral mass removed. D, Right view of the anterior foregut. E, Mantle complex. Abbreviations: aldg, anterior lobe of digestive gland; cm, columellar muscle; cme, cut mantle edge; ct, ctenidium; fgo, female genital opening; gL, gland of Leiblein; hg, hypobranchial gland; ml, mantle lobe; ne, nephridium; nr, circumesophageal nerve ring; odr, odontophoral retractor; op, operculum; os, osphradium; par, parapodium; pg, pallial gonoduct; poe, posterior esophagus; pr, proboscis; prp, propodium; prr, proboscis retractor; re, rectum; rnh, rhynchodeum (= proboscis sheath); rns, rhynchostome; rsg, right salivary gland; s, siphon; sd, salivary duct; st, stomach; tn, cephalic tentacles; vL, valve of Leiblein.



Figure 29. Scanning electron micrographs of the radula of *Calyptoliva bolis* sp. nov. A, Dorsal view of the central portion of the radular ribbon. B, Enlarged dorsal view of the rachidian teeth. C, Left lateral view of the rachidian teeth. D, Left lateral view of the lateral teeth. Scale bars = $10 \mu m$.

esophagus (Fig. 28D, vL), which becomes very narrow immediately posterior to the valve and passes through the nerve ring.

Circumesophageal nerve ring comparatively large. Gland of Leiblein small, colorless, narrow, tubular. Opening of the duct into esophagus not traced during dissection. Salivary glands medium-sized, apparently (but not certainly due to small size) broad-tubular, left one slightly smaller than right, situated on either side of esophagus posterior to the proboscis and not fusing. Salivary ducts rather thick, entering the esophageal walls shortly after leaving the glands and passing towards their opening along esophagus dorsal side. Accessory salivary glands not found. Stomach large, spanning about 0.3 whorls, with long and narrow posterior mixing area (Fig. 28B, st). Stomach anatomy not studied in detail due to poor fixation.

Remarks

The second specimen is very similar to the holotype, except that its apertural lip is not thickened and its color is pure white.

Etymology

From the Greek *bolis*, a missile, with reference to the general shell profile; used as a noun in apposition.

Calyptoliva tatyanae Kantor and Bouchet sp. nov. (Fig. 27D-G)

Type material

Holotype (Moll 9481) and 2 paratypes (Moll 9482) in MNHN.

Material examined

Coral Sea, Fairway Bank. EBISCO, st. CP2647, 21°32'S, 162°27'E, 737 m (3 dd).

Type locality

Coral Sea, southeastern part of Fairway Bank, 21°32'S, 162°27'E, 737 m (EBISCO, st. CP2647).

Description (holotype)

Shell solid, glossy, elongate, nearly biconic (BWL/SL = 0.61, AL/SL = 0.50, D/SL = 0.35), with narrow aperture and

high spire, consisting of about 0.8 protoconch and 4.75 teleoconch whorls. Protoconch very large, tall, globular evenly rounded, diameter 2340 µm, exposed height 1640 µm, smooth, protoconch-teleoconch transition indistinctly marked by the appearance of the callus overlapping the suture on teleoconch whorls. Profile of whorls weakly convex, evenly rounded. Suture shallowly impressed and overlain by very narrow and thin smooth callus, extending slightly adapically. Filament channel (seen by transparency through callus) narrow, closed by overlaid callus but not filled. Aperture narrow, tapering adapically. Outer lip slightly convex adapically and nearly straight along most of its length. Parietal plate narrow, clearly microshagreened, broadening and thickening in its abapical part prior to anterior band. Anterior plating without any plicae, similarly microshagreened. Color uniformly off-white, sutures slightly darker than the rest of the shell surface.

Dimensions (holotype, largest specimen): SL 13.1 mm, SW 4.6 mm, BWL 8.1 mm, AL 6.6 mm.

Remarks

Calyptoliva tatyanae sp. nov. differs from Calyptoliva bolis sp. nov. by its narrower shell with taller spire, less convex whorls, narrower aperture, and much larger protoconch (diameter 2340 μ m versus 1650 μ m in *C. bolis*). All three specimens are very similar in shape, with some variance in the convexity of the whorls.

Etymology

The species is named after the biologist and wife of the senior author, Tatiana Steyker, from the P.P. Shirshov Institute of Oceanology of the Russian Academy of Sciences.

> Calyptoliva amblys Kantor and Bouchet sp. nov. (Fig. 27H-J)

Type material

Holotype in AMS, 2 paratypes in MNHN.

Material examined

Coral Sea, CORAIL2, Mellish Reef, st. DW172, 18°26'S, 155°12'E, 1100 m (4 dd).

Type locality

Coral Sea, Mellish Reef, 18°26'S, 155°12'E, 1100 m (CORAIL 2, st. DW172).

Description (holotype)

Shell solid, glossy, elongate-oval, white (BWL/SL = 0.78, AL/SL = 0.54, D/SL = 0.46), with medium-wide aperture and low spire. Shell consists of 0.75 whorl of protoconch and 2.75 teleoconch whorls. Protoconch large, low, evenly

rounded, diameter 1330 μ m, exposed height 590 μ m, smooth, protoconch-teleoconch transition is indistinctly marked by the appearance of the callus overlapping the suture on teleoconch whorls. Profile of whorls moderately convex, evenly rounded.

Suture is shallowly impressed and overlain by very narrow, thin smooth callus, extending slightly adsuturally. Filament channel (seen by transparency through callus) narrow, closed by overlaid callus but not filled. Aperture medium wide, obtuse adapically. Outer lip thickened, convex adapically, nearly straight along most of the length and rounded abapically. Parietal plate narrow, slightly broadens in its abapical part prior to anterior band, microshagreened. Anterior plating smooth, similarly microshagreened.

Dimensions (holotype largest specimen): SL 9.2 mm, SW 4.2 mm, BWL 7.2 mm, AL 5.0 mm.

Animal unknown.

Remarks

Calyptoliva amblys differs from Calyptoliva bolis sp. nov. by its smaller adult size with more convex whorls, wider aperture with straight lip in its middle part, and smaller protoconch. All four known specimens are very similar in shape, with some variance in the convexity of the whorls.

Etymology

From the Greek *amblys*, obtuse, with reference to the shell shape.

DISCUSSION

Revised diagnosis of Belloliva

Iredale (1924) described Gemmoliva as a subgenus of Belloliva, with Olivella pardalis A. Adams and Angas, 1864 as type species, based on minor differences in radulae (Peile 1922) namely the additional marginal cusps on the rachidian tooth were said to be "very small and apparently sometimes missing." We found this character to be of not more than specific value in the species of Belloliva we studied and, the shell and anatomical characters being otherwise equal, we agree with Wilson (1994) in synonymizing Gemmoliva with Belloliva. Thiele (1929 in 1929-1931) also described Olivellopsis as a subgenus of Belloliva, with Olivella simplex Pease, 1868 as type species based on subtle shell differences (essentially suture more appressed and columellar callus without lower fold). However, its radula and gross morphology do not differ significantly from other species of Belloliva, including its type species, and thus do not support segregation of O. simplex in a separate genus-group taxon.

As a result of the new data presented in this paper and

comparison with other taxa, the following is a revised diagnosis of *Belloliva*.

Shell less than 15 mm long, olivelliform, elongate-oval, with attenuated spire, and open filament channel. Protoconch paucispiral, consisting of about one whorl or less, smooth, evenly rounded, large in comparison with the teleoconch, diameter 1000-1800 µm, protoconch-teleoconch transition marked by the onset of filament channel. Aperture elongate or lanceolate-oval, gradually narrowing abapically. Parietal plate narrow, slightly thickened, anterior plating smooth or plicate. Foot with well developed parapodia and crescent-shaped propodium. Operculum usually present, narrow. Mantle with mantle filament, without mantle lobe. Head with two separate vertical flaps, separated by furrow. Rhynchostome opening below the right flap. Proboscis short or of medium length when retracted. Salivary glands paired, ramified tubular, accessory salivary glands absent, valve of Leiblein medium-sized to large, gland of Leiblein bulky, stomach with long posterior mixing area. Rachidian radular teeth with 3 main cusps, central cusp narrower and shorter than the lateral ones, and additional small, but usually distinct, cusps abutting each side of the main lateral cusps. Lateral teeth with subrectangular or subtriangular bases and long curved hook-like cusps.

Composition of the genera

Four Australian species have traditionally been included in *Belloliva* (Kaicher 1987, Wilson 1994, see below). In addition, a couple of other taxa have been, at one time or another, allocated to the genus and need to be discussed separately.

(1) Based on his examination of the radula of Olivella tabulata Dall, 1889 from off Cuba, Olsson (1956) tentatively included it in Belloliva, and this placement was followed by Kaicher (1987). We concur with Olsson that Olivella tabulata bears an overall resemblance to Belloliva, especially in the large size of the protoconch. However, Olsson described the radula with a rachidian bearing 3 cusps, of which the central one is the largest, whereas in Belloliva from Australia (including the type species) and the South-West Pacific, the central cusp is the smallest. In addition, O. tabulata lacks an operculum (Dall 1889), a character admittedly shared with Belloliva apoma but with no other species of Belloliva. The diverging distributions and the radular differences suggest that O. tabulata is probably not congeneric with the Australia-South-West Pacific clade, but probably belongs to some other, possibly still unnamed, genus of the subfamily Olivinae.

(2) Hunon (2000) attributed *Oliva lacanientai* Greifeneder and Blöcher, 1985 to *Belloliva* based on the presence of two fasciolar bands and protoconch shape; Hunon also stated he had found remains of an operculum. We have examined material of *O. lacanientai* and find Hunon's statement misleading, since shell shape and protoconch (multispiral, consisting of about 4.25 whorls) are typical for *Oliva*. Examination of the anatomy and radula (Fig. 30A) confirm a placement in *Oliva*. We did not find an operculum and we suggest that Hunon mistakenly interpreted the presence of an operculum from the presumably rotten and dried (as this was dealer's material from tangle nets) soft parts of his specimen.

The present study thus brings to 10 the number of species included in *Belloliva*, and three in *Calyptoliva*, and highlights the Coral Sea as their center of diversity: In fact, our material still contains one additional undescribed species from Lansdowne-Fairway Banks (represented by a single empty juvenile shell), suggesting that additional findings of new species of *Belloliva* in the Coral Sea are still possible. By contrast, it should be emphasized that cruises conducted since 1992 in other South Pacific archipelagoes (Solomons, Vanuatu, Fiji, Wallis and Futuna, Tonga, Marquesas) did not yield any deep-water material of *Belloliva* or *Calyptoliva*.

Thus the following species are currently recognized: Belloliva alaos sp. nov., northern New Caledonia, alive in 668 m, shells in 397-660 m (Fig. 31), Belloliva apoma sp. nov., northern New Caledonia, alive in 502-516 m, shells in 470-550 m (Fig. 31), Belloliva brazieri (Angas, 1877), type species of the genus, coastal waters of south-eastern Australia (New South Wales, Victoria, and Tasmania) (Fig. 32A-B), Belloliva dorcas sp. nov., Coral Sea, Chesterfield Plateau and Lansdowne-Fairway Bank, shells in 230-355 m (Fig. 31), Belloliva ellenae sp. nov., Coral Sea, Chesterfield plateau, alive in 386-486 m (Fig. 31), Belloliva exquisita (Angas, 1871), coastal waters of eastern Australia, Coral Sea and New Caledonia, alive in 26-345 m (Fig. 31), Belloliva leucozona (A. Adams and Angas, 1864), coastal waters of the eastern seaboard of Australia from Caloundra, Queensland to Lorne, Victoria (Fig. 32C-D), Belloliva obeon sp. nov., Coral Sea, Chesterfield Plateau and Lansdowne-Fairway Bank, alive in 500-672 m, shells from 252 m (Fig. 31), Belloliva simplex (Pease, 1868), coastal waters of Tuamotu Island (French Polynesia), Samoa, Tonga, Loyalty Islands, New Caledonia, and Vanuatu, alive in 10-45 m (Fig 31), Belloliva triticea (Duclos, 1835) (= O. pardalis A. Adams and Angas, 1864), coastal waters of southern Australia (New South Wales to Albany, Western Australia) (Fig. 32E-F), Calyptoliva amblys sp. nov., Coral Sea, Mellish Reef, shells in 1100 m, Calyptoliva bolis sp. nov., Coral Sea, Lansdowne-Fairway Bank, alive in 745-825 m, shells from 650-660 m (Fig. 31), Calyptoliva tatyanae sp. nov., Coral Sea, Fairway Bank, shells in 737 m (Fig. 31).

All species of *Belloliva* and *Calyptoliva* have a paucispiral protoconch indicating non-planktotrophic development, and therefore inferred limited larval dispersal, which probably account for restricted ranges and multiple speciation



Figure 30. Scanning electron micrographs of the radulae of different members of Olividae. A, *Oliva lacanientai* Greifeneder and Blöcher, 1985 (Coral Sea, MUSORSTOM 5, sta. 380). B, *Ancila cinnamomea* Lamarck, 1801 (Southern India, Rameshwaran). C, *Ancillina* sp. (northern New Caledonia, BATHUS 4, st. DW914). D, *Amalda fuscolingua* Kilburn and Bouchet, 1988 (northern New Caledonia, BATHUS 2, st. DW729). E, *Turrancila* sp. (Indonesia, KARUBAR, st. CP71). F, *Belloliva alaos* sp. nov. (northern New Caledonia, MUSORSTOM 4, st. DW160). Scale bars = 10 µm (A, C, E, F), 100 µm (B, D).

events on the isolated seamounts and banks in the middle of the Coral Sea. However, it is difficult to ascertain whether the very narrow ranges of some of the new species are real or represent sampling artefacts. For instance, *Belloliva ellenae* is known from 8 stations that straddle only 30 km on the Chesterfield Plateau (Fig. 31), and *Belloliva apoma* is known from 4 stations over a distance of 35 km. Conversely, Belloliva exquisita ranges from Australia to New Caledonia, including isolated guyots and banks in the Coral Sea. Limited sampling in the Coral Sea may explain the apparently extremely narrow ranges, such as that of *B. ellenae*, but the more than one thousand hauls taken in New Caledonia suggest that the very limited range of *B. apoma* is real. A similar pattern of narrow endemism has been de-



Figure 31. General distributions of Coral Sea and New Caledonian species of *Belloliva* and *Calyptoliva*. Holotypes illustrated when named in this paper, all at the same scale.

scribed in the family Volutomitridae (Bouchet and Kantor 2004).

Position of *Belloliva* and *Calyptoliva* in the family Olividae

Although the genus Belloliva has been referred to Olivellidae (or Olivelliinae) in the recent literature (e.g., by Wilson 1994, Tursch and Greifeneder 2001, Sterba 2003), this is not supported by its radular morphology, a point already made by Olsson (1956), who referred the genus to the Olivinae. The current consensus (Bouchet and Rocroi 2005) on the composition and classification of the family Olividae is to recognize two subfamilies, the nominal subfamily Olivinae (synonyms Agaroniinae and Olivancillariinae) and the Ancillariinae (= Ancillinae). Surprisingly few anatomical data are available, essentially only for various species of Oliva (Marcus and Marcus 1959, Kantor 1991, Kantor and Tursch 2001) and two of Olivancillaria (Marcus and Marcus 1959); for Ancillariinae, the information is restricted to just two species of Amalda (Marcus and Marcus 1968, Kantor 1991).

One of the characteristic traits of the family Olividae is the presence of mantle appendages. The most complex assemblage is present in the Olivinae, which have anterior mantle tentacle, a mantle filament, and a mantle lobe. The mantle filament is a muscular, contractile, and mobile organ which originates on the right side of the mantle edge, extending through the aperture adapically and positioning in the filament channel. It is present in all oliviform gastropods (including the Olivellidae) that have channelled sutures, and its function remains unknown. The anterior mantle tentacle is situated near the siphon and, when the snail is crawling, it passes through the siphonal canal and rests on the dorsal side of the shell. Its function is not known either. The small posterior mantle lobe is situated at the base of the mantle filament (when present). In Belloliva, only a rather short (in preserved animals) mantle filament is present; neither an anterior mantle tentacle nor a mantle lobe were found in dissections. By contrast, in Calyptoliva, the mantle filament is absent but the mantle lobe is well-developed. Judging from the differences in shell morphology, it may be inferred that the mantle lobe is responsible for secreting the primary spire callus (following the terminology of Kilburn 1977) that overlies the suture, rather than producing the columellar callus (as suggested by Marcus and Marcus 1959), which is equally developed in the two genera.

With the Olivinae Belloliva shares a canaliculate suture



Figure 32. A-B, *Belloliva brazieri* (Angas, 1877), AMS C388726, dissected specimen (SL 12.9 mm). C-D, *Belloliva leucozona* (A. Adams and Angas, 1864), probably illustrated syntype, BMNH 1870.10.26.93 (SL 13.8 mm). E-F, *Belloliva triticea* (Duclos, 1835), illustrated syntype, MNHN 1273 (SL 10.6 mm), photo by D. Brabant.

and, correspondingly, the presence of a mantle filament, a foot that is rounded posteriorly, a stomach that has a long posterior mixing area, and the radula type. The olivine radula is rather uniform (Troschel 1866, Marcus and Marcus 1959, Kantor and Tursch 2001), with rachidians with 3 nonserrated cusps and laterals that are leaf-shaped, concave posteriorly, and convex anteriorly with long curved hook-like tips (Fig. 30A). However, Belloliva (and Calyptoliva) differs from all Olivinae in having an operculum; it also differs from Oliva in the absence of the anterior mantle tentacle (which is also absent in Olivancillaria) and mantle lobe. The absence of tentacles on the vertical flaps on the head of Belloliva and Calvptoliva is a character shared with Olivancillaria, but not with Oliva. Calyptoliva differs from Olivinae in its open filament channel overlain by thin callus; superficial examination of two ancillariines (Entomoliva mirabilis Bouchet and Kilburn, 1991 and Amalda aureomarginata Kilburn and Bouchet, 1988) revealed complex multi-layered structure of the shell but no sign of the filament channel. At this moment we do not know whether the peculiar suture of *Calyptoliva* should be regarded as ancestral (representing an intermediate stage between Olivinae and Ancillariinae), or an autapomorphy of *Calyptoliva*.

With the Ancillariinae *Belloliva* and *Calyptoliva* share the presence of an operculum and the head morphology. *Calyptoliva* also shares with the Ancillariinae the suture covered by a thin callus. *Belloliva* differs from Ancillariinae in having a channelled suture and a mantle filament. Both *Belloliva* and *Calyptoliva* differ from Ancillariinae in a stomach with a long posterior mixing area (the only genus of Ancillariinae studied in this respect, *Amalda*, has a narrow tubular U-shaped stomach without posterior mixing area), and a rounded versus posteriorly deeply notched foot. Ancillariine radulae (Fig. 30B-E) are much more variable than those of the Olivinae and essentially follow a genus-specific pattern; rachidians are multicuspid in *Turrancilla* Martens, 1903 (Fig. 30E) and *Ancillina* Bellardi, 1882 (= *Gracilancilla* Thiele, 1925) (Fig. 30C), or have three major cusps and numerous

	Olivinae				Ancillariinae
Character	Oliva*	Olivancillaria**	Belloliva	Calyptoliva	Amalda***
Suture of the shell	Canaliculate	Canaliculate	Canaliculate	Non-canaliculate, overlaid by callus	Non-canaliculate, overlaid by callus
Operculum	Absent	Absent	Present	Present	Present
Foot	Rounded posteriorly	Rounded posteriorly	Rounded posteriorly	Rounded posteriorly	Notched posteriorly
Head morphology	Vertical flaps with tentacles	Vertical flaps without tentacles	Vertical flaps without tentacles	Vertical flaps without tentacles	Dorso-ventrally compressed flaps without tentacles
Anterior mantle tentacle	Present	Absent	Absent	Absent	Absent
Mantle filament	Present	Present	Present	Absent	Absent
Mantle lobe	Present	Present	Absent	Present	Present
Stomach	With long posterior mixing area	?	With long posterior mixing area	With long posterior mixing area	U-shaped, without posterior mixing area
Rachidian of the radula	Tricuspid, with non-serrated cusps	3 main non-serrated cusps and additional cusps abutting each side of the main lateral cusps	3 main non-serrated cusps and additional cusps abutting each side of the main lateral cusps	3 main non-serrated cusps and additional cusps abutting each side of the main lateral cusps	3 main serrated cusps
Lateral teeth of the radula	Leaf-shaped, concave posteriorly, and convex anteriorly with long curved hook-like tips	Leaf-shaped, concave posteriorly, and convex anteriorly with long curved hook-like tips	Leaf-shaped, concave posteriorly, and convex anteriorly with long curved hook-like tips	Leaf-shaped, concave posteriorly, and convex anteriorly with long curved hook-like tips	Nearly flat, without complex, bent tips

Table 1. Summary of major characters of Olivinae, Ancillariinae and Belloliva and Calyptoliva.

* Data based on Marcus and Marcus (1959), Kantor (1991), and Kantor and Tursch (2001).

** Data based on Marcus and Marcus (1959).

*** Data based on Marcus and Marcus (1968), and Kantor (1991).

smaller denticles or serrations on the rachidian in *Amalda* (Fig. 30B, D). In addition, the lateral teeth of the Ancillariinae are nearly flat, without complex, bent tips. The radulae of *Belloliva* and *Calyptoliva* are therefore much closer to that of Olivinae than to that of Ancillariinae.

In conclusion, *Belloliva* and *Calyptoliva* share morphological and conchological characters with both Olivinae and Ancillariinae (Table 1). The general similarity between *Belloliva* and *Calyptoliva* in most shell characters, external anatomy, anatomy of the digestive system, and radula is remarkable, and is not likely to be the result of convergence. Thus, their differing in the presence/absence of an open canaliculate suture puts into question the validity of this character, which was hitherto considered to be a fundamental difference between, respectively, the Olivinae and Ancillariinae. Clearly, the validity of the two subfamilies requires examination of the anatomy of additional genera.

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