The Systematic Position of the Genus *Nucella* (Prosobranchia: Muricidae: Ocenebrinae)

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ABSTRACT

The muricid genus *Nucella* Röding, 1798 has commonly been placed in Thaidinae Jousseaume, 1888 (Prosobranchia: Muricidae). The Thaidinae (*sensu* Kool, 1989) is monophyletic with and thus synonymous with Rapaninae Gray, 1853 (Kool, 1993, in press). Comparative anatomical investigations of the type species of *Nucella* Röding, 1798 (*Buccinum filosum* Gmelin, 1791 [=*Nucella lapillus* (Linnaeus, 1758)]) and of *Thais* Röding, 1798 (*Murex fucus* Gmelin, 1791 [=*Thais nodosa* (Linnaeus, 1758)]) as well as other rapanines have revealed that inclusion of *Nucella* in Rapaninae would result in polyphyletic groups (Kool, 1989; 1993, in press). Studies of the anatomy, radula, protoconch, shell ultrastructure, and operculum of the type species of *Nucella*, *Ocenebra* Gray, 1847 (*Murex erinaceus* Linnaeus, 1758 [=*Ocenebra erinacea*]) (Ocenebrinae Cossmann, 1903), and *Trophon* Montfort, 1810 (*Murex magellanicus* Gmelin, 1791 [=*Trophon geversianus* (Pallas, 1774)]) (Trophoninae Cossmann, 1903), indicate that *Nucella* has close affinities with Ocenebrinae and Trophoninae. Based on cladistic analyses, it is here proposed that *Nucella* be placed in Ocenebrinae. Results further reveal that the distinctions between Ocenebrinae and Trophoninae are less clear than previously accepted.

Key words: Nucella; Ocenebrinae; phylogeny; systematics; comparative anatomy.

INTRODUCTION

The Thaidinae of authors, also referred to as Thaididae, Purpurinae/dae Swainson, 1840, Drupinae Wenz, 1941, etc., has been shown to be a conglomerate of disparate taxa (Kool, 1989; 1993, in press). The taxonomic coherence of the Thaidinae and the boundaries of its genera were based primarily on external shell characters, which are often convergent, obscuring phylogenetic relationships.

Rigorous cladistic analyses based primarily on characters derived from anatomy, radula, operculum, and shell ultrastructure, have shown that para- and polyphyly were wide-spread in the Thaidinae/dae of authors (Kool, 1989). Subsequent phylogenetic studies have revealed that the genus *Rapana* Schumacher, 1817, and the Thaidinae (*in partem*) constitute a monophyletic group, making Thaidinae a junior subjective synonym of Rapaninae (Kool, 1993, in press). The name Rapaninae will herein be used for the clade that includes *Rapana* and *Thais*.

Several species of the genus *Nucella* have been used extensively in ecological studies (Colton, 1922; Crothers, 1983, 1985; Emlen, 1966; Etter, 1987; Kincaid, 1957; Moore, 1936, 1938; Palmer, 1983, 1985; Spight, 1972, 1976). In most of these studies *Nucella* was regarded as a subgenus or synonym of *Thais*. Anatomical studies (Kool, 1986, 1989) of the type species of *Nucella* [*Buccinum filosum* = *Nucella lapillus* (see Kool & Boss, 1992)] and *Thais* [*Murex fucus* = *Thais nodosa*] revealed major differences between these genera. Kool (1988) therefore excluded *Nucella* from the Thaidinae and tentatively placed *Nucella* in the Ocenebrinae (Kool, 1989) on the basis of radular (Sabelli & Tommasini, 1987; Bandel, 1977) and protoconch (Bandel, 1975) morphology as well as anatomical descriptions (Graham, 1941) of *Ocenebra erinacea*.

Although the anatomy of *Nucella lapillus* is well known (Fretter & Graham, 1962; Kool, 1986, 1989; Oehlmann *et al.*, 1988), relatively little is known about the soft parts of *Ocenebra erinacea*. Aspects of the anatomy of *Trophon geversianus* were described by Harasewych (1984), who suggested that similarities (e.g. radular morphology) between members of *Trophon* and *Nucella* may be due either to convergence resulting from similar environmental conditions or to phylogenetic affinity.

The object of this study is to discern the phylogenetic affinities among *Nucella*, *Trophon* and *Ocenebra*.

MATERIALS AND METHODS

The following specimens were used for anatomical studies:

Nucella lapillus; Kittery, Maine, U.S.A. (USNM 857053) (7 ♀, 5 ♂).

Trophon geversianus; Daniel Este, Isla Grande, Tierra del Fuego, Chile (LACM 86-270.2); Puerto Basil Hall,

Table 1. List of characters and character states for *Muricanthus, Thais, Trophon, Nucella,* and *Ocenebra.*

Character	Mur	Tha	Tro	Nuc	Oce
1. Protoconch whorls	0	0	1	1	1
2. Calcitic layer	0	1	1	1	1
3. Number of aragonitic layers	0	1	2	2	0
4. Position of opercular nucleus	0	3	1	2	1
5. Opercular shape	0	1	0	1	1
6. Pigmentation pattern on head-foot region	0	0	1	1	1
7. Duct(s) for accessory boring organ and ventral pedal gland	0	0	0	1	1
8. Bursa copulatrix	0	2	1	1	0
9. Seminal receptacles at dorsal periphery of albumen gland	0	1	0	0	0
10. Penial shape	0	2	1	0	0
11. Penial vas deferens	0	1	0	0	2
12. Prostate	0	1	0	0	0
13. Accessory salivary gland(s)	0	1	1	2	2
14. Straw-like membrane around gland of Leiblein	0	0	1	1	1
15. Posterior duct of gland of Leiblein	0	0	1	1	1
16. Central cusp of rachidian	0	0	0	1	1
17. Margin of rachidian basal plate	0	0	1	1	1

Isla de los Estados, Tierra del Fuego, Argentina (LACM 71-289); Punta Catalina, Isla Grande, Tierra del Fuego, Chile (LACM 80-87.2) (4 ♀, 3 ♂).

Ocenebra erinacea; Roscoff, France (MCZ 298425) (2 ♀, 1 ♂).

Morphological data were compiled from soft tissues, radulae, shell ultrastructures, protoconchs, and opercula. Living specimens of *Nucella* and preserved specimens of *Nucella*, *Trophon* and *Ocenebra* were dissected.

Radulae (2-4 per species) were cleaned using a potassium hydroxide solution, rinsed in distilled water, air-dried, sputter-coated with carbon and gold, and examined with a Hitachi S-570 scanning electron microscope. Photomicrographs were taken of the unused, matured central portion of each radular ribbon.

Shell fragments from at least two individuals of each species were obtained by crushing the shell. Portions from the central region of the body whorl about one-half to three-quarters of a whorl away from the edge of the apertural lip were mounted, sputter-coated with carbon and gold, and their fracture surfaces observed with a Hitachi S-570 scanning electron microscope. An apparently amorphous outer layer was interpreted as consisting of calcite, while layers with organization in crystal lamellar structure were considered aragonitic (data from x-ray diffraction methods confirm these identifications; Kool and Harasewych, in preparation).

Cladistic Analysis: Seventeen characters, divided into 41 character states (Table 1), were used in a cladistic analysis performed with Hennig86 (Copyright J.S. Farris, 1988). The six multistate characters were entered as unordered. Most characters were derived from soft tissues (mainly from the male and female reproductive and alimentary systems), the remainder from radulae, opercula, protoconchs, and shell ultrastructure. Two additional species, *Thais nodosa* and *Muricanthus fulvescens* (Sowerby, 1841), are used in the cladistic analysis, based on data in Kool (1989; 1993, in press). *Muricanthus fulvescens*, a muricine and member of a sister group of Ocenebrinae, Trophoninae and Rapaninae, is used as outgroup for the cladistic analysis.

Table 1 lists characters and character states, and reflects the sequence in which organs and other morphological features are described for each of the three species.

RESULTS

DESCRIPTIONS OF TAXA

Nucella lapillus:

Shell: Protoconch (Figs. 26, 29) conical, low, of about 1¼ smooth whorls, with impressed suture; transition to teleoconch smooth, difficult to discern. Teleoconch highly polymorphic; usually elongate, oval, of 6-7 whorls (Figs. 1-6, 21, 22). Adult shell to 55 mm in height, 30 mm in width. Body whorl rounded, about 80% of shell height, smooth or sculptured with pattern of about 15 spiral, occasionally lamellose, ridges. Aperture (to 65% of shell height) oval; outer lip wide, smooth, occasionally with 3-4 denticles on edge of thickened lip. Columella with moderate callus, flat to concave. Siphonal canal short, open (Fig. 3) to partly closed (Fig. 1). Siphonal fasciole poorly developed, adjacent to callus layer. Shell color variable: white, grey, yellow, brown, orange-red; often banded; aperture, columella white.

Shell Ultrastructure: Innermost layer of crossed-lamellar aragonite, with crystal planes oriented perpendicular to growing edge [15-20% of thickness; often absent (Fig. 28)]; middle layer of crossed-lamellar aragonite, with crystal planes oriented parallel to growing edge [15-25% of thickness]; outermost layer of calcite [55-85% of thickness] (Fig. 27).

Operculum: D-shaped, with lateral nucleus just below center right (Figs. 7, 8). Outer surface (Fig. 7) with arch-shaped growth lines recurved at both ends; inner surface (Fig. 8) with 3-5 arch-shaped growth lines, with broad (35-40% of opercular width), callused, glazed outer rim.

Head and Foot: Uniformly light yellow to white. Cephalic tentacles elongate, thin. Incurrent siphon short. Mantle edge smooth. Accessory boring organ (Fig. 56, abo) large, well developed, (in females) anterior to, separate from equally large ventral pedal gland (Fig. 56, pg).

Mantle Cavity: Osphradium slightly more than ⅓ ctenidial length, less than ½ ctenidial width. Right pectin usually wider than left. Each lamella (8-10/mm) attached to mantle roof along ½ its base. Anteriormost portion of ctenidium straight, extending slightly anterior of osphradium. Ctenidial lamellae (9-11/mm) wider than high or equally wide as high, with strongly convex or straight lateral edges, translucent. Thick supporting rod extending beyond lateral edge of each lamella, forming small papilla.

Female Reproductive System: Vaginal opening round with slightly swollen edges, located below and posterior to anus. Bursa copulatrix (Fig. 47, 48, bc) small diverticulum, connected to vagina, ventral channel (vc) by wide ventral passage. Ventral channel formed by two small interlocking flanges located under ventral lobe of capsule gland, one arising from left lobe, the other from ventral epithelium. Single-chambered ingesting gland located between capsule gland and albumen gland. Albumen gland (Fig. 49) arch-shaped, elongate, opening anteriorly into ovi-sperm duct (osd), posteriorly into oviduct (od). Ovary yellow to light golden. Many specimens with pseudo-penis of variable size (see also Bryan *et al.*, 1986).

Male Reproductive System: Penis (Fig. 60) simple, elongate, dorso-ventrally flattened, often slightly curved, with abruptly tapering, papilla-like end. Penial vas deferens (Fig. 62, pvd) minute, simple duct, semi-closed by transverse ridges on overlapping ventral and dorsal sides of penis. Cephalic vas deferens (Fig. 57, cvd) well developed, extending from penis (p) to prostate gland (pr). Prostate gland (Fig. 57, pr) white; prostate duct (prd) dorso-ventral slit in cross section; duct open to mantle cavity posteriorly. Posterior vas deferens (along visceral mass) well developed, white to dirty white, iridescent. Testis light brown to golden.

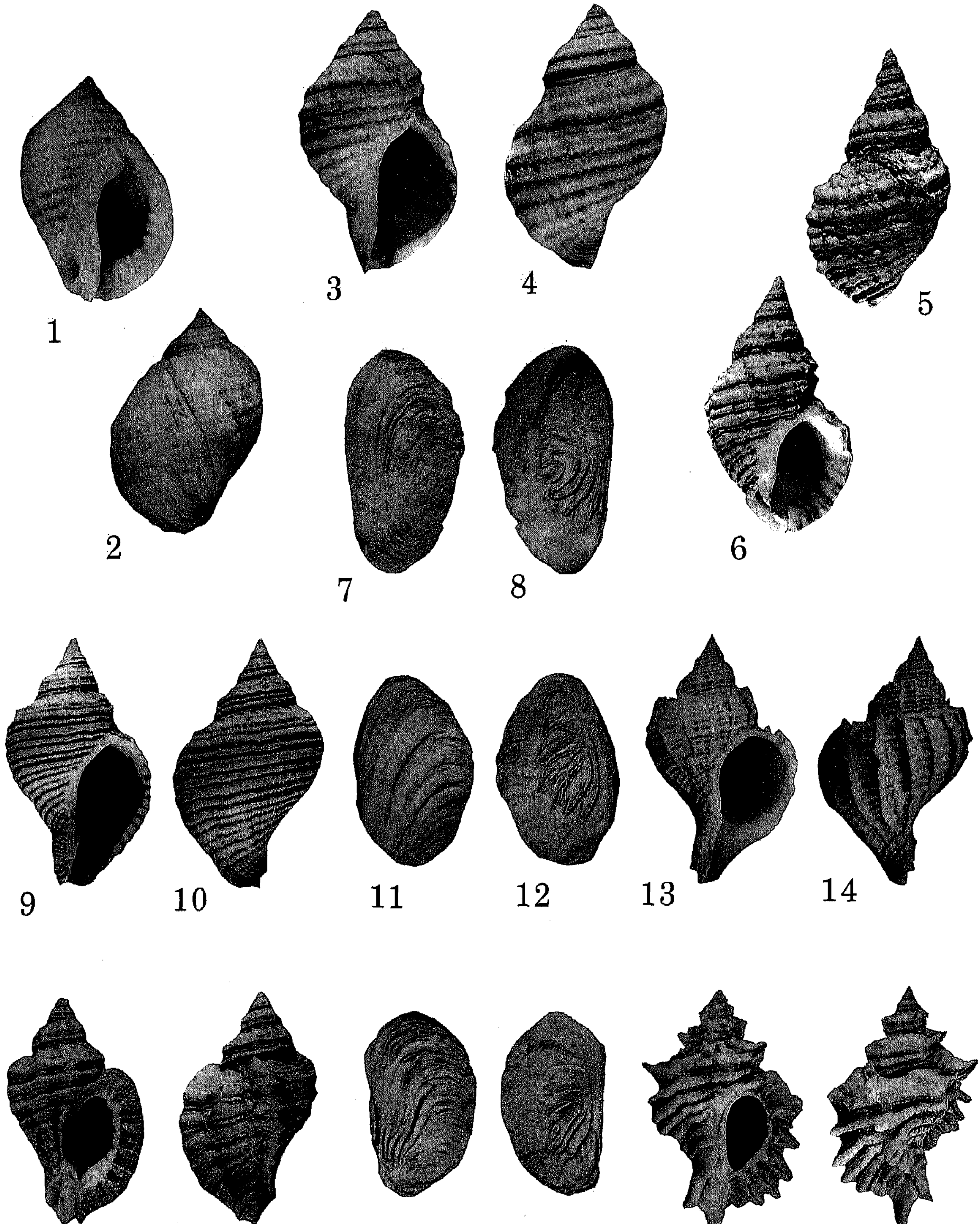
Alimentary System: Paired accessory salivary glands extremely long, usually equal to or slightly longer than one-half of shell height; left gland intertwined with salivary glands, right gland separate from salivary glands, situated in right anterior corner of buccal cavity. Salivary glands in center of dorsal buccal cavity between gland of Leiblein and short, pear-shaped valve of Leiblein. Salivary ducts attached to anterior esophagus at some distance from valve. Glandular folds in mid-esophageal region inconspicuous. Connection between mid-esophagus and gland of Leiblein short, thick. Posterior esophagus appressed to left side of gland of Leiblein in loop-shaped fashion. Gland of Leiblein yellowish; posterior blind duct very short (<½ length of gland), with small terminal ampulla. Stomach tubular, with 8-12 large, radially oriented folds on wall. Stomach typhlosole extending dorsally onto left portion of posterior mixing area. Intestinal typhlosole thick, wide. Two digestive diverticula present. Rectal gland inconspicuous. Large papilla overlying equally large anus.

Radula: Ribbon length 30-35% of shell height. Base of rachidian tooth expanded below base of neighboring rachidian tooth; central cusp of rachidian thin, flame-shaped, leaning more anteriorly (*in situ*) than lateral cusps; inner lateral denticle low on base of lateral cusp, occasionally bifurcate (within same specimen); outer edge of lateral cusp with several denticles; large marginal cusp pointing straight forward and parallel to elongate, lateral extension at base of rachidian tooth (Figs. 23-25), resulting in bifid appearance of rachidian basal plate. Lateral teeth shorter than rachidian width (Fig. 23).

Egg capsules: Elongate-oval, vase-shaped, up to 9 mm in height, 3 mm in width. Capsules yellow, light brown or purple (Lebour, 1937), each attached by short, thin stalk about 1 mm long. Apex tapered with rounded, cap-shaped top with mucous plug. Capsules interconnected at base. Number of embryos varying from two (Risbec, 1937) to one thousand (Fretter & Graham, 1962, 1985), most being nurse eggs (75-95%) (Crothers, 1985; Fretter & Graham, 1985; Lamy, 1928) (see also Pelseneer, 1911; Ankel, 1937; Thorson, 1941, 1946; Robertson, 1974).

Ecology: More is known about *Nucella* ecology than about any other muricoidean [for an extensive bibliography on the biology (primarily ecology) of *Nucella lapillus*, see Crothers, 1985]. *Nucella lapillus* and its western American congeners have been the topic of many comprehensive studies (Crothers, 1985; Emlen, 1966; Etter, 1987; Kincaid, 1957; Spight, 1972). *Nucella* feeds on barnacles and mussels (Colton, 1922; Connell, 1970; Crothers, 1973; Graham, 1955; Kool, 1987; Largen, 1967; Murdoch, 1969; Spight, 1982) in the rocky intertidal zone and is eaten by crabs and birds (Spight, 1976). Studies of Agersborg (1929), Colton (1922), and Moore (1936) show that environmental factors (wave action, food availability, etc.) influence shell morphology. Moore (1938) reported the main spawning period to be during winter and spring; but breeding occurs throughout the year (Lebour, 1937; Thorson, 1946). Juveniles hatch from the eggs after 4-7 months (Fretter & Graham, 1985).

Distribution: North Atlantic Ocean from southern Por-



Figures 1–8. *Nucella lapillus.* **1-6.** Shells (**1,2** MCZ 69192, Freshwater Bay, Isle of Wright, England, height 25 mm; **3,4** MCZ 115093, Sullivan, Maine, U.S.A., height 35 mm; **5,6** MCZ 50600, Wales, height 34 mm). **7,8.** Operculum (MCZ 302404, Braunton, North Devon, England, height 15 mm); **7.** Outer surface; **8.** Inner surface. **Figures 9-14.** *Trophon geversianus.* Shells (**9,10** MCZ

tugal to Novaya Zemblya [records from western Mediterranean, Azores, Morocco, Senegal, and Canary Islands are suspect (Cooke, 1915)]; Great Britain; Ireland; Iceland; Greenland; New Jersey, U.S.A., to northern Canada [for extensive list of geographical range and localities, see Cooke, 1915].

Trophon geversianus:

Harasewych (1984) described aspects of the anatomy of *Trophon geversianus* (Figs. 9, 10, 13, 14, 30, 31). Because my observations were congruent with the descriptions in Harasewych's paper, only the most essential and supplemental data are presented to avoid unnecessary duplication.

Shell ultrastructure: Innermost layer of crossed-lamellar aragonite, with crystal planes oriented perpendicular to growing edge [10-15% of thickness; often absent (Fig. 37)]; middle layer of crossed-lamellar aragonite, with crystal planes oriented parallel to growing edge [15-20% of thickness]; outermost layer of calcite [70-80% of thickness] (Fig. 36).

Operculum: Ovate, with lateral nucleus in lower right (Figs. 11, 12). Outer surface (Fig. 11) with growth lines recurved at upper ends, progressively upright; inner surface (Fig. 12) with 3-4 narrow horseshoe-shaped growth lines, broad (> ⅓ opercular width), lightly callused, glazed outer rim.

Head and foot: Uniformly light yellow. Cephalic tentacles elongate, thin. Incurrent siphon short. Mantle edge smooth. Accessory boring organ (Fig. 55, abo) well developed, sharing common duct with ventral pedal gland (pg) in females.

Mantle Cavity: Osphradium small (⅓-⅔ ctenidial length, ⅔ ctenidial width), usually partially overlying ctenidium. Right pectin usually wider than left. Each lamella (9-10/mm) attached to mantle roof along most of its length. Anteriormost portion of ctenidium straight, extending slightly anterior of osphradium. Ctenidial lamellae (10-12/mm) translucent, wider than high anteriorly, equally wide as high posteriorly, with straight to convex lateral edges.

Female Reproductive System: Vaginal opening (Fig. 47, vo) round, with swollen edges, located below, slightly anterior to anus. Bursa copulatrix (Figs. 47, 48, bc) small diverticulum, connected to vagina and ventral channel (vc) by wide duct. Wall of posterior vagina with folds decreasing in number posteriorly. Capsule gland with simple, inconspicuous ventral channel posteriorly connected to large, well-developed ingesting gland filled with whitish substance. Albumen gland (Fig. 49) large, arch-shaped, elongate, opening anteriorly into ovi-sperm duct (osd), posteriorly into oviduct (od).

Male Reproductive System: Penis (Fig. 59) bulbous, short, dorso-ventrally flattened, with large papilla. Penial vas deferens (Fig. 62, pvd) minute, simple duct, closed by overlapping ventral and dorsal sides of penis. Cephalic vas deferens (Fig. 57, cvd) well developed. Prostate gland (Fig. 57, pr) light yellow; prostate duct (prd) dorso-ventral slit in cross section; duct open to mantle cavity posteriorly.

Alimentary System: Paired accessory salivary glands short (<1/10 shell height); left gland intertwined with left salivary gland, right gland free, situated in right anterior corner of buccal cavity. Salivary glands in center of dorsal buccal cavity between gland of Leiblein and elongate valve of Leiblein. Salivary ducts attached to anterior esophagus immediately anterior to valve. Glandular folds in mid-esophageal region well developed. Connection between mid-esophagus and gland of Leiblein short, thick. Posterior esophagus appressed to left side of gland of Leiblein in loop-shaped fashion. Gland of Leiblein yellowish; posterior blind duct short, without terminal ampulla. Stomach tubular, with 10-15 thin, elevated folds on wall; posterior ones oriented toward center, anterior ones merging into elevated section of sorting area. Intestinal typhlosole thin. Two digestive diverticula present. Rectal gland light brown, extending along ½ of pallial gonoduct.

Radula: Ribbon length 40-45% of shell height. Base of rachidian tooth expanded below base of neighboring rachidian tooth; central cusp thin, with wide base; inner lateral denticle small protrusion from base of lateral cusps; outer edge of lateral cusp straight, with several faint denticles; large marginal cusp pointing straight forward and parallel to faint, elongate, lateral extension at base of rachidian tooth (Figs. 32-34), resulting in bifid appearance of rachidian basal plate. Lateral teeth shorter than rachidian width, with wide bases positioned close together (Fig. 32).

Egg capsules: Discoidal, laterally flattened, with wide, equally flattened base, up to 20 mm in height (including base), 12 mm in width (Harasewych, 1984, Fig. 23). Capsules yellowish in color, and containing 74-112 embryos (Melvill & Standen, 1898). Capsules deposited in rows with flattened edges adjacent to one another (Lamy, 1928; D'Asaro, 1991).

Ecology: This species lives in the rocky intertidal and subtidal zones where barnacles and mussels are plentiful.

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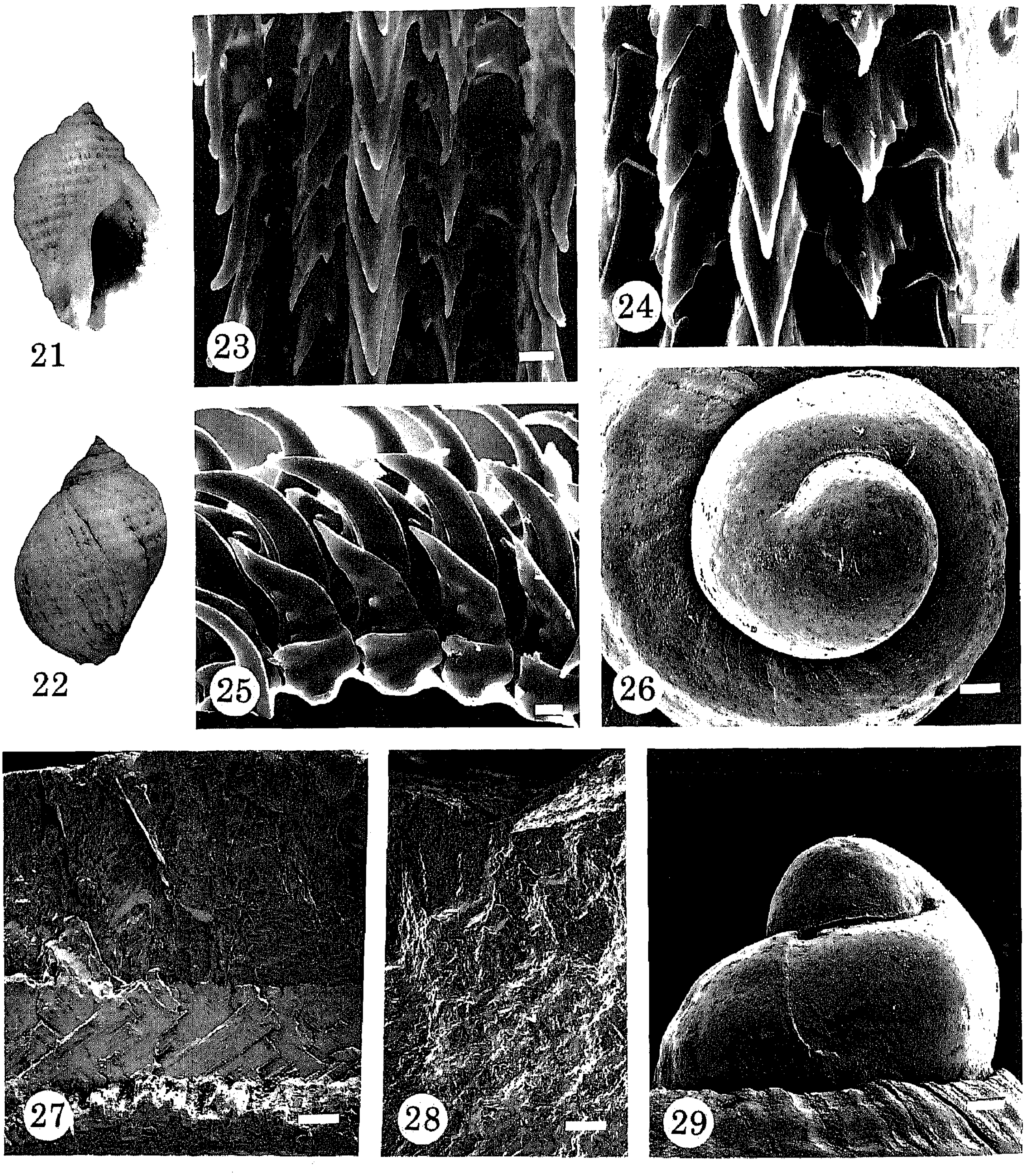
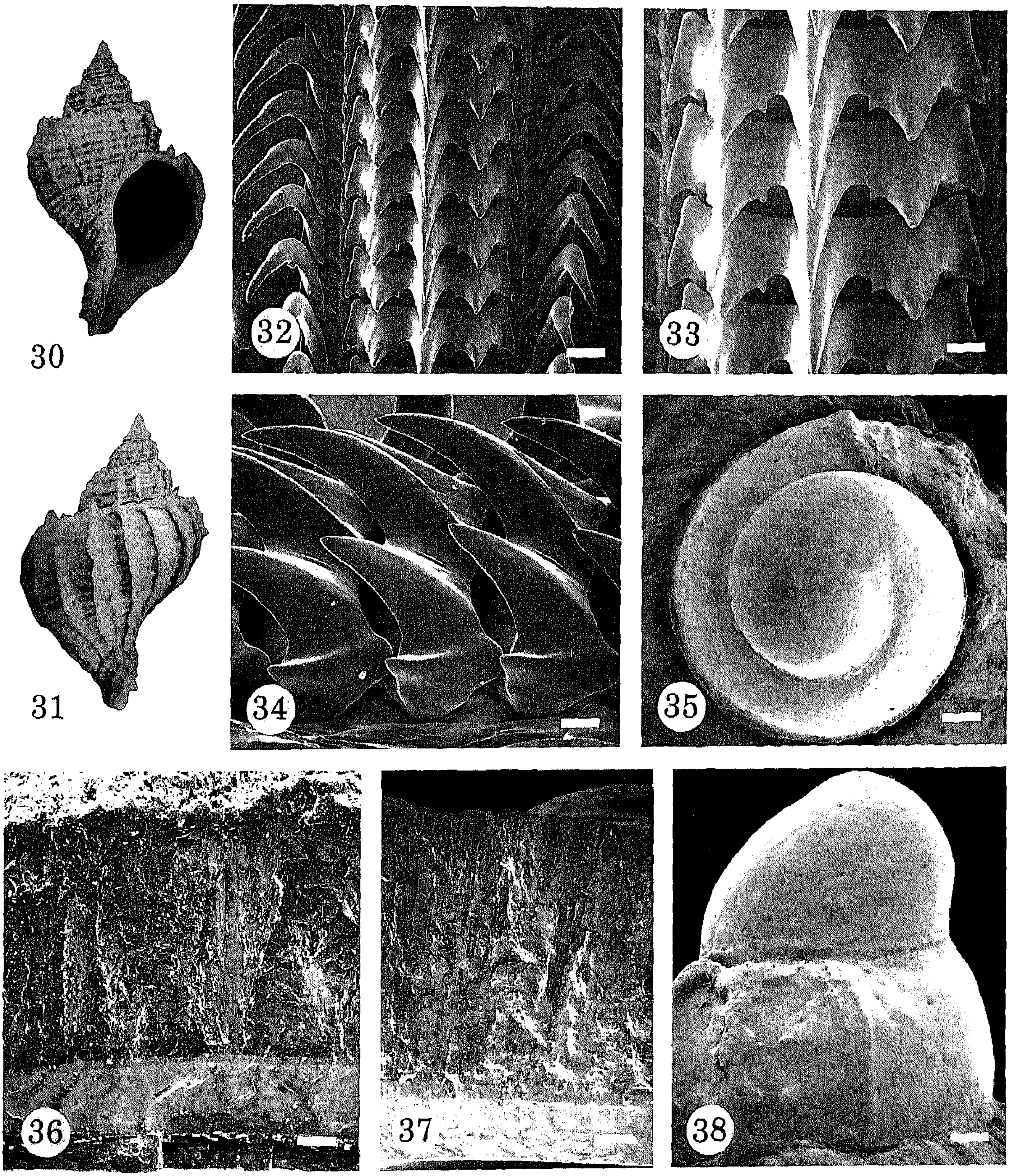
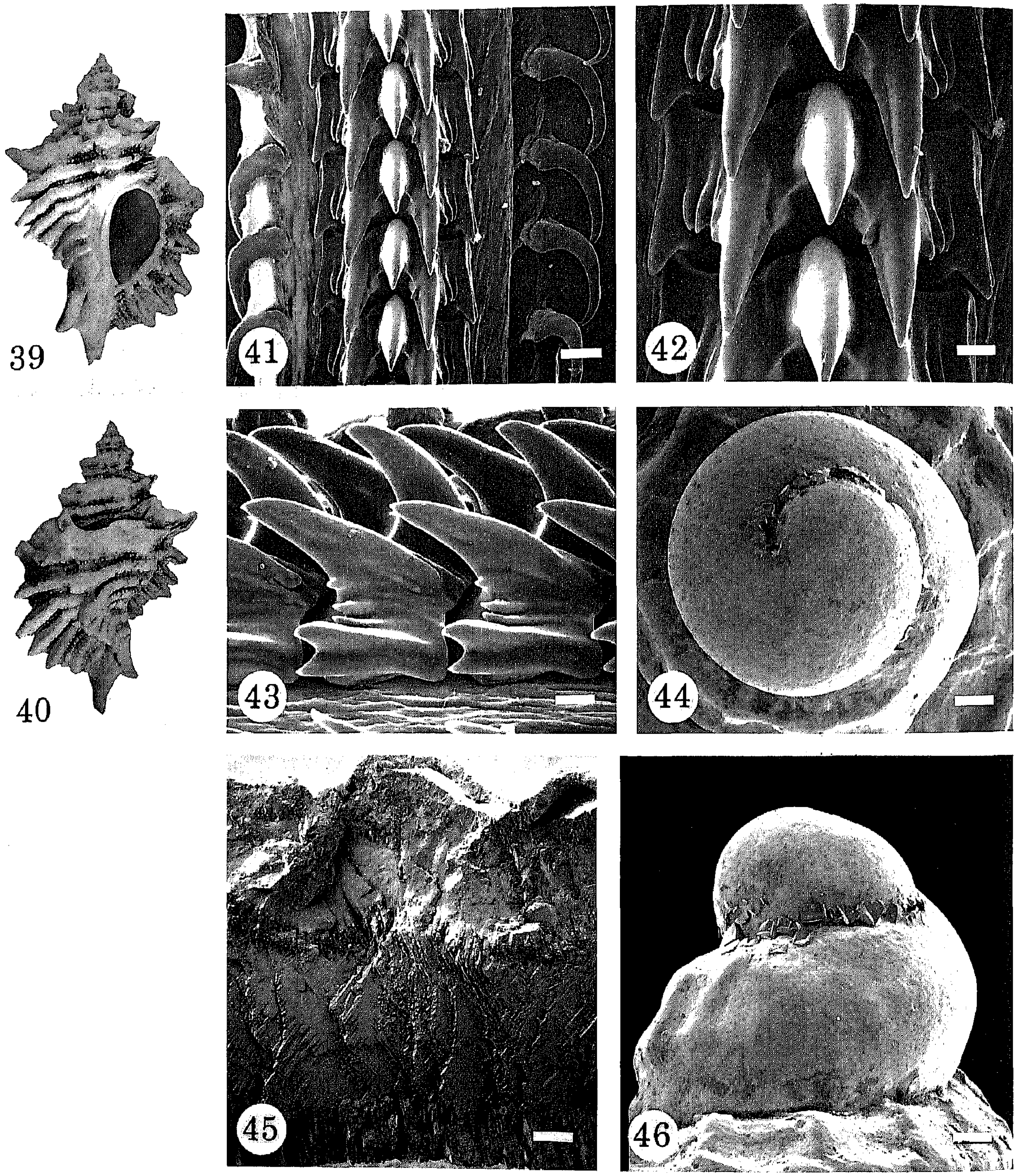
109413, Ushaia, Tierra del Fuego, Argentina, height 41 mm; **13,14** MCZ 132566, Falkland Islands, Argentina, height 47 mm). **11,12**. Operculum (LACM 86-270.2, Daniel Este, Isla Grande, Tierra del Fuego, Chile, height 11 mm); **11**. Outer surface; **12**. Inner surface. **Figures 15-20**. *Ocenebra erinacea*. Shells (**15,16** MCZ 87662, Weymouth, England, height 31 mm; **19,20** MCZ 172450, Fos-sur-Mer, Bouches-du-Rhône, France, height 56 mm). Operculum (**17,18** MCZ 302405, St. Lunaire, France, height 8.0 mm); **17**. Outer surface; **18**. Inner surface.



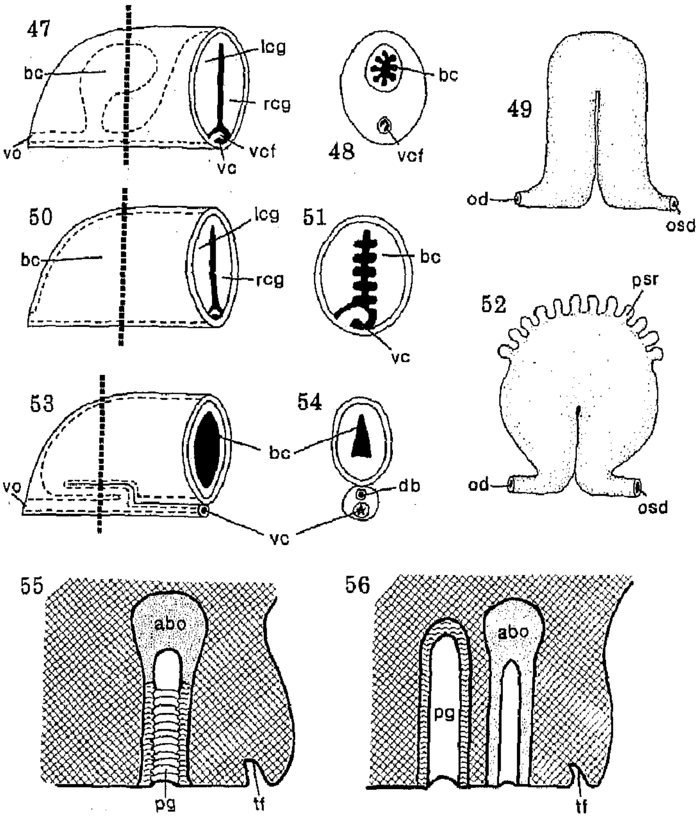
Figures 21–29. *Nucella lapillus*. **21,22.** Shell (MCZ 69192, Freshwater Bay, Isle of Wight, England, height 25.1 mm). **23-25.** Radula (USNM 857053, Kittery, Maine, U.S.A.). **23.** Central portion of radular ribbon. Scale bar = 15 μm. **24.** Rachidian teeth. Scale bar = 10 μm. **25.** Side view of rachidian teeth (right row of lateral teeth removed). Scale bar = 10 μm. **26,29.** Protoconch (MCZ 14184, Isle au Haut, Maine, U.S.A.). **26.** Apical view. Scale bar = 12 μm. **29.** Side view. Scale bar = 12 μm. **27,28.** Shell ultrastructure (view of growing edge; innermost layer on bottom) (MCZ 69192, Freshwater Bay, Isle of Wight, England). Scale bars, 45 μm and 70 μm, respectively.



Figures 30–38. *Trophon geversianus.* **30,31.** Shell (MCZ 132566, Falkland Islands, Argentina, height 47 mm). **32-34.** Radula. (LACM 86-270.2, Daniel Este, Isla Grande, Tierra del Fuego, Chile). **32.** Central portion of radular ribbon. Scale bar = 45 μm. **33.** Rachidian teeth. Scale bar = 25 μm. **34.** Side view of rachidian teeth. Scale bar = 20 μm. **35,38.** Protoconch (LACM 86-270.2, Daniel Este, Isla Grande, Tierra del Fuego, Chile). **35.** Apical view. Scale bar = 150 μm. **38.** Side view. Scale bar = 150 μm. **36,37.** Shell ultrastructure (LACM 86-270.2, Daniel Este, Isla Grande, Tierra del Fuego, Chile); Scale bars, 60 μm and 150 μm, respectively.

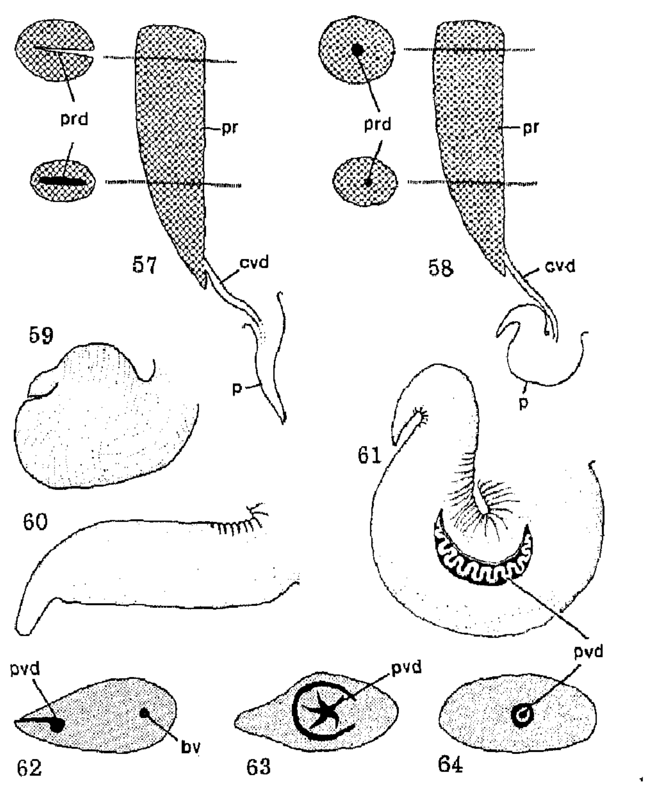


Figures 39–46. *Ocenebra erinacea*. **39,40.** Shell (MCZ 172450, Fos-sur Mer, Bouches-du-Rhône, France, height 56 mm). **41-43.** Radula (MCZ 298425, Roscoff, France). **41.** Central portion of ribbon. Scale bar = 17 μm. **42.** Rachidian teeth. Scale bar = 8 μm. **43.** Side view of rachidian teeth. Scale bar = 9 μm. **44,46.** Protoconch (MCZ 38369, Kent, England). **44.** Apical view. Scale bar = 90 μm. **46.** Side view. Scale bar = 90 μm. **45.** Shell ultrastructure (MCZ 298425, Roscoff, France). Scale bar = 130 μm.



Figures 47–56. Anatomical structures of the female reproductive system of *Nucella lapillus*, *Trophon geversianus*, *Ocenebra erinacea*, *Muricanthus fulvescens*, and *Thais nodosa*. **47,50,53.** Bursa copulatrix in *N. lapillus* and *T. geversianus* (**47**), *Th. nodosa* (**50**), *O. erinacea* and *M. fulvescens* (**53**). **48,51,54.** Cross sections through bursa copulatrix (location indicated by vertical bar). **49,52.** Albumen glands in *N. lapillus*, *T. geversianus*, *O. erinacea*, *M. fulvescens* (**49**), and *Th. nodosa* (**52**). **55,56.** Sagittal section through foot showing accessory boring organ and pedal gland of *Th. nodosa*, *T. geversianus*, *M. fulvescens* (**55**), *N. lapillus*, and *O. erinacea* (**56**).

abo, accessory boring organ; bc, bursa copulatrix; db, duct to bursa copulatrix; lcg, left lobe of capsule gland; od, oviduct; osd, ovi-sperm duct; pg, ventral pedal gland; psr, posterior seminal receptacles; rcg, right lobe of capsule gland; tf, transverse fold; vc, ventral channel; vcf, flange of the ventral channel; vo, vaginal opening.



Figures 57–64. Anatomical structures of the male reproductive system of *Nucella lapillus*, *Trophon geversianus*, *Ocenebra erinacea*, *Muricanthus fulvescens*, and *Thais nodosa*. Prostate gland with proximal and distal cross sections in *N. lapillus*, *T. geversianus*, *O. erinacea*, *M. fulvescens* (**57**) and *Th. nodosa* (**58**). Penial morphologies with cross sections in *T. geversianus* (**59,62**), *N. lapillus*, *M. fulvescens* (**60,62**), *O. erinacea* (**60,63**), and *Th. nodosa* (**61,64**).

bv, blood vessel; cvd, cephalic vas deferens; p, penis; pr, prostate; prd, duct through prostate; pvd, penial vas deferens.

Sculpture of the shell may vary with the type of habitat.

Distribution: Southern Argentina to Chile.

Ocenebra erinacea:

Shell: Protoconch (Figs. 44, 46) conical, low, of 1½ smooth whorls, and with impressed suture; transition to teleoconch smooth, difficult to discern. Teleoconch elongate, fusiform, biconical (Figs. 15, 16, 19, 20, 39, 40), of 7-8 whorls. Adult shell highly variable in shape, to 55 mm in height, 25 mm in width (not including spine length; 35 mm including spine length). Body whorl 55-60% of shell height, with 3-9 varices, often with frilled edges, and with 6-8 spiral cords. Aperture (to 30% of shell height) round to oval; outer lip with crenulated edge. Moderately callused columella. Siphonal canal partly or completely closed, often nearly equal in length to aperture in larger specimens. Siphonal fasciole pointing away from siphonal canal. Shell color yellowish to cream or dark brown; aperture, columella white.

Shell ultrastructure: Innermost layer of crossed-lamellar aragonite, with crystal planes oriented perpendicular to growing edge [15-20% of thickness]; followed by layer of crossed-lamellar aragonite, with crystal planes oriented parallel to growing edge [40-45% of thickness]; followed by layer of crossed-lamellar aragonite, with crystal planes oriented perpendicular to growing edge [5-8% of thickness]; outermost layer of calcite [35% of thickness] (Fig. 45).

Operculum: D-shaped, with lateral nucleus in lower right (Figs. 17, 18). Outer surface (Fig. 17) with arch-shaped growth lines progressively upright, recurved at upper end; inner surface (Fig. 18) with 4-5 arch-shaped growth lines, with broad (≈ ½ opercular width), lightly callused, glazed outer rim.

Head and foot: Uniformly light yellow to white. Cephalic tentacles elongate, thin. Incurrent siphon well developed. Mantle edge smooth, occasionally with crenulations (possibly an artifact). Sole of foot with large lateral

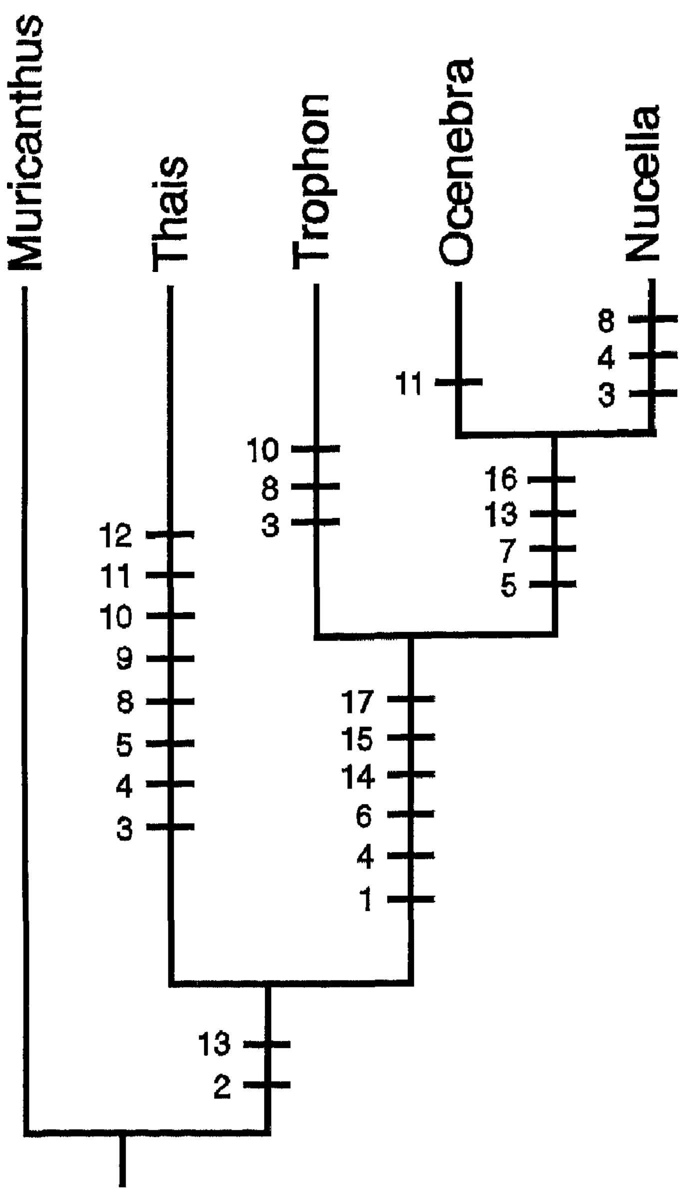


Figure 65. Cladogram, based on analysis of data in Table 1, showing high phylogenetic affinity between *Nucella* and *Ocenebra*. Numbers next to character changes correspond to numbers given to characters in Table 1. Alternative, equally parsimonious character state transformation series are possible for characters 3, 4, 5, and 8 (see text).

folds. Accessory boring organ (Fig. 56, abo) large, well developed, (in females) anterior to, separate from equally large ventral pedal gland (Fig. 56, pg).

Mantle Cavity: Osphradium (<½ ctenidial length, ¾ ctenidial width) partially extending over ctenidium. Right pectin usually wider than left. Each lamella (10-11/mm) attached to mantle roof along short basal portion. Anteriormost portion of ctenidium straight, extending anteriorly of osphradium. Ctenidial lamellae (11-12/mm) basically triangular, longer than high with convex lateral edges posteriorly. Lamellar support rods not well developed.

Female Reproductive System: Vaginal opening (Fig. 53, vo) round to elongate, on short, extension of pallial gonoduct, situated below, posterior to anus. Bursa copulatrix (Figs. 53, 54, bc) large diverticulum (equal in diameter to capsule gland), connected at its anterior portion to duct running parallel to ventral channel for some length prior to connecting with it (Figs. 53, 54, db). Lumen of bursa copulatrix filled with loose flocculent material and iridescent spherules. Capsule gland posterior to, shorter than bursa copulatrix. Ventral channel (Figures 53, 54, vc) well developed anteriorly, less distinct posteriorly. Ingesting gland situated between capsule gland, albumen gland. Albumen gland (Fig. 49) arch-shaped, elongate, opening anteriorly into ovi-sperm duct (osd) posteriorly into oviduct (od). Ovary orange-yellow. Pseudo-penis occasionally present (see also Féral, 1976).

Male Reproductive System: Penis (Fig. 60) simple, dorso-ventrally flattened, elongate, slightly curved, with abruptly tapering, papilla-like end. Penial vas deferens (Fig. 63, pvd) a wide, straight tube star-shaped in cross section; tube partially attached to penial wall. Cephalic vas deferens (Fig. 57, cvd) large, similar to penial vas deferens in structure, extending from penis (p) to prostate gland (pr). Prostate gland (Fig. 57, pr) white to yellow; prostate duct (prd) a dorso-ventral slit in cross section anteriorly, a triangular large space posteriorly; duct open to mantle cavity posteriorly (Fig. 57). Posterior vas deferens white to dirty white, iridescent. Testis yellowish.

Alimentary System: Paired accessory salivary glands very long (≈ ½ shell height); left gland intertwined with left salivary gland, right gland free,situated in right anterior corner of buccal cavity. Salivary glands in center of dorsal buccal cavity between gland of Leiblein and short, pear-shaped valve of Leiblein. Salivary ducts attached to anterior esophagus at short distance from valve. Glandular folds in mid-esophageal region swollen, especially well developed at connecting point between esophagus and gland of Leiblein. Connection between mid-esophagus and gland of Leiblein short, thick. Posterior esophagus appressed to left side of gland of Leiblein in loop-shaped fashion. Gland of Leiblein yellowish; posterior blind duct very short (<½ length gland of Leiblein), with prominent terminal ampulla. Stomach tubular, with faint folds on stomach wall oriented toward center of stomach (poorly preserved in specimens examined). Rectal gland thin, green, extending along ½ of pallial gonoduct. Large papilla overlaying anus.

Radula: Ribbon length 35-40% shell height. Base of rachidian tooth expanded below base of neighboring rachidian tooth; central cusp of rachidian thin, flame-shaped, leaning more anteriorly (*in situ*) than lateral cusps; inner lateral denticle low on base of lateral cusp, occasionally bifurcate (within same specimen); outer edge of lateral cusp straight, with several short denticles; large marginal cusp pointing straight forward and parallel to elongate, lateral extension at base of rachidian tooth (Figs. 41-43), resulting in bifid appearance of rachidian basal plate. Lateral teeth with narrow base, widely spaced, shorter than rachidian width (Fig. 41).

Egg capsules: Oval-elongate, vase-shaped, triangular in cross section. Capsules yellowish, up to 13 mm in height, 6 mm in width, each on narrow stalk, attached by flat base. Apex with short elevated protuberance with mucous plug. Each capsule containing 4-167 embryos, of which none are nurse eggs (Fretter & Graham, 1985; Lebour, 1937).

Ecology: *Ocenebra erinacea* lives in the rocky intertidal and subtidal zones (Jeffreys, 1867) to 150 meters (Fretter & Graham, 1985) where it feeds on oysters and other bivalves (Fretter & Graham, 1985), barnacles and limpets (Graham, 1955). Lebour (1937) reported breeding in late spring and summer. Juveniles hatch from the eggs after 12-14 weeks (Fretter & Graham, 1985). A comprehensive ecophysiological study was done on *Ocenebra erinacea* by Hawkins (1985).

Distribution: North Atlantic Ocean (Spain to Norway, Great Britain, Ireland); Mediterranean Sea (southern Europe, northern Africa).

CLADISTIC ANALYSIS

The cladistic analysis yielded one tree with a consistency index of 0.88 (Fig. 65). This cladogram indicates that: 1) placement of *Nucella* in Thaidinae or its senior synonym, Rapaninae, creates polyphyletic groups (see also Kool, 1989); 2) *Nucella* is more closely related to *Ocenebra* than to *Trophon* and should be placed in Ocenebrinae; 3) the subfamilial boundaries between Ocenebrinae and Trophoninae are much less distinct than previously accepted.

Characters and character state distribution among the taxa Nucella, Trophon, Ocenebra, Thais, and the outgroup, Muricanthus:

Character 1. Protoconch: 0. multispiral ($>$ 2 whorls); 1. paucispiral ($\leq$ 1½ whorls).

Nucella, *Trophon* and *Ocenebra* (Figs. 26, 29, 35, 38, 44, 46) have a paucispiral, smooth protoconch without a sinusigeral notch or outwardly-flared lip. This morphology reflects direct development. The outgroup and the rapanines have a multispiral (and generally sculptured) protoconch with a sinusigeral notch and outward-flaring lip, typical for species with a planktonic larval stage.

Character 2. Calcitic layer: 0. absent; 1. present.

The outgroup lacks an outer calcitic shell layer that is present in the other four taxa. The presence of calcite appears to be the derived condition.

Character 3. Number of aragonitic layers: 0. 3; 1. 4; 2. 2.

The outgroup and *Ocenebra* have three layers of aragonite (transverse, collabral, transverse). *Thais* has an additional, innermost fourth layer of crystals oriented in a 45° angle; both *Nucella* and *Trophon* have two layers (transverse, collabral), but may lack the innermost transverse layer (Figs. 28, 37).

Character 4. Nucleus of operculum: 0. terminal nucleus in lower right; 1. lateral nucleus in lower right; 2. lateral nucleus below center right; 3. lateral nucleus in center right.

The outgroup has a terminal nucleus in the lower right. All ingroup taxa have a lateral nucleus, the position of which varies. The nucleus of the operculum in *Nucella* is located below the center right; that of *Trophon* and *Ocenebra* in the lower right (Figs. 7, 11, 17, respectively). The nucleus is located in the center right in rapanines.

Character 5. Shape of operculum: 0. oval; 1. D-shaped.

The opercula of *Nucella*, *Thais*, and *Ocenebra* are roughly D-shaped. Those of *Muricanthus* and *Trophon* are elongate-oval.

Character 6. Pigmentation pattern of head-foot region: 0. present; flecked with black and gray; 1. absent, uniformly colored (faint yellow).

The head-foot regions of *Nucella*, *Trophon*, and *Ocenebra* are uniformly faint yellow. Both *Thais* and the outgroup are densely flecked with black blotches and specks (this pattern generally survives preservation in alcohol although other colors, such as white and yellow, fade).

Character 7. Ventral pedal gland and accessory boring organ: 0. sharing one duct; 1. with separate ducts.

In *Nucella* and *Ocenebra*, the accessory boring organ and ventral pedal gland (Fig. 56, abo, pg) have separate ducts to the sole of the foot, while in *Trophon*, rapanines, and the outgroup these structures share a common duct (Fig. 55, abo, pg).

Character 8. Bursa copulatrix: 0. large diverticulum, separate from capsule gland; 1. small diverticulum, separate from capsule gland; 2. small chamber with lumen continuous with capsule gland.

The bursa copulatrix is a small blind sack in *Nucella* and *Trophon* (Fig. 47), a large separate diverticulum in *Ocenebra* (Fig. 53) and the outgroup, while in rapanines the bursa is continuous with the capsule gland (Figs. 50, 51).

Character 9. Seminal receptacles at dorsal periphery of albumen gland: 0. absent; 1. present.

In *Thais*, a row of posterior seminal receptacles (Fig. 52, psr) at the dorsal periphery of the albumen gland presumably increases efficiency in the fertilization process (Kool, 1988, 1989). These posterior seminal receptacles are absent in *Nucella*, *Trophon*, *Ocenebra*, and in the outgroup, *Muricanthus* (Fig. 49). This character is a synapomorphy for Rapaninae (Kool, 1993, in press).

Character 10. Penial shape: 0. simple, elongate to lightly curved; 1. bulbous, with papilla; 2. strongly recurved with pseudo-papilla.

Penial shape in *Nucella*, *Ocenebra*, and the outgroup is elongate (Fig. 60). The penis in *Thais* is strongly recurved, and sinuous (Fig. 61), while that of *Trophon* is short, bulbous, with a distinct papilla (Fig. 59).

Character 11. Penial vas deferens: 0. simple duct; 1. small, loose duct-within-a-duct; 2. large duct-within-a-duct, partially attached to penial inner wall.

Nucella, *Trophon* and the outgroup have a penial vas deferens that is loosely closed, while rapanines have a "duct-within-a-duct" system (Figs. 61, 64) (Kool, 1988, 1989). *Ocenebra* differs from both types in having a rather wide inner duct that is partially attached to the penial inner wall (Fig. 63).

Character 12. Prostate Gland: 0. open to mantle cavity posteriorly; 1. without opening to mantle cavity.

Males of *Nucella*, *Trophon*, *Ocenebra*, and the outgroup have a prostate gland that is open to the mantle cavity along its posterior portion (Fig. 57). The prostate of rapanine males does not open to the mantle cavity (Fig. 58).

Character 13. Accessory salivary gland length: 0. right gland small, left gland absent; 1. glands < ¼ shell height; 2. glands ≥ ½ shell height.

Character 14. Straw-like membrane around gland of Leiblein: 0. present; 1. absent.

In most rapanines and the outgroup, the gland of Leiblein is covered by a thick membrane of interwoven fibers of connective tissue, producing a straw-like appearance. Such a membrane is absent in *Nucella*, *Trophon* and *Ocenebra*.

Character 15. Posterior duct of gland of Leiblein: 0. longer than ½ of gland length; 1. shorter than ½ gland length.

In *Nucella*, *Trophon* and *Ocenebra*, the gland of Leiblein tapers posteriorly into a thin, very short posterior duct that runs adjacent to the posterior esophagus and is often filled with secretory material from the gland; in the majority of rapanines and in the outgroup this duct is much longer, extending into the dorsal branch of the afferent renal vein.

Character 16. Central cusp of rachidian: 0. oriented in same plane as lateral cusps; 1. leaning more anteriorly than lateral cusps.

In *Nucella* (Fig. 25) and *Ocenebra* (Fig. 43) the central cusp on the rachidian leans more anteriorly (*in situ*) than the lateral cusps. In *Thais*, *Trophon* (Fig. 34), and the outgroup, the lateral cusps and central cusp are aligned in the same plane.

Character 17. Margin of rachidian basal plate: 0. straight; 1. bifid.

The bifid condition of the rachidian basal plate (Figs. 25, 34, most developed in Fig. 43) is found in *Nucella*, *Trophon* and *Ocenebra*, but not in *Thais* or the outgroup.

Synapomorphies for the Nucella-Ocenebra clade (Fig. 65):

Character 5: The character for opercular shape is homoplastic; a D-shaped operculum occurs in *Thais* as well.

Character 7: Both *Nucella* and *Ocenebra* have separate openings for the ventral pedal gland and accessory boring organ (Fig. 56, abo, pg). Female specimens of *Trophon geversianus*, *Thais nodosa*, and the outgroup, have a single duct and opening for these organs (Fig. 55, abo, pg). A shared duct for the accessory boring organ and ventral pedal gland, as found in *Trophon geversianus*, may not be as advantageous as an arrangement as when the ducts originating from the accessory boring organ and ventral pedal gland are separate. It would appear that an arrangement where one duct serves both as ventral pedal gland and as a passage for the accessory boring organ and its secretions during boring activities (Carriker, 1981) prevents the female from boring activity, and thus perhaps feeding in general, during stages of egg-laying.

Character 13: *Nucella* and *Ocenebra* have a pair of very long accessory salivary glands (≥ ½ shell height). *Trophon* and *Thais* have much smaller glands (< ¼ shell height). The outgroup has only one extremely small right accessory salivary gland.

Character 16: In *Nucella*, and to a much greater degree in *Ocenebra*, the central cusp leans more anteriorly (Figs. 25, 43, respectively) (*in situ*) than the lateral cusps, whereas in *Trophon*, the central cusp is aligned with the lateral cusps (Fig. 34).

Synapomorphies for the Trophon-Nucella-Ocenebra Clade:

Character 1: The paucispiral protoconch is indicative of having crawl-away larvae, rather than a planktonic larval stage that is found in *Thais* and other rapanines (Kool, 1993, in press) and the outgroup.

Character 4: The cladogram suggests that an opercular nucleus below the center right (*Nucella*; character state 2) evolved from the ancestral condition for the taxa in this clade of having a nucleus in the lower right (*Ocenebra* and *Trophon*; character state 1).

Character 6: All three taxa lack a pigmentation pattern on their head-foot region that is found in the outgroup, *Thais*, and other members of the Rapaninae.

Character 14: The straw-like outer membrane of the gland of Leiblein is absent in the species of this clade, but present in the outgroup, and most members of Rapaninae (Kool, 1989; 1993, in press).

Character 15: The posterior duct of the gland of Leiblein is shorter than ½ the length of the gland itself in this clade, but much longer in the remaining taxa, reaching into the dorsal branch of the afferent renal vein.

Character 17: The bifid condition of the basal plate, especially well developed in *Ocenebra* (Fig. 43), is absent in *Thais* and the outgroup.

Synapomorphies for the Thais-Trophon-Nucella-Ocenebra Clade:

Character 2: An outer layer of calcite is present in all ingroup taxa, but is absent in the outgroup.

Character 13: The outgroup has only one extremely small right accessory salivary gland. A situation of having a pair of medium-size accessory salivary glands appears to have evolved from the condition described above and to have given rise to the most derived condition (extremely long glands).

DISCUSSION

According to the topology of the cladogram (Fig. 65), two characters have evolved in a parallel manner in *Nucella lapillus* and *Trophon geversianus*. Out of the context of the cladogram, these similarities would suggest a closer relationship between these two species than is suggested by the tree topology:

Character 3: Shell ultrastructure in both *Nucella* and *Trophon* consists of two aragonitic layers and an outer layer of calcite. Specimens of both may lack the innermost (transverse) layer (Figs. 28, 37). More detailed studies may reveal the cause of this variation. Perhaps environmental factors may play a role (Etter, personal communication).

Character 8: The morphology of the bursa copulatrix of *Nucella* is very similar to that of *Trophon*. In both taxa, a relatively small, muscular blind sack branches off from the vagina (Figs. 47, 48). In *Ocenebra* the bursa is thin-walled and equal in width and height to the capsule gland, extending for up to ½ the length of the pallial complex. The ventral channel loops backwards towards the anterior portion of the bursa in *Ocenebra* (Fig. 53), rather than straight up into the bursa as in *Trophon* and *Nucella* (Fig. 47).

The above two characters could be considered synapomorphies for an alternative, but less parsimonious, tree in which *Trophon* and *Nucella* would be united in one clade. However, in the proposed phylogenetic hypothesis (Fig. 65), four synapomorphies support a clade consisting of *Nucella* and *Ocenebra*, rendering the above two characters as homoplastic.

Fretter and Graham (1962) mention several similarities in egg capsule morphology between *Nucella lapillus* and *Ocenebra erinacea*. Both species lay vase-shaped capsules, whereas *Trophon geversianus* produces discoidal egg capsules. However, having discoidal egg capsules is only an autapomorphic trait for *Trophon* and does not provide clues about relationship in this case. Alternative, equally parsimonious transformation series are possible for characters 3, 4, 5, and 8. For Characters 3, 5, and 8, I chose the scenario involving homoplasy over one involving a reversal to avoid an "artificial" increase in synapomorphies. Similarly, for Character 4, I chose the least linear trans-formation series ("zero state" evolving into both the "three state" and the "one state").

Zoogeographical data reveal that members of *Nucella*, *Ocenebra* and *Trophon* occur primarily in colder waters of the temperate and boreal zones, whereas rapanines and the outgroup occur primarily in warmer waters of the (sub)tropics (Kool, 1989).

Nucella lapillus and *Ocenebra erinacea* overlap for much of their ranges in primarily temperate western European waters. In addition, *N. lapillus* occurs in the western Atlantic, where *O. erinacea* does not, and *O. erinacea* occurs in the Mediterranean, where *N. lapillus* has not occurred since the Pleistocene [Malatesta (1960) cited records of *N. lapillus* from the Pleistocene of Sicily]. Cooke (1915), in a comprehensive list of localities for *Nucella lapillus*, showed that the southernmost record for this species is the Algarve coast of Portugal and alleged that any records from Northern Africa (see Nordsieck, 1982), the western Mediterranean, the Azores, and the Canary Islands, are highly suspect. Other members of what can be assumed to be *Ocenebra s.s.* and *Nucella s.s.* are found in the eastern Pacific (Abbott, 1974) and the northern Pacific. Furthermore, *Ocenebra s.s.* occurs in western Africa (Houart, 1989) and South Africa (Kilburn & Rippey, 1982). Ranges of these genera may be revised when more *Ocenebra*-like taxa (for example from Japan) and *Nucella*-like species have been examined with respect to their anatomy, radula, shell ultrastructure, etc. Such studies are also necessary to determine if, for example, species such as *Nucella dubia* and *Nucella squamosa*, both from the South African Province, are indeed members of *Nucella s.s.* It appears from preliminary dissections that the genus *Nucella* can no longer be considered restricted to the temperate waters of the northern hemisphere (Kool, in preparation).

Trophon geversianus, limited to the South American continent, lives in temperate to boreal waters, as do *Nucella lapillus* and *Ocenebra erinacea*.

SYSTEMATIC CONCLUSIONS

The high degree of similarity in anatomy, radula, protoconch, shell ultrastructure and operculum in *Ocenebra erinacea*, *Trophon geversianus* and *Nucella lapillus* indicates that these three taxa are more closely related to one another than any one of them is to *Thais* or other representatives of Rapaninae. *Nucella* should therefore be excluded from Rapaninae to maintain monophyly (Kool, 1989; 1993, in press). The difficulty of correctly allocating *Nucella* to a subfamily is indicative of the dilemma of our lack of understanding of higher muricoidean systematics. The cladistic analysis and the resulting cladogram (Fig. 65) suggest that *Nucella* is better placed in Ocenebrinae than in Trophoninae. It is obvious that the boundaries of groups at the higher taxonomic categories, traditionally based on shell characters, become less clear after completion of thorough anatomical studies of members from different genera and subfamilies. Results shown here suggest that *Trophon geversianus*, the type species of Trophoninae, is closely related to *Nucella* and *Ocenebra*. Perhaps it is more closely related to the latter two taxa than to other species hitherto included in Trophoninae. It is beyond the scope of this paper to suggest synonymization of Trophoninae with Ocenebrinae. However, I suspect that future studies will show that Trophoninae is not a monophyletic group and that a new name for some of its members may be warranted. The following systematic arrangement is proposed for the taxa treated herein:

MURICOIDEA Rafinesque, 1815
MURICIDAE Rafinesque, 1815
RAPANINAE Gray, 1853 (*sensu* Kool, 1993, in press)
Thais Röding, 1798
OCENEBRINAE Cossmann, 1903
Ocenebra Gray, 1847
Nucella Röding, 1798
TROPHONINAE Cossmann, 1903)
Trophon Montfort, 1810

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