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Micromolluscs in Japan: taxonomic composition, habitats, and future topics

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Abstract

Studies of micromolluscs are essential in the malacology of the 21st century. Our understanding of molluscs has been chiefly based on large-sized species, and there are little-known taxa that comprise only of small-sized species. In Japan, an obvious change occurred from classic conchology to more advanced microscopic work in the 1990s, but further research must be accelerated to reveal the entire fauna. In this review, a summary of the current state of knowledge is given for all known micromolluscan families distributed in Japan. Since the 1990s new micromolluscs have been described from various microhabitats such as the undersides of half-buried boulders, burrows of other invertebrates, submarine caves, sunken wood, deep-sea hydrothermal vents and cold seeps. These are promising habitats for more intensive sampling in addition to unexplored environments. Basic taxonomy is still necessary in advancing biological studies at all levels including anatomy, molecular phylogenetics, development, ecology, and paleontology. The importance of micromolluscs is also rising in the field of conservation biology, especially with regard to endangered and introduced species. The genus *Lepetella* (Lepetellidae) is recorded for the first time from Japan.

Keywords: Gastropoda, Bivalvia, diversity, fauna, Lepetellidae

Introduction

Discovering and describing micromolluscan faunas is an unlimited frontier anywhere in the world. In Japan, more than 8,000 species of molluscs have been recorded since the 18th century (Higo *et al.* 1999; Minato 1988a). But there are still numerous unidentifiable or undescribed species, and most of them are micromolluscs. According to estimations by various malacologists, there may be more than 1,400 undescribed species of molluscs in Japan (Union of Japanese Societies for Systematic Biology 2002–2003).

The study of micromolluscs is obviously essential to Japanese malacology in this century. Macromolluscs are already well examined as a whole (Okutani 2000), and the forefront for the future is clearly in studies of micromolluscs. This is true of all fields, including taxonomy, anatomy, molecular phylogenetics, ecology and development. The importance of micromolluscs can be readily understood by referring to the history of Japanese malacology.

The study of Japanese molluscs started around the 1860s (see Cosel 1998 for review). The fauna was examined by European and American expeditions, and many small species were described by malacologists such as A. Adams, Dunker and Martens. A. Adams especially introduced numerous names for micromolluscs.

In the 1900s the finding of new species was further accelerated by Henry A. Pilsbry and Yoichiro Hirase, especially in the field of land snails (Callomon 2003; Callomon & Tada 2006). Hirase em-

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ployed several people and sent them throughout the Japanese territories, including remote oceanic islands, and collected all species within reach. The majority of common species in Japan had been given names by this period. Hirase's huge personal investment was by far the most important contribution to the beginning of Japanese malacology.

During or before Hirase's time, some publications were made by Japanese zoologists such as Isao Iijima, Yoshio Tanaka, Ryotaro Uchiyama and Goto Seitaro. But their interest in molluscs was as part of general zoology. Tomotaro Iwakawa was another well-known malacoloigst of that era but his chief contribution was limited to cataloging a collection of the Tokyo Imperial Museum.

The leader of the first generation of professional malacological taxonomist in Japan was Dr. Tokubei Kuroda. He was trained in the private museum of Mr. Hirase, later obtained a position at Kyoto University, and worked with the leader of the next generation, Dr. Tadashige Habe. Their most important work together was a complete list of Japanese shell-bearing marine molluscs (Kuroda & Habe 1952) and their collaboration further developed into *Shells of Sagami Bay* (Kuroda *et al.* 1971). The illustrations of small-sized species in that book were clearer than any other publications of that age.

Dr. Habe was a leading malacologist, who described numerous molluscs mainly between the 1950s and the 1980s. He had already started studying micromolluscs, including the larvae of marine gastropods, by the 1940s, and carried out taxonomic revisions of whole groups of shell-bearing molluscs in Japan. A fundamental part of our current knowledge of Japanese molluscan taxonomy was established by him.

The frontier for the third generation was the exploration of the deep-sea fauna. Dr. Takashi Okutani took the initiative by engaging in a faunal survey using the research ship R/V *Soyo-Maru* of the Tokai Regional Fisheries Research Laboratory in the 1960s. He described molluscs from the bathyal and deeper levels (*e.g.*, Okutani 1963, 1968) and established faunal research into molluscs from hydrothermal vents and seeps since the late 1980s (see Sasaki *et al.* 2005 for detail).

Paleontology is another field that has greatly contributed to molluscan taxonomy. Dr. Matajiro Yokoyama and Dr. Shichihei Nomura are two representative paleontologists, who described numerous small species from the Pliocene to Holocene. However, since their retirement new descriptive work has slowed down, and the study of fossil micromolluscs is still only half accomplished.

Unfortunately malacologists and paleontologists of previous generations could not use a scanning electron microscope (SEM), because such facilities were not yet common before the 1990s. Monographs of faunal descriptions with SEM figures began appearing in the early 1990s (*e.g.*, Fukuda 1993; Hayami & Kase 1993). After this period, the SEM became widely used for the examination of various characters including the radula, soft parts and protoconch (*e.g.*, Hasegawa 1997a; Sasaki 1998).

Therefore, in Japanese malacology, the 1990s were a clear turning point from classic conchology to a new phase of micromolluscan studies. In addition to the introduction of the SEM, interesting taxa were discovered from previously unexplored habitats such as submarine caves, hydrothermal vents, sunken wood and other cryptic environments. Since the late 1990s, new micromolluscs have been described mainly by Dr. Hiroshi Fukuda, Dr. Kazunori Hasegawa, Dr. Itaru Hayami, Dr. Tomiki Kase and Dr. Yasunori Kano, and some have been added by the present author (see below for details).

In the late 2000s the importance of micromolluscs to a wider range of biological fields, including anatomy, molecular phylogenetics, ecology, paleontology and conservation, became better recognized. In this context, this review is intended to show an overview of the current knowledge on Japanese micromolluscs and gives accounts of the gaps in knowledge and what we need to do for the future.

Material and methods

This paper reviews the knowledge of the taxonomic composition of micromolluscs in Japan at the family level up to the end of 2007. To present a thorough review of micromolluscan fauna, extensive surveys were made of the malacological literature (books, monographs, and journals) related to the Japanese fauna. Most importantly, all articles in *Venus*, *Chiribotan*, (1928–2007: published by Malacological Society of Japan; see also The Malacological Society of Japan 1979; Tsuchiya & Sasaki 2005 for index of *Venus*) and *Yuriyagai* (1990–2002: Malacozoological Society of Yamaguchi) were searched. Various reports of faunal research exist, but are cited here only if high-quality figures of micromolluscs were given. Relevant foreign publications were also consulted, especially concerning the phylogeny and definition of higher taxa distributed in Japan.

In addition to data concerning literature, some examples of Japanese micromolluscs are illustrated to facilitate readers' understanding (Figs. 1–22). The figures contain some new distributional records and the sampling data are listed in the figure captions. All material was collected in Japan, mainly during field work by the author. Specimens were photographed with a scanning electron microscope (Hitachi S2250N, The University Museum, The University of Tokyo: UMUT). The details of methods for specimen treatment and photography were described in Geiger *et al.* (2007). All figured specimens are registered and deposited in the Department of Historical Geology and Paleontology of UMUT.

In this review, the word 'micromolluscs' mainly indicates molluscs whose shell is 4 mm in size or smaller. However, slightly larger species are also mentioned if they are related to smaller species. Possibly or obviously juvenile specimens are also included in the figures, because comparison of juveniles, immature subadult and adults is frequently important for species recognition.

The arrangement of families and higher taxa in the text follows a provisional classification by Bouchet *et al.* (2005) for Gastropoda and Bieler & Mikkelsen (2006) for Bivalvia. Species-level taxonomy is mainly based on Okutani (2000), Higo *et al.* (1999), Azuma (1995) and Minato (1988a). The size ranges of shells are quoted from Okutani (2000) for marine species, Azuma (1995) for terrestrial snails, and Masuda & Uchiyama (2005) for freshwater species.

Gastropoda

The species diversity of micromolluscs is the highest in Gastropoda. Small species of microscopic size exist in almost every higher taxonomic group. True micromolluscs are rare or yet unknown in groups such as the Patellogastropoda, Tonnoidea, and most of the Nudibranchia, but it is still possible that small species have been overlooked in these groups.

In the majority of caenogastropods and pulmonates, the adult can be easily distinguished from immature stages by determinate growth, in which adult characters appear in the shell morphology (Fig. 1). Most typically, the aperture margin is markedly thickened (Fig. 1E–F). In other cases, a projection is formed (Fig. 1A–B) or the last part of the whorl becomes disjunct (Fig. 1C–D). Determinate growth is unknown or uncommon in basal groups (*e.g.*, the Patellogastropoda, Vetigastropoda, Neritimorpha) and shelled Opisthobranchia.

The currently used phylogenetic framework was established by Ponder & Lindberg (1997). The latest phylogenetic analysis is presented by Aktipis *et al.* (2008).

PATELLOGASTROPODA. The taxonomy and phylogeny of patellogastropods in Japan are relatively well known, at least as regards shallow-water species (*e.g.*, Sasaki *in* Okutani 2000: 24–33; Nakano & Ozawa 2004, 2007). Generally the number of species that are mature at small size is limited in the Patellogastropoda. In particular, the species of Patellidae and Nacellidae all attain at least 2 cm.

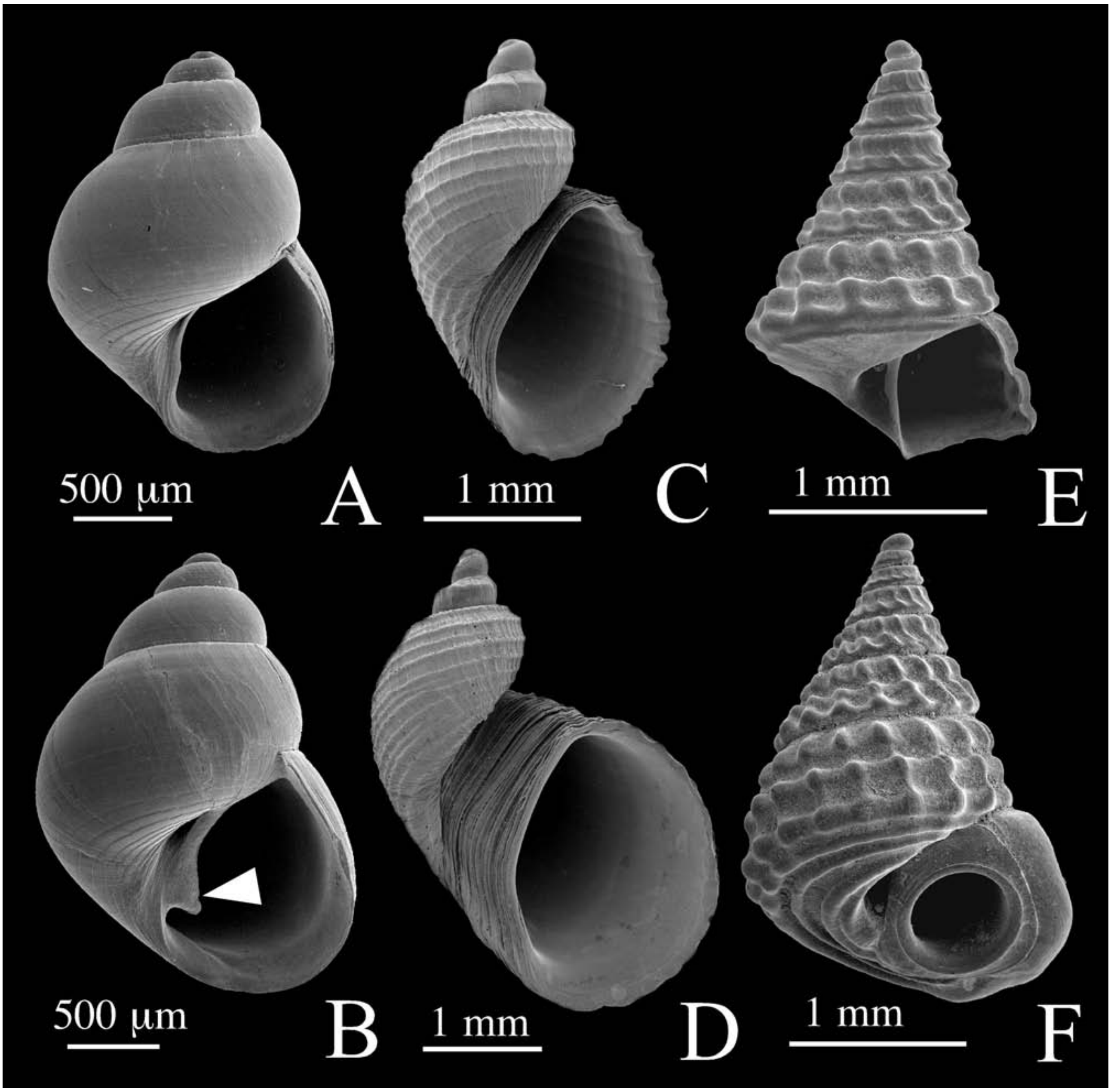


Figure 1. Determinate growth in Gastropoda with comparison between immature (upper) and adult (lower) stages. **A–B.** Trochidae, *Alcyna ocellata* A. Adams, 1860. Arrowhead indicates projection formed at adult. **C–D.** Vanikoridae, *Macromphalus* sp. **E–F.** Pickworthiidae, *Sansonia umbilicata* Jousseaume, 1892. Locality data: **A–B.** Banda, Tateyama, Chiba, date unknown. **A.** UMUT RM29570. **B.** UMUT RM29571. **C–D.** R/V *Tansei-Maru*, cruise KT-99-17, station SH-2, off Shirahama, Wakayama, 41–42 m, 33°40.700'N, 135°19.170'E–33°40.629'N, 135°19.231'E, Nov. 30, 1999. **C.** UMUT RM29572. **D.** UMUT RM29573. **E–F.** Agonohama, Aka Island, Okinawa, from sediments in rock crevices by diving, Sep. 29, 1997. **E.** UMUT RM29574. **F.** UMUT RM29575.

Species of the Lottioidea (Lepetidae, Lottiidae, Acmaeidae) and Eoacmaeidae (see Nakano & Ozawa 2007) are smaller than those in the Patellidae and Nacellidae on average. There is no clear character showing sexual maturity in the shell.

Lottiidae. The smallest species confirmed so far in Japan is *Yayoiacmaea oyamai* (Habe, 1955), which grows up to 6 mm (Sasaki & Okutani 1993). The species lives attached to reddish coralline algae in the shallow subtidal level of warm temperate zones. The shell is encrusted entirely with algae and hardly discernible from the substrate in its natural habitat.

Two subarctic species of *Erginus*, *E. sybaritica* (Dall, 1871) *and E. moskalevi* (Golikov & Kussakin, 1972), attain 8–10 mm, but most specimens collected in the field are smaller. They are known to brood juveniles in the pallial cavity (Sasaki 1988: fig. 21A–C). This genus is also associated with reddish coralline algae. There is no small patellogastropod associated with sea grass in Japan.

Lepetidae. Unidentified small lepetids have been collected from the lower subtidal to bathyal levels, but they have been poorly studied. *Iothia* sp. (Sasaki 1998: fig. 15) is one example of such an uncommon species. Some of the species described by Kuroda & Habe (1949) seem also to be lepetids, and this needs confirmation in future studies.

VETIGASTROPODA. The Vetigastropoda contains numerous micromolluscs, mainly in the families Fissurellidae, Scissurellidae, Anatomidae, Trochidae and Turbinidae. There are no small species in the Haliotidae or Pleurotomariidae. Family-level systematics should be further revised on the basis of phylogenetic analysis. A review and recent status of vetigastropod subgroups was given by Geiger *et al.* (2008).

'Trochaclididae' (= Ataphridae). The occurrence of this family in Japan was first recorded by Hasegawa (2005: 150, fig. 5C). A single, undescribed species, *Trochaclis* sp. (3 mm in width) was obtained from two localities off southern Okinawa at depths of 955–1618 m. The family Trochaclididae was synonymized with the Ataphridae by Bouchet *et al.* (2005: 243).

Fissurellidae (Fig. 2A–C)**.** Members of the ghe genus *Emarginula* (Fig. 2A) are the most typical small fissurellids (Sasaki *in* Okutani 2000: 44–53). Some large species of the genus exceed 2 cm (*e.g., E. imaizumi* Dall, 1926), but many are smaller than 1 cm. This genus contains numerous unidentified species, especially from warm-water regions, and needs taxonomic revision. *Zeidora* has an elongated depressed shell with posteriorly projected apex (Fig. 2B). *Zeidora calceolina* A. Adams, 1860 (Sasaki 1998: fig. 39a–b) is the best-known species, but there are a few more (*cf.* Horikoshi 1944). *Rimula* has a closed slit in the middle part of the anterior slope, and one species, *R. cumingii*, is 4 mm or less. *Cranopsis* (Fig. 2C) has a strongly inclined apex and is 6 mm or less in size (Fig. 2C). *Fissurisepta* (*cf.* McLean & Geiger 1998) is a rare genus distributed in the lower subtidal to bathyal zones and reaching 3 mm or less in Japanese species.

The taxonomy of the Japanese Fissurellidae has not been seriously revised since Habe (1951c). From the author's observations there are numerous unidentifiable or possibly new species in Japan, especially in subtropical waters.

LEPETELLOIDEA. The superfamily Lepetelloidea was originally defined as a member of Cocculiniformia (Haszprunar 1988a) but later transferred to the Vetigastropoda (Ponder & Lindberg 1997; Bouchet *et al.* 2005: 243). This superfamily is restricted to the lower subtidal to bathyal levels

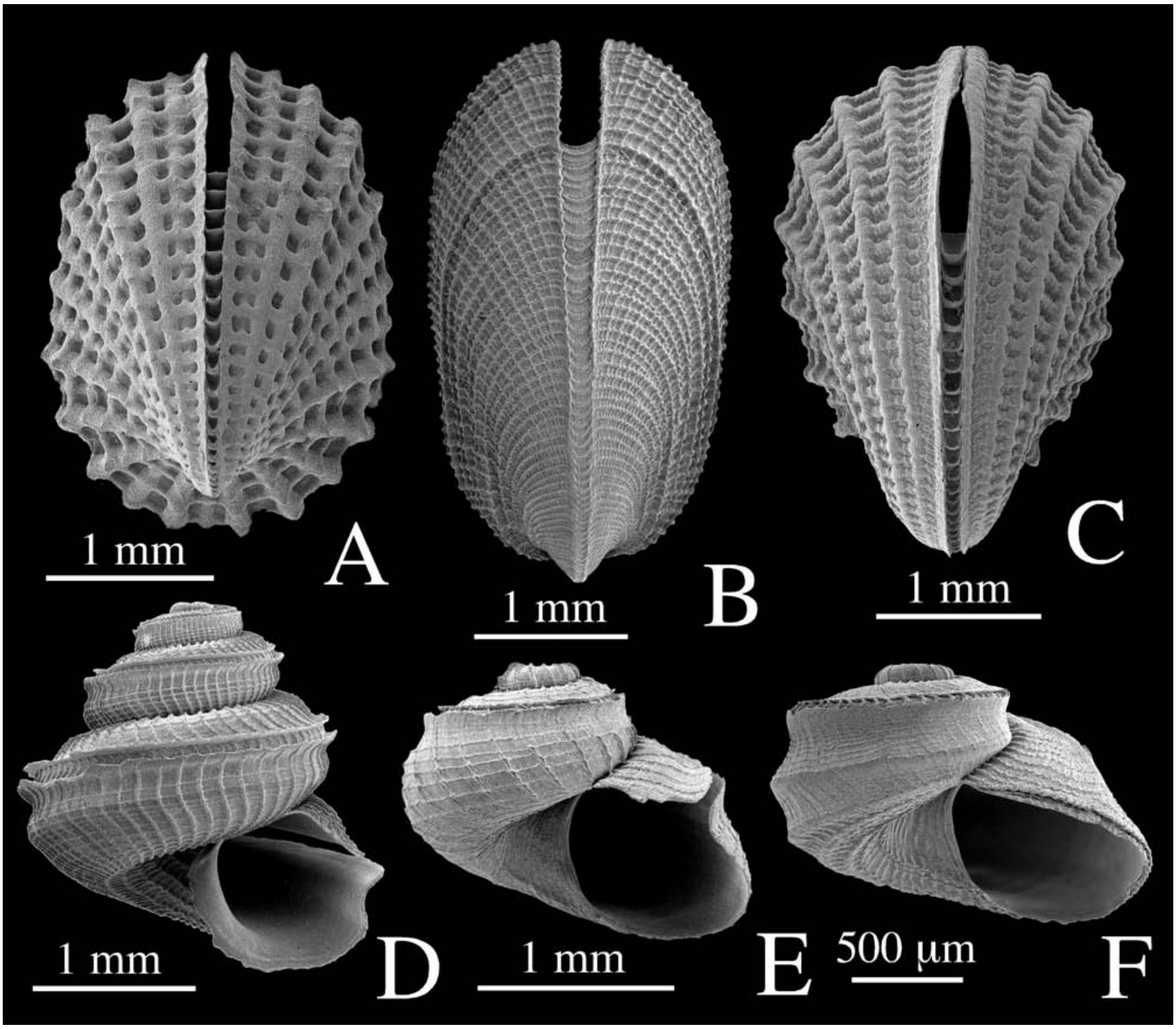


Figure 2. Vetigastropoda (1). **A–C.** Fissurellidae. **A.** *Emarginula* aff. *concinna* A. Adams, 1852. **B.** *Zeidora* sp. **C.** *Cranopsis pileolus* A. Adams, 1860. **D.** Anatomidae, *Anatoma munieri* (Fischer, 1862). **E–F.** Scissurellidae. **E.** *Scissurella staminea* (A. Adams, 1862). **F.** *Sukashitrochus carinatus* (A. Adams, 1862). Locality data: **A.** R/V *Shinyo-Maru*, station 1997-2, off Ogasawara Islands, 70–68 m, 27°47.72'N, 142°02.97'E–27°47.76'N, 142°02.90'E, Oct. 15, 1997, UMUT RM28752. **B.** Kushibaru, Aka Island, Okinawa, 7 m deep by diving, Sep. 30, 1997, UMUT RM28751. **C.** R/V *Tansei-Maru*, cruise KT-98-17, station 3, off Ashizuri-Misaki, 140–145 m, 32°38.57'N 132°47.55'E–32°38.541'N 132°47.204'E, Sep. 26, 1998, UMUT RM29576. **D.** R/V *Tansei-Maru*, cruise KT-05-30, station KM3(1), off Kushimoto, Wakayama, 95.19–96.36 m, 33°26.18'N, 135°43.64'E–33°26.27'N, 135°43.50'E, Nov. 25 2005, UMUT RM29577. **E.** R/V *Tansei-Maru*, cruise KT-05-30, station KM3(1), off Kushimoto, Wakayama, 95.19–96.36 m, 33°26.18'N, 135°43.64'E–33°26.27'N, 135°43.50'E, Nov. 25 2005, UMUT RM 29578. **F.** R/V *Shinyo-Maru*, station 1997-10, off Ogasawara Islands, 55–59 m, 27°06.35'N, 142°10.48'E–27°06.35'N, 142°10.28'E, Oct. 16, 1997, UMUT RM29579.

and is generally difficult to collect. It has not been sufficiently studied taxonomically in Japan. The Addisoniidae, Bathyphytophilidae, Caymanabyssiidae and Osteopeltidae (see Bouchet *et al.* 2005: 243–244), are not known from Japanese waters.

Lepetellidae (Fig. 3A)**.** Lepetellids have been unrecorded from Japan to date in literature, but an empty shell of a possible member of this family was collected from Tosa Bay (*Lepetella* sp.: Fig. 3A). The species is tall, its aperture is not planar, and the overall shell morphology is similar to that of *Lepetella* in Europe (see Warén 1972; Dantart & Luque 1994). The species possibly attaches to some biogenic substrate that has a rounded surface, but its habitat is unknown.

Lepetellidae: Choristellinae (Fig. 3B–C)**.** The 'Choristellidae' is listed as a subfamily of the Lepetellidae by Bouchet *et al.* (2005: 243). In general *Choristella* (Sasaki *in* Okutani 2000: 34–35; Fig. 3B–C) is known to live within shark egg cases (McLean 1992; Haszprunar 1988a). The Japanese species *Choristella vitrea* (Fig. 3B–C) grows up to 1 cm. The shell of *Granigyra nipponica* (Okutani, 1964a) is similar in outline but the species belongs in the Skeneinae. See McLean (1992) for a world-wide revision of taxonomy.

Cocculinellidae (Fig. 3D)**.** Cocculinellids are extremely rare in Japan. There has hitherto been only a single record of *Cocculinella minutissima* (E.A. Smith, 1904), by Habe *et al.* (1986), and this species has never been collected alive in Japan. Figure 3D represents an additional record from Tosa Bay, also a dead shell. Marshall (1983) figured the radular morphology of this species and Haszprunar (1988b) discussed its anatomy.

Pseudococculinidae. The shells of this family are very similar to those of the Cocculinidae in overall morphology but the animals are distinct in radular (Hickman 1983) and anatomical characters (Haszprunar 1988c). Three Japanese species [*Pseudococculina subcingulata* (Kuroda & Habe, 1949), *Notocrator pustulosa* (Thiele, 1925) *and Copulabyssia similaris* Hasegawa, 1997] were critically revised by Hasegawa (1997a: 82–89). Until that point *P. subcingulata* and *N. pustulosa* had been treated as belonging respectively to the Cocculinidae and Phenacolepadidae.

Pyropeltidae. The Pyropeltidae is one of the vent-endemic limpet families proposed in the 1980s (McLean & Haszprunar 1987). There are two described species in Japan (Sasaki *et al.* 2003, 2005, in press).

Neomphalidae. The superfamily Neomphaloidea (= Neomphalina) (Bouchet *et al.* 2005: 244) is one of the major groups that are almost absent from the Japanese fauna. The only known species *is Retiskenea deploura* Warén & Bouchet, 2001 from cold seeps in the Japan Trench at 5,343–6,920 m (*e.g.,* Okutani & Fujikura 2002; see Sasaki *et al.* 2005 for summary of records). There are no recorded Japanese species in the Melanodrymiidae or Peltospiridae.

Scissurellidae (Fig. 2E–F)**.** The family Scissurellidae generally comprises species smaller than 6 mm. In Japan, a very limited number of species have been recorded in the genera *Scissurella* (Fig. 2E), *Sukashitrochus* (Fig. 2F) and *Sinezona* (Okutani & Hasegawa *in* Okutani 2000: 36–37). *Trogloconcha*

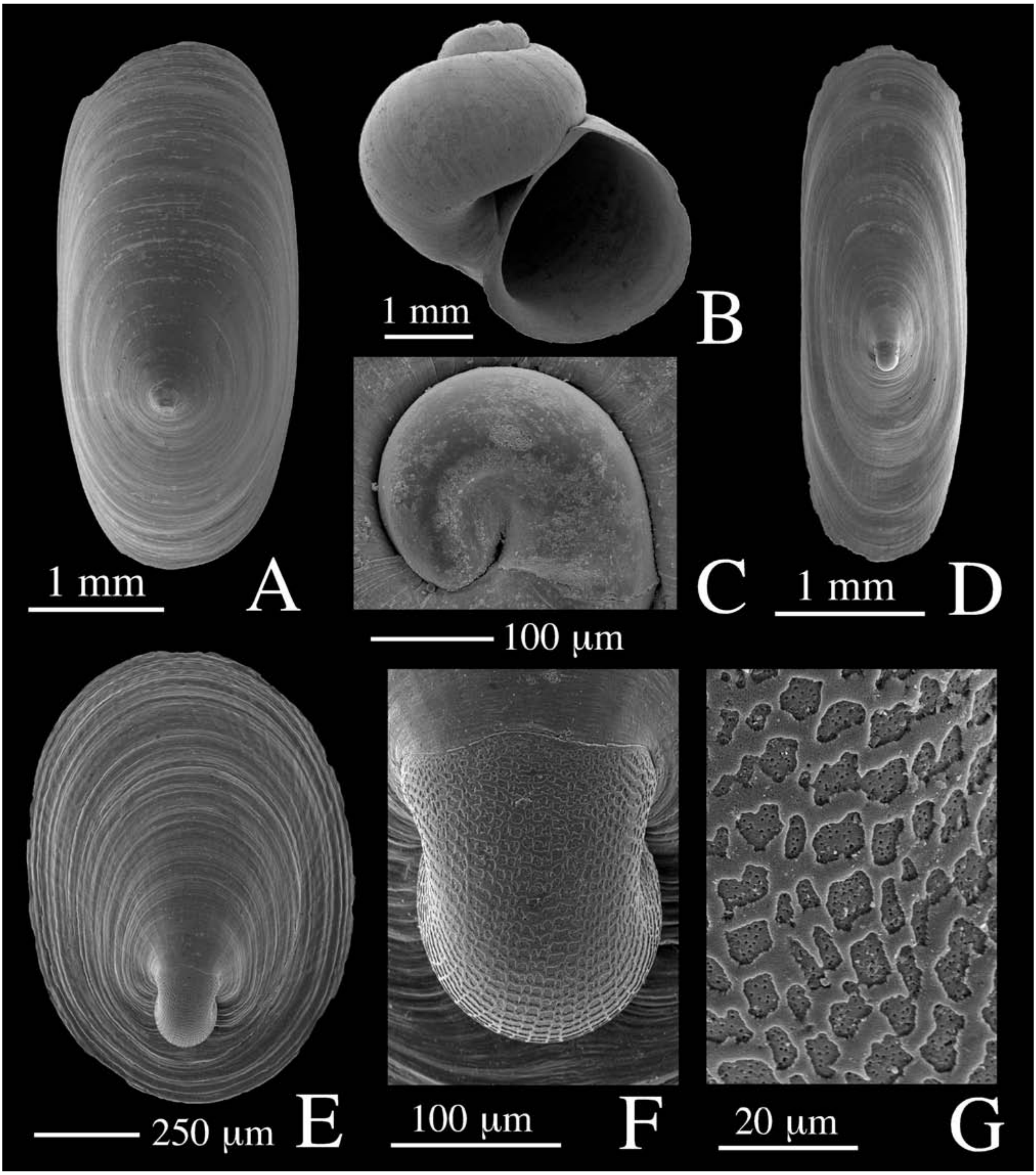


Figure 3. Vetigastropoda (2) and Cocculiniformia. **A.** Lepetellidae, *Lepetella* sp. **B–C.** Choristellinae of Lepetellidae, *Choristella vitrea* (Kuroda & Habe, 1971). **C.** Protoconch. **D.** Cocculinellidae, *Cocculinella minutissima* (E.A. Smith, 1904). **E–G.** Cocculinidae, *Cocculina* sp. **E.** Protoconch. **F.** Enlargement of protoconch sculpture. Locality data: **A.** R/V *Tansei-Maru*, cruise KT-05-30, station OS1(2), off Okinoshima Island, Kochi, 131.4–136.4 m, 32°43.95'N, 134°41.99'E–32°43.98'N, 132°41.80'E, Nov. 22 2005, UMUT RM29580. **B–C.** Off Ushibuka, Kumamoto, depth unknown, from shark egg case. **B.** UMUT RM29581. **C.** UMUT RM29582. **D.** R/V *Tansei-Maru*, cruise KT-98-17, station 3, off Ashizuri-Misaki, 140–145 m, 32°38.57'N 132°47.55'E–32°38.541'N 132°47.204'E, Sep. 26, 1998, UMUT RM29583. **E–G.** Off Saga, Kochi Prefecture, depth unknown, from sunken wood, Nov. 6, 1998, UMUT RM28757.

is a specialized genus from submarine caves (Kase & Kano 2002). The taxonomy of the Japanese scissurellid species was once revised by Habe (1951a) but needs reinvestigation in the context of world-wide revisions (*cf.* Geiger 2003, 2004b, 2006a; Zelaya & Geiger 2007).

Hasegawa (2004) reported the occurrence of an undescribed swimming species of the Scissurellidae, which was collected by a light trap in southwestern Japan (*cf.* also Hickman & Porter 2007 for similar examples). Scissurellids can be mainly collected from the intertidal to shallow subtidal zones. The species from shallow-water subtropical regions are particularly poorly studied.

Anatomidae (Fig. 2D)**.** The Anatomidae were traditionally included in the Scissurellidae but have been separated based on the results of molecular phylogenetic analyses (Geiger & Thacker 2005). The habitat of *Anatoma* is from the lower subtidal zone to the abyssal plain, but the genus has been insufficiently investigated in Japan. The taxonomy of this group also should be completely revised in accordance with world-wide revisions (*cf.* Geiger 2004a; 2006a,b,c; Zelaya & Geiger 2007). For example, the well-known species *Anatoma turbinata* (A. Adams, 1862) was revealed to be a junior synonym of *Anatoma munieri* (Fischer, 1862) by Geiger (2006a).

Seguenziidae (Fig. 4A–B)**.** This family is diversified at the bathyal and deeper levels (Okutani 2000: 86–87; *cf.* also Marshall 1991). The Japanese species are smaller than 5 mm except those in *Basilissa* (*e.g.*, *Basilissa superba* Watson, 1879: Okutani 1982). This family can be collected from wide geographic areas with muddy sediments, but its taxonomy is still unsettled. For example, unidentified species of *Seguenzia* and *Halystina* were reported by Sasaki (1998: fig. 66), Hasegawa (2001: pl. 1, figs K–N) and Hasegawa (2005: fig. 5E–F).

TROCHOIDEA. The superfamily Trochoidea is the largest group in the Vetigastropoda. Recent phylogenetic analyses suggest the necessity of conceptual changes in family level relationships and systematics (Hickman & McLean 1990; Williams & Ozawa 2006; Bouchet *et al.* 2005: 245; Kano 2008).

Trochidae (Fig. 4C–D)**.** Small species occur in several genera in the Japanese trochids (Sasaki *in* Okutani 2000: 54–83).

The genus *Margarites* is of variable size, with a maximum of up to 15 mm in adults. The smallest Japanese species, *Margarites margaritiferus* Okutani, 1964, from the bathyal zone, is below 3 mm (Sasaki *in* Okutani 2000: 61). This genus apparently contains several undescribed species in Japan.

Alcyna ocellata A. Adams, 1860 (less than 3–4 mm in height: Fig. 1A–B) is similar to *Tricolia* (Fig. 4G) in shell shape but distinct in the presence of a columellar process and a non-calcareous operculum. Its morphology is one unusual example of determinate growth in the Trochoidea.

The genus *Lirularia* is a typical micromollusc of the intertidal zone. *Lirularia iridescens* (Schrenck, 1863) is found on algae in cold-water regions, and *L. pygmaea* (Yokoyama, 1922) (Sasaki *in* Okutani 2000: 76) is attached to seagrass in temperate areas. There seem to be a few more as yet unnamed species in this genus (*e.g.*, Fukuda *et al.* 2000).

The genus *Conotalopia* (Sasaki *in* Okutani 2000: 81) also needs further investigation. In particular, the species in the subtidal zone are little known. For example, a possibly undescribed species was figured by Hasegawa *et al.* (2001: fig. 2) and Hasegawa (2006: fig. 2E–F). *Conotalopia minima*

Golikov, 1967, is relatively common in the intertidal zone of temperate areas, but its occurrence was first noticed by Ekawa only recently (1993b).

Small species can also be found in more uncommon genera. *Roya eximia* (Nevill, 1869) (Sasaki *in* Okutani 2000: 70) is a small trochoidean limpet and is very rare. The related genus *Broderipia* is more

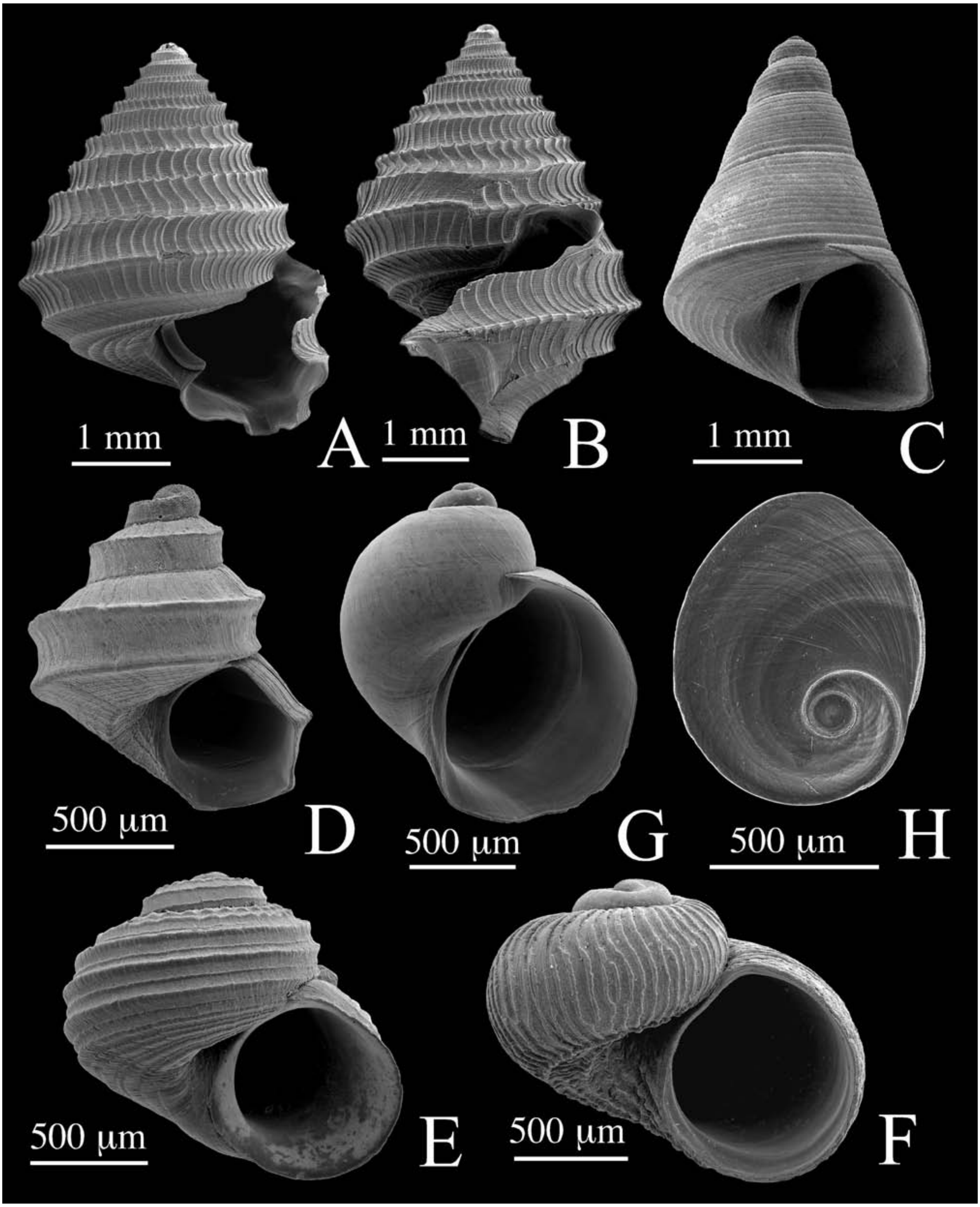


Figure 4 (previous page)**.** Vetigastropoda (3). **A–B.** Seguenziidae, *Seguenzia mirablis* Okutani, 1964. **C–D.** Trochidae. **C.** *Komaitrochus pulcher* Kuroda & Iw. Taki, 1958, juvenile. **D.** *Conotalopia minima* Golikov, 1967. **E–F.** Turbinidae. **E.** *Leptothyra rubricincata* (Mighels, 1845). **F.** *Moelleria* sp. **G–H.** Phasianellidae, *Tricolia variabilis* (Pease, 1860). **H.** Inner veiw of operculum. Locality data: **A–B.** R/V *Tansei-Maru*, cruise KT-99-06, station 15, southeast off Kamogawa, Chiba, 2089–2096 m, 34°43.56'N, 140°44.359'E–34°43.43'N, 140°41.47'E, May 22, 1999 **A.** UMUT RM28756. **B.** UMUT 29584. **C.** R/V *Tansei-Maru*, cruise KT-05-30, station SS4(2), off Shirahama, Wakayama, 27.68–35.29 m, 33°37.43'N, 135°22.09'E–33°37.31'N, 135°21.85'E, Nov. 26 2005, UMUT RM29585. **D.** Mitsuishi, Manazuru, Kanagawa, intertidal zone, May 17 2003, UMUT RM29586. **E.** Agonohama, Aka Island, Okinawa, Sep. 29, 1997, UMUT RM29587. **F.** R/V *Tansei-Maru*, cruise KT-97-15, station HY2(2), off Matsumaekojima Island, southern Hokkaido, 127–136 m, 41°22.251'N, 139°55.178'E–41°22.170'N 139°55.081'E, June 11, 1997, UMUT RM29588. **G–H.** Mitsuishi, Manazuru, Kanagawa, intertidal zone, May 17 2003. **G.** UMUT RM29589. **H.** UMUT RM29590.

common and can be collected in grooves on rock platforms. *Synaptocochlea pulchella* (A. Adams, 1850) (3 mm in width) is stomatellid-like but bears an operculum (Sasaki *in* Okutani 2000: 56).

The identification of juvenile trochids is a difficult problem. Currently, there are no clear criteria to distinguish juveniles of most trochids by shell morphology, although they are frequently abundant in unsorted micromollusc samples. In particular, juveniles of *Chlorostoma* (Sasaki 1998: fig. 54a–c) and *Cantharidus* (Sasaki 1998: fig. 59e–h) are predominant everywhere in rocky intertidal zones, and there are a few sympatric species.

Turbinidae (Fig. 4E–F)**.** The family has mostly large and robust shells (*e.g.*, *Turbo* and *Bolma*). One representative small species *Leptothyra rubricincata* (Mighels, 1845) (Fig. 4E) is widely distributed in the tropical to subtropical Pacific. It has a conspicuously reddish shell, but was known from Japan before being reported by Ekawa (1990).

A species of *Moelleria* (Fig. 4F; *cf.* McLean & Hickman 1990; Warén 1991) was collected from off northern Japan, and this is the second record of the genus from Japan. *Moelleria* sp. reported from Sagami Bay (Hasegawa 2006: fig. 3C) has a more prominently elevated apex.

Turbinidae: Skeneinae (Fig. 5)**.** The so-called ‘‘Skeneidae’’ or skeneimorph gastropods are one of the least studied groups in the Vetigastropoda. This group was recently listed as a subfamily of Turbinidae by Bouchet *et al.* (2005: 245). The taxon is a possibly polyphyletic assemblage of small trochoid shells without nacreous structure (see Hickman & McLean 1990; Warén 1991). The members are all small and white, without color patterns.

Skeneines can be found in various environments from shallow water to bathyal depths (Hasegawa *in* Okutani 2000: 82–87). In the intertidal and adjacent subtidal zones, *Leucorhynchia* (Fig. 5A–B) is the most typical group in the subtropical islands. A similarly low-spired species, *Cyclostremisus emeryi* (Ladd, 1966) was first reported from Japan by Fukuda (1993) and later by Sasaki (1998: fig. 61).

Munditiella ammonoceras (A. Adams, 1863) (Fig. 5C) has a flat shell with prominent axial ribs. It is uncommon but collectable from the undersides of boulders in the lower intertidal zone from temperate to subtropical regions.

Species of *Conradia* (Fig. 5D) are distributed from the shallow to middle subtidal zones, and all are rarely collected alive. *Conradia doliaris* A. Adams, 1863, is variable in sculpture (see Ekawa 1989).

Crossea miranda A. Adams, 1865, (Fig. 5E) from around 100 m depth, is an unusual species in that it has varices. The positions of the varices are not synchronized (*cf.* Savazzi & Sasaki 2004 for synchronization) or even constant among individuals.

It is still uncertain whether the true *Skenea*, the type genus, occurs in Japan, because neither the radula nor the anatomy of any Japanese species havebeen compared with those of the type species from Europe. Hasegawa (2006: fig. 3A) identified one undescribed species as *Skenea* sp. based on the similarity in shell morphology to northen Atlantic *Skenea trochoides* (Friele, 1874).

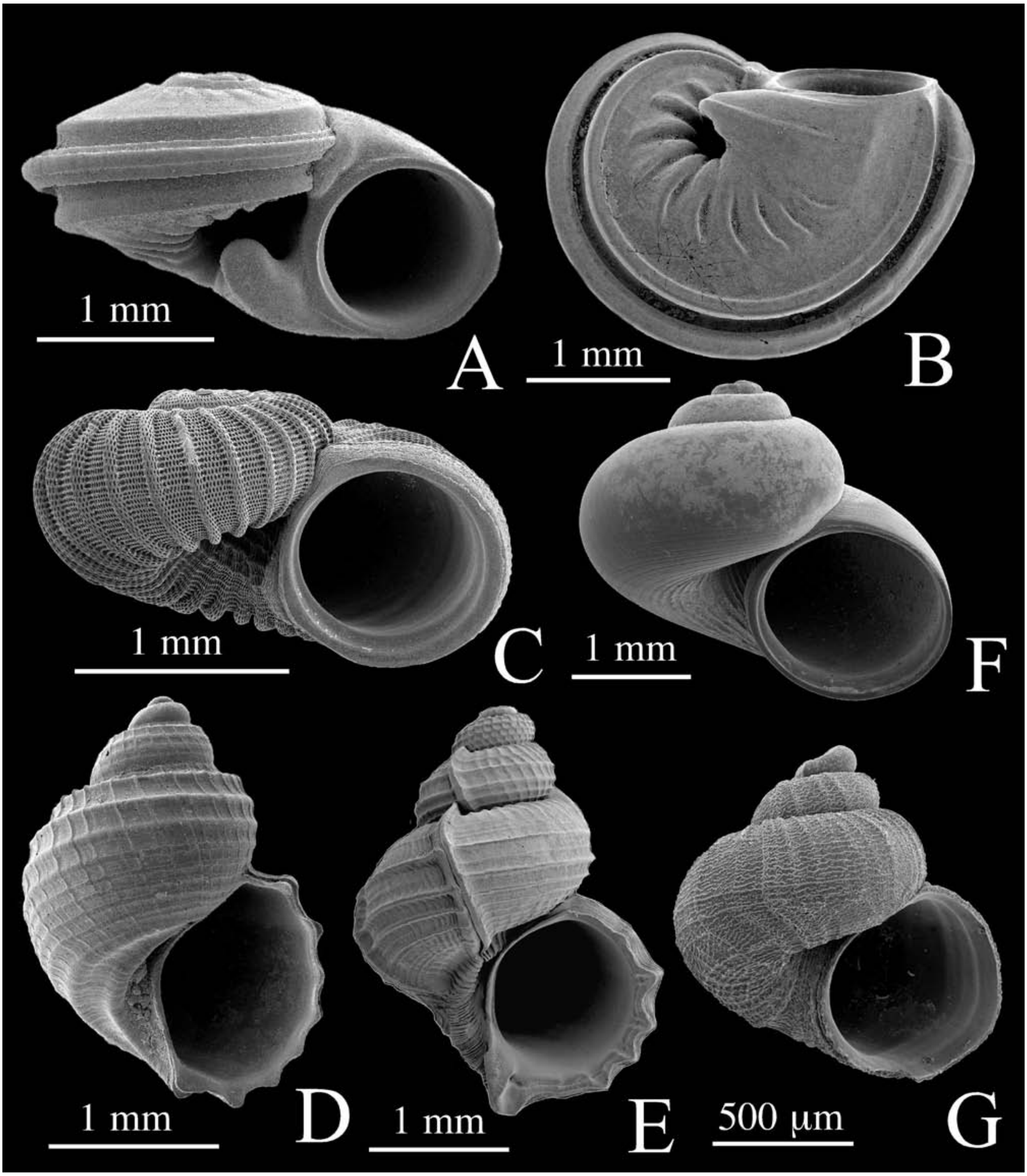


Figure 5 (previous page)**.** Vetigastropoda (4). **A–G.** Skeneinae of Turbinidae. **A–B.** *Leucorhynchia tricarinata* Melvill & Standen, 1896. **C.** *Munditiella ammonoceras* (A. Adams, 1863). **D.** *Conradia doliaris* A. Adams, 1863. **E.** *Crossea miranda* A. Adams, 1865. **F.** *Cirsonella* sp. **G.** Gen. et sp. Locality data: **A–B.** Kushibaru, Aka Island, Okinawa, 7 m deep, Sep. 30, 1997. **A.** UMUT RM28754. **B.** UMUT RM28755. **C.** R/V *Shinyo-Maru*, station 1997-10, off Ogasawara Islands, 55–59 m, 27°06.35'N, 142°10.48'E–27°06.35'N, 142°10.28'E, Oct. 16, 1997, UMUT RM29591. **D.** Nagahama, Maizuru, Kyoto, beach-drifed, Oct. 16 2004, UMUT RM29592. **E.** R/V *Shinyo-Maru*, station 1997-12, off Ogasawara Islands, 150–160 m, 27°11.99'N, 142°09.18'E–27°11.75'N, 142°08.92'E, Oct. 16, 1997, UMUT RM28753. **F.** R/V *Tansei-Maru*, cruise KT-00-05, station 1, southeast off Kamogawa, Chiba, 240–273 m, 34°59.963'N, 140°27.159'E–35°00.020'N, 140.28.427'E, May 17, 2000, UMUT RM29593. **G.** R/V *Tansei-Maru*, cruise KT-01-08, station TK-4, off Chiba, 2,234–2,240 m, 34°42.350'N, 140°45.820'E–34°41.220'N, 140°44.600'E, June 23, 2001, UMUT RM29594.

Sunken wood in the lower subtidal to bathyal zone is known as a major habitat of specialized genera. For example, Hasegawa (1997a) reported six species from Suruga Bay, in the genera *Dilwynella* (four species), *Bathyxylophila* (one species) and *Leptogyropsis* (one species). Most confusingly, *Leptogyropsis inflata* Hasegawa, 1997 is very similar to the vitrinellid *Ponderinella major* Hasegawa, 1997 (Hasegawa 1997a: figs 25, 28).

In the bathyal zone, some rare species can be occasionally collected, but they have been little studied in Japan taxonomically (*cf. e.g.*, Hasegawa 2005: fig. 5A, B). In one described deep-sea species, *Granigyra nipponica*, the surface is roughened with minute vermicular granules. Figure 5F shows one example of an unidentified species from the bathyal zone (ca. 2,200 m).

Phasianellidae (Fig. 4G–H)**.** Species of *Tricolia* (Fig. 4G) were clearly diagnosed in the world-wide revision by Robertson (1985). In this genus, sexual dimorphism is common both in shell and radular characters (Robertson 1985, 1997). The Japanese *T. variabilis* (Pease, 1860) and *T. oligomphala* (Pilsbry, 1895) were once treated as separate species due to clear differences in shell shape (*e.g.*, Kuroda *et al.* 1971), but in fact *T. oligomphala* is the female of the broader male called *T. variabilis*. This case shows how careful biological studies can influence the taxonomy of micromolluscs. Among *Tricolia*-related groups, the occurrence of *Gabrielona* in Japan was first reported by Hasegawa (1997b).

COCCULINIFORMIA. Two families are included in this clade (Bouchet *et al.* 2005: 245). The occurrence of the Bathysciadiidae has not yet been unquestionably confirmed from Japan, although there is a single record in literature (*Bonus petrochenckioi* Moskalev, 1973: Higo *et al.* 1999: G544 based on Moskalev 1973).

Cocculinidae (Fig. 3E–G)**.** In the earlier period of Japanese malacology, pale limpets from lower subtidal or deeper levels were all identified as *Cocculina*. Kuroda & Habe (1949) described Japanese species mainly on shell characters, and their species comprised heterogeneous groups of patelliform gastropods. Up to now nine species have been described in the family in Japan (Higo *et al.* 1999: G535–543). Most importantly, Hasegawa (1997a) intensively investigated the species of *Cocculina* (*C. tenuitesta* Hasegawa, 1997, *C. surugaensis* Hasegawa, 1997, and *C.* cf. *pacifica* Kuroda & Habe, 1949, *C.* sp.) as well as *Coccopigya* [*C. punctoradiata* (Kuroda & Habe, 1949), *C. okutanii* Hasegawa, 1997, *C.* sp.], illustrating the shell, radula and external anatomy using an SEM. Additional distributional records were given by Hasegawa (2001, 2005), and the internal anatomy was described by Sasaki (1998).

NERITIMORPHA. The Neritimorpha is a clade that has most successfully adapted to a wide range of habitats from terrestrial to deep-sea communities. The Recent species are classified in nine families (Bouchet *et al.* 2005: 246). The phylogenetic relationships among neritimorphs were best analyzed by Kano *et al.* (2002) based on molecular data of all major subgroups. A close correlation between the mode of development and opercular nucleus morphology was revealed by Kano (2006).

Helicinidae. The species in Japan are less diverse than in tropical regions and they are grouped into three genera. The species of *Waldemaria* in temperate areas are 7–15 mm in shell width; *Aphanoconia* in the Ryukyu Islands are 3.4–6.5 mm; *Ogasawarana* are 3.7–6.1 mm (Azuma 1995: 183–184). The genus *Ogasawarana* is one of the major land snail groups that are endemic to the Ogasawara Islands and consists of as many as 14 species (Minato 1980a; Azuma 1995). They are now seriously endangered or already extinct due to habitat destruction.

Neritiliidae (Fig. 6A–B)**.** The family Neritiliidae had been included in Neritidae for a long time (*e.g.*, Sasaki 1998). Before the late 1990s little attention had been paid to this group, but Dr. Yasunori Kano revealed a surprising diversity and greatly advanced the knowledge of their taxonomy, anatomy and molecular phylogeny (Kano & Kase 2000a,b, 2001, 2002, 2003, 2004, 2008; Kano *et al.* 2001, 2003).

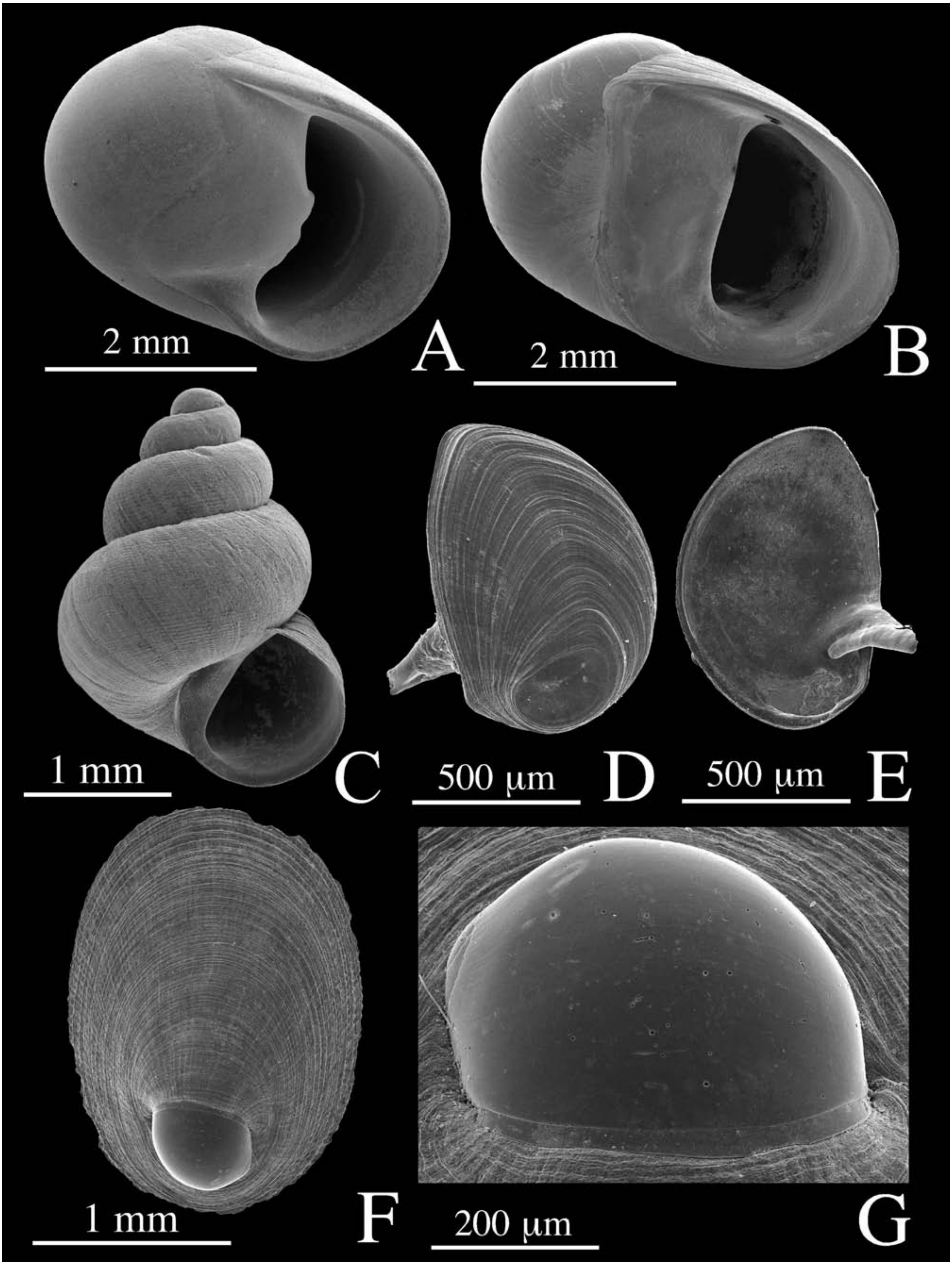
The family comprises four Recent genera in Japan (*Neritilia*, *Pisulina*, *Platinerita* and *Laddia*: Kano 2006, 2008). *Pisulina* has a thickened, polished shell with prominent columellar denticles (Fig. 6A). The species from the Indo-Pacific region had been identified as *P. adamsiana* G. & H. Nevill, 1869 (*e.g.*, Fukuda 1993; Sasaki 1998 in Japan), but Kano & Kase (2000b) revealed that it is a complex of four distinct species. Before being discovered in submarine caves, *Pisulina* was an enigmatic gastropod that had never been collected alive (Kano & Kase 2000b, 2002).

The genus *Neritilia* has a thinner shell than *Pisulina*, that lacks columellar teeth. Members of the genus are also typical of cryptic environments such as the undersides of stones in rivers and estuaries, interstices under rocks in the intertidal zone, and anchialine lakes, which are connected to the sea below ground. An unidentified species was even collected from an underground well 12 km from the seashore (Sasaki & Ishikawa 2002), and this was the first record of the Neritimorpha from phreatic communities. Additional species in this genus might remain to be discovered in cryptic environments. For a list of known species, see Kano (2006).

The genus *Platynerita* is distinguished from *Pisulina* by the paucispiral operculum and characteristic denticles in the marginal teeth (Kano & Kase 2003). The *Laddia* was separated from the other

Figure 6 (next page)**.** Neritimorpha. **A–B.** Neritiliidae. **A.** *Pisulina biplicata* Thiele, 1925. **B.** *Neritlia rubida* (Pease, 1865). **C–E.** Hydrocenidae, *Georissa shikokuensis* Amano, 1939. **D.** Exterior of operculum. **E.** Interior of operculum. **F–G.** Phenacolepadidae, *Phenacolepas* sp. **G.** Enlargement of Protoconch. Locality data: **A.** Tokashiku Beach, Tokashiki Island, Okinawa, beach-drifed, Mar 13–27, 1990, UMUT RM28758. **B.** Fukido River, Ishigaki Island, Okinawa, Apr. 2002, UMUT RM28759. **C–E.** Omine, Mine, Yamaguchi, Dec. 15, 1993, limestome area. **C.** UMUT RM29595. **D.** UMUT RM29596. **E.** UMUT RM29597. **F–G.** Koajiro Bay, Kanagawa, dredged empty shell, Nov. 12 2001, UMUT RM29598.

genera mainly based on fine spiral ridges on the early teleoconch and the absence of a protuberance in the aperture (Kano & Kase 2008).



Neritidae. This is the most diversified neritimorph family in Japan. The shells of most species are medium-sized (1–3 cm) but *Smaragdia* is smaller (Tsuchiya *in* Okutani 2000: 101–109).

All species of *Smaragdia* are known to occur on sea grass. *Smaragdia paulucciana* Gassies, 1870, (Fukuda *in* Wada *et al.* 1996: pl. 1, fig. 10; but treated as *Clithon* by Komatsu 1986) is distributed on subtropical islands and southwards. Another unidentified species (*Smaragdia* sp.: Fukuda *in* Wada *et al.* 1996: pl. 1, fig. 11) is said to live on sea grass in temperate areas but is uncommon.

Hydrocenidae (Fig. 6C–E)**.** This terrestrial group is particularly small in size (below 3 mm in height for Japanese species). Only four species (*Georissa japonica* Pilsbry, 1900, *G. hukudai* Kuroda, 1960, *G. shikokuensis* Amano, 1939, and *G. luchana* Pilsbry, 1901) have been described from Japan (Habe 1951b; Minato 1980b; Azuma 1995: 1), and they are irregularly distributed over temperate to subtropical islands. Their protoconch is unique (Sasaki 1998: fig. 87), and the operculum has a peg like that in the Neritidae (Fig. 5D–E; *cf.* Sasaki 2001 for the operculum structure of *Nerita*).

Phenacolepadidae (Fig. 6F–G)**.** The shell is limpet-shaped. Species diversity is highest in subtropical to tropical waters, and it is highly likely that there are more unrecognized small species in this family. The habitat is exclusively cryptic, most typically below half-buried boulders in most species. In southern Japan, one unidentified species was found in the burrows of crustaceans (Kano 2007). The live animal is vividly red (Kimura & Kimura 1999; Fukuda *et al.* 2000) and contains discoidal blood cells (Sasaki 1998: fig. 85d). Because of the specialized habitat, many species are rarely collected alive. The genus *Shinkailepas* is a separate subgroup endemic to hydrothermal vents (Sasaki *et al.* 2003, 2006). The protoconch is smooth and globular (Fig. 6G). The internal whorls of the protoconch are resorbed (Sasaki 1998: fig. 86d).

CAENOGASTROPODA. This is a large clade comprising the Architaenioglossa and Sorbeoconcha. Based on the results of phylogenetic analysis (Ponder & Lindberg 1997), the large clade Sorbeoconcha is defined as comprising the superfamily Cerithioidea + superfamily Campaniloidea + clade Hypsogastropoda. The Hypsogastropoda in turn comprises the clade Littorinimorpha + ‘Ptenoglossa’ + clade Neogastropoda. See Ponder *et al.* (2008) for a review of earlier and more recent hypotheses regarding caenogastropod phylogeny.

ARCHITAENIOGLOSSA. This is a possibly a non-monophyletic group, living in non-marine environments. Ten Recent families are recognized in three superfamilies: the Ampullarioidea, Cyclophoroidea and Viviparoidea (Bouchet *et al.* 2005: 247–248). Among their families, the Cyclophoridae (which includes the Alycanae) and Diplommatinidae are important groups with regard to Japanese micromolluscs.

Cyclophoridae (Fig. 7A)**.** The family consists of the genera *Leptopoma*, *Cyclophorus, Japonia, Spirostoma, Platyrhaphe, Cyclotus, Nakadaella, Cyathopoma* and *Nobuea* in the Japanese fauna. Among these, *Nakadaella* [two species: *N. micron* (Pilsbry, 1900) in Fig.7A and *N. ogaitoi* Minato, 1988] are the smallest in the family and also among land snails in Japan: the shell width is below 2 mm. *N. ogaitoi* is separable from *N. nakadai* in having a disjunct body whorl (Minato 1988b).

The genus *Cyathopoma*, also about 2 mm in diameter, differs from *Nakadaella* in having 5–6 spiral cords. The only Japanese species (*C. nishinoi* Minato, 1980) is distributed in the Amakusa Islands in western Japan, and related species are known from Taiwan (Minato 1980c).

Nobuea kurodai Minato & Tada, 1978 (5.5 mm in width) was described as a member of the Diplommatinidae (Minato & Tada 1978) because of the presence of dense axial ribs, but was later transferred to the Cyclophoridae (Minato & Nishi 1996).

All species of *Japonia* are 4–5 mm. The shell is covered with a thick periostracum, and each species is diagnosed primarily by the detailed morphology of the long periostracal hairs (*e.g.*, Minato 1985).

Cyclophoridae: Alycaenae (Fig. 7B)**.** This group has been treated as an independent family by Japanese malacologists, but is now considered a subfamily of Cyclophoridae (Bouchet *et al.* 2005: 248). The shell is characterized by a vermicular tube and a constriction in the body whorl; the function of this unusual morphology has not been identified, and the growth process has not been described in literature.

This group is highly diversified in the Japanese main islands and the Ryukyu Islands, and more than 43 nominal species have been described (Higo & Goto 1993: no. 761–803). Most were described in the 1980s or earlier, but new species can still be discovered (*e.g.*, Minato 2005). There are three genera in Japan: *Chamalycaeus*, *Cipangocharax* and *Awalycaeus*. All are smaller than 6 mm; most species are less than 4 mm.

Diplommatinidae (Fig. 7C–D)**.** The family is composed entirely of small-sized species. Most Japanese species are allocated to the genus *Diplommatina*. The genus *Arinia*, with a single species *A. japonica*, is diagnosed by well-swollen whorls; the genus *Palaina* is sinistral in contrast to the dextral species of the other genera (Azuma 1995: pls. 5–7). Nearly 80 nominal species have been cited in Japan (Higo & Goto 1993: no. 813–889).

CERITHIOIDEA. The superfamily is one of the basal groups of the Sorbeoconcha (Ponder & Lindberg 1997; Bouchet *et al.* 2005: 248–249). Small species are found in the families Planaxidae, Dialidae, Litiopidae and Scaliolidae, and in part of the Cerithiidae. There are no micromolluscs in the Batillariidae, Melanopsidae, Modulidae, Pleuroceridae, Potamididae, Siliquariidae or Turritellidae.

Cerithiidae (Fig. 8A)**.** This family is most intensively diversified in tropical regions and also extends to warm temperate areas. Representatives are found mostly in shallow water habitats, with a few exceptions [*e.g.*, *Cerithium ophioderma* (Habe, 1968) from 50–275 m: Hasegawa *in* Okutani 2000: 118]. Most members of the major genera, *Cerithium*, *Clypeomorus* and *Rhinoclavis*, are large and robust (1.5–7 cm in height).

Species in the genus *Argyropeza* are 4 or 5 mm in height (except *A. divina* Melvill & Standen, 1901, at 7 mm: Hasegawa *in* Okutani 2000: 123–125). *Argyropeza verecunda* (Melvill & Standen, 1903) was first recorded by Tamura & Okutani (1989) from Japan, and now four species are known in the genus.

Bittium and related genera have been classified separately in the past but are now treated as members of Cerithiidae (Houbrick 1993). The species of *Bittium*, *Ittibittium* and *Cerithidum* attain 5–7 mm or less (Hasegawa *in* Okutani 2000: 124–125).

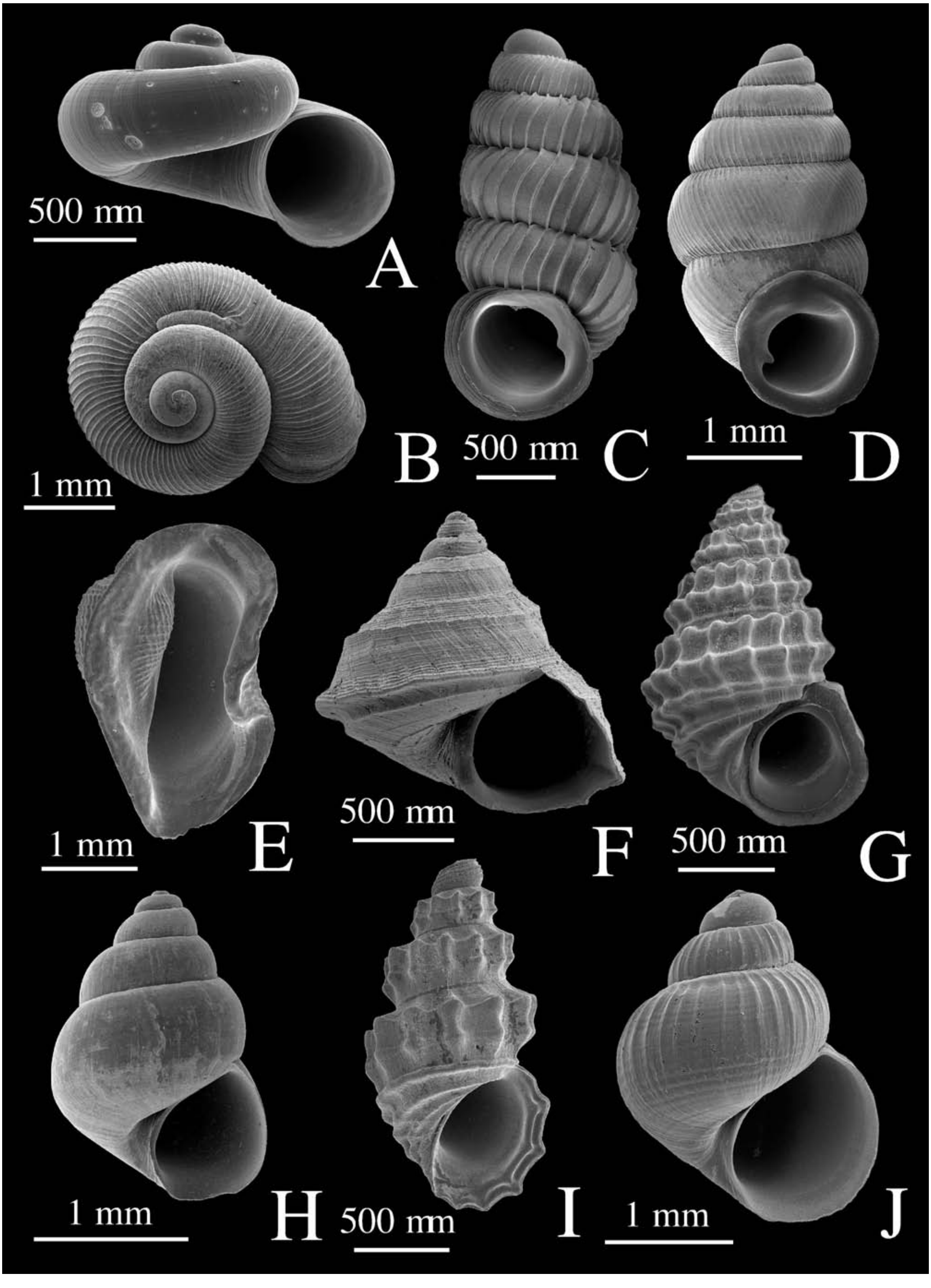

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Figure 7 (previous page)**.** Taenioglossate Caenogastropoda (1). **A.** Cyclophoridae, *Nakadaella micron* Pilsbry, 1900. **B.** Alycaeidae, *Chamalycaeus oshimanus* (Pilsbry & Hirase, 1904). **C–D.** Diplommatinidae. **C.** *Palaina paucicostata* Pilsbry & Hirase, 1905. **D.** *Diplommatina kyushuensis* Pilsbry & Hirase, 1904. **E.** Pediculariidae, *Pedicularia* sp. **F.** Littorinidae, *Peasiella conoidalis* (Pease, 1868). **G.** Pickworthiidae, *Sansonia iredalei* (Bavay, 1922). **H–J.** Rissoidae. **H.** *Voorwindia* sp. **I.** *Merelina* sp. **J.** *Alvania flava* (Okutani, 1964). Locality data: **A.** Heta, Tokuyama, Yamaguchi, UMUT RM28766. **B.** En, Tatsugo, Amami-Oshima, Kagoshima, June 5 2000, UMUT RM28767. **C.** Sawara, Hokkaido, July 1989, UMUT RM28768. **D.** Ninomiya, Tokuji, Yamaguchi, Apr. 29, 1984, UMUT RM29599. **E.** R/V *Tansei-Maru*, cruise KT-00-05, station OS-2, west off Izu Oshima, 305–320 m, 34°44.706'N, 139°19.529'E–34°44.971'N, 139°19.538'E, May 21 2000, UMUT RM29600. **F.** Maehama, Aka Island, Okinawa, intertidal zone, Oct. 1, 1997, UMUT RM28777. **G.** Kushibaru, Aka Island, Okinawa, 7 m deep, by diving, Sep. 30, 1997, UMUT RM29601. **H.** R/V *Tansei-Maru*, cruise KT-05-30, station SS4(2), off Shirahama, Wakayama, 27.68–35.29 m, 33°37.43'N, 135°22.09'E–33°37.31'N, 135°21.85'E, Nov. 26, 2005, UMUT RM29602. **I.** Ayamaru, Kasari, Aami-Oshima, Kagoshima, intertidal zone, June 4, 2000, UMUT RM29603. **J.** R/V *Tansei-Maru*, cruise KT-05-30, station HB, Hyuga Basin, 1644.3–1656.6 m, 32°22.58'N, 132°30.54'E–32°22.61'N, 132°29.24'E, Nov. 22, 2005, UMUT RM29604.

Hasegawa (1998) revised the taxonomy of small cerithiform gastropods previously assigned to '*Eufenella'* and '*Clathrofenella'* and demonstrated that there are only two valid species of Japanese *Cerithidium*: *C. fusca* (A. Adams, 1860) and *C. perparvulum* (Watson, 1886).

Dialidae. All Japanese species of Dialidae are 5 mm or less in height and live on algae on shallow subtidal rocky shores (Hasegawa *in* Okutani 2000: 124–125). The taxonomy of the family was revised by Ponder & de Keyzer (1992), and there are three species, *Diala semistriata* (Philippi, 1849), *D. albugo* (Watson, 1886), and *D. sulcifera* (A. Adams, 1862), in Japan. For the anatomy of *Diala*, see Ponder (1991).

Litiopidae (Fig. 8B)**.** The family consists of the genera *Litiopa* and *Alba* (Hasegawa *in* Okutani 2000: 127). The genus *Litiopa* (*L. nipponica* Kuroda & Kawamoto, 1956; 5 mm in height) attaches to floating algae and other objects, and is widely distributed in oceanic warm currents. The genus *Alba* lives on algae in the intertidal zone and there are three species in Japan: *A. goniochila* (A. Adams, 1860), *A. picta* (A. Adams, 1861), and *A. hungerfordi* Sowerby, 1894. *Alba goniochila* (A. Adams, 1860) has a polished transparent shell (Fig. 8B).

Planaxidae. This group lives in the intertidal zone and has a shell height of less than 3 cm (Hasegawa *in* Okutani 2000: 129–131). Shells in the genus *Fossarus* are smaller than 5 mm; *F. trochlearis* (A. Adams, 1853) lives among byssi of the bivalves *Septifer virgatus* and *Isognomon nucleus* in the intertidal zone. *Planaxis suturalis* Smith, 1872 (8 mm in maximum height) has never been collected alive. Its pure white shell may suggest a cryptic habitat as in the Neritiliidae.

Scaliolidae (Fig. 8C)**.** All members of this family inhabit sandy bottoms in the shallow subtidal zone, and their adult shells reach 3–7 mm in height. Japanese species are assigned to two genera, *Scaliola* and *Finella*. The anatomy and relationships of the family were discussed by Ponder (1994a).

The genus *Scaliola* characteristically attaches sand grains to the shell surface. Hasegawa (1999) revised the Japanese species based on type material and redefined them as three valid species, *S. bella* A. Adams, 1860, *S. arenosa* A. Adams, 1862 and *S. glareosa* A. Adams, 1862. For fossil records and phylogeny of the genus, see Bandel & El-Nakhal (1993).

The genus *Finella* has been variously classified historically (*e.g.*, in the Finellidae or Diastomatidae). The Japanese species were revised by Hasegawa (1998) into three valid species, *F. pupoides* (A. Adams, 1860), *F. purpureoapicata* (Preston, 1905) and *F. rufocincta* (A. Adams, 1861).

CAMPANILOIDEA. Two families, the Campanilidae and Plesiotrochidae, have been considered to form a distinct clade based on uniquely shared sperm characters (Healy 1993). The only extant species of Campanilidae (*Campanile symbolicum* Iredale, 1917) grows up to 24 cm and occurs only in southwestern Australia (Houbrick 1981).

Plesiotrochidae. This family was anatomically examined in detail by Houbrick (1990). There are two Japanese species: *P. acutangulus* (Yokoyama, 1924) is 8 mm in height, and *P. souverbianus* (Fisher, 1878) is 5 mm. Both are known from algae (Hasegawa *in* Okutani 2000: 134–135, 137).

LITTORINIMORPHA. There are many micromollucs among the remaining taenioglossate families, especially in the Rissooidea. However, most of the well-known families comprise only large-sized species, including the Capulidae, Calyptraeidae, Cypraeidae, Xenophoridae, Strombidae and Vermetidae. In particular, shells in the Tonnoidea (Tonnidae, Cassidae, Ranellidae, Pisanianuridae, Personidae, Bursidae and Laubierinidae) are at least 1 cm and generally attain 10 cm or larger.

Cingulopsoidea. The Cingulopsidae (see Ponder & Yoo 1980 for revision of genera) forms the Cingulopsoidea together with the Eatoniellidae and Rastodentidae (Bouchet *et al.* 2005: 250). This rissoiform family had not been recognized at all in Japan until Fukuda *et al.* (1998) reported a new species, *Eatonia kitanagato* Fukuda, Nakamura & Yamashita, 1998. Fukuda *et al.* (2000: 127) reported two unidentified species, *Eatonina* sp. and *Tubbreva* sp., and Hasegawa *in* Okutani (2000: 146–147) added *Pseudopisinna balteata* Ponder & Yoo, 1977, as a Japanese species.

Eatoniellidae. This family was established by Ponder (1965) but it is still little-known to Japanese malacologists. The first report from Japan was an unidentified species from the Ogasawara Islands (Fukuda 1993: pl. 13, fig. 180). Fukuda *et al.* (2000: 128) also reported *Eatoniella* sp. and a species in an undescribed genus from the mainland. The species in Japan need fundamental taxonomic study and comparison with those of other western Pacific regions (*cf.* Ponder & Yoo 1978).

Ovulidae. Except for a few genera (*e.g.*, *Ovula* 3–10 cm in length, *Volva* 8 cm, and *Phenacovolva* 1.3–7 cm), most species are between 6 mm and 2 cm (*e.g.*, *Prinovolva*, *Dentiovula*, *Pseudosimnia* and *Primovula*) (Okutani & Sasaki *in* Okutani 2000: 210–223). The smallest species in Japan is *Pseudocypraea exquista* Petuch, 1979, 4 mm in length (Omi & Habu 2003).

Ovulidae: Pediculariinae (Fig. 7E)**.** The best-known Japanese species *Pedicularia pacifica* (Pease, 1865) lives attached to hydrocorals (Habe 1976a) in the lower subtidal zone and broods veliger, larvae in the pallial cavity (Omi & Sasaki 2005). A few different species might be present in Japan (Fig. 7E). Because the shell shape seems highly variable, reflecting host morphology, careful examination is required assessing in the taxonomy of this group. The record of *Pedicularia stylasteris* Hedley, 1903, var. by Habe (1955) needs reinvestigation.

Littorinidae (Fig. 7F)**.** Almost all species are abundant in the intertidal rocky shore. The genus *Littorina* generally attains 1–2 cm, but some are smaller: two unnamed species are 5 mm in length (Reid 1996; Hasegawa *in* Okutani 2000: 141). *L. horikawai* Matsubayashi & Habe, 1979 attains 7 mm but often is smaller than 5 mm locally. Other genera such as *Tectarius*, *Echinius* and *Littoraria* are all larger than 1.5 cm.

The three Japanese species in the genus *Peasiella* are 3–5 mm in width [*P. habei* Reid & Mak, 1998, *P. roepstorffiana* (Nevill, 1884) and *P. conoidalis* (Pease, 1868): Fig. 7F]. These all live in small depressions in rocks or among small barnacles and epibyssate bivalves in the upper level of the intertidal zone.

The genus *Lacuna* (3–10 mm in height) had previously been treated as separate and placed in the family Lacunidae (*e.g.*, Habe 1953) but now is considered a group within the Littorinidae. The genus is generally associated with sea grass in the shallow subtidal zone in temperate to subarctic waters.

Pickworthiidae (Figs 1E–F, 7G)**.** This family was formerly little-known in Japan. However, abundant occurrences of the genera *Sansonia, Reynellona, Microliotia* and *Ampullosansonia* were reported by Kase (1998a,b,c, 1999) from submarine caves in the subtropical to tropical regions of the western Pacific. Before his publications, only a few eroded empty shells had been known from southwestern Japan (Shikano 1990; Ekawa 1993a), and their habitat was unknown. The shells of all species of this family are pure white, and this represents a typical case in which pale color is tied to cryptic environments. A world-wide revision including Japanese species was published by Le Renard & Bouchet (2003).

Pickworthiidae: Pelycidiinae (Fig. 8D)**.** This group was described by Ponder & Hall (1983) as the family Pelycidiidae. There are two Japanese species: *Pelecydion japonica* and *P*. sp. (Hasegawa *in* Okutani 2000: 146–147), and both are rare. The former has a brown punctate protoconch, while the latter possesses a white smooth protoconch. Living specimens can rarely be obtained in Japan.

Naticidae. The smallest known species in Japan is *Naticarius pumilus* Kubo, 1997 (2–4 mm), which was described from the shallow water of Okinawa (Kubo 1997a). Other small species, *Natica buriasensis* Récluz, 1843 (Saito *in* Okutani 2000: 260) and *Sigatica bathyraphe* (Pilsbry, 1925) are 8 mm in height (Saito *in* Okutani 2000: 256). There might be more small species in this family. The recognition of adult stages is not easy, because the shell does not show determinate growth.

PTEROTRACHEOIDEA = 'HETEROPODA'. There are three holoplanktonic families in this group. The Atlantidae is one of the major components of the planktonic micromollusc assemblages. The other two families, the Carinariidae and Pterotracheidae, grow to large size. The largest species, *Carinaria cristata*, attains nearly 50 cm in body length. (Okutani 2000: 297). For general biological accounts of this group, including information on Japanese species, see Lalli & Gilmer (1989: 27–57).

Pterotracheoidea has been known as the Heteropoda, but now is regarded as one of the superfamilies in the clade Littorinimorpha (Bouchet *et al.* 2005: 251).

Atlantidae. Two genera are known in this family. In *Atlanta*, the shell is up to 11 mm wide (*A. peroni* Lesueur, 1817), though some are smaller than 2–3 mm (*e.g., A. lesueuri* Souleyet, 1852, *A. inflata* Souleyet, 1852, and *A. fusca* Souleyet, 1852). The protoconch is turrate in *Atlanta*, while it is globular and *Bellerophon*-like in *Oxygyrus*. A survey of the Japanese species was conducted by Dr. Takashi Tokioka (1955b,c, 1961), but no additional information has been published since. The atlantid species in Japan must be reinvestigated with a scanning electron microscope, as in the taxonomic revision carried out by Seapy (1990) for Hawaii.

Rissoidae (Figs 7H–J, 8E–I)**.** Shells in this family are generally 5 mm or smaller in height. The largest two species in Japan, *Rissoina gigantea* (Deshayes, 1850) and *Zebina lamellata* (Kuroda, 1960), reach 1.5 cm. Historically the family was a large mixture of various rissoiform taxa, but the genera were clearly redefined by Ponder (1985). Most of the common species were clearly illustrated by Hasegawa *in* Okutani (2000: 148–161). Before this work, Kosuge (1965a, b) described a limited number of species, and Hasegawa (2000) published a very detailed taxonomic revision of rissoids from the Seto Inland Sea.

The genus *Alvania* is one of the common members of the family. *Alvania ogasawarana* (Pilsbry, 1904) and *A. concinna* (A. Adams, 1861) are locally abundant in the temperate intertidal zone.

The genus *Rissoina* is the most diverse among the family, and *Zebina* and *Schwartziella* are also typical of subtropical islands in Japan (*e.g.*, Fukuda 1993). *Rissoina costulata* (Dunker, 1860) (Fig. 8H) and *Stosicia annulata* (Dunker, 1860) (Fig. 8I) are representative species of the mainland, but these genera are less common in temperate areas.

Other genera of the family are more difficult to collect than the above groups. They include *Pusillina*, *Manzoina*, *Frigidoalvania*, *Boreocingula*, *Parashiela*, *Lucidesta*, *Voorwindia* and *Merelina*.

The habitat of this family is mostly the shallow subtidal zone. *Microstelma japonica* (A. Adams, 1863) and *Rissoina benthicola* (Habe, 1961) prefer lower subtidal zones down to 200 m deep. A few species are distributed in the bathyal zone. *Frigidoalvania asura* (Yokoyama, 1926) lives between 200–600 m and *Alvania flava* (Okutani, 1964) (Fig. 7J) occurs between 500 and 1,500 m (Hasegawa *in* Okutani 2000: 148–149).

Anabathridae (Fig. 9A)**.** This was also one of the little-known rissoiform families in Japan. Hasegawa (1995) first reported the occurrence of *Amphithalamus fulcira* (Laseron, 1956) from Japan, and additional records were illustrated by Fukuda *et al.* (2000). This species is locally common from warm temperate to subtropical zones in Japan and is distributed widely in the Western Pacific.

Assimineidae. This family is a highly diversified group from estuarine, supralittoral and terrestrial zones, and probably there are more than 40 species in Japan. It has also been notorious in Japan as a taxonomically difficult group. The taxonomic revision of the Japanese species was initiated by Drs Kuroda and Habe (Habe 1942, 1943; Habe & Habe 1983; Kuroda 1958, 1959). More recently this group has been under intensive review by Dr. Hiroshi Fukuda (Fukuda & Mitoki 1995, 1996a,b).

For Japanese species, see also Fukuda *in* Wada (1996), Hasegawa *in* Okutani (2000: 166–169) and Masuda & Uchiyama (2004: 104–110).

The species of *Assiminea* and other related genera (*e.g.*, *Angustassiminea*) live around estuaries, and they are important in terms of conservation due to the crisis of habitat destruction. Many species are endangered or potentially endangered (*e.g.*, Fukuda *in* Wada *et al.* 1996; Kimura & Kimura 1999).

Species of *Paludinella* live in the supralittoral zone. A few species (*e.g.*, *Paludinella kuzuuensis* Suzuki, 1937, and *P. miyakoinsularis* Minato, 1980) are truly terrestrial (Minato 1980d; Azuma 1995: 23, 189; Masuda & Uchiyama 2004: 110).

Most interestingly in this family, small-sized genera new to Japan were reported by Fukuda *in* Wada *et al.* (1996: 19–20, pl. 10, figs 1–9). Four undescribed species of *Ditropisena* have strongly keeled and low-spired shells. Species of two undescribed genera are also depressed in height and vitrinellid-like. These little-known species are no more than 2 mm in width and very small for the family.

Barleeidae (Fig. 9B)**.** This family had been treated as part of the Rissoidae before being raised to family rank by Ponder (1983). No serious taxonomic study has been made of the Japanese species. The only well-known species, *Barleeia angustata* (Pilsbry, 1901) (Fig. 9B), is abundant on algae in the intertidal to very shallow subtidal zones throughout the temperate area of Japan. Hasegawa *in* Okutani (2000: 146–147) illustrated two other species, but these are much less common.

Bithyniidae. The Japanese species are classified into three genera, *Bithynia*, *Gabbia* and *Parafossarulus*. Their size is between 6 and 8 mm in height (Masuda & Uchiyama 2004: 112–114).

Caecidae (Fig. 9E–F)**.** The shell of *Caecum* is a weakly curved tube in adults, and all are below 4 mm (Hasegawa *in* Okutani 2000: 170–173). The shell is planispiral at the veliger, stage but abandons normal coiling after metamorphosis. With growth, the posterior end of the shell is sealed with a secondarily secreted septum, and the protoconch is usually cast off. The habitat of all known species is the intertidal to shallow-subtidal zone. The taxonomy of Japanese species was relatively well examined by Dr. Habe (*e.g.*, Habe 1978a). For the systematics of entire family, see Bandel (1996).

Caecum glabella (A. Adams, 1868) is the most common species in Japan. It is collected from sand deposited in rock crevices and from branching coralline algae. The aperture is simple in this species, even in adults. *Caecum gracile* Carpenter, 1858, (Fig. 9E–F) is coarsely sculptured by annular rings. In contrast to *C. glabella*, the aperture of the adults is thickened, apparently representing determinate growth. In other species, *e.g.*, *C. kajiyamai* (Habe, 1963), the aperture is markedly narrowed and thickened at the end of growth (Hasegawa *in* Okutani 2000: 172).

Parastrophia japonica Hinoide & Habe, 1978, was once described as a species in a different family, the Ctiloceratidae (Hinoide & Habe 1978). The extremely thin shell is gently curved, and the protoconch is retained even at the adult stage.

Elachisinidae. There are only two described species (Hasegawa *in* Okutani 2000: 164–165). *Laeviphitus japonicus* Okutani, Fujikura & Sasaki, 1993, (1.8 mm in height) was described from hydrothermal vents off the Ogasawara Islands at a depth of 440 m (Okutani *et al.* 1993). *Elachisina ziczac* Fukuda & Ekwa, 1997, (1.8 mm in height) was found on the undersides of deeply buried rocks in an estuary (Fukuda & Ekawa 1997). Two undescribed species of *Pseudocrisope* were reported from Sagami Bay (Hasegawa 1996: figs 4H, 4I). This family was established by Ponder (1985).

Falsicingulidae. The family is mainly from cold-water regions. The habitat ranges from estuaries to algae in the intertidal zone. There are three known species in Japan: *Falsicingula kurilensis* (Pilsbry, 1905), *F. athera* Bartsch in Golikov & Scarlato, 1967, and *F. mundana* (Yokoyama, 1926) (Hasegawa *in* Okutani 2000: 164–165).

Hydrobiidae (Fig. 9C–D)**.** This family is uncommon in the Japanese freshwater fauna. All of the Japanese species are less than 2 mm in height. Species of *Bythinella* (*B. nipponica* Mori, 1937 and allied species: Fig. 9C–D) prefer clean water in creeks on mountain sides. Species of *Saganoa* live below ground. They were once collected from well pumps, but are now hard to obtain with the disappearance of old-fashioned wells for water. Species of *Akiyoshia* (*A. uenoi* Kuroda & Habe, 1954, and *A. kobayashii* Kuroda & Habe, 1958) live in freshwater caves.

Pomatopyrgus antipodarum (Gray, 1843) (also known as *P. jenkinsi* E.A. Smith, 1889) was already introduced in the 1980s in Japan. However, it is still scarce and confined to areas around freshwater fish culturing ponds.

The taxonomy of the Japanese Hydrobiidae was established by Drs Kuroda and Habe (Kuroda & Habe 1954, 1958; Habe 1961). The current information in the literature is largely based on their publications.

Iravadiidae (Fig. 8J–K)**.** The family has adapted widely to coasts with brackish water, intertidal boulder shores, and the lower subtidal zone, but each species inhabits a quite narrow range of habitat as a rule. For example, *Iravadia sakaguchii* is restricted to the undersides of rocks on mud in estuaries, *I. elegantula* (A. Adams, 1863) lives in mud in estuaries, and *I. quadrasi* (Böttger, 1902) is known from the underside of stones in mangrove swamps (Hasegawa *in* Okutani 2000: 162–165). *Ceratia nagashima* Fukuda, 2000 was described from the upper intertidal zone of a rocky shore (Fukuda 2000). *Nozeba lignicola* Hasegawa, 1997 (Fig. 8K) was described from sunken wood in Suruga Bay at 140–400 m (Hasegawa 1997a: 108–110). Habitat details for other species have not been determined. There are still several unidentified rare species in the intertidal zone (*e.g.*, Fukuda *in* Wada 1996; Fukuda *et al.* 2000; Sasaki 2006a). The genera of the family were revised by Ponder (1984).

Pomatiopsidae. The members of this family are mainly terrestrial. In the truly terrestrial genus *Blanfordia*, Ando & Habe (1983) recognized three valid taxa out of eight nominal species described from Japan. The genus *Fukuia* lives on constantly moist surfaces on land. *Fukuia minima* (Bartsch, 1936) is 3 mm in height, and other species reach up to 1 cm (Masuda & Uchiyama 2004: 102–103). *Cecina manchurica* A. Adams, 1861, (less than 5 mm in height) is found under drift debris in the supralittoral zone. The juvenile has a tall spire, but the upper part is lost by decollation with growth (Hasegawa *in* Okutani 2000: 164). *Oncomelania nosophora* (Robson, 1915) (7 mm in height) is a freshwater species that has been heavily decimated due to the presence of a parasite that causes a serious disease.

Stenothyridae (Fig. 9J)**.** The habitat of this family ranges from freshwater to brackish-water zones (Hasegawa *in* Okutani 2000: 170–171; Masuda & Uchiyama 2004: 115–117). The taxonomy of the

Japanese species was revised by Kuroda (1962) and is relatively well examined for Japanese non-marine micromolluscs. The anatomy was described by Kosuge (1969).

Most Japanese species are threatened by environmental degradation (Fukuda *in* Wada *et al.* 1996: 27). Hosaka & Fukuda (1996) reported a well-preserved locality of *S. japonica* Kuroda, 1962, but the species is already extinct in most previously known localities. Tamaki *et al.* (2002) reported an unidentifiable *Stynothyra* species as possibly introduced from China. The operculum of *Stenothyra* bears a pair of transverse ridges on the interior.

Tornidae (Fig. 9G–I)**.** This family had been variously classified. The name 'Vitrinellidae' had been used independently or instead of Tornidae (*e.g.*, Hasegawa *in* Okutani 2000: 173), but it is now treated as a subfamily of Tornidae (Bouchet *et al.* 2005: 252).

'Vitrinelliform' gastropods are one of the most extreme cases of shell convergence across different higher taxa (*e.g.*, Skeneidae and Cornirostridae). There remains the possibility that many species currently in this family will be transferred to other remotely related groups in the future.

Most genera inhabit the shallow subtidal zone, and some species extend into the middle subtidal zone down to 100 m (Hasegawa *in* Okutani 2000: 172–179).

The most typical genus, *Vitrinella*, has a smooth-surfaced shell of 1.5–5 mm in width. Its habitat is generally in the intertidal to very shallow waters. The shell of *Pseudoliotia* is sculptured by rough spiral ribs, granules on the ribs, and lamellate axial ribs connecting the granules. *Pseudoliotia pulchella* (Dunker, 1860) (Fig. 9G) can be collected from the undersides of buried stones in embayments, and the living shell is completely covered with a dark, rusty substance. The genera *Pygmaerota* and *Circulus* (Fig. 9I) are sculptured only by spiral ribs of varying thickness. The genus *Teniostoma* is distinguished from *Vitrinella* (Fig. 9H) in lacking the umbilicus.

Exceptionally in this family, *Ponderina major* Hasegawa, 1997, was collected from sunken wood in Suruga Bay at depths of 140–400 m (Hasegawa 1997a: 111–112). There is no other species recorded from the bathyal zone.

The problem with biological studies in this group is the difficulty in finding live specimens. The microhabitat of the majority of species is not precisely known. *Sigaretornus planus* (A. Adams, 1850) is known to live in the burrows of echiurans and scale worms. Such a habitat was first reported by Ponder (1994b) in Hong Kong.

Vanikoridae (Fig. 8L)**.** This family name had been previously used only for the genus *Vanikoro*, but also for various genera that were later transferred from the Trichotropidae or Fossaridae (*e.g.*, Habe 1978) to this family (Warén & Bouchet 1988).

The genus *Vanikoro* is between 8 mm and 1.5 cm in size, and thus not a micromollusc. However, one earlier misidentification illustrates the importance of studing juveniles: a juvenile of *Vanikoro japonica* Pilsbry, 1895 was mistaken for an independent small species, *Fossar fenestratus* A. Adams, 1863, for a long time (Habe 1978b: 165).

The Japanese fauna includes many uncommon vanikorids (Hasegawa *in* Okutani 2000: 192–195. The shell of *Macromphalus* (Fig. 1C–D) is sculptured by many spiral cords. There are little-known species (*e.g.*, Fukuda 1993: pl 12, fig. 158; Fukuda *et al.* 2000: fig. 12b; Haseagawa, 2006: fig. 5A,B) and a renewed taxonomic revision is necessary for the genus.

The habitat of some species is a complete mystery. *Halotapada okamotoi* (Habe, 1962) (1 cm in height) and *Amamiconcha sakuraii* Habe, 1961 (1 cm) are both known only from worn dead shells. *Japanonoba patula* (A. Adams, 1863) (3.5 mm) has never been collected alive, but its distribution has been better recorded than that of other rare species (Habe & Ando 1987; Yoshizaki *et al.* 1997). *Berthais egregia* (A. Adams, 1863) (Fig. 8L) is also an example of a rare species.

Caledoniella montrouzeri Souverbie, 1869 was once assumed to be a lamellarid, but is now classified in Vanikoridae (Hasegawa *in* Okutani 2000: 195). The species is commensal on the stomatopod *Gonodactylus* spp. (Ishikawa 1989).

Haloceratidae. The morphology and systematics of this family was investigated in most detail by Warén & Bouchet (1991). The family is exclusively from the deep sea. There are two described species of *Haloceras* in Japan: *H. japonica* Okutani, 1964, (6 mm in length) is distributed between 1,230–1,580 m, and the shell is tall for the family; *H. millestriata* (Okutani, 1964) is from 1,230–1,350 m, and the shell is more depressed.

Velutinidae. A few described species of *Velutina* are below 5 mm in shell size (*e.g.*, *Velutina abyssicola* Okutani, 1964: Okutani 2000: 249). The shell is external in *Vetulina* but in *Marsenia*, *Lamellaria* and other related genera it is completely covered with the mantle and invisible from the outside. The largest species, *Onchidiopsis nihonkaiensis* Okutani & Numanami, 1993, from 400–500 m in the Sea of Japan, reaches 11 cm in body length. It is well known that the *Echinospira* larvae in this family have a secondary outer shell. The larvae of the Japanese *Lamellaria* were described by Habe (1944c).

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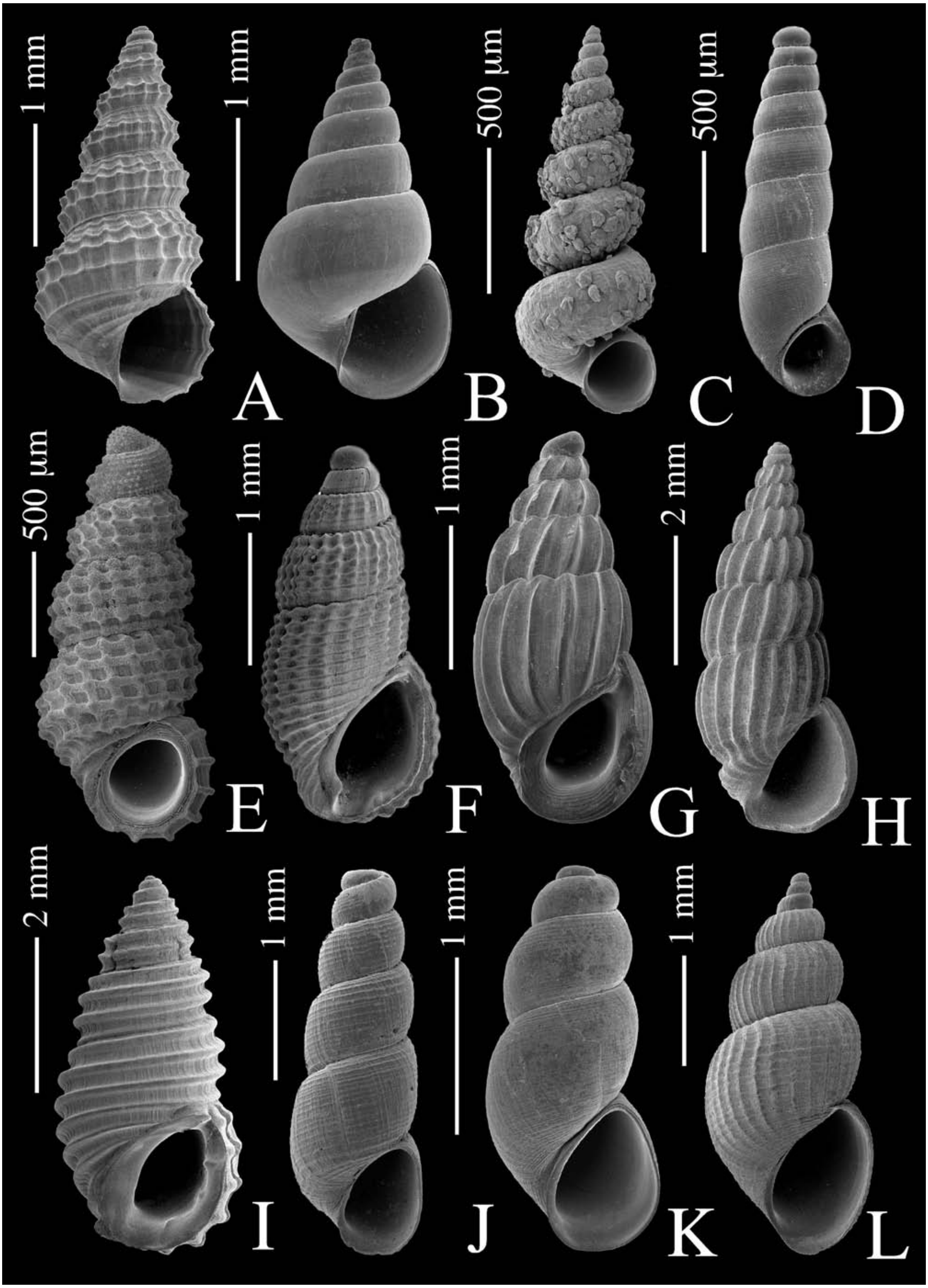
Figure 8 (next page)**.** Taenioglossate Caenogastropoda (2). **A.** Cerithiidae, *Cerithidium fusca* (A. Adams, 1860). **B.** Litiopidae, *Alaba goniochila* (A. Adams, 1860). **C.** Scaliolidae, *Scaliola bella* A. Adams, 1860. **D.** Pelycidiinae of Pickworthiidae, *Pelecydion* sp. **E–I.** Rissoidae. **E.** *Merelina* sp. **F.** *Stosicia incisa* (Dunker, 1860). **G.** Rissoidae, *Schwartziella triticea* (Pease, 1860). **H.** *Rissoina costulata* (Dunker, 1860). **I.** *Stosicia annulata* (Dunker, 1860). **J–K.** Iravadiidae. **J.** *Iravadia yendoi* (Yokoyama, 1927). **K.** *Nozeba lignicola* (Hasegawa, 1997). **L.** Vanikoridae, *Berthais egregia* (A. Adams, 1863). Locality data: **A–B.** R/V *Tansei-Maru*, cruise KT-05-30, station SS4(2), off Shirahama, Wakayama, 27.68–35.29 m, 33°37.43'N, 135°22.09'E–33°37.31'N, 135°21.85'E, Nov. 26 2005. **A.** UMUT RM29605. **B.** UMUT RM29606. **C.** R/V *Tansei-Maru*, cruise KT-99-17, station SH-2, off Shirahama, Wakayama, 41–42 m, 33°40.700'N, 135°19.170'E–33°40.629'N, 135°19.231'E, Nov. 30, 1999, UMUT RM28769. **D.** R/V *Tansei-Maru*, cruise KT-95-17, station OM2(1), Omurodashi, 116–121 m, 34°289.77'N, 139°29.780'E–34°28.839'N, 139°29.678'E, Dec. 13, 1995, coll. by Eiji Tuschida, UMUT RM28770. **E.** Aka Island, Okinawa, UMUT RM29607. **F.** Agonohama, Aka Island, by diving, Okinawa, Sep. 29, 1997, UMUT RM28773. **G.** Yaebishi, off Miyako Island, intertidal zone, Okinawa, Apr. 18, 1995, UMUT RM28774. **H.** Kuwabara, Shunan, Yamaguchi, intertidal zone, May 16, 2006, UMUT RM29608. **I.** Kuwabara, Shunan, Yamaguchi, intertidal zone, May 16, 2006, UMUT RM29609. **J.** Kuwabara, Shunan, Yamaguchi, shallow subtidal zone, empty shell from sediment, UMUT RM28775. **K.** Off Saga, Kochi Prefecture, depth unknown, from sunken wood, Nov. 6, 1998, UMUT RM28776. **L.** R/V *Tansei-Maru*, cruise KT-05-30, station OS1(2), off Okinoshima Island, Kochi, 131.4–136.4 m, 32°43.95'N, 134°41.99'E–32°43.98'N, 132°41.80'E, Nov. 22, 2005, UMUT RM29610.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Triviidae (Fig. 9K–L)**.** The members are generally below 1 cm except for the large genus *Pseudotrivia* (2 cm in height: Okutani 2000: 242–245). The shells of *Trivirostra* (5–12 mm) and *Niveria* (5 mm, Fig. 9L) are cypraeid-like, and are covered with a secondary shell layer bearing dense transverse ridges. In the genus *Erato* (4–9 mm), the surface is polished, except for *E. sulcifera* Sowerby II, 1832, which has granules (Fig. 9K).

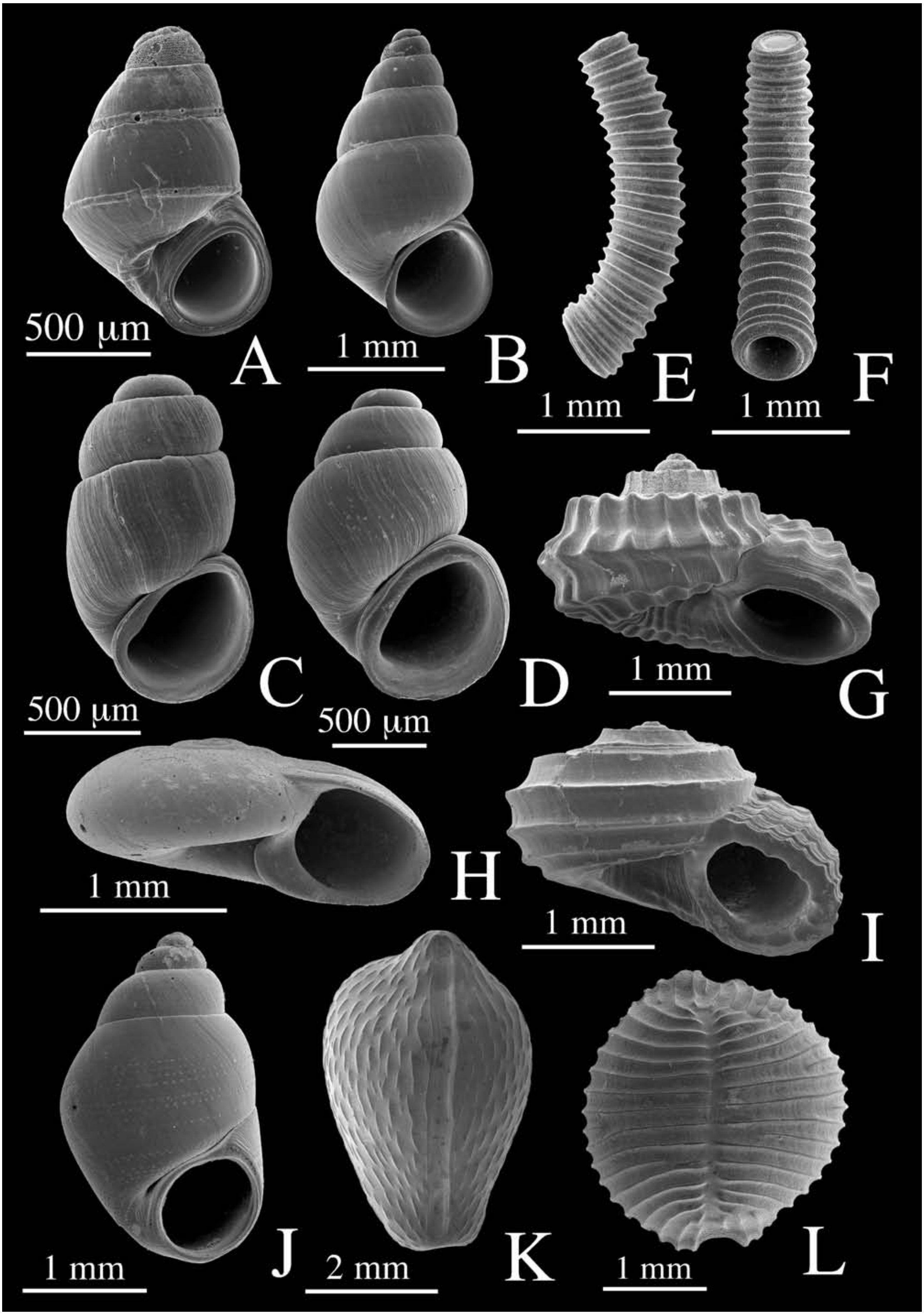
Tsuchida *et al.* (1999) reported from Okinawa *Trivia hallucinata* Liltved, 1984, which was originally described from South Africa. This might be a case of connected faunas between the western Pacific and the entire Indian Ocean, but the identification should be reconfirmed. A similar distribution is also known from *Cypraea iutsui* Shikama, 1974, and *Conus teramachii* (Kuroda, 1956).

‘**PTENOGLOSSA’.** Eight families are grouped into three superfamilies: the Epitonioidea, Eulimoidea and Triphoroidea (Bouchet *et al.* 2005: 254), but this grouping is regarded as para- or polyphyletic (Ponder & Lindberg 1997).

Epitoniidae (Fig. 10A–E)**.** This diverse family includes at least 130 Japanese species (Higo *et al.* 1999: G1804–1933). Nakayama (2003) published a more complete revision of the Japanese species, including synonymy and literature information. Very probably the Japanese epitoniid fauna is underrepresented in the literature, especially in the case of small species. For example, Nakayama (2007) reported six little-known species, which are all around 2 mm in height.

It is difficult to identify fully mature stages without biological inspection in this family. The shell maintains an identical form and sculpture during ontogeny, and does not show determinate growth. Some species form varices irregularly, but these do not represent the termination of growth. In one case study in Japan, Yamashiro (1990) gave the shell length at which the animal deposited eggs and thus confirmed the sexually mature size of *Epitonium bullatum* (Sowerby, 1844). Similar studies should be carried out on various small species.

Figure 9 (next page)**.** Taenioglossate Caenogastropoda (3). **A.** Anabathronidae, *Amphithalamus fulcira* (Laseron, 1956). **B.** Barleeidae, *Barleeia angustata* (Pilsbry, 1901). **C–D.** Hydrobiidae. **C.** *Bythinella nipponica* Mori, 1937.**D.** *Bythinella kubotai* Kuroda & Habe, 1958. **E–F.** Cacidae, *Caecum gracile* (A. Adams, 1868). **G–I.** Tornidae. **G.** *Pseudoliotia pulchella* (Dunker, 1860). **H.** *Vitrinella* sp. **I.** *Circulus* sp. **J.** Stenothyridae, *Stenothyra edogawensis* (Yokoyama, 1927). **K–L.** Triviidae, *Erato sulcifera* Sowerby II, 1832. **L.** *Niveria pilula* (Kiener, 1843). Locality data: **A–B.** Mitsuishi, Manazuru, intertidal zone, Kanagawa, May 17, 2003. **A.** UMUT RM28772. **B.** UMUT RM28771. **E–F.** Utsu, Mishima Island, Hagi, Ymaguchi, intertidal zone, Aug. 5, 1985. **E.** UMUT RM29611. **F.** UMUT RM29612. **C.** Iwanagahongo, Shuho, Yamaguchi, Apr. 30, 1984, UMUT RM28784. **D.** Mie, Nagasaki City, Nagasaki, Jan. 2, 1985, coll. by Kinzo Matsubayashi, UMUT RM28783. G–**H.** Kuwabara, Shunan, Yamaguchi, intertidal zone, May 16, 2006. **G.** UMUT RM29613. **H.** UMUT RM29614. **I.** R/V *Tansei-Maru*, cruise KT-05-30, station OS1(2), off Okinoshima Island, Kochi, 131.4–136.4 m, 32°43.95'N, 134°41.99'E–32°43.98'N, 132°41.80'E, Nov. 22, 2005, UMUT RM29615. **J.** Edogawa, Tokyo, estuary, date unknown, UMUT RM28782. **K.** Yaebishi, off Miyako Island, Okinawa, intertidal zone, Apr. 18, 1995, UMUT RM29616. **L.** R/V *Shinyo-Maru*, station 1997-4, off Ogasawara Islands, 57–62 m, 27°47.70'N, 142°03.25'E–27°47.80'N, 142°03.30'E, Oct. 15, 1997, UMUT RM28781.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Eulimidae (Fig. 10F–H)**.** This is a surprisingly diversified group in shell morphology, anatomy and parasitic ecology (see Warén 1983a for general review). Most of the described species are medium-sized, but it is highly likely that there are more undescribed small species.

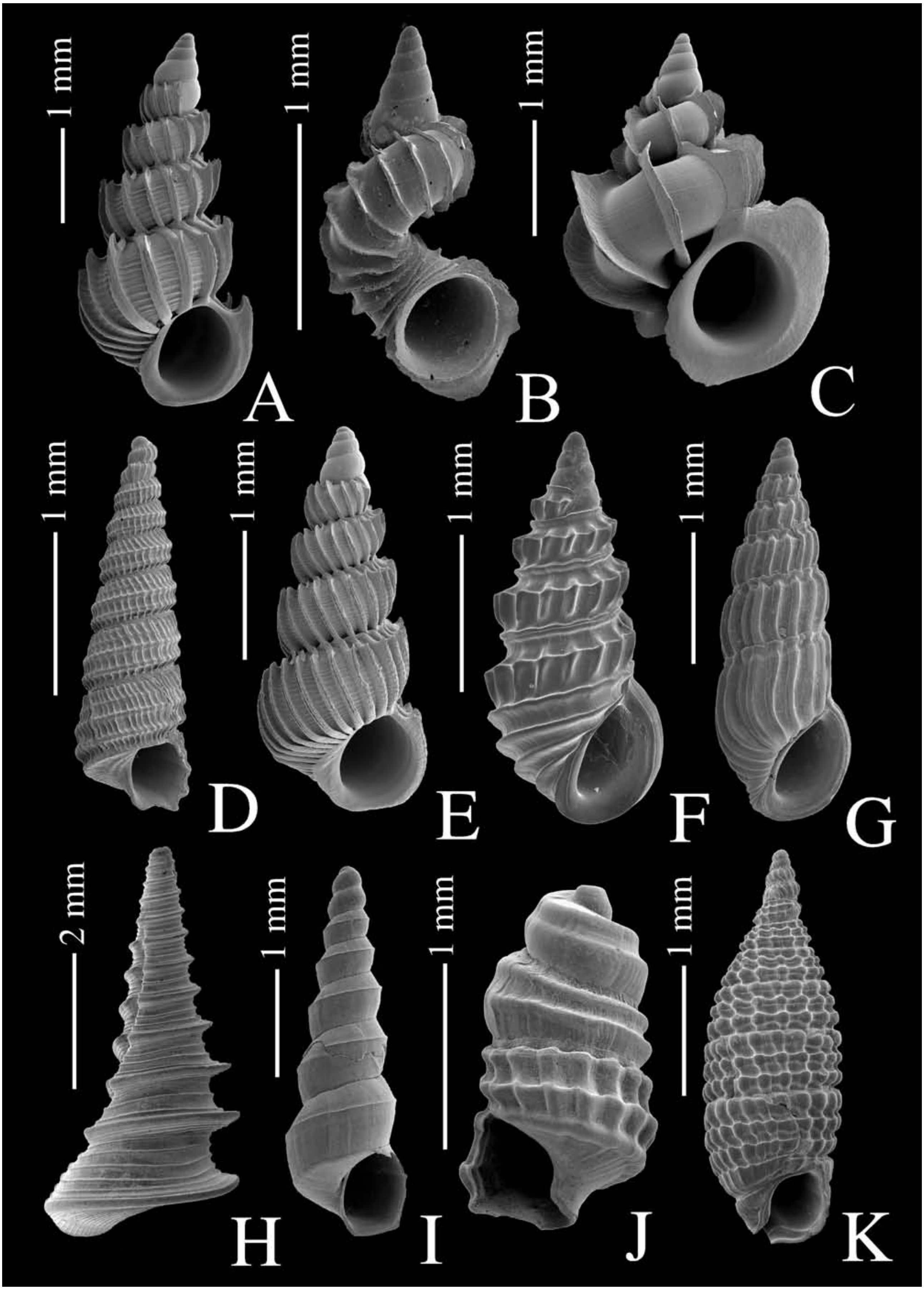
Anatomical and ecological studies are particularly important for the study of this family. For example, species of *Pyramidelloides* (Fig. 10F–G) were revealed to be eulimids anatomically by Warén (1983b), but before that they were regarded as rissoids. The host-parasite relationships are also essential to describe the habitat of each species precisely. The earlier records were summarized by Habe (1976c), Hori & Koda (1997) and Kubo (2006) later added ecological data for some species.

Because their habitats are specialized, special efforts are frequently required to obtain live material. For example, *Asteriophila japonica* could not be found by any Japanese malacologists following the original description, but its occurrence in Japan was confirmed by echinoderm workers investigating the life history of asteroideans by collecting numerous specimens on a monthly basis (Sasaki *et al.* 2007a).

The determination of the adult state is also a vexing problem in this group. Gonad histology is the only reliable method for both shell-bearing and shell-less species. In the shell-bearing groups, the whorls are marked with characteristic growth increments, but this feature does not change with maturation.

Aclididae (Fig. 10I)**.** The shell is strikingly multispiral, turrate, sculptured by spiral cords, and lacking color pattern. There are two well-known species [*A. angulifera* (Yokoyama, 1992) and *A. loveniana* Adams, 1861] and six problematic species that were described by A. Adams (Higo *et al.* 1999: G1934–1941; Hasegawa *in* Okutani 2000: 318–319). The habitat of the Japanese species is

Figure 10 (next page)**.** Ptenoglossa. **A-E.** Epitonidae. **A.** *Epitonium* sp. 1. **B.** *Cycloscala hyaline* (Sowerby, 1844). **C.** *Epitonium* sp. 2. **D.** *Amaea* sp. **E.** *Epitonium* sp. 3. **F-H.** Eulimidae. **F.** *Pyramidelloides miranda* (A. Adams, 1861). **G.** *Pyramidelloides angusta* (Hedley, 1898). **H.** *Bacula morisyuichiroi* (Habe, 1968). **I.** Aclididae, *Aclis angulifera* (Yokoyama, 1922). **J.** Triphoridae, Gen. et sp., juvenile. **K.** Cerithiopsidae, *Jaculator* sp. Locality data: **A.** R/V *Tansei-Maru*, cruise KT-99-17, station KU-2, off Katsuura, Wakayama, 37-38 m, 33°37.454'N, 135°58.394'E – 33°37.402'N, 135°58.470'E, Nov. 29, 1999, UMUT RM28790. **B.** R/V *Shinyo-Maru*, station 1997-1, off Ogasawara Islands, 98–99 m, 27°48.52'N, 142°02.62'E – 27°48.47'N, 142°02.55'E, Oct. 15, 1997, UMUT RM29617. **C.** R/V *Tansei-Maru*, cruise KT-99-17, station KU-3, off Katsuura, Wakayama, 39–43 m, 33°37.289'N, 135°58.631'E – 33°37.228'N, 135°58.660'E, Nov. 29, 1999, UMUT RM29618. **D.** R/V *Shinyo-Maru*, station 1997-12, off Ogasawara Islands, 150–160 m, 27°11.99'N, 14°09.18'E – 27°11.75'N, 142°08.92'E, Oct. 16, 1997, UMUT RM29619. **E.** R/V *Tansei-Maru*, cruise KT-99-17, station KU-2, off Katsuura, Wakayama, 37–38 m, 33°37.454'N, 135°58.394'E – 33°37.402'N, 135°58.470'E, Nov. 29, 1999, UMUT RM29620. **F.** R/V *Shinyo-Maru*, station 1999-16, Omurodashi, 88 m, 34°32.66'N, 139°29.65'E -34°32.66'N, 139°29.65'E, Oct. 16, 1999, UMUT RM29621. **G.** Majanohama, Aka Island, Okinawa, by diving, Sep. 30, 1997, UMUT RM29622. **H.** Tsuchihama, Amami-Oshima, Kagoshima, beach-drifted, Apr. 4, 1990, UMUT RM28786. **I.** R/V *Tansei-Maru*, cruise KT-99-17, station SH-2, off Shirahama, Wakayama, 41–42 m, 33°40.700'N, 135°19.170'E – 3°40.629'N, 135°19.231'E, Nov. 30, 1999, UMUT RM28789. **J.** R/V *Tansei-Maru*, cruise KT-95-17, station OM2(1), Omurodashi, 116–121 m, 34°289.77'N 139°29.780'E – 34°28.839'N 139°29.678'E, Dec. 13, 1995, coll. by Eiji Tuschida, UMUT RM29623. **K.** Yaebishi, off Miyako Island, Okinawa, intertidal zone, Apr. 18, 1995, UMUT RM28787.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sandy bottoms in the middle subtidal zone between 50 and 100 m. Live specimens are scarcely collected, for unknown reasons. The Japanese species obviously need further revision.

Triphoridae (Fig. 10J)**.** The shell is multispiral, tall, and sinistral in most species except some (*e.g., Trituba*: Sasaki 2006b). The protoconch varies from paucispiral, possibly representing lecithotrophic development, to multispiral, possibly representing planktotophic development, and is used as a criterion for generic delimitation (*cf.* Marshall 1983). In all species, the adult stage is readily recognizable by the thickened and reflected apertural margin. In addition, one or two canal(s) are formed at maturity.

The species diversity is highest in the shallow subtidal zone of subtropical coral reef regions in Japan, and many genera are also distributed in the warm temperate zone. The species richness is also probably very high on subtidal banks in subtropical areas, but the micromolluscan fauna of such environments has been poorly explored in Japan.

The species-level taxonomy was well studied by Dr. Kosuge in the 1960s (Kosuge 1961a,b, 1962, 1963a,b, 1964, 1965c, 1966). At least 110 species have been recorded (Higo *et al.* 1999: G1656–1765), and most of the well-known species were beautifully illustrated by Hasegawa *in* Okutani (2000: 302–317). Individual species are diagnosed mainly by shell characters, including color pattern, surface sculpture of whorls, siphonal canal morphology and protoconch.

Cerithiopsidae (Fig. 10K)**.** This family is also diverse but has been studied less than the Triphoridae. Shells in this family are dextral (except *Leiocochlis*) and sculptured most typically by spiral and axial cords or spiral cords only (*e.g.*, *Notoseila*). Unidentifiable specimens can be collected throughout Japan in such genera as *Cerithiopsis, Jaculator* and *Metaxia* in shallow water (*e.g.,* Fukuda 1993; Fukuda *et al.* 2000; Hasegawa *et al.* 2001; Sasaki 2006a) and *Cerithiella* in deeper zones (Hasegawa 2005). For an overview of the systematics of the family, see Marshall (1978).

NEOGASTROPODA. The Recent Neogastropoda are classified into 30 families (Bouchet *et al.* 2005: 254–256), and most of them are distributed in Japan. Small species are most common in the families Columbariidae, Cystiscidae and Turridae. There are no species mature at 4 mm or less in the family Muricidae (*cf.* Kubo 2003 for examples of relatively small groups), Buccinidae, Melongenidae, Fasciolariidae, Vasidae, Turbinellidae, Volutidae, Olividae, Harpidae, Cancellariidae, Conidae or Terebridae.

Columbariidae (Fig. 11A–B)**.** The family is diversified mainly in shallow waters in warm temperate to tropical zones (Tsuchiya *in* Okutani 2000: 424–437). Small species are especially numerous in the genus *Zafra* (Fig. 11A). Their taxonomy needs revision.

Nassariidae. The members of this family are mostly medium-sized (1–2 cm) (Tsuchiya *in* Okutani 2000: 438–451). Examples of small species in Japan are *Zeuxia macrocephalus* (Schepman, 1911) (0.5 mm in height) and *Nassarius* (*Zeuxis*) *tabescens* Marrat, 1880 (6 mm). The latter species is known to brood embryos in the pallial cavity (Kubo 1996).

Costellaridae (Fig. 11C–D)**.** The shells are mostly larger than 1 cm, robust and vividly colored (Tsuchiya *in* Okutani 2000: 556–575). Examples of small species can be found in the genera *Thala*, *Pusia* (Kubo 1997b) and *Thaluta* (Rosenberg & Callomon 2004).

Cystiscidae (Fig. 11E)**.** This family contains micromolluscs typical of shallow, warm-water regions. The shell is strongly polished and white in most species (Cossignani 2006). From Japan at least 13 species have been recorded (Habe 1951b; Higo *et al.* 1999: G6173–3180; Hasegawa *in* Okutani 2000: 576–579). The status of this family was established by Coovert & Coovert (1995).

Marginellidae (Fig. 11F)**.** Species of *Dentimargo* are 4 mm or smaller in length. Species similar to *D. kawamurai* (Habe, 1951) need taxonomic revision. *Tateshia yadai* (Kosuge, 1986) described as Olividae belongs to this family.

Volutomitridae. A small species, *Microvoluta hondoana* (Yokoyama, 1922), lives on shallow sandy bottoms in central Japan (Okutani 2000: 574–575). It was described as a Pliocene fossil, and living specimens are rarely collected. The best known species, *Volutomitra alaskana* Dall, 1902, is distributed in the cold-water bathyal zone, and is relatively large (3.5 cm in height).

Turridae (Fig. 11G–J)**.** This family is the largest group in the Neogastropoda (Hasegawa, Okutani & Tsuchida *in* Okutani 2000: 618–667; see also Tucker 2004 for listing of species). Small species have historically been poorly known. For example, the distinctive species *Microdaphne trichodes* (Dall, 1919) (Fig. 11H), was first recorded in Japan by Ekawa only recently (1992a). *Aliceia okutanii* Sasaki & Warén, 2007 (4.9 mm in height) was described as the first record of the genus from the western Pacific. Another small species is *Carinapex minutissima* (Garrett, 1873) (4 mm in height; Fukuda 1994: pl. 29, fig. 588; Hasegawa *in* Okutani 2000: 640). In adults, the aperture is distinctly thickened, with a deep notch. Some of the species in *Mitromorpha* are below 5 mm and relatively small for the family.

'Lower HETEROBRANCHIA'. The lower heterobranchs include many small-sized species. Their importance came to light in the 1990s (*e.g.*, Ponder 1990a,b; Warén *et al.* 1993), but their relationships still remain to be resolved. There are some species with uncertain familial assignment.

Cimidae. The family is represented in Japan by two species of *Graphis* (Hasegawa *in* Okutani 2000: 686–687). They are both below 2.5 mm.

Orbitestellidae. The shell is flat and discoidal with prominent peripheral keel(s) and numerous axial ribs. They live on algae or below boulders. There are only three known species in the shallow waters of Japan (Fukuda 1994: pl. 37, fig. 725; Hasegawa *in* Okutani 2000: 686–687). A species of *Lurifax* (1.5 mm in width) has been found at a vent site in Japan (Sasaki & Okutani 2005). Warén & Bouchet (2001) assigned this genus to the Orbitestellidae based on radular characters but Kiel (2006) pointed out the orthostrophic protoconch is of a caenogastropod type. The anatomical definition of the family was given by Ponder (1990).

Xylodisculidae. Only two specimens have been obtained from Japan: *Xylodiscula* sp. cf. *vitrea* Marshall, 1988, was collected from sunken wood in Suruga Bay at 140–500 m (Hasegawa 1997a: 117)

Acteonidae (Fig. 13A)**.** The known species are all 5 mm or larger (Hori *in* Okutani 2000: 732–735). One of smallest, *Obrussena moeshimaensis* Habe, 1952, is very rare (Tsuchida 1991). This family is traditionally placed among the cephalaspideans but recently has come to be regarded as a more basal group (Bouchet *et al.* 2005: 257).

Architectonicidae (Fig. 12A)**.** The shells of *Architectonica* attain 5 cm or more in diameter and are relatively large; those of *Psilaxis*, *Heliacus* and other similar genera are generally 1–2 cm (Hasegawa *in* Okutani 2000: 691–700; see also Bieler 1993 for world-wide revision; Bieler & Petit 2005 for list of species). The genus *Pseudotorinia* is 5 mm or less and normally coiled, but *Spirolaxis* reaches only 4 mm or less, and some of its members have an open-coiled shell (Fig. 12A). These small-sized genera both have been recorded from the lower subtidal zone off the Ryukyu Islands (Ekawa 1995; Tsuchida & Ikebe 1998)

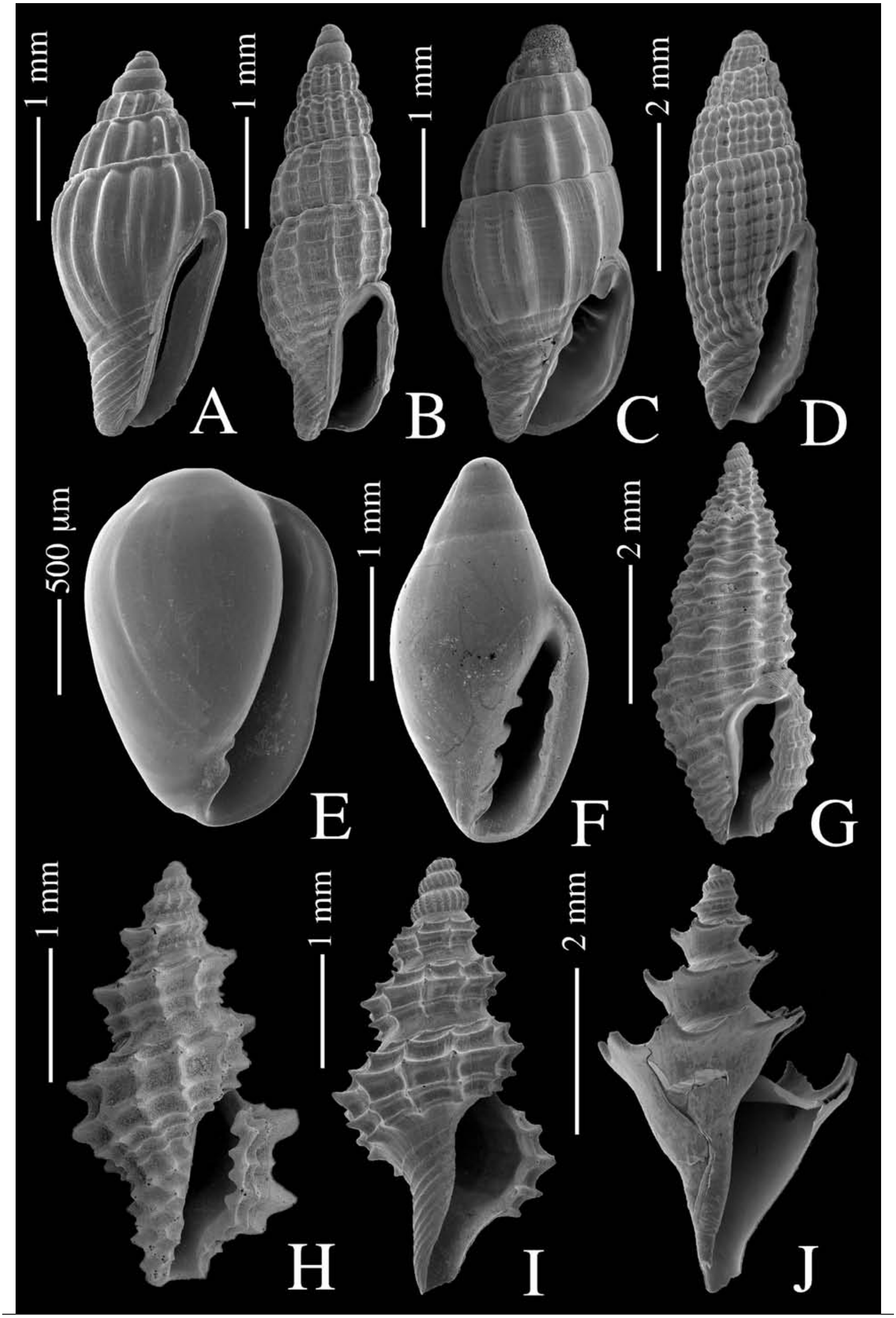
Mathildidae (Fig. 12B)**.** The known species in Japan are 7 mm or larger in height (Hasegawa *in* Okutani 2000: 688–689), but there might be additional, smaller species (*cf.* Bieler 1995). All members of this family are uncommon and difficult to collect alive, for unknown reasons. Further taxonomic studies are necessary for this family.

Omalogyridae (Fig. 12C)**.** Two genera (*Ammonicera* and *Omalogyra*: Hasegawa *in* Okutani 2000: 700–701) represent the smallest Japanese gastropods. The maximum adult size is 0.6 mm in diameter. This group can be collected from rocky shores in the intertidal zone. In the first molecular study on Japanese micromolluscs, Kurabayashi & Ueshima (2000a) set out the partial mitochondrial genome organization of *Omalogyra atomus* (Philippi, 1841).

Pyramidellidae (Fig. 12D)**.** More than 700 nominal species have been described in the Japanese Pyramidellidae (Dr. Shigeo Hori, personal communication), and most are below 1 cm (Hori *in* Oku-

→

Figure 11 (next page)**.** Neogastropoda. **A–B.** Columbellidae. **A.** *Zafra* sp. **B.** Gen. et sp. **C–D.** Costellariidae. **C.** *Pusia* sp. **D.** *Thala* sp. **E–F.** Cystiscidae. **E.** *Gibberula sueziensis* (Issel, 1869). **F.** *Dentimargo* sp. **G–J.** Turridae. **G.** *Kermia barnardi* (Brazier, 1867). **H.** *Microdaphne trichodes* (Dall, 1919). **I.** *Veprecula* sp. **J.** *Thatcheriasyrinx orientis kawamurai* (Kuroda, 1959). Locality data: **A.** R/V *Shinyo-Maru*, station 1997-10, off Ogasawara Islands, 55–59 m, 27°06.35'N, 142°10.48'E–27°06.35'N, 142°10.28'E, Oct. 16, 1997, UMUT RM29624. **B.** Aoku, Amami-Oshima Island, Kagoshima, beach-drifted, Mar. 30, 1990, UMUT RM29625. **C–D.** Majanohama, Aka Island, Okinawa, by diving, Sep. 30, 1997. **C.** UMUT RM29626. **D.** UMUT RM29627. **E.** Chojagasaki, Hayama, Kanagawa, intertidal zone, May 17, 1995, UMUT RM29628. **F–G.** Majanohama, Aka Island, Okinawa, by diving, Sep. 30, 1997. **F.** UMUT RM29629. **G.** UMUT RM29630. **H.** Kushibaru, Aka Island, Okinawa, 7 m deep, by diving, Sep. 30, 1997, UMUT RM29631. **I.** R/V *Tansei-Maru*, cruise KT-98-17, station 3, off Ashizuri-Misaki, 140–145 m, 32°38.57'N 132°47.55'E–32°38.541'N 132°47.204'E, Sep. 26, 1998, UMUT RM29632. **J.** R/V *Shinyo-Maru*, station 1998-37, off Ogasawara Islands, 121 m, 27°10.36.6'N, 142°10.16.7'E–27°10.45.6'N, 142°10.19.5'E, Oct. 21, 1998, UMUT RM29633.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tani 2000: 702–731). The taxonomy of the family has been best revised by Dr. Hori (1996, 1998; Hori & Okutani 1995, 1996, 1997; Hori *et al.* 2002) but still remains uncompleted, especially for the species from the subtidal or deeper zones. Paleontologists in the early 20th century (*e.g.*, Matajiro Yokoyama and Shichihei Nomura: see references in Higo *et al.*, 1999) described numerous small species, and their names are considered to represent valid Recent taxa (*e.g.*, see Oyama 1973 for types of Yokoyama; Higo *et al.* 2001 for types of Nomura).

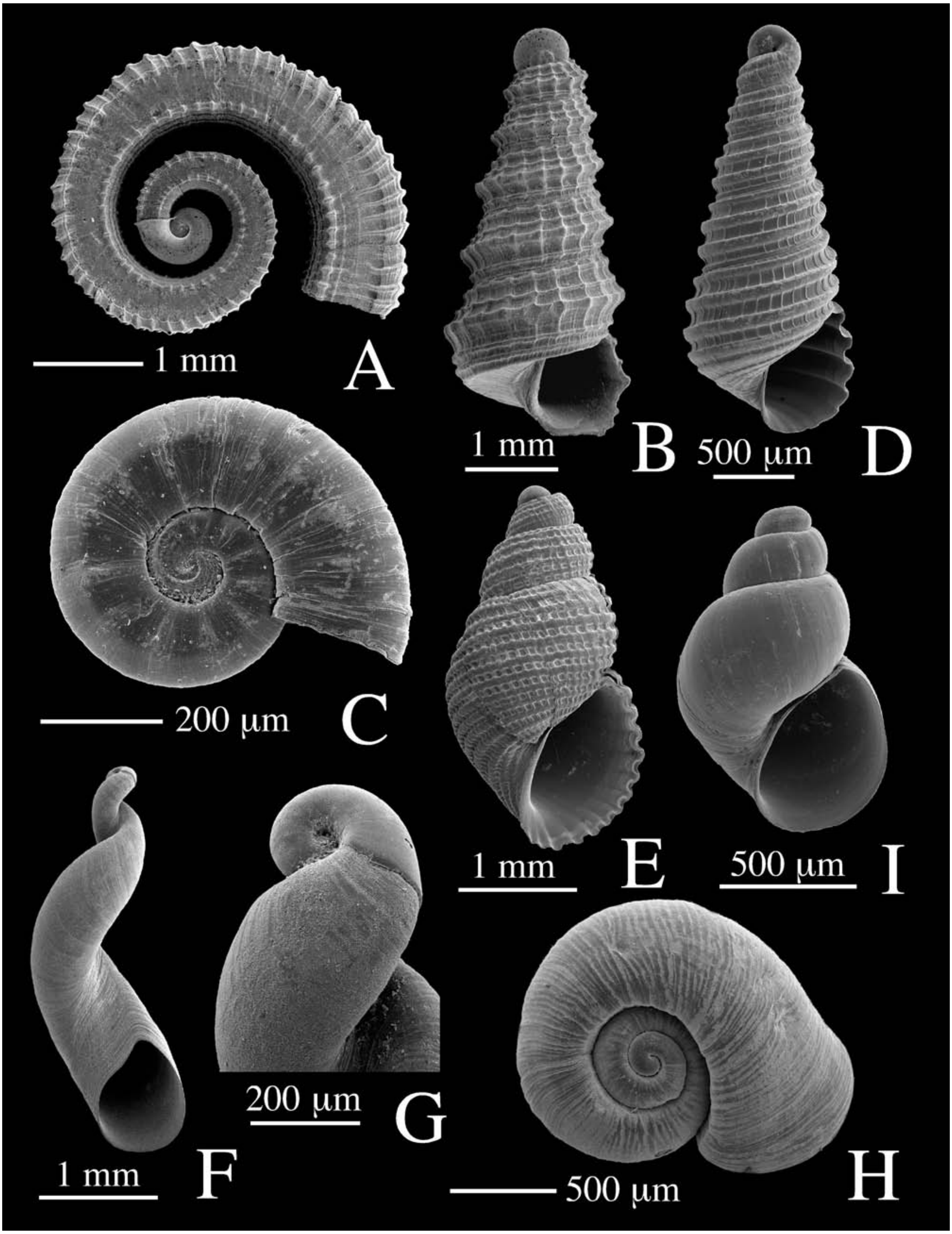
Amathinidae (Fig. 12E)**.** The family was defined based on anatomy by Ponder (1987). Later Hori & Tsuchida (1995) confirmed that *Leucotina* is anatomically an amathinid. Small species may exist in the genus *Leucotina*, but this has not been investigated sufficiently.

Murchisonellidae (= Ebalidae). In shell morphology this group is pyramidellid-like (*Ebala* and *Murchisonella*: Hori *in* Okutani 2000: 730–731) but can be distinguished by the presence of a pair of jaws (Warén 1994). There are two described species in Japan [*Ebala pagodula* (Yokoyama, 1927), *Murchisonella densistriata* (Nomura, 1936)] and they are all below 5 mm. Fukuda *et al.* (1998) and Hasegawa (2006: fig. 8D) reported unidentified species. The family Ebalidae was synonymized with Murchisonellidae by Bouchet *et al.* (2005: 258).

Uncertain groups of possibly pyramidelloid character (Figs. 12F–H)**.** There are several species of unknown systematic position in the lower Heterobranchia that possibly belong in the Pyramidelloidea. In the species in Figure 12F–G the whorls are loosely coiled, and the protoconch (Fig. 12G) is heterostrophic. *Morchinella obvoluta* (A. Adams, 1860) (Fig. 12H) has been regarded as a vitrinellid species in the past, but the slightly heterstrophic protoconch suggests it is possibly a heterobranch. *Microthyca crenellifera* (A. Adams, 1862) has more inflated whorls (Ekawa 1992b), and it may also be related to the Pyramidelloidea.

Ringiculidae (Fig. 13B)**.** There are more than ten Recent species in Japan (Higo *et al.* 1999: G4766–4777) and many of them are below 4 mm in length (Hori *in* Okutani 2000: 738–739). They were first revised

Figure 12 (next page)**.** Lower Heterobranchia. **A.** Architectonicidae, *Spirolaxis exornatus* Bieler, 1993. **B.** Mathildidae, *Mathilda* sp. **C.** Omalogyridae, *Ammonicera japonica* Habe, 1972. **D.** Pyramidellidae, *Cingulina cingulata* (Dunker, 1860). **E.** Amathinidae, *Leucotina* sp. **F–G.** Family uncertain, gen. & sp. **G.** Enlarged view of apical part. **H.** Family uncertain, *Morchinella obvoluta* (A. Adams, 1860). **I.** Rissoellidae, *Rissoella* sp. Locality data: A R/V *Toyoshio-Maru*, cruise TO-94-12, station 8, off Kakeroma Island, Amami Islands, Kagoshima, 310 m deep, Nov. 10, 1994, coll. by Eiji Tsuchida, UMUT RM28793. **B.** R/V *Toyoshio-Maru*, cruise TO-94-12 station 8, off Kakeroma Island, Amami Isalnds, Kagoshima, 310 m, Nov. 10, 1994, coll. by Eiji Tsuchida, UMUT RM28796. **C.** Mitsuishi, Manazuru, Kanagawa, intertidal zone, May 17, 2003, UMUT RM28794. **D.** Banda, Tateyama, Chiba, intertidal zone, May 27–28, 1998, UMUT RM28797. **E.** R/V *Shinyo-Maru*, station 1997-11, off Ogasawara Islands, 53–47 m, 27°06.47'N, 142°10.51'E–27°06.40'N, 142°10.29'E, Oct. 16, 1997, UMUT RM29634. **F–G.** Off Saga, Kochi Prefecture, depth unknown, from sunken wood, Nov. 6, 1998, UMUT RM29635. **H–I.** Banda, Tateyama, Chiba, intertidal zone, 1995. **H.** UMUT RM29636. **I.** UMUT RM29637.



by Takeyama (1935). Since then only a few articles on their taxonomy have been published (*e.g.*, Habe 1950a; Kuroda 1961; Mimoto 2007). This group also awaits taxonomic revision.

Rissoellidae (Fig. 12I)**.** Undoubtedly this family is the least studied group among Japanese intertidal micromolluscs (Hasegawa *in* Okutani 2000: 700–701; *cf.* Ponder & Yoo 1997). There are several species in the intertidal zone from warm-temperate regions (Fukuda 1994: pls. 22, 35, figs 695, 696; Fukuda *et al.* 2000; Sasaki 2006a), but none of them has been described taxonomically. The shell is small and transparent, and lacks a color pattern. The species thus cannot be readily distinguished by shell characters alone. The existence of several species is nevertheless suggested by the different color patterns of the animals (*e.g.*, Fukuda 1994).

Valvatidae. This family occurs exclusively in fresh water. Currently four species, *Valvata hokkaidoensis* Miyadi, 1935, *Cincinna kizakikoensis* Fujita & Habe, 1991, *C. japonica* (Martens, 1877), and *Biwakovalvata biwaensis* (Preston, 1916) are known from Japan (Masuda & Uchiyama 2004: 118–119). Their taxonomy was first established by Miyadi (1935), and Fujita & Habe (1991) described one additional species. Kawabe *et al.* (2006) recently reported an isolated new locality of *C. japonica*. All species of this family prefer clean environments in good natural condition, and they are discontinuous in distribution.

Cornirostridae. The diagnosis of the family was established by Ponder (1990) and it was entirely unknown from Japan until two new species were described by Fukuda & Yamashita (1997). Later Fukuda *et al.* (2000: 135–136, figs 13–16) also reported one unidentified species of *Tomura*. Like the other known species in the world (see Ponder 1990b; Warén *et al.* 1993; Bieler *et al.* 1998) the size of the shell is below 2 mm. The species can be collected from the underside of half-buried boulders in slightly reducing environments.

Hyalogyrinidae. This family includes some of the least known micromolluscs in Japan. *Hyalogyrina depressa*, described from sunken wood in Suruga Bay by Hasegawa (1997a: 113) is the only representative of this family in Japan. For species outside Japan, see Marshall (1988: as Skeneidae), Warén & Bouchet (1993) and Warén *et al.* (1993).

OPISTHOBRANCHIA. The systematics of ‘Opisthobranchia’ has undergone considerable refinements based on phylogenetic analyses (Wägele *et al.* 2008), and the traditional concept of opisthobranchs is now maintained as an informal group (Bouchet *et al.* 2005: 258). No true micromolluscs are known in the ‘Aplysiomorpha’ (Akeridae and Aplysiidae), ‘Pleurobranchomorpha’ (Pleurobranchaeidae and Pleurobranchidae) or ‘Umbraculomorpha’ (Umbraculidae and Tylodinidae).

CEPHALASPIDEA. This group of mainly shelled opisthobranchs includes many micromolluscs. The majority of cephalaspidean families have small-sized species, but there are no micromolluscs in the Bullinidae, Hydatinidae, Bullidae or Gastropteridae. The taxonomy of the Japanese shelled Cephalaspidea was founded by Dr. Habe (Habe 1952a,b). The Acteonidae has traditionally been considered a member of the Cephalaspidea but is possibly more basal in position, as listed by Bouchet *et al.* (2005).

Diaphanidae. There are three described species in Japan (*Diaphana watanabei* Habe, 1976, *D. sakuraii* Habe, 1976, and *D. tibai* Habe, 1976) and they are all smaller than 3 mm (Higo *et al.* 1999:

G4890–4892; Hori *in* Okutani 2000: 738–739). This group is known from soft sediments in the lower subtidal zone. All species are uncommon and the currently used taxonomy is based on Habe (1976b).

Haminoeidae. The shell is well inflated in this family. *Mimatys fukuokaensis* Habe, 1952, and *Micratys ovum* Habe, 1952, are both 2 mm in height (Hori *in* Okutani 2000: 754–759). The habitat of these species is sandy bottoms in the shallow subtidal zone.

Philinidae (Fig. 13C)**.** Some species are below 2 mm in shell length, but the animal is always larger than the shell (Hori *in* Okutani 2000: 750–753). This family lives in fine sediments in the intertidal to subtidal zones. The external morphology and color pattern of the animal is useful for species-level taxonomy. The Japanese species were conchologically reviewed by Habe (1950b).

Smaragdinellidae (Fig. 13D)**.** This family can be found among algae or in crevices and on rocks in the intertidal zone. The shell is small and dorsally covered with well-developed parapodia, contained in the posterior part of the body (Hori *in* Okutani 2000: 758–759).

Aglajidae (Fig. 13E)**.** Members of the Aglajidae have a reduced internal shell (Hamatani *in* Okutani 2000: 752–755). *Nakamigawaia spiralis* Kuroda & Habe, 1961, (Fig. 13E) has a planispirally open-coiled shell.

Cylichnidae (Fig. 13F–G)**.** Japanese species attain 4 cm at the maximum (*Bucconia centa* Okutani, 1987) and several species are small, between 4 and 5 mm (Hori *in* Okutani 2000: 740–747). In particular, *Acteocina* and similar forms are generally small. This family inhabits sandy and/or muddy bottoms in the subtidal to upper bathyal zones.

Retusidae (Fig. 13H)**.** The family comprises many small species (Higo *et al.* 1999; Hori 2000; Hori *in* Okutani 2000: 746–748). Most species of *Retusa* and *Rhizorus* are below 4 mm. This family also lives in soft sediments in subtidal to upper bathyal zones.

THECOSOMATA. These shell-bearing holoplanktonic molluscs are a major component of the zooplankton in the ocean, and are traditionally called ‘Pteropoda’ together with the Gymnosomata. Some families include small-sized species. The Clioidae and Cuvierinidae [*Cuvierina columnella* (Rang, 1827)] are mostly between 1 and 3 cm in shell length, and their shells can be symmetrical, spicular, acutely triangular or cylindrical. All species are widely distributed in the world’s oceans (see Lalli & Gilmer 1989: 58–166 for review of the group). In Japan, multiple species were investigated by Tokioka (1955a), but subsequently only limited information has been published (*e.g.*, Okutani 1964b; Kobayashi & Terazaki 1995).

Cavolinidae. The shell is symmetrical, and dorsoventrally curved; the aperture is constricted with an extended lip. Most species are 1 cm or larger in length but some are smaller (*e.g.*, *Diacria quadridentata* Blainville, 1821; 4 mm) (Okutani 2000: 772–775).

Limacinidae. The shell is planispirally or conically coiled, polished, transparent, and smaller than 2 mm (Okutani 2000: 772–773). All species are widely distributed, mainly in warm oceans. The aperture can be closed with the operculum.

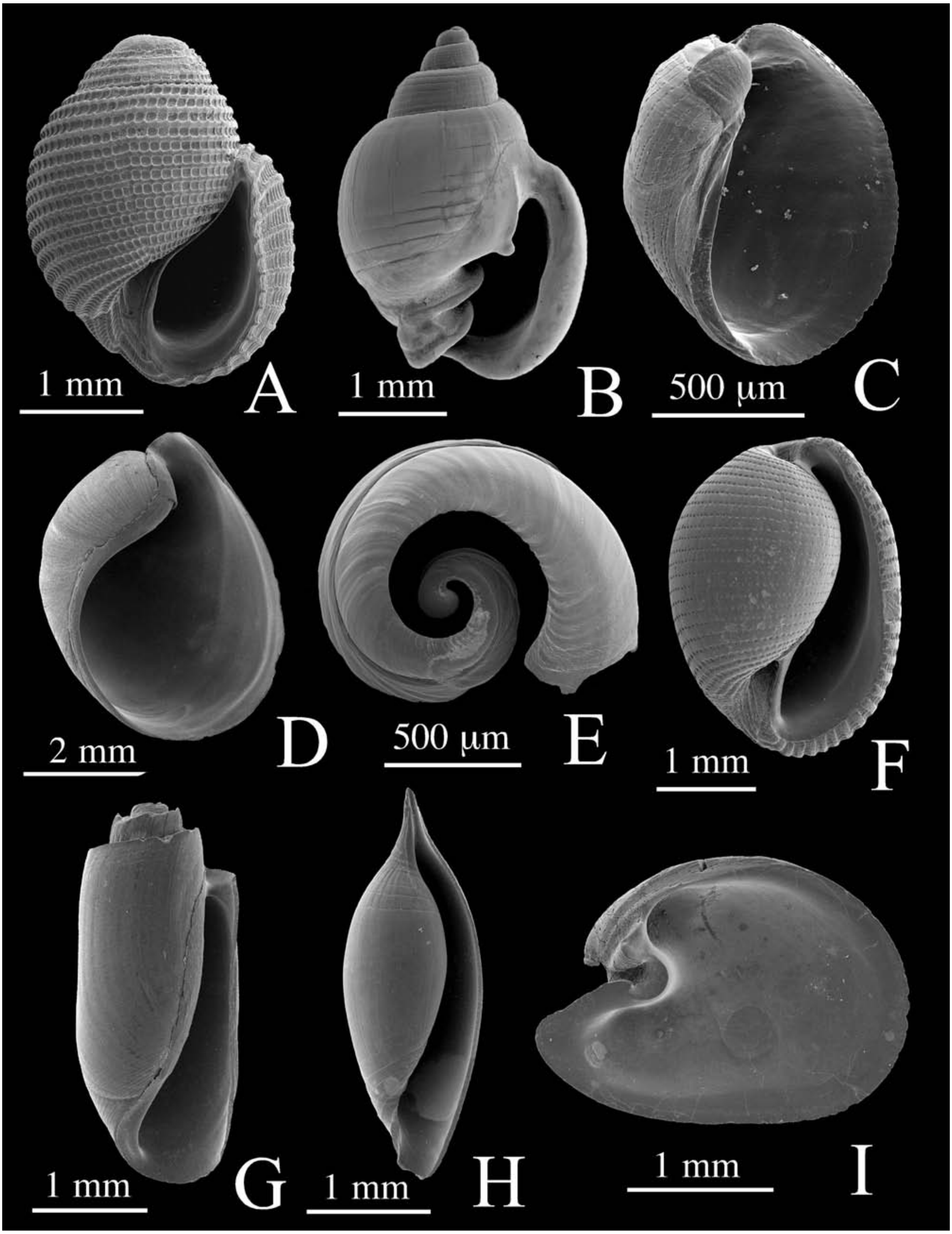
Desmopteridae. *Desmopterus papilo* Chun, 1889 ranges from 2 to 5 mm in body length. This species is different from other members of the family with respect to its well-developed foot lobes, which are larger than the main body (Okutani 2000: 777).

Peraclidae. The shell of *Peraclis* is sinistrally coiled and covered with obliquely crossed reticular sculpture. The columella is strongly reflected to form an acute spine. An operculum is present. Shell length is around 6 mm in Japanese species (Okutani 2000: 774–775). The genus is widely distributed in temperate and warm oceans in the world, but rather rare in Japan.

GYMNOSOMATA. This shell-less holoplanktonic group is carnivorous and known to feed on Thecosomata (see Lalli & Gilmer 1989: 167–213 for the review of biology). The foot is markedly deformed into a pair of lobes for swimming. Five families are known in Japan. Among them, *Clione limacina* (Phipps, 1774) (Clionidae) and *Cliopsis krohnii* Troschel, 1854, (Cliopsidae) attain 4 cm and 2.5 cm, respectively. *Hydromyles globulosa* (Rang, 1825) (8 mm in length, Hydromylidae) and *Pneumoderma atlanticum pacificum* (Dall, 1817) (less than 1 cm, Pneumodermatidae) are of more moderate size.

ACOCHLIDEA. This specialized group of opisthobranchs is interstitial and mostly small. Characteristically the visceral mass is cylindrical and separated from the foot. See Neusser *et al.* (2006) & Neusser & Schrödl (2007) for the anatomy of Acochlidea.

Figure 13 (next page)**.** Opisthobranchia (in traditional sense). **A.** Acteonidae, *Obrussena moeshimaensis* Habe, 1952. **B.** Ringiculidae, *Ringiculina doliaris* (Gould, 1860). **C.** Philinidae, *Philine rubrata* Gosliner, 1988. **D.** Smaragdinellidae, *Smaragdinella sieboldi* A. Adams, 1864. **E.** Aglajidae, *Nakamigawaia spiralis* Kuroda & Habe, 1961. **F–G.** Cylichnidae. **F.** *Roxania punctulata* A. Adams, 1862. **G.** *Didontoglossa koyasensis* (Yokoyama, 1927). **H.** Retusidae, *Rizorus* cf. *radiolus*. **I.** Juliidae, *Julia japonica* Kuroda & Habe, 1951. Locality data: **A.** R/V *Shinyo-Maru*, station 1998-33, 106–101 m, 27°06.48'N 142°09.12'E–27°06.56'N 142°09.14'E, Oct. 21, 1998, UMUT RM28800. **B.** Banda, Tateyama, shallow subtidal zone, by diving, Chiba, 1995, UMUT RM28799. **C.** Shibasaki, Hayama, Kanagawa, intertidal zone, Apr. 29, 1998, UMUT RM29638. **D.** Tomori, Kasari, Amami-Oshima Island, Kagoshima, beach-drifed, Apr. 4, 1990, UMUT RM29639. **E.** R/V *Tansei-Maru*, cruise KT-99-17, station SH-2, off Shirahama, Wakayama, 41–42 m, 33°40.700'N, 135°19.170'E–33°40.629'N, 135°19.231'E, Nov. 30, 1999, UMUT RM28804. **F.** R/V *Tansei-Maru*, cruise KT-99-17, station TN-5, off Tanabe, Wakayama, 91–93 m, 33°41.583'N, 135°14.917'E–33°41.647'N, 135°14.777'E, Nov. 30, 1999, UMUT RM28801. **G.** Isahaya Bay, Nagasaki, Mar. 23, 1997, shallow subtidal zone, dredged, coll. by Dr. Shinichi Sato, UMUT RM29640. **H.** R/V *Tansei-Maru*, cruise KT-99-17, station KU-3, off Katsuura, Wakayama, 39–43 m, 33°37.289'N, 135°58.631'E–33°37.228'N, 135°58.660'E, Nov. 29, 1999, UMUT RM28803. **I.** Agonohama, Aka Island, Okinawa, by diving, Sep. 29, 1997, UMUT RM29641.



Hedylopsidae. One unidentified *Hedylopsis* species smaller than 3 mm in length has been recorded from Okinawa (Hamatani *in* Okutani 2000: 760–761). The real diversity of this group is unknown, since no one has seriously examined the interstitial molluscan fauna in Japan.

SACOGLOSSA. This group is well defined by the presence of a single row of blade-like radular teeth, by a sac-like structure (saccus) to store used teeth, and by feeding on green algae. Most species are below 2 cm. The shell-less sacoglossans, the Caliphillidae, Hermaeidae and Plakobranchidae are 15 mm or larger in size and range up to 5 cm in animal length.

Oxynoidae. The shell is bulliform and external but covered with parapodia when living, and much shorter than the animal. Japanese species are smaller than 8–10 mm in shell length and 20–30 mm in body length (Hamatani *in* Okutani 2000: 760–762).

Juliidae (Fig. 13I)**.** Two genera, *Julia* and *Tamanovalva*, represent this family in Japan, although the latter has been placed separately in the Berthelinidae. The shell of *Julia* is thickened, and the protoconch is on the apex of the left valve. There are three species in Japan, *Julia japonica* Kuroda & Habe, 1951, *J. zebra* Kawaguti, 1981 and *J. mishimaensis* Kawaguti & Yamasu, 1982. They are mainly distinguished by the color pattern of the shell (Hamatani *in* Okutani 2000: 762–763). The shell is smaller than 3–6 mm in shell length, and *J. mishimaensis* (3 mm at maximum) is distinctly smaller than the others. *Julia zebra* is known also from Hawaii and South Africa; the other two are distributed only in southwestern Japan. Live specimens of *J. japonica* were first reported by Kawaguti & Yamasu (1966).

Tamanovalva becomes larger than *Julia* (ca. 8 mm), and the shell is very fragile. The protoconch is on the left valve, as in *Julia*. Kawaguti & Baba (1959) first noticed that *Tamanovalva* is an opisthobranch, not a bivalve as believed before. Later they published excellent descriptions of its reproduction and development (Kawaguti & Yamasu, 1960).

Volvatellidae (= Ascobullidae). In *Volvatella* the aperture of the shell is well inflated, and the apical (posterior) side is constricted into a short canal. Several species are known in Japan. The shell reaches 16 mm in length in the largest species (*V. kawamurai* Habe, 1946) but is smaller than 6 mm in the smallest (*V. angeliniana* Ichikawa, 1993) (Hamatani *in* Okutani 2000: 760–761). In *Ascobulla* the shell is cylindrical and extremely fragile, with *A. japonica* (Hamatani, 1969) being smaller than 6 mm. All species are associated with the green algae *Caulerpa* (Hamatani *in* Okutani 2000: 760–761).

NUDIBRANCHIA. In this group small-sized species are probably more common than currently known. Most of the well-examined families such as the Polyceridae, Chromodorididae, Dorididae and Phyllidiidae are mostly 2 cm or larger in body length (Hamatani *in* Okutani 2000: 779–811; Debelius & Kuiter 2007). The largest species, *Hexabranchus lacera* (Cuvier, 1804) (Hexabranchidae) and *Melibe japonica* (Tethydidae), reach over 30 cm in body length.

Okadaiidae (= Vayssieriidae). The size of *Okadaia elegans* Baba, 1930, which might be synonymized with *Vayssierea felis* (Collingwood, 1881), is 7 mm at maximum (Hamatani *in* Okutani 2000: 782–783).

Eubranchidae. Species of *Eubranchus* are generally smaller than 10–15 mm and have numerous branchial papillae on the dorsum (Hamatani *in* Okutani 2000: 802–803). *Eubranchus inabai* Baba, 1964, is smaller than 5 mm.

Pseudovermidae. From Japan, the single interstitial species *Pseudovermis japonicus* was described from Wakayama Prefecture by Hamatani & Nunomura (1973). Its body is vermiform and translucent, and the branchial papillae are vestigial. The anterior end of the body is rounded. See also Hamatani *in* Okutani (2000: 802–803).

Tergipedidae: Cuthoninae. Species of *Cuthona* are generally smaller than 10–15 mm in body length (Hamatani *in* Okutani 2000: 804–805). *Cuthona pupillae* (Baba, 1961) is below 5 mm, and the smallest species, *Tenellia papillida* (Alder & Hancock, 1854), is 2 mm. The latter species is also recorded from the Mediterranean Sea and Brazil.

PULMONATA. The monophyly of the Pulmonata has been tested actively within the last decade and has not always been accepted (see review by Mordan & Wade 2008). In the current systematic list, the informal group Pulmonata is composed of the informal group Basommatophora + clade Hygrophila + clade Eupulmonata (Bouchet *et al.* 2005: 263–270). The Basommatophora consists of the Amphibolidae and Siphonariidae. Families living in freshwater are united as Hygrophila.

Amphibolidae (Fig. 14A)**.** The only described Japanese species, *Lactiforis takii* (Kuroda, 1928) (Fig. 14A), is distributed on muddy bottoms of embayed areas (Kurozumi *in* Okutani 2000: 822–823) and is now seriously threatened by habitat destruction. Tanaka (1959) documented its development briefly and Kosuge (2000) investigated its ecology and life history. It has long been known as *Salinator takii* but was recently transferred to the newly proposed genus *Lactiforis* (Golding *et al.* 2007). Nawa *et al.* (1998) also reported an undentified species from Okinawa.

Siphonariidae (Fig. 14B)**.** The average size of *Siphonaria* species is between 15 and 20 mm (Kurozumi *in* Okutani 2000: 812–815), but there are smaller species in Japan. *Siphonacmea oblongata* (Yokoyama, 1926) is smaller than 5 mm. It is exceptional for this family in its cold-water distribution in the subarctic area of northern Japan. The localities of extant populations are poorly known but it has been collected alive from subtidal seagrass beds in Iwate Prefecture (Tsuchida *et al.* 1998). Toyohara *et al.* (2001) examined its population dynamics by periodic sampling. *Williamia radiata* (Pease, 1860) (Fig. 14B, 6 mm in length) inhabits lower intertidal to shallow subtidal zones in subtropical to tropical regions. See Ruthensteiner (2006) for the anatomy of the genus.

Lymnaeidae (Fig. 14C–D)**.** Japanese species in this family are below 20 mm in height. Some are 6 mm or smaller, such as *Lymnaea hamadai* Habe, 1968, *Radix onychia* (Westerlund, 1887) (Fig. 14C) and *Galba truncatula* (Müller, 1774) (Fig. 14D). A few species endemic to Japan are now critically endangered (*e.g.*, *L. hamadai*). In contrast, some introduced species (*e.g.*, *Physa acuta* Draparnaud, 1805) are widely distributed.

Planorbidae (Fig. 14E–G)**.** The typical shape of the family is discoidal. *Cyranulus chinensis* Dunker, 1854 (Fig. 14F) is the most common species throughout Japan, but there is the possibility that this represents a complex of similar species (Masuda & Uchiyama 2004: 160). *Polypylis hemisphaerula* (Benson, 1842) (Fig. 14E) is another common species that differs from others by its narrow umbilicus. The size of the discoidal form is between 10 mm and 4 mm (Masuda & Uchiyama 2004: 158–163).

Camptoceras hirasei Walker, 1919, (Fig. 14G) is markedly tall in shell shape. The maximum size is 10 mm in height and 3 mm in diameter. The species was known in the past from a large area, but now only from a very limited number of localities (Marui 2002; Masuda & Uchiyama 2004: 158).

Planorbidae: Ancylini (Fig. 14H)**.** There are a few species of freshwater limpets in Japan. *Laevapex nipponica* (Kuroda, 1947) (Fig. 14H) is common in temperate areas. *Laevapex japonica* (Habe & Burch, 1965) was described from Lake Biwa (Habe & Burch 1965) but now is regarded as a variety of *L. nipponica* with striations. *Pettancylus pettardi* (Johnston, 1879) is an introduced species (Masuda & Uchiyama 2004: 165).

EUPULMONATA. The clade Eupulmonata is divided into Trimusculoidea + Ellobioidea + Otinoidea + Systellommatophora + Stylommatophora (Bouchet *et al.* 2005: 264, note 231).

Trimusculidae. In the literature there is no record of freshly collected specimens in Japan. The descriptions of two Japanese species, *Trimusculus kurodai* Habe, 1958 and *T. yamamotoi* Habe, 1958, were based on shells only. The size is up to 8–9 mm in length (Kurozumi *in* Okutani 2000: 812–813) but normally smaller.

Ellobiidae (Fig. 14I–J)**.** Small-sized species exist in various genera such as *Laemodonta* and *Microtralia* (Kurozumi *in* Okutani 2000: 816–823; Masuda & Uchiyama 2004: 121–149). Generally the diversity is higher in warmer regions, and the taxonomy of the species from Ryukyu Islands is the most complicated among Japanese ellobiids. The Japanese species were well treated by Fukuda *in* Wada (1996), Kimura (1997, 2000), Masuda & Uchiyama (2005: 121–149) and Kimura *et al.* (2006). The occurrence of this family is rather limited in temperate areas.

Ellobiidae: Carychiinae (Fig. 15A)**.** This group has been treated as an independent family, but it is nowadays positioned as a subfamily of Ellobiidae (Bouchet *et al.* 2005: 264). The shell is white, small, with strong denticles on the columella (Fig. 15A). Among the six Japanese species of *Carychium*, the largest species, *C. noduliferum* Reinhardt, 1877, is 2.5 mm in height, and *C. nipponense* Pilsbry & Hirase, 1904, is the smallest at 1.3 mm.

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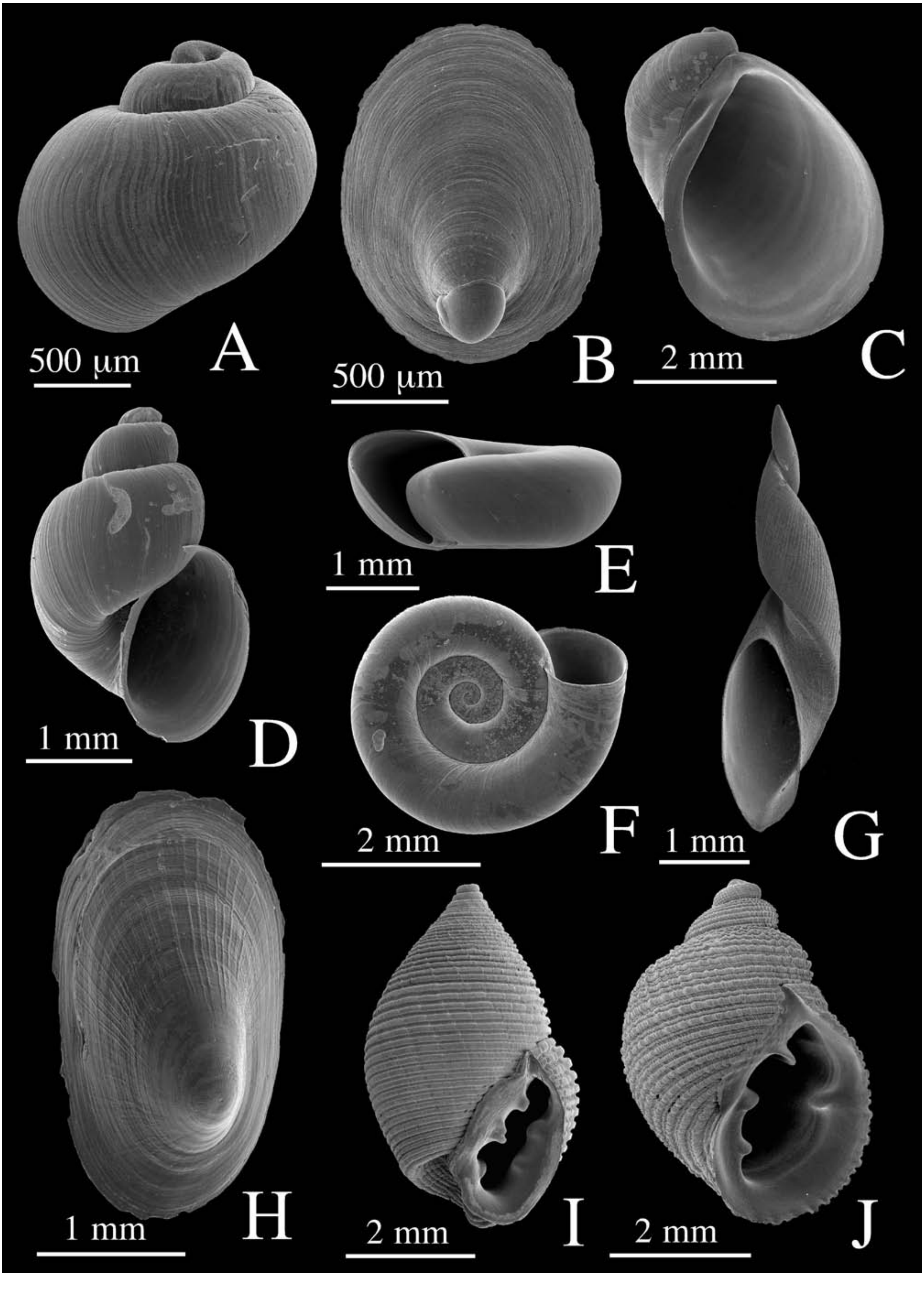
Figure 14 (next page)**.** Pulmonata (1). **A.** Amphiboridae, *Lactiforis takii* (Kuroda, 1928). **B.** Siphonariidae, *Williamia radiata* (Pease, 1860). **C–D. C.** *Radix onychia* (Westerlund, 1887). **D.** *Galba truncatula* (Miller, 1774). **E–H.** Planorbidae. **E.** *Polypylis hemisphaerula* (Benson, 1842). **F.** *Gyraulus chinensis* Dunker, 1854. **G.** *Camptoceras hirasei* Walker, 1919. **H.** *Laevapex nipponica* (Kuroda, 1947). **I–J.** Ellobiidae. **I.** *Laemodonta typica* (H. & A. Adams, 1854). **J.** *Pedipes jouani* Montrouzier, 1862. Locality data: **A.** Isahaya Bay, Nagasaki, Mar. 23, 1997, shallow subtidal zone, dredged, coll. by Dr. Shinichi Sato, UMUT RM29642. **B.** R/V *Shinyo-Maru*, station 1997-10, off Ogasawara Islands, 55–59 m, 27°06.35'N, 142°10.48'E–27°06.35'N, 142°10.28'E, Oct. 16, 1997, UMUT RM29643. **C.** Okinoshima Island, Lake Biwa, UMUT RM29644. **D.** Hetayama, Heta, Shunan, Yamaguchi, UMUT RM29645. **E–F.** Heta, Tokuyama, Yamaguchi, 1980, UMUT RM28809. **F.** UMUT RM29646. **G.** Hatacho, Kasai, Hyogo, ex Kenji Ishikawa Collection, UMUT RM28808. **H.** Tonda River, Shinnanyo, Yamaguchi, July 1989, UMUT RM28807. **I.** Chinen, Okinawa, May 2000, UMUT RM28810. **J.** Miyako Island, Okinawa, Nov. 1996, UMUT RM28811.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STYLOMMATOPHORA. The Stylommatophora is the largest main group of Pulmonata. There are no small species among the Japanese Enidae, Clausiliidae, Trochomorphidae, slugs (Philomycidae, Limacidae, Milacidae and Arionidae), Corillidae, Camaenidae or Bradybaenidae. The family Succineidae (*e.g.*, *Succinea*), Cionellidae (*Cochlicopa*) and Subulinidae (*e.g.*, *Allopeas*) are relatively small but not really minute.

Achatinellidae: Tornatellininae (Fig. 15B)**.** The spire in the Japanese species is tall and pointed apically. The aperture is not thickened but shows a single small lamella on the parietal wall. *Tornatellides* species are 3–4 mm in height (Azuma 1995: 28); *Elasmias* and *Lamellidea* are around 3 mm in height (Azuma 1995: 190–191).

Pupillidae. The shell of *Pupilla* is somewhat cylindrical and yellowish brown, and some carry weak denticles on the parietal wall. The Japanese species of *Pupilla* are about 3 mm in height (Azuma 1995: 191). The best publication with clear illustrations was that by Yamashita & Fukuda (1996). Kurozumi & Yamashita (1996) reported a possible introduced species of *Pupoides*.

Pleurodiscidae. *Pyramidula conica* Pilsbry & Hirase, 1902, is between 2–3 mm and restricted to limestone areas in warm-temperate zones, as is the case with *Georissa shikokuensis* (Fig. 5C) and *Bensonella plicidens* (Fig. 15F).

Strobilopsidae. The clearest diagnostic character of this group is the presence of a few horizontal lamellae on the parietal wall and also on the basal side in a slightly deeper position (Azuma 1995: 32). The Japanese species (2–3 mm in width) belong to two genera (Minato 1982). *Eostrobilops nipponica* Pilsbry, 1927, is distributed in the northern part of the Japanese mainland, and a subspecies was discovered from remote localities in the more western part (Matsumura & Minato 1998; Kawabe *et al.* 2000). *Enteroplax yaeyamensis* Habe & Chinen, 1974, is distributed in the Yaeyama Islands and Okinawa; Minato & Tada (1992) described a similar species from Taiwan.

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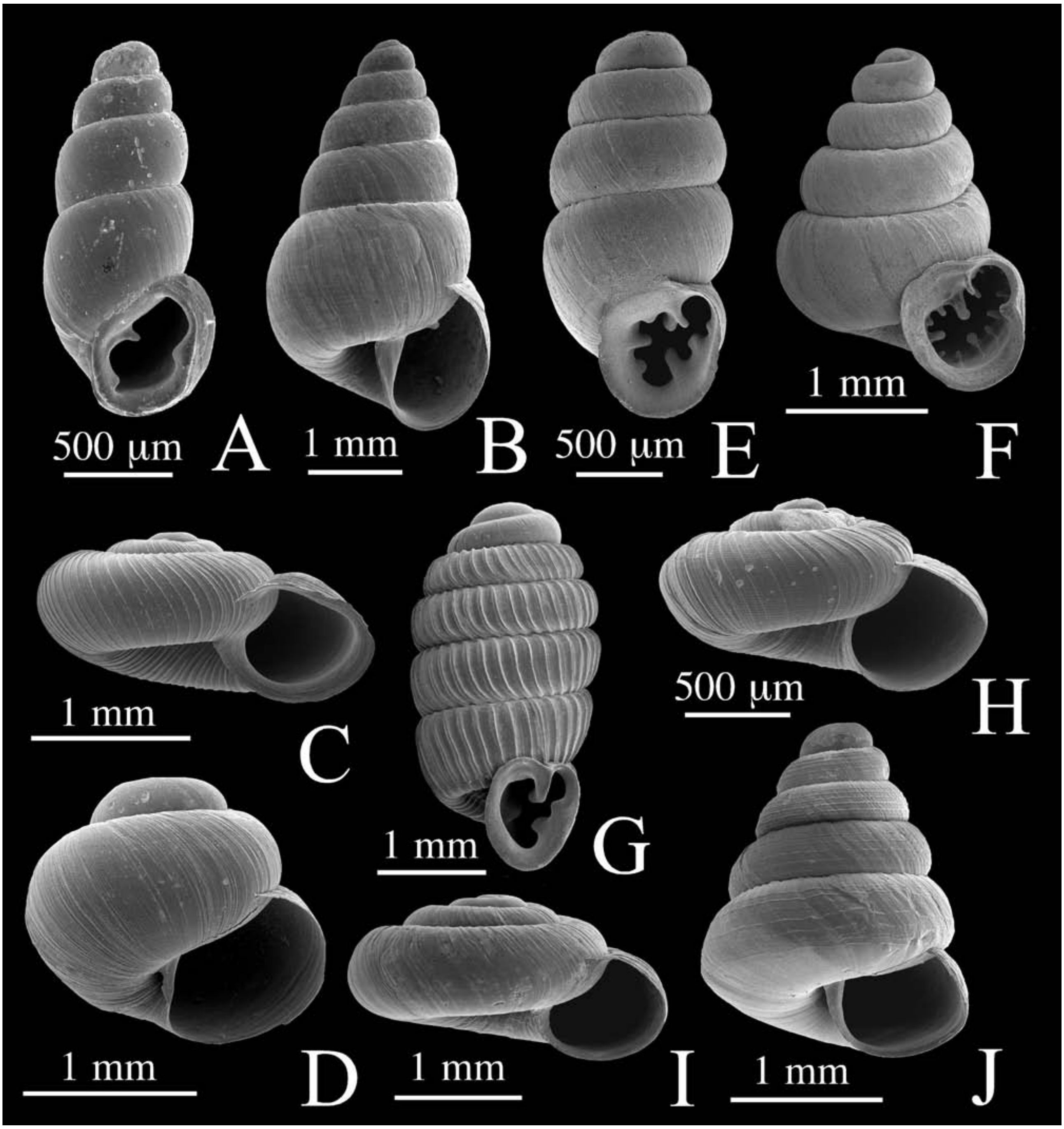
Figure 15 (next page)**.** Pulomonata (2). **A.** Carychiidae, *Carychium nipponense* Pilsbry & Hirase, 1904. **B.** Tornatellininae of Achatinellidae, *Tornatellides boeningi* (Schmacher & Boettger, 1891). **C–D.** Valloniidae. **C.** *Vallonia costata* (Miller, 1774). **D.** *Parazoogenetes orcula* (Benson, 1850). **E–F.** Vertiginidae, *Vertigo shimochii* Kuroda & Amano, 1960. **F.** *Bensonella plicidens* (Benson, 1849). **G.** Streptaxidae, *Sinoennea iwakawa* (Pilsbry, 1900). **H.** Punctidae, *Punctum* sp. **I.** Zonitidae, *Hawaiia minuscule* (Binney, 1840). **J.** Helicarionidae, *Sitalina circumcincta* (Reinhardt, 1883). Locality data: **A.** Otsuchi, Iwate, July 16, 1999, UMUT RM29647. **B.** Taketomi Island, Okinawa, Mar. 1, 2001, coll. by Michiko Okada, UMUT RM28812. **C.** Seto Marine Biological Station, Kyoto University, Shirahama, Wakayama, Mar. 10, 2000, UMUT RM29648. **D.** Tanaka, Nijo, Fukuoka, Feb. 29, 2004, UMUT RM29649. **E.** Seikai National Fisheries Research Institute, Ishigaki Island, Okinawa, Apr. 26, 2002, coll. by Dr. Takeharu Kosuge, UMUT RM28813. **F.** Iwanagahongo, Shuho, Yamaguchi, Apr. 30, 1984, UMUT RM28814. **G.** Furen Limestone Cave (outside of cave), Oita, Feb. 12, 1985, UMUT RM28817. **H.** Heta, Shunan, Yamaguchi, May 15, 2006, UMUT RM29650. **I.** Ube, Yamaguchi, Apr. 2002, UMUT RM29651. **J.** Seto Marine Biological Station, Kyoto University, Shirahama, Wakayama, Mar. 10 2000, UMUT RM29652.



Valloniidae (Fig. 15C–D)**.** The shell is discoidal with a thickened prosocline aperture. *Vallonia costata* (Müller, 1774) (2 mm in width) is widely distributed in Japan near the sea shore. A population in Soujima, Wakayama Prefecture, has a polished surface and has been identified as *V. excentrica* Sterki, 1892, which was originally described from Europe. *Vallonia patens* (Reinhardt, 1883) from northern Japan was illustrated by Kuwahara *et al.* (1997: fig. 2a).

The so-called 'Acanthinulidae' is now synonymized with the Valloniidae (Bouchet *et al.* 2005: 265). The whorls are rounded and elevated, and the aperture is not thickened. The Japanese species are in two genera and are all less than 2–3 mm in width (Azuma 1995: 32–33). *Zoogenetes harpa* (Say, 1824) is distributed in northern Japan (Kuwahara *et al.* 1997: fig. 2d). *Parazoogenetes* (Fig. 15D) is widely distributed in temperate areas of Japan.

Vertiginidae (Fig. 15E)**.** The shell of the type genus, *Vertigo*, is yellowish brown with several denticles in the thickened aperture. The Japanese species are less than 2–3 mm in height. Species are distinguished by the outline of the shell and the morphology of the denticles (Azuma 1995: 29–30, 191–192). The species in northern Japan were compared by Kuwahara *et al.* (1997). *Truncatella insulivaga* (Pilsbry & Hirase, 1904) was reported by Minato & Nishi (2005).

Vertiginidae: Gastrocoptinae (Fig. 15F)**.** The shell of *Gastrocopta* is translucent white and 2–3 mm or smaller in height (Azuma 1995: 30–31 192–193). The aperture is markedly narrowed with denticles on the parietal, columellar, basal and palatal sides.

Two species of 'Hypselostomatidae' (= Vertiginidae: Gastrocoptinae) are distributed in Japan (Azuma 1995: 31–32). *Hypselostoma insularum* Pilsbry, 1908 (1.6 mm in height) is found only on islands in the southernmost part of Okinawa. The last part of the whorl is slightly detached from the previous whorls. The inside of the aperture bears six denticles. *Bensonella plicidens* (Benson, 1849) (2.5 mm in height) is a temperate species on the mainland and its habitat is restricted to limestone areas. Several small lamellae are formed in the thickened aperture.

Streptaxidae (Fig. 15G)**.** All the native Japanese species belong to *Sinoenna*, and are 4–7 mm in height (Azuma 1995: 181–182, 227). The aperture is strikingly thickened and narrowed with projections (Fig. 15G). *Indoenna bicolor* (Hutton, 1834) is an introduced species.

Punctidae (Fig. 15H)**.** About ten species of *Punctum* were described in the 1900s and all the Japanese species are between 2–3 mm in width (Azuma 1995: 93–95; 200–201). They are difficult to distinguish morphologically and need revision with clear illustrations.

Discidae. The only Japanese species of this family, *Discus pauper* (Gould, 1859), is 6.5 mm in width (Azuma 1995: 96). Its shell is distinguishable from that of other similar-looking snails by its wide umbilicus and rough axial streaks.

Endodontidae. The genus *Hirasea* (3–7 mm in diameter) is a well-known genus endemic to Ogasawara Islands. This group has long been assigned to the Endodontidae, but Ueshima & Kurozumi (1988) proposed to transfer *Hirasea* to Helicarionidae: Euconulinae based on the anatomy of *Hirasea diplomphalus* Pilsbry, 1902. About 20 species were described around the 1900s and most of them are already extinct or critically endangered (Azuma 1995: 95 201–203).

Helicodiscidae. This family was first discovered in Japan by Kano (1996). At least three species are distributed in Japan (*Helicodiscus singleyanus inermis* Baker, 1929; *H.* sp. A, *H.* sp. B).

Zonitidae (Fig. 15I)**.** The shell is discoidal, multispiral, polished on the surface, and with a deep umbilicus. The members of the family are all small (7.5–2.1 mm in diameter) in Japan (Azuma 1995: 96–98), although there are large species in Europe. The most famous species, *Hawaiia minuscula* (Binney, 1840), was introduced from North America. Kano (1996) demonstrated that the species called '*H. minuscula*' in Japan actually represents a mixture of taxa, including Helicodiscidae.

Helicarionidae (Fig. 15J). More than 150 nominal species have been described from Japan (Higo & Goto 1993: no. 7010–7166), and their taxonomy is the most seriously confused among Japanese land snails. This group is currently under revision by Dr. Rei Ueshima (*e.g.*, Ueshima 1989, 1995, 2007).

Bivalvia

The Bivalvia is the second largest group of molluscs, and the second major component of the micromolluscs. The latest concepts of family-level taxa were proposed by Bieler & Mikkelsen (2006), and a new classification at higher rank is proposed by Giribet (2008). In contrast to gastropods, bivalve shells generally do not exhibit determinate growth.

PROTOBRANCHIA. Small-sized protobranchs are common in soft sediments in the lower subtidal to hadal zones. The Protobranchia is divided into the three orders Nuculoida, Solemyoida and Nuculanoida (Bieler & Mikkelsen 2006). Giribet (2008) proposes the new group Opponobranchia for the Nuculoida and Solemyoida. In the Nuculanoidea, six families are recognized in Japan: the Malletiidae, Neilonellidae, Tindariidae, Sareptidae and Nuculanidae. Most members of these families are 1 cm or larger.

Nuculidae (Fig. 16A). Most species are within the range of 0.6–3 cm in length in Japan (Kurozumi & Tsuchida *in* Okutani 2000: 835–837). The smallest species is *Pronucula insignis* Hayami & Kase, 1993, (2.1 mm in length) from submarine caves (Hayami & Kase 1993). *Nucula paulula* A. Adams, 1856, a common species in the intertidal to shallow subtidal zones, attains 4 mm in length. A few species are also around 4 to 6 mm, including *e.g., N. gemmulata* Habe, 1953, and *N. dorsocrenata* (Habe, 1977).

'**Nucinellidae' (= Manzanellidae)** (Fig. 16B–C). There are five Japanese species in the family (Matsukuma *et al.* 1982; Okutani 2000: 832–833). *Nucinella viridis* Matsukuma, Okutani & Tsuchi, 1982, is about 1 cm in length, and the remaining four, *Huxleyia sulcata* A. Adams, 1860, *N. cavernicola* Hayami & Kase, 1993, *N. kanekoi* Matsukuma, Okutani & Tsuchi, 1982, and *N. surugana* Matsukuma, Okutani & Tsuchi, 1982, are about 2 mm in length. All live at lower subtidal to bathyal depths except for *Huxleyia cavernicola* Hayami & Kase, 1993, which comes from submarine caves (Hayami & Kase 1993: 12–14).

Nuculanidae (Fig. 16D–F). One species, *Yoldiella philippiana* (Nyst, 1844) (Fig. 16E), is 3–4 mm in length. Sasaki *et al.* (2006b) reported this species as a food source of *Ctenodiscus crispatus* (Retzius, 1805) (Asteroidea). Other Japanese species in the family are 1 cm or larger.

Tindariidae. Three species are distributed between 250 and 6,000 m off Japan (Kurozumi & Tsuchida *in* Okutani 2000: 839). *Tindaria soyoae* Habe, 1953, is ca. 5 mm in length and others are larger, while *T. antarctica* Thiele, 1931, (7 mm) is known as an example of a cosmopolitan deep-sea mollusc.

PTERIOMORPHIA. This large group of bivalves consists mainly of epifaunal species that are cemented or byssally attached to the substrate. The shape of the dissoconch is highly variable, but the prodissoconch is regularly rounded in most families (Fig. 17A–H). In current systematics, the Pteriomorphia consists of five orders: the Arcoida, Mytiloida, Pterioida, Limoida, and Pectinoida

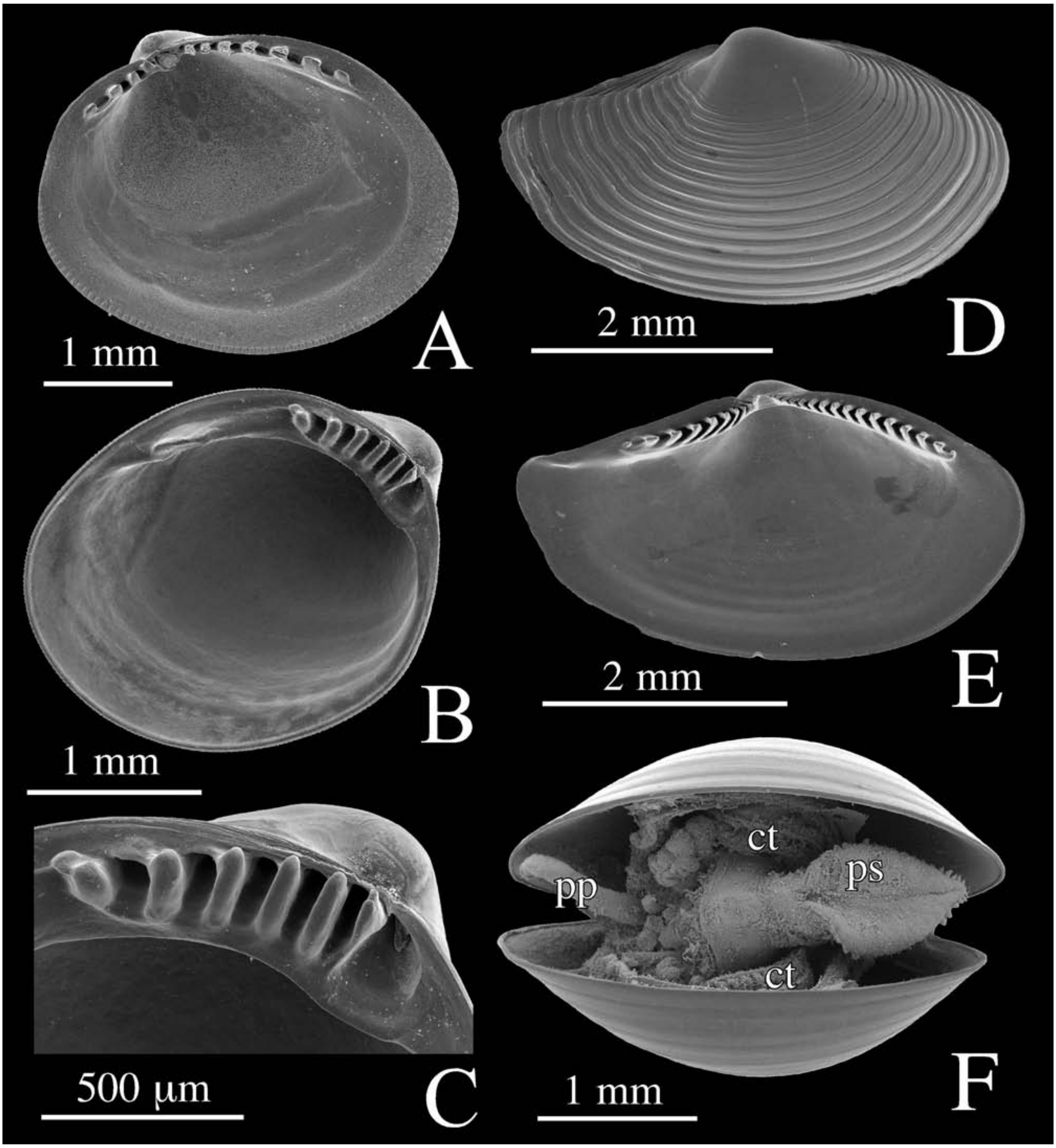


Figure 16. Protobranchia. **A.** Nuculidae, *Nucula* sp. **B–C.** Nucinellidae, *Huxleyia sulcata* A. Adams, 1960. **C.** Enlarged view of hinge. **D–F.** Nuculanidae, **D–E.** *Jupiteria confusa* (Hanley, 1860), young specimens. **F.** *Yoldiella philippiana* (Nyst, 1844), ventral view with animal. Abbreviations: ct, ctenidium; pp, palp proboscides; ps, pedal sole. Locality data: **A.** R/V *Tansei-Maru*, cruise KT-05-30, station HB, Hyuga Basin, 1644.3–1656.6 m, 32°22.58'N, 132°30.54'E–32°22.61'N, 132°29.24'E, Nov. 22 2005, UMUT RM29653. **B–C.** Off Minabe, Wakayama, depth unkown, Dec. 6, 1999, UMUT RM28726. **D–E.** R/V *Tansei-Maru*, cruise KT-99-17, station KU-2, off Katsuura, Wakayama, 37–38 m, 33°37.454'N, 135°58.394'E–33°37.402'N, 135°58.470'E, Nov. 29, 1999. **D.** UMUT RM28725. **E.** UMUT RM28724. **F.** Off Shinminato, Toyama, depth unkown, Apr. 21 2004, coll. by Kentaro Muro, UMUT RM29654.

(Bieler & Mikkelsen 2006). There are no small species in the families Parallelodontidae, Cucullaeidae, Glycymeridae, Pteriidae, Vulsellidae, Malleidae, Pinnidae, Pectinidae, Spondylidae, Anomiidae, Plicatulidae, Dimyidae, Gryphaeidae or Ostreidae.

Arcidae (Fig. 18A)**.** All species attach to hard bottoms or grains in soft bottoms with byssi. They are most abundant in shallow water but some are also found in the abyss (*e.g.*, *Bentharca asperula* Dall, 1881) (Matsukuma & Okutani *in* Okutani 2000: 844–855). Small species are considerably restricted among this family. Adult shells smaller than 5 mm are found only in species of *Bentharca* from submarine caves (Hayami & Kase 1993: 19–26) and in a few species of *Bathyarca* from muddy bottoms in the lower subtidal and bathyal zones and also submarine caves (Hayami & Kase 1993: 26–27).

Limopsidae. Most species range from 1 to 3 cm in length (Matsukuma *in* Okutani 2000: 856–859). The species of *Nipponolimopsis* are below 1 cm, and a recently-discovered new species in the intertidal zone is below 4 mm (Sasaki & Haga, 2007).

Philobryidae (Fig. 19A–E)**.** The species of this family are exclusively below 2 mm in length (Okutani 2000: 860–861) and there is little information in literature except for Hayami & Kase (1993). There are several species in the genera *Cosa* [*C. waikikia* (Dall, Bartsch & Rehder, 1938), *C. kinjyoi* Hayami & Kase, 1993, *C. uchimae* Hayami & Kase, 1993, and *C.* sp.: Hayami & Kase 1993: 28–36] and *Cratis* (*C. kanekoi* Hayami & Kase, 1993, and *C. ohashii* Hayami & Kase, 1993: Hayami & Kase 1993: 36–41) in Japan. They are common in submarine caves (Hayami & Kase 1993). The relation with the Limopsidae needs further investigation (*cf.* Sasaki & Haga 2007).

Mytilidae. This family is highly variable in size (Kurozumi *in* Okutani 2000: 862–877). The largest species in Japan, *Gigantidas horikoshii* Hashimoto & Yamane, 2005, attains nearly 20 cm (Hashimoto & Yamane 2005). The small groups include species of *Dacrydium* (2–5 mm) and *Crenella yokoyamai* Nomura, 1922 (3 mm). The smallest species, *Uremella concava* Hayami & Kase, 1993, is around 1.1 mm in length and found only in submarine caves (Hayami & Kase 1993: 50–52). *Dacrydium* and *Crenella* are also known from submarine caves (*D. zebrum* Hayami & Kase, 1993; Hayami & Kase 1993: 46–48; *C.* sp. Hayami & Kase 1993: 45).

Limidae (Fig. 18B–C)**.** The members are mostly large (Hayami *in* Okutani 2000: 890–895). In the largest species in Japan, *Acesta marissinica* Yamashita & Habe, 1969, the maximum size is 20 cm in height. In other genera (*Lima*, *Limaria* and *Ctenoides*), most species are larger than 2 cm. Small species are typical of the genus *Limatula* (Fig. 18C). The largest species of this genus are 15 mm in height [*L. strangei* (Sowerby, 1872) and *L. japonica* A. Adams, 1863] but some are below 5 mm. The genus *Divarilima* (Fig. 18B) is also small and known from the lower subtidal zone and submarine caves (Hayami & Kase 1993: 69–71).

Propeamussiidae (Fig. 18D–I)**.** Uniquely among bivalves, this family is characterized by the difference in shell microstructure between left and right valves (Hayami 1988; Hayami *in* Okutani 2000: 912–915). The shell is extremely thin and fragile. The largest species, *Propeamussium watsoni* (Smith, 1885), reaches 4 cm in height, but most species are below 2 cm. This family is well-known as one of the typical faunal element of deep-sea habitats, but is also found in submarine caves (*Parvamussium*, *Cyclopecten* and *Chlamydella*: Hayami & Kase 1993: 54–67). The species of *Chlamydella* (Fig. D–E) are especially small, about 2 mm in shell height. Live specimens have been collected only from submarine caves, but dead valves are also obtained by dredging from sediments outside of caves (Fig. 18D–F).

HETEROCONCHIA. The monophyly of Heteroconchia has been recognized in phylogenetic analyses in the 2000s. It consists of the Palaeoheterodonta (orders Trigonioida + Unionoida) and Heterodonta (orders Carditoida + Anomalodesmata **+** Veneroida + Myoida). The freshwater Unionidae is the only member of this clade in Japan, and contains no small-sized species.

HETERODONTA. The Heterodonta is the most diverse group of bivalves. They are mostly infaunal, with some exceptions such as the Chamidae. In the traditional classification, the Heterodonta has been treated as a distinct subclass from the Anomalodesmata. However, in a recently proposed classification the Heterodonta consists of four orders: the Carditoida, Anomalodesmata, Veneroida and Myoida (Bieler & Mikkelsen 2006).

CARDITOIDA. It has been recently revealed that the families Crassatellidae, Astartidae and Carditidae are basal among Heterodonta, and a new name, Archiheterodonta, is proposed for these groups by Giribet (2008; see also Taylor *et al.* 2007). A large heterodont group excluding the Archiheterodonta is called Euheterodonta (Giribet & Distel 2003).

Crassatellidae. All Japanese species are larger than 1 cm except *Salaputium unicum* Hayami & Kase, 1993, from submarine caves, which is smaller than 3 mm in length (Hayami & Kase 1993: 86–88).

Carditidae. Species of *Cardita* are larger than 1.5 mm in length, but, one species from submarine caves, *Cardita urema* Hayami & Kase, 1993, is 3–4 mm (Hayami & Kase 1993: 80–81).

Condylocardiidae (Fig. 20A)**.** The Japanese species are all 2 mm or less, and uncommon or poorly known. *Cuna iriomotensis* Habe, 1992, was described from Okinawa by Habe (1992) but it has never been recollected. *Carditella* and the similar genus *Carditellopsis* were once allocated to Carditidae: Carditellinae (*e.g.*, Kuroda *et al.* 1971) but are now regarded as a member of this family (Bieler & Mikkelsen 2006). Hayami & Kase (1993) described the two species *Carditella iejimensis* Hayami & Kase, 1993, and *C. shimojiensis* Hayami & Kase, 1993, from submarine caves. *Carditella hanazawai*

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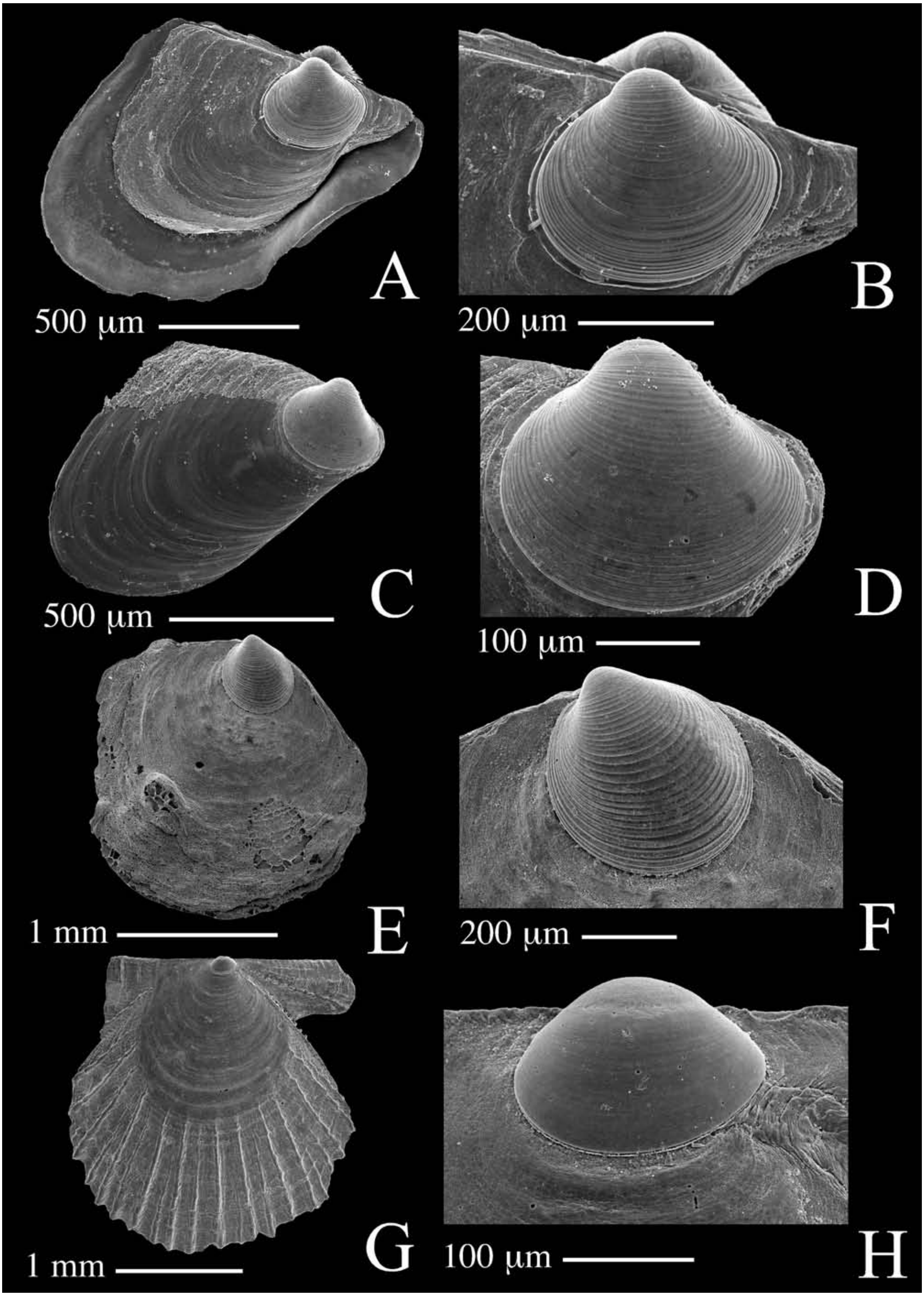
Figure 17 (next page)**.** Pteriomorphia (1). Entire view of juvenils (left) and enlarged view of prodissoconch (right). **A–B.** Pteriidae, possibly *Pinctada martensii* (Dunker, 1873). **C–D.** Isognomonidae, *Isognomon acutirostris* (Dunker, 1848). **E–F.** Ostreoidea, gen. et sp. **G–H.** Ptectinidae, *Patinopecten yessoensis* (Jay, 1856). Locality data: **A–B.** Izu-Oshima Island, south off Tokyo, date unknown, UMUT RM29655. **C–D.** Maehama, Aka Island, Okinawa, upper intertidal zone, Oct. 1, 1997, UMUT RM29656. **E–F.** R/V *Tansei-Maru*, cruise KT-05-30, station SS4(2), off Shirahama, Wakayama, 27.68–35.29 m, 33°37.43'N, 135°22.09'E–33°37.31'N, 135°21.85'E, Nov. 26 2005, UMUT RM29657. **G–H.** Otsuchi, Iwate, date unknown, UMUT RM29658.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(Nomura, 1933) and *Carditellopsis toneana* (Yokoyama, 1922) have not been clearly illustrated in literature and need reinvestigation.

ANOMALODESMATA. In general, species diversity in the Anomalodesmata is limited to shallow-water environments. The shells of some of the families are characterized by rough spicular or granular sculpture (Fig. 21A–G) and nacreous structure. Species smaller than 4 mm are known in the Verticordiidae and Cuspidariidae in Japan. The remaining anomalodesmatans—the Lyonsiidae, Poromyidae and Myochamidae—are relatively small, but there are no truly small species. In the Thraciidae, some *Asthenothaerus* are around 8 mm. In the other families, the Pholadomyidae, Parilimyidae (Sasaki & Okutani 2007), Periplomatidae, Laternulidae, Clavagellidae and Pandoridae, the shell size is medium to very large for anomalodesmatans. The largest species, *Nipponoclava gigantea* (Sowerby, 1888), is about 30 cm in tube length.

It is now obvious that Anomalodesmata is a subgroup of the Heterodonta (Taylor *et al.* 2007; Giribet 2008). See also Harper *et al.* (2006) for the phylogeny within the Anomalodesmata, and see Poutiers & Bernard (1995) for a species list of the Anomalodesmata from the western Pacific.

Verticordiidae (Fig. 21C–G)**.** The shell is mostly small, except for *Acreuciroa rostrata* (Thiele & Jäckel, 1931) (5 cm) and *Halicardia nipponensis* Okutani, 1957, (3.5 cm) (Kuroda 1952; Okutani 2000: 1039–1041). The most minute genus, *Haliris*, is 4 mm or less in length. It is distributed on muddy bottoms at lower subtidal to bathyal depths.

Cuspidariidae (Fig. 21H–I)**.** Most species are between 1.5 and 4 cm (Okutani 2000: 1042–1047). In the smallest Japanese species, *Cuspidaria sadoensis* Okutani & Ito, 1983, the shell length is 2–3 mm. The species of *Cardiomya* (Fig. 21I) are all relatively small for the family but attain 1 cm in maximum size.

Interestingly, one species of the family, *Halonympha asiatica* Hayami & Kase, 1993 (5 mm in length), was described from submarine caves at a depth of 20 m or less (Hayami & Kase 1993: 103–105). This is the shallowest habitat for the family in Japan.

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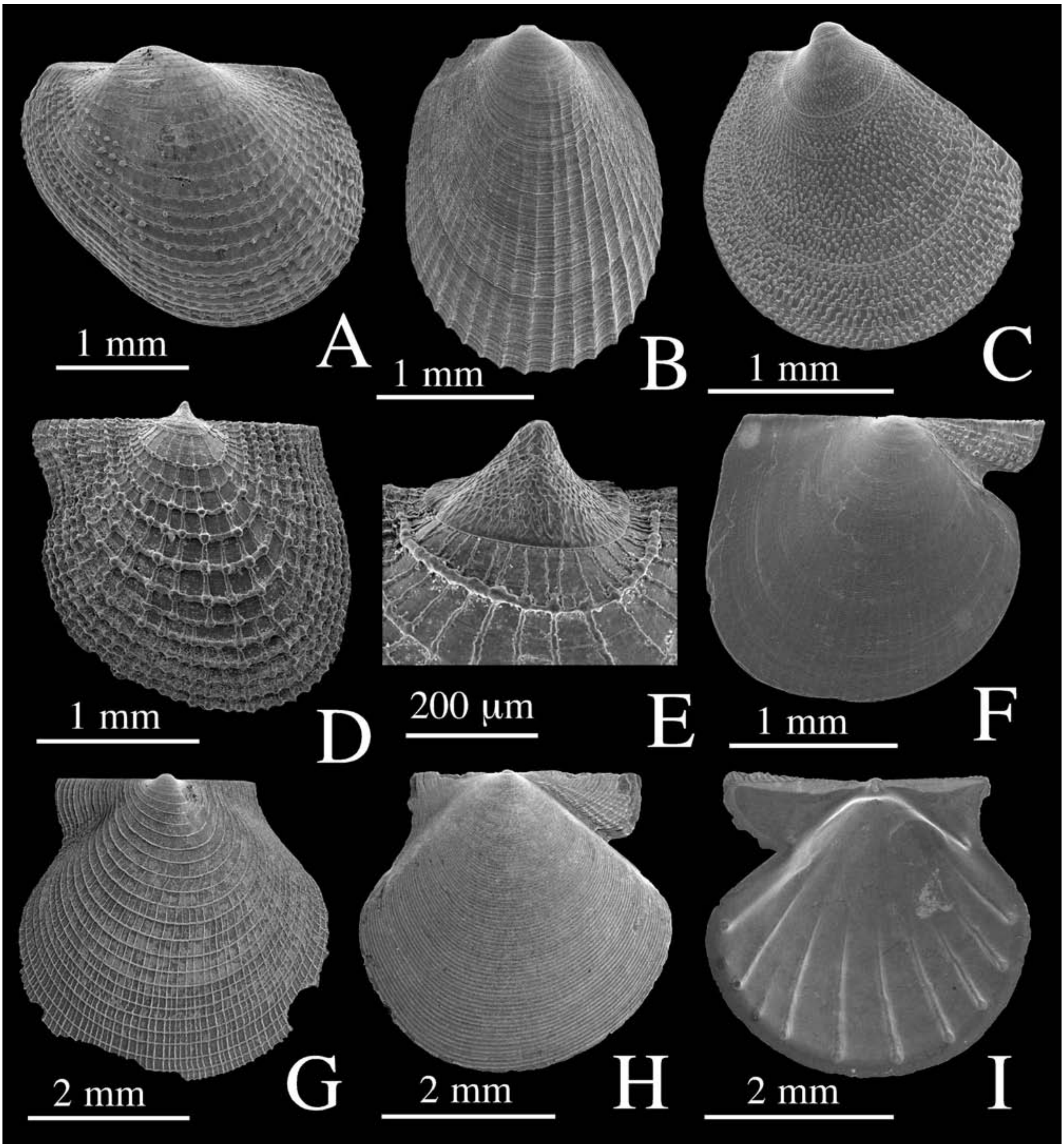
Figure 18 (next page)**.** Pteriomorphia (2). **A.** Arcidae, *Bathyarca kyurokusimana* (Nomura & Hatai, 1940). **B–C.** Limidae. **B.** *Limatula* sp. **C.** *Divarilima iwaotakii* (Habe, 1961). **D–I.** Propeamussiidae, **D–F.** *Chlamydella incubata* Hayami & Kase, 1993. **G.** *Cyclopecten* sp. **H–I.** *Parvamussium scitulum* (E.A. Smith, 1885). Locality data: A R/V *Tansei-Maru*, cruise KT-98-17, station 3, off Ashizuri-Misaki, 140–145 m, 32°38.57'N 132°47.55'E–32°38.541'N 132°47.204'E, Sep. 26, 1998, UMUT RM29659. **B–C.** R/V *Tansei-Maru*, cruise KT-00-05, station OS-2, west off Izu Oshima, 305–320 m, 34°44.706'N, 139°19.529'E–34°44.971'N, 139°19.538'E, May 21, 2000, UMUT RM29660. **C.** UMUT RM29661. **D.** Yaebishi, off Miyako Island, lower intertidal zone, Okinawa, Apr. 18, 1995, UMUT RM28732. **E.** Agonohama, Aka Island, by scula diving, Okinawa, Sep. 29, 1997, UMUT RM29662. **F.** R/V *Tansei-Maru*, cruise KT-05-30, station SS4(2), off Shirahama, Wakayama, 27.68–35.29 m, 33°37.43'N, 135°22.09'E–33°37.31'N, 135°21.85'E, Nov. 26 2005, UMUT RM29663. **G.** R/V *Tansei-Maru*, cruise KT-05-30, station HB, Hyuga Basin, 1644.3–1656.6 m, 32°22.58'N, 132°30.54'E–32°22.61'N, 132°29.24'E, Nov. 22 2005, UMUT RM 29664. **H–I.** R/V *Shinyo-Maru*, station 1997-12, off Ogasawara Islands, 150–160 m, 27°11.99'N, 142°09.18'E–27°11.75'N, 142°08.92'E, Oct. 16, 1997. **H.** UMUT RM 29665. **I.** UMUT RM29666.



VENEROIDA. Some species are small but there are no described micromolluscs in the families Lucinidae (Fig. 20B–C), Cardiidae (Fig. 20G), Tellinidae, Psammobiidae (Fig. 20I), Trapeziidae or Vesicomyidae. The size varies greatly in these families. There are no described small species in the Fimbriidae, Chamidae, Tridacnidae, Mactridae, Anatinellidae, Cardiliidae, Donacidae, Glossidae, Corbiculidae, Glauconomidae, Petricolidae, Pharellidae, Solenidae or Cultellidae.

Thyasiridae (Fig. 20D)**.** Relatively small-sized species are common in this family (Matsukuma *in* Okutani 2000: 932–935). In the genus *Thyasira*, most species are 1 cm or less, and species of similar size also exist in other related genera (*e.g.*, *Axinulus*). Because of the simplicity of shell morphology, the taxonomy is in dire need of revision. The largest species, *Conchocele bisecta* (Conrad, 1849), attains more than 10 cm, but this size is exceptional for the family.

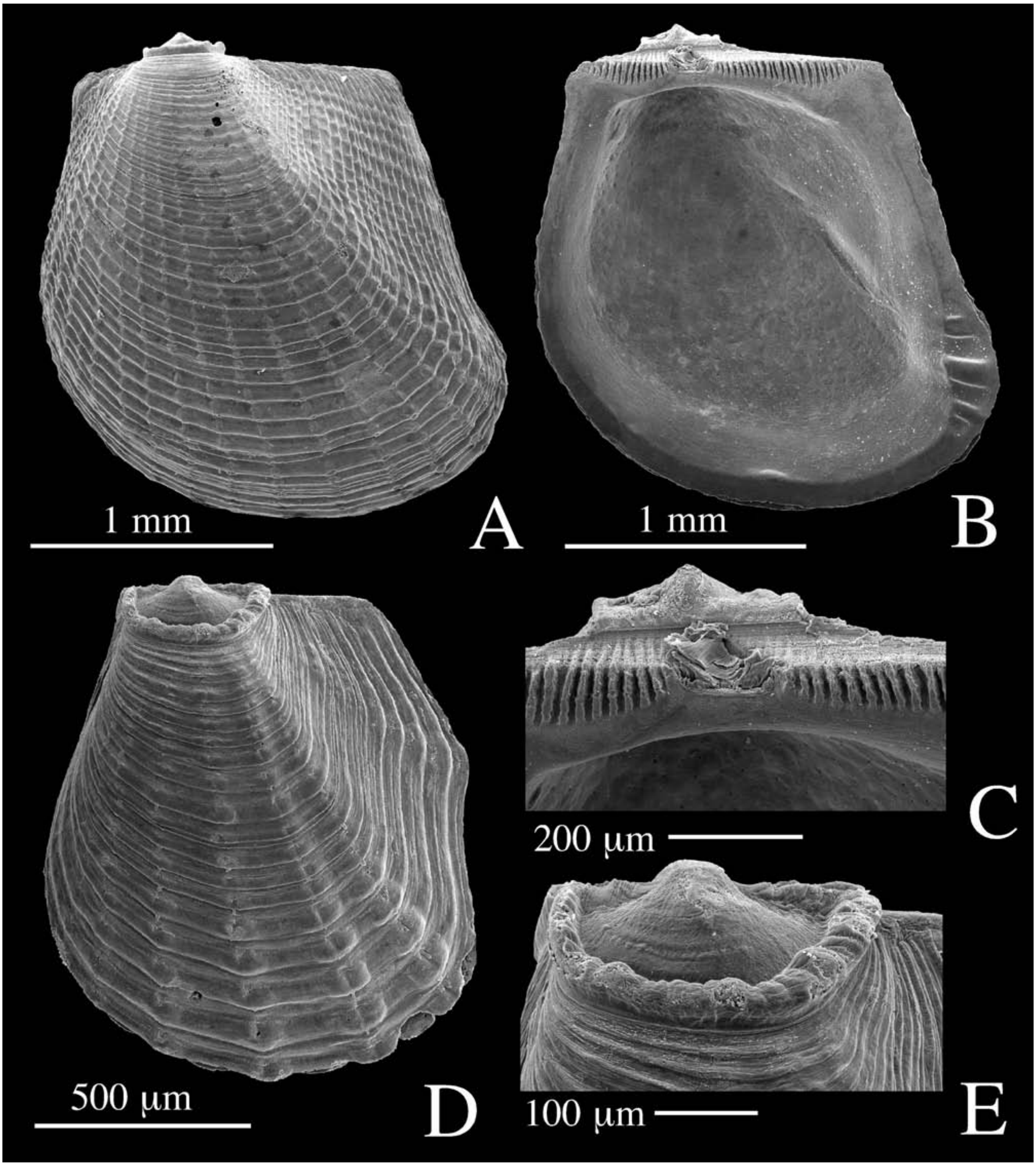


Figure 19. Pteriomorphia (3). **A–E.** Philobryidae, **A–C.** *Cosa waikikia* (Dall, Bartsch & Rehder, 1938). **C.** Enlargment of hinge. **D–E.** *Cratis kanekoi* Hayami & Kase, 1993. **E.** Enlargement of prodissoconch. Locality data: **A–C.** R/V *Shinyo-Maru*, station 1997-11, off Ogasawara Islands, 47–53 m, 27°06.47'N, 142°10.51'E–27°06.40'N, 142°10.29'E, Oct. 16, 1997, UMUT RM29667. **D–E.** Gahi, Miyako Island, lower intertidal zone, Okinawa, Apr. 17, 1995, UMUT RM29668.

GALEOMMATOIDEA. The systematics of this superfamily is still controversial. Similar-looking groups have been variously classified in such families as Galeommatinidae, Lasaeidae, Montacutidae, Leptonidae and Kellidae. See Bieler & Mikkelsen (2006: 232) for a listing of existing names at the family level. Members are commensal with various invertebrate hosts. Morton & Scott (1989) reviewed 22 species from Hong Kong and half of them are also distributed in Japan. In the currently used systematic arrangement in Japan, galeommatoideans are assigned to the three families below.

Lasaeidae (Fig. 20E–F)**.** All members are exclusively smaller than 1 cm (Matsukuma *in* Okutani 2000: 937–939). The most typical species in Japan is *Lasaea undulata* (Gould, 1861) (Fig. 20E), which is around 3 mm in shell length and inhabits intertidal rocky shores (see Iwasaki 1996a, b for ecology). This family contains many uncommon or taxonomically little-known species. Some of the species are known to be symbiotic with other organisms. For example, Lützen & Kosuge (2006) described a new species commensal with a species of *Sipuncula*. *Pseudophthina macrophthalamensis* Morton & Scott, 1989, lives attached to the appendages of crabs with byssi (Kosuge & Itani 1994).

Montacutidae. This family is also composed of small species (Matsukuma *in* Okutani 2000: 939–941). Many are symbiotic with other organisms and difficult to collect alive. *Nipponomysella oblongata* (Yokoyama, 1922) was reported to be commensal with a species of *Sipuncula* (Lützen *et al.* 2007). *Fronsella philippinensis* Habe & Kanazawa, 1981, is also associated with a sipunculan (Kosuge & Kubo 2002).

Leptonidae. This family is a little-known group in Japan. Lützen & Takahashi (2003) described a small species commensal with a pinnnotherid crab.

Kelliellidae. Two known species from Japan are both ca. 2 mm in shell length (Okutani 2000: 993–994). *Alvenius ojianus* (Yokoyama, 1927) is collected from muddy bottoms in sheltered shallow bays and *Kelliella japonica* Hayami & Kase, 1993, (less than 2.5 mm) was described from submarine caves in the Ryukyu Islands (Hayami & Kase 1993: 91–93). The anatomy and shell morphogensis of *Alveinus ojianus* were examined by Evseev *et al.* (2004a, b).

Sphaeriidae (= Pisidiidae). This freshwater group is usually small in size (5 mm or smaller in length). About 30 nominal species have been proposed, mainly before 1940 (Higo & Goto 1993: no. 1208–1238), but their taxonomy is in the state of complete confusion (see Ieyama & Mitou 1999; Ieyama & Takayashi 2000 2004; Masuda & Uchiyama, 216–219; Inaba & Ieyama 2007). Overall revision, including reinvestigation of old type material, is necessary for all the species in Japan.

‘**Turtoniidae**’ **(= Veneridae).** *Turtonia minuta* (Fabricius, 1780) (3 mm in length) attaches to algae in the intertidal to shallow subtidal zones and is distributed from northern Japan to the North Atlantic through Alaska (Matsukuma *in* Okutani 2000: 940–941). See Mikkelsen *et al.* (2006) for the phylogenetic position within Veneroida.

Semelidae (Fig. 20J–K)**.** This family is similar to the Tellinidae in overall shell morphology, but is distinguished by the presence of a resilium. The well-known genus *Semele* is more than 5 cm in length, but other genera are mostly smaller than 1.5 or 1 cm (Matsukuma *in* Okutani 2000: 982–985). The smallest two species, *Leptomyaria trigona* Habe, 1960, (Fig. 20J) and *Leptomya minuta* Habe, 1960 (Fig. 20K), are less than 3 mm. These two species have a translucent, smooth shell.

Mesodesmatidae (Fig. 20L)**.** In terms of shell characters the family is defined primarily by the presence of a resilium between the anterior and posterior cardinal teeth. Among the Japanese species, *Spondervilia bisculpta* (Deshayes, 1863) and *Rochefortina sandwichensis* (E.A. Smith, 1885) (Fig. 20L), are smaller than 4 mm (Matsukuma *in* Okutani 2000: 967–969). *Rochefortina sandwichensis* was reported from submarine caves (Hayami & Kase 1993: 90–91) but can also be collected alive outside caves (*e.g.*, the dredged specimen in Fig. 20L).

MYOIDA. This group was previously regarded as a suborder of the order Veneroida, but was listed as a separate higher taxon by Bieler & Mikkelsen (2006). The monophyly of this group was not supported by the molecular phylogenetic analysis by Taylor *et al.* (2007). There are no described small species in the families Myidae, Hiatellidae, Gastrochaenidae or Pholadidae.

Corbulidae. The Japanese species in this family are below 2.5 cm in length (Okutani 2000: 1022–1023). In the smallest genus, *Varicorbula* (*V. yokoyamai* Habe, 1949), the maximum shell length is 4 mm. *Varicorbula rotalis* (Hinds, 1843) grows to slightly larger size (6 mm).

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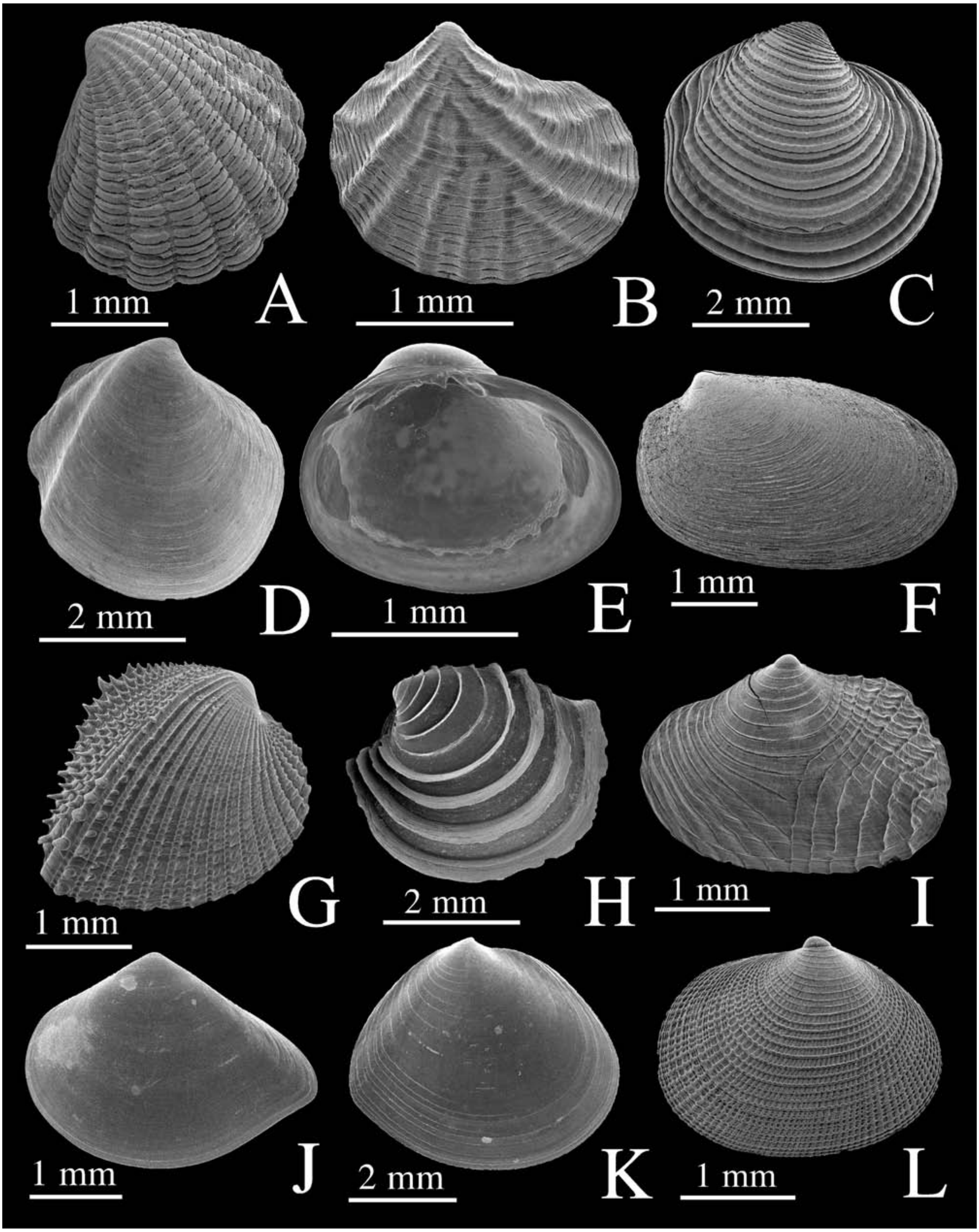
Figure 20 (next page)**.** Heterodonta **A.** Condylocardiidae, *Carditella* sp. **B–C.** Lucinidae. **B.** *Epicodakia delicatula* (Pilsbry, 1904), young specimen. **C.** *Bellucina civica* (Yokoyama, 1927). **D.** Thyasiridae, *Thyasira tokunagai* Kuroda & Habe, 1951. **E.** Lasaeidae, *Lasaea undulata* (Gould, 1861). **F.** Montacutidae, *Nipponomysella oblongata* (Yokoyama, 1922). **G.** Cardiidae, *Fragum* sp., possibly juvenile. **H.** Veneridae, *Placamen tiara* (Dillwyn, 1817), juvenile. **I.** Psammobiidae, *Heteroglypta contraria* (Deshayes, 1863). **J–K.** Semelidae. **J.** *Leptomya minuta* Habe, 1960. **K.** *Leptomyaria trigona* Habe, 1960. **L.** Mesodesmatidae, *Rochefortina sandwichensis* (E.A. Smith, 1885). Locality data: **A.** R/V *Tansei-Maru*, cruise KT-94-16, station MS-7, off Mishima Island, Hagi, Yamaguichi, 96–99 m, 34°50.45'N, 131°50.12'E–34°50.53'N, 131°05.18'E, Sep. 27, 1994, coll. by Eiji Tsuchida, UMUT RM29669. **B.** R/V *Tansei-Maru*, cruise KT-05-30, station SS4(2), off Shirahama, Wakayama, 27.68–35.29 m, 33°37.43'N, 135°22.09'E–33°37.31'N, 135°21.85'E, Nov. 26 2005, UMUT RM29670. **C–D.** R/V *Tansei-Maru*, cruise KT-00-17, station KN-1, off Koshikiji-ma-Nomamisaki, Kagoshima, 160–161 m, 31°35.269'N, 130°01.710'E–31°35.446'N, 130°01.637'E, Dec. 13, 2000. **C.** UMUT RM29671. **D.** UMUT RM29672. **E.** Aburatsubo, Kanagawa, intertidal zone, June 9–14, 2003, UMUT RM29673. **F.** Kuwabara, Shunan, intertidal zone, Yamaguchi, May 16 2006, UMUT RM29674. **G.** Majanohama, Aka Island, Okinawa, by diving, Sep. 30, 1997, UMUT RM28734. **H.** R/V *Tansei-Maru*, cruise KT-99-17, station KU-3, off Katsuura, Wakayama, 39–43 m, 33°37.289'N, 135°58.631'E–33°37.228'N, 135°58.660'E, Nov. 29, 1999, UMUT RM28737. **I.** R/V *Tansei-Maru*, cruise KT-99-17, station SH-2, off Shirahama, Wakayama, 41–42 m, 33°40.700'N, 135°19.170'E–33°40.629'N, 135°19.231'E, Nov. 30, 1999, UMUT RM28735. **J–K.** R/V *Tansei-Maru*, cruise KT-05-30, station SS4(2), off Shirahama, Wakayama, 27.68–35.29 m, 33°37.43'N, 135°22.09'E–33°37.31'N, 135°21.85'E, Nov. 26, 2005. **J.** UMUT RM29675. **K.** UMUT RM29676. **L.** R/V *Shinyo-Maru*, station 1997-4, off Ogasawara Islands, 57–62 m, 27°47.70'N, 142°03.25'E–27°47.80'N, 142°03.30'E, Oct. 15, 1997, UMUT RM28736.



‘Xylophagainidae’ (= Pholadidae). The shell form is similar to that of Teredinidae, but the cardinal tooth, ligament and internal apophysis are absent. There might be small species in this family, but details are unknown. Taxonomic work specific to this group has not been published in Japan since Taki & Habe (1950).

Teredinidae. The family contains many small species (Okutani 2000: 1030–1031). All are smaller than 1 cm in shell length, and some are below 5 mm, although the animal is much longer than the shell. The taxonomy of the Japanese species was established by Kuronuma (1931) and Taki &

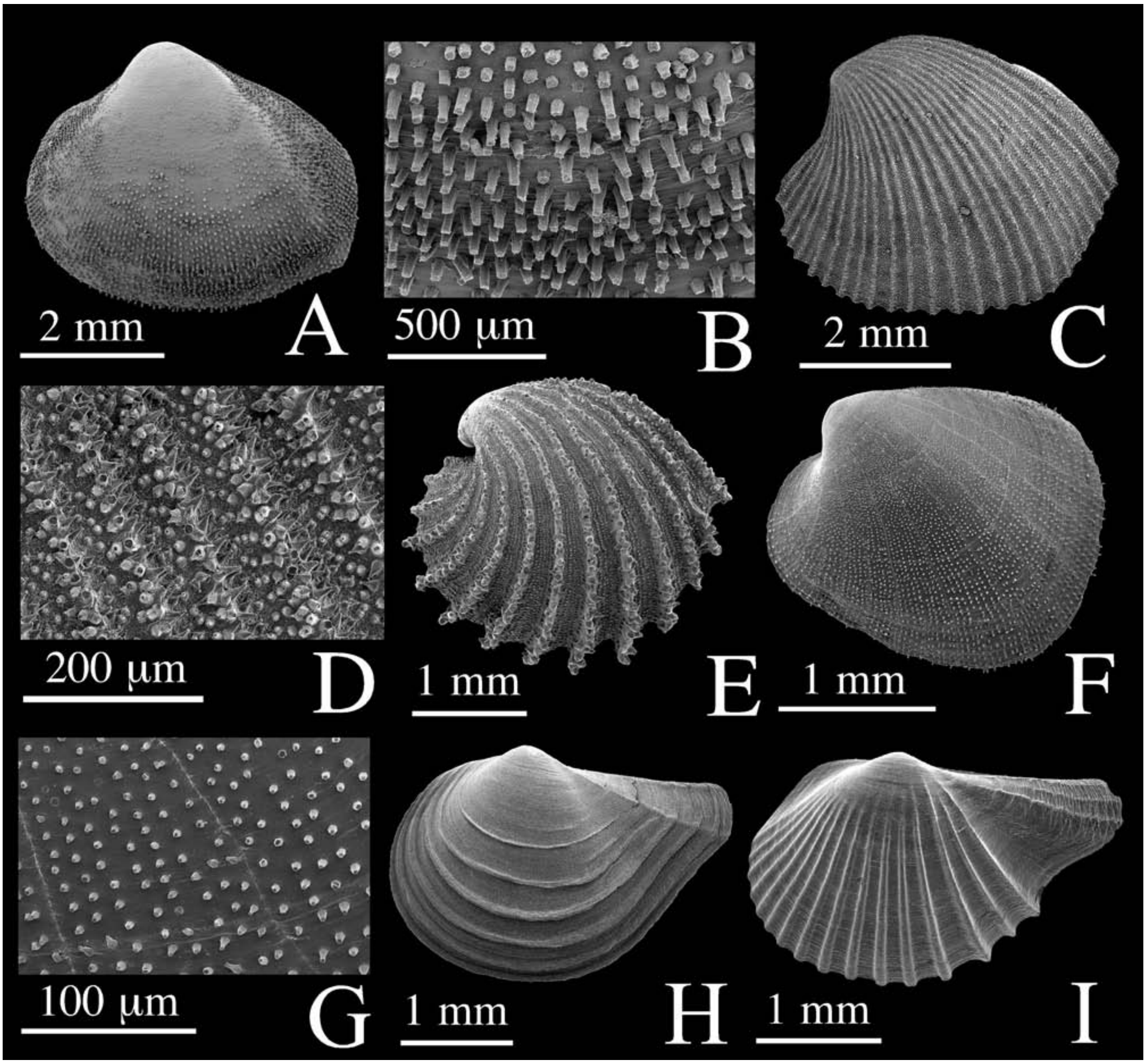


Figure 21. Anomalodesmata. **A–B.** Poromyidae, *Poromya flexuosa* Yokoyama, 1922, young specimen. **C–G.** Verticordiidae, **C–D.** *Haliris* sp. **E.** *Haliris multicostata* (A. Adams, 1862). **F–G.** *Lyonsiella parva* Okutani, 1962. **H–I.** Cuspidariidae. **H.** *Cuspidaria* sp. **I.** *Cardiomya* sp. Locality data: **A–B.** R/V *Tansei-Maru*, cruise KT-99-17, station KU-2, off Katsuura, Wakayama, 37–38 m, 33°37.454'N, 135°58.394'E–33°37.402'N, 135°58.470'E, Nov. 29, 1999, UMUT RM28744. **C–D.** R/V *Tansei-Maru*, cruise KT-99-17, station TN-1, off Tanabe, Wakayama, 63 m, 33°41.201'N, 135°17.905'E–33°41.210'N, 135°17.900'E, Nov. 30, 1999. **E.** R/V *Shinyo-Maru*, station 1997-12, off Ogasawara Islands, 150–160 m, 27°11.99'N, 142°09.18'E–27°11.75'N, 142°08.92'E, Oct. 16, 1997, UMUT RM28742. **F–H.** R/V *Tansei-Maru*, cruise KT-05-30, station KB1(3), Shima Spur, 839. 1–846 m, 33°59.09'N, 136°52.26'E –33°59.88'N, 136°51.68'E, Nov. 24 2005, **F–G.** UMUT RM29677. **H.** UMUT RM29678. **I.** R/V *Tansei-Maru*, cruise KT-99-17, station SG-4, off Shingu, Wakayama, 60–61 m, 33°45.373'N, 136°05.050'E–33°45.284'N, 136°04.977'E, Dec. 3, 1999, UMUT RM28745.

Habe (1945), when damage to wooden structures by boring was a more serious problem than it is now. Since the 1940s only limited new data has been published in Japan (*e.g.*, Haga 2001). *Zachsia zenkewitschi* Bulatov & Ryabtschikov, 1933 is a specialized species boring in sea grass only. It has not been clearly illustrated since the original description, but was recently reported by Sasaki *et al.* (2006c) and Haga (2006).

Other classes

Solenogastres and Caudofoveata. the so-called 'Aplacophora' is the most seriously unstudied higher group in Japan. Most of the known species were described in a classic work by Heath (1911). Recent studies on Japanese aplacophorans have been limited to development (Okutsu 2002), feeding habit (Sasaki & Saito 2005), hox-gene sequences (Iijima *et al.* 2006) and neuroanatomy (Shigeno *et al.* 2007), and taxonomic work is urgently needed. According to recent estimates, there are 98 undescribed species (25 Caudofoveata and 75 Solenogastres) in addition to 13 described species (3 Caudofoveata and 10 Solenogastres) (Union of Japanese Societies for Systematic Biology 2002–2003: data by Dr. Hiroshi Saito). Therefore, any research on this group must start from basic taxonomy in the present state.

Polyplacophora. The Polyplacophora in Japan are relatively well-studied taxonomically and consist of about 80 species (Saito *in* Okutani 2000: 4–23). Most major families such as the Ischnochitonidae, Chitonidae and Acanthochitonidae are larger than 2 cm. Species smaller than 1 cm in adult size are mostly in the Leptochitonidae. *Leptochiton hirasei* (Taki & Taki, 1929) (5 mm in body length) inhabits the undersides of partly buried boulders, and two small congeneric species [*L. torishimensis* (Wu & Okutani, 1984) *and L. habei* Saito, 1997] are also known from sunken wood (Saito 1997; Saito *in* Okutani 2000: 7). Another small species, *Connexochiton kaasi* Saito, 1997 (Ischnochitonidae), described from Suruga Bay, is 3.2 mm in length (Saito 1997).

Monoplacophora. It would be of great interest to confirm whether the Monoplacophora are really missing from the Northwest Pacific. So far 29 living species have been described in the world (Haszprunar 2008). In the Pacific, several species have been recorded from off the eastern coast of America (from California to northern Chile), Hawaii and New Zealand. Most species are below 2–3 mm, and some are even below 1 mm. The present author has repeatedly sorted sediments at this size range from bathyal to abyssal depths but never been able to find a single shell.

Scaphopoda. Scaphopods are generally difficult to identify because of their relatively simple shell morphology and the absence of distinct color patterns in most species. In particular, very small specimens with smooth surface generally lack any striking taxonomic characters. All the known taxa were listed by Higo *et al.* (1999) and by Steiner & Kabat (2001, 2004), but the taxonomy of the Japanese species has not been updated very much since Habe's (1964) revision. There may be species that mature at 4 mm less, but small scaphopods are completely unstudied so far in Japan.

The protoconch of the Scaphopoda has been described for only two species in Japan (Sasaki 2007). In *Dentalium octangulatum* Donovan, 1804, the protoconch is of a unique type (Sasaki 2007). The protoconch morphology of another unidentified species matches well the type 1 of Steiner (1995), which is typical of the Dentaliida.

Cephalopoda. There are no 'microcephalopods' among the described species, although there is the possibility of future discovery of minute species. The smallest species so far is *Idiosepius paradoxus* (Ortmann, 1888), of 2 cm mantle length. By contrast, the largest cephalopod *Architeuthis japonica* Pfeffer, 1912 (Architeuthidae) attains 2 m in mantle length (Kubodera *in* Okutani 2000: 1067), and the largest octopod, *Octopus dofleini* (Wülker, 1910), reaches 3 m in total length (Kubodera *in* Okutani 2000: 1083).

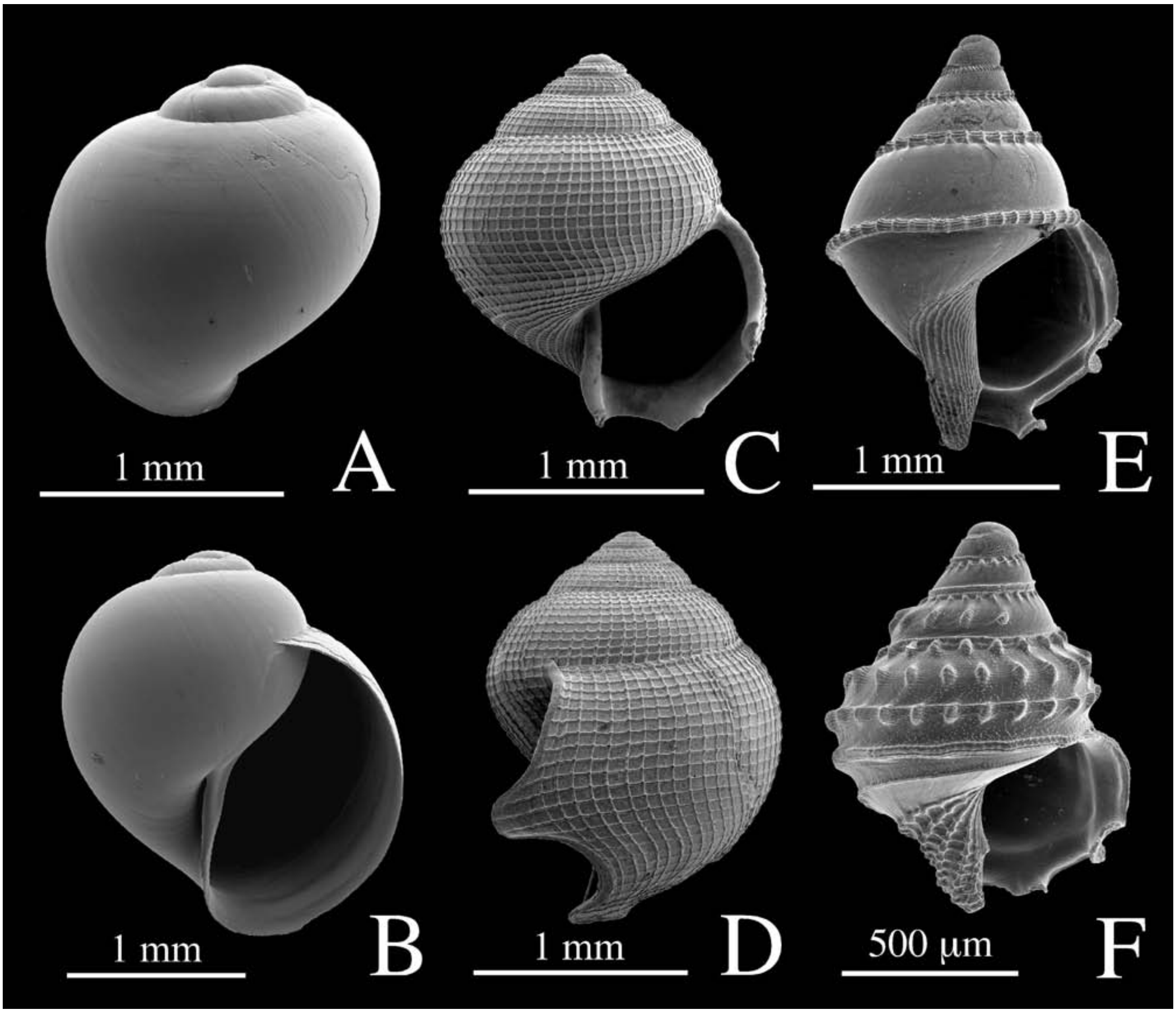


Figure 22. Examples of unidentified gastropod larval shells collected in the field. **A–B.** Naticidae. **A.** Gen. et sp. 1. **B.** Gen. et sp. 2. **C–D.** Cypraeidae. **C.** *Cypraea* sp. 1. **D.** *Cypraea* sp. 2. **E–F.** Family uncertain, possibly Muricidae. **E.** Gen. et sp. 1. **F.** Gen. et sp. 2. Locality data: **A–C.** R/V *Tansei-Maru*, cruise KT-99-17, IKMT-station 22, 33°20'N, 135°00'E, Nov. 1999, IKMT (= Isaacs-Kidd Midwater Trawl) net. **A.** UMUT RM29679. **B.** UMUT RM29680. **C.** UMUT RM29681. **D.** R/V *Shinyo-Maru*, station 1997-1, off Ogasawara Islands, 98–99 m, empty shell, dredged, 27°48.52'N, 142°02.62'E–27°48.47'N, 142°02.55'E, Oct. 15, 1997, UMUT RM29682. **E.** R/V *Shinyo-Maru*, station 1998-N04, 33°15.50'N, 140°14.22'E–33°15.14'N, 140°14.01'E, Oct. 14, 1998, larval fish net on water surface, UMUT RM29683. **F.** R/V *Shinyo-Maru*, station 1999-16, Omurodashi, 88 m, 34°32.66'N, 139°29.65'E–34°32.66'N, 139°29.65'E, dredged from bottom, Oct. 16, 1999, UMUT RM29684.

Habitat, fauna and sampling methods

Micromolluscs exist in almost every environment that molluscs have colonized. Knowledge of the habitat is essential for biological studies, since obtaining fresh material with the animal intact is a starting point. Based on the review given above, the currently known habitats of Japanese micromolluscs are briefly summarized below.

Intertidal rocky shore. The intertidal zone is generally a mollusc-rich environment. The rocky shore provides different types of microhabitat for molluscs including rock surfaces, crests, grooves and undersides of shelves. Rock is often covered with algae, which produces a suitable habitat for phytal groups (see below).

In most cases, micromolluscs prefer narrow interspaces of rocks or other organisms, and few micromolluscs can be found on a smoothly exposed surface or vertical slopes. For example, *Peasiella* (Littorinidae) and *Lasaea* (Lasaeidae) are the most common groups in small depressions of rocks and in small spaces among barnacles and other sessile organisms.

Algae and sea grass. Some marine molluscs are associated exclusively with algae or sea grass. Because sunlight is necessary for plants, phytal molluscs are restricted to shallow-water areas in the euphotic zone.

The micromolluscs associated with algae are largely gastropods. Most typically, some trochoideans (*e.g.*, *Cantharidus, Lirularia, Tricolia*), cerithioideans (*e.g.*, *Alba*) and rissoiform gastropods (*e.g.*, *Barleeia, Amphithalamus*) are dominantly found on the algae. Such species can be easily collected by washing algae in water (Geiger *et al.* 2007).

More specialized plant-associated species are exclusive to sea grass beds. Typical examples include *Smaragdia* (Neritidae), *Lacuna* (Littorinidae) and *Siphonacmea* (Siphonariidae). Some sacoglossans are strictly confined to specific groups of green algae. The terenidid *Zachsia zenkewitschi* bores only into the stems of sea grass (Haga 2006; Sasaki *et al.* 2006c). These species may be easily collectable if associated plants or algae are found in the field.

Among bivalves, *Turtonia minuta* (‘Turtonidae’ = Veneridae) is attached to various algae with its byssus. Some species of *Musculus* (Mytilidae) are also byssaly attached to algae. These species may not be collected by algal washing, but must be collected individually.

Half-buried boulders. It is widely known that exposed surfaces and undersides of boulders yield different fauna (Geiger *et al.* 2007). Species tolerant of strong sunlight can live on the outer surface, but those having negative phototaxis conceal themselves on the underside of boulders. If there is enough space for water passage, the underside is well oxygenated. However, the underside becomes reduced or anoxic if a boulder is deeply buried into sediments. Along the boundary between aerated and anoxic zones (also called dysaerobic zone), a specialized fauna is formed.

The importance of half-buried bounders as habitats of micromolluscs was recognized by Japanese malacologists in the late 1990s. For example, *Tomura* (Cornirostridae) was discovered on the undersides of boulders (Fukuda *et al.* 2000). Similarly, live specimens of *Phenacolepas* (Phenacolepadidae) can be found only beneath boulders. *Tomura* is often accompanied by *Leptochiton hirasei, Stosicia* *annulata* (Fig. 8I) and *Pseudoliotia pulchella* (Fig. 9G). These species are often coated with a dark, rusty substance when alive.

Chevallieria sp. (Iravadiidae, Fukuda *in* Wada *et al.* 1996: pl. 9, figs 5–6) was discovered by Dr. Hiroshi Fukuda from a very specialized boulder habitat, where it prefers the undersides of the deepest level of a multiple layer of large boulders. Therefore, the species can only be collected by removing numerous heavy boulders.

Intertidal to shallow-water soft bottom. In the soft sediments, micromolluscs are always on the surface, because the small species cannot burrow deeply due to the limited size of their in- and exhalent organs (siphons). Some trochoideans, cerithioideans, various pyramidellids and cephalaspideans are typical micromolluscs found on sandy bottoms. These can be collected effectively by sediment screening.

Burrows of others invertebrates. There are still some little-explored environments in the intertidal zone in Japan. Recently, Kano (2007) reported a new phenacolepadid from within the burrows of crustaceans. *Sigaretornus planus* (Tornidae) is similarly known from the burrows of echiurans and scale worms. *Cryptomya truncata* (Gould, 1861) (Myidae) is not a micromollusc, but this species is also associated with thalassidean shrimp burrows (Itani & Kato 2002). Some galeommatoidean bivalves (*e.g.,* Montacutidae) are known to live commensally with burrowing invertebrates such as sipunculans. These species can never be collected alive without knowledge about their hosts.

Interstitial fauna. Interstices of sands are another little explored molluscan habitat in Japan. For example, interstitial opisthobranchs are widely known in sandy beaches of the world, but there are only two records in Japan: *Hedylopsis* sp. from Okinawa (Hedylopsidae, Hamatani *in* Okutani 2000: 761) and *Pseudovermis japonicus* from Wakayama Prefecture (Hamatani & Nunomura 1973; see also Hamatani *in* Okutani 2000: 803). Certain molluscan groups like the Solenogastres and Caecidae might also be found in this type of environment in the future (*cf.* Giere 1993: 121–124).

Subtidal zone. The subtidal zone is a relatively flat area of the continental shelf that is normally shallower than 200 m. The fauna of the upper subtidal zone is generally similar to that of the intertidal zone. Algae are abundant and harbor various micromolluscs. Sessile invertebrates such as sponges and cnidarians also attract micromolluscs such as Triphoridae and Ovulidae on hard bottoms.

At the middle to lower levels, the fauna is gradually replaced with groups typical of deeper waters such as Cuspidariidae and Nuculanidae. The fauna of this depth range can be regarded as intermediate between the upper subtidal and bathyal zones.

Sampling opportunities are relatively limited compared to the intertidal zone. Subtidal molluscs can be effectively collected by SCUBA at shallow depths, but this is generally restricted to a maximum depth of 30 m. Dredging and grab sampling from a boat can be used at greater depths.

The subtidal zone of oceanic banks generally has a distinct fauna and is a rich field for micromolluscs (*e.g.,* Tsuchida & Ikebe 1990, 1991, 1993). The species from this environment have been poorly investigated in Japan, mainly because of the limited accessibility of localities. Poorly surveyed banks are especially numerous among the Izu-Ogasawara Islands and the Ryukyu Islands at depths of 50–300 m.

Submarine caves. A very characteristic fauna was discovered from submarine caves in subtropical islands in the 1990s (*e.g.*, Hayami & Kase 1993, 1996). The majority of the collected species was new to science or collected alive for the first time. Among the gastropods, these included species in the Neritiliidae and Pickworthiidae.

The fauna has several distinctive features such as (1) the high rate of endemism relative to the outside fauna, (2) small adult size, possibly induced by poor nutritional conditions with no primary producers except for a few large-sized species like *Glossocardia obesa* (Reeve, 1843) and *Pycnodonte taniguchii* Hayami & Kase, 1992, (3) the predominance of non-planktotrophic development and brooding in connection with progenesis, (4) a taxonomic composition somewhat similar to that of lower-subtidal or deeper faunae, an example of which is the occurrence among the bivalves of the manzanellid genus *Huxleyia*, propeamussiids and cuspidariids, and (5) the presence of relic 'living fossil' taxa like *Neritopsis radula* (Linnaeus, 1758) (Neritopsidae) and *Pycnodonte taniguchii* (Osteoidea: Gryphaeidae) (Kase & Hayami 1992; Hayami & Kase 1993, 1996).

It is notable that a small number of species can be collected also from outside the caves. For example, *Rochefortia sandwichensis* (Fig. 20L) can be collected alive both inside and outside caves. Shells of *Cosa* have also been collected from the outside (Fig. 19), and dead valves of *Chlamydella* (Fig. 18D–F) have been collected by dredging. Therefore, the range of their actual microhabitat might be wider than currently known.

The submarine-cave fauna can be found over a wide range of tropical regions of the world, but its mechanism of dispersal is controversial. In the recent study of the Neritiliidae, Kano & Kase (2006) revealed the presence of both planktotrophic and non-planktotrophic species in cave-dwelling members, and there is no direct correlation between distribution range and developmental mode. A possible hypothesis is that planktotrophic larvae can survive outside of caves for long-range migration, and non-planktotrophic species might be passively transported with drifting substrata (Kano & Kase, 2006: 39). Likewise, long-distance rafting by byssate juveniles was assumed for small bivalves (Hayami & Kase, 1993: 122).

Bathyal to hadal zones. The fauna of the deep sea (bathyal to hadal zones) differs significantly from that of shallow waters. This is possibly associated with various extreme environmental factors, for instance, the lack of light (and hence the absence of algae), lower water temperature and increased pressure at greater depths (McLain & Rex, 2001; Rex *et al.*, 2005a, b).

There are no herbivorous gastropods in the deep sea, but instead deposit feeders are common on muddy bottoms. Groups well-known for deposit feeding include Anatomidae, Seguenziidae and some trochoideans (*e.g.*, *Bathybembix*: Hickman 1981) among gastropods, and the bivalve families Nucinellidae, Nuculidae and Yoldiellidae.

Carnivores are also diversified. Gastropod species in the Buccinidae and Turridae can be found almost in every area. Among the bivalves, families in the Anomalodesmata like the Cuspidariidae and Verticordiidae are known as deep-sea dwellers that display carnivorous feeding habits.

The deep-sea fauna exhibits gradual transitions between the bathyal, abyssal and hadal zones with increasing depths. The Japanese fauna has been described by Dr. Takashi Okutani (*e.g.*, Okutani 1964, 1968), Mr. Eiji Tsuchida (*e.g.*, Tsuchida 1994) and Dr. Kasunori Hasegawa (*e.g.*, Hasegawa 2001, 2005) mainly between bathyal and abyssal depths. Knowledge of the hadal zone is still extremely fragmentary because of limited sampling opportunities. The best information regarding the deepest level was a list of molluscs from the Japan Trench summarized by Okutani (2003). Molluscs are known to occur down to around 8,000 m off Japan.

In the deep sea, sampling with a small dredge is not effective, because the biomass per unit area of molluscs is too low. Trawling is a widely used method on deep-sea soft sediments, but it is not suitable for hard bottoms. A submersible with an underwater camera system is very useful, but this method involves problems of limited availability and extraordinary operating cost.

Sunken wood. It is well-known that a specialized molluscan fauna exists on sunken driftwood from the lower subtidal to the abyssal zones (*e.g.*, Marshall 1988 in New Zealand). In Japan, sunken-wood molluscs were best described by Hasegawa (1997a). In his work, numerous interesting new species were described in the Cocculinidae, Pseudococculinidae, Skeneidae, Iravadiidae, Vitrinellidae (= Tornidae), Hyalogyrinidae and Xylodisculidae. In the other classes, polyplacophorans have also been collected from sunken wood (Saito 1997). Despite high densities, bivalves from sunken wood have been poorly studied. New taxonomic revisions are necessary for Teredinidae and Xylophagainidae.

Sunken bone. Sunken bones are also an interesting habitat that harbors a specialized fauna of molluscs. Fujiwara *et al.* (2007) reported on a three-year faunal survey from an artificially sunken whale. In their survey, cocculinids and skeneids were found that were similar to the fauna of sunken wood. However, the location of that study was in the lower subtidal zone, and not very deep. Sunken bones in the bathyal or deeper zones probably have a different fauna but nothing has been documented taxonomically for the Japanese fauna.

Vents and seeps. Deep-sea chemosynthesis-based communities have been major sources of new species since the 1980s (see Sasaki *et al.* 2005 for review). Various small species have been described, but the main focus of past studies was on large-size species such as *Calyptogena*, *Bathymodiolus* and *Phymorhynchus*. Compared to those in other areas (*cf.* Warén & Bouchet 1989, 1993, 2001), studies of micromolluscs from Japanese vents and seeps are still insufficient.

Submersibles with underwater cameras and manipulators such as the Japanese *Shinkai 6500* and *Hyperdolphin* are the most powerful tools for exploring the vent/seep fauna. Normal trawling and dredging are nearly useless for this purpose, because the communities are patchy and restricted to small areas. With the finest camera, species around 1 cm can be clearly observed on a screen on a supporting ship (*e.g.,* Sasaki *et al.* 2007b), but true micromolluscs can still only be found by sorting them from collected sediments.

Planktonic fauna. Holoplanktonic molluscs are widely distributed between the water surface and sea bottom. Among them, the Atlantidae, Gymnosomata and Thecosomata include many small species. It is quite unsatisfactory that no detailed SEM-level study has been made of this fauna in Japan. In addition to true planktonic groups, most benthic molluscs also have a planktonic phase as larvae. Thus, the water column is an important habitat for all molluscs.

Micromolluscs in the water column can be collected with a plankton net from a boat. Most holoplanktonic micromolluscs can be found at the surface, but some occur in the mid-water or deeper. Sometimes planktonic species can be obtained with a dredge by accidental trapping, and empty shells can be collected from bottom sediments such as pteropod ooze. Larvae with tiny shells are common in plankton samples but they have been almost completely neglected in Japan.

Estuaries. Estuaries and adjacent environments are the main habitats for various groups like the Assimineidae and Ellobiidae. Some uncommon species of Neritiliidae and Iravadiidae are also distributed in estuaries. Mangroves in the estuaries of the subtropical region have a characteristic fauna (Fukuda *in* Wada *et al.* 1996). It is not widely known that some ellobiids are strictly nocturnal. Such species can be easily collected at night but are rarely obtainable in the daytime.

Anchialine ponds. Anchialine ponds were discovered to be a habitat of *Neritilia* by Kano *et al.* (2001). They are brackish-water ponds connected to the sea only through underground passages. There are only a few molluscs in this environment but they are worth special attention.

Freshwater environments. Molluscs are less diverse in fresh water than in marine and terrestrial environments, but characteristic micromolluscs exist there as well. The Lymnaeidae, Planorbiidae and Pisididae are the most common families containing freshwater micromolluscs in Japan. These can be collected by plant washing and sediment screening in the water. In contrast to other regions of the world, the Hydrobiidae and Valvatidae form a very minor component of the Japanese freshwater fauna.

Underground freshwater. Since the 1950s it has been noticed that phreatic communities include molluscs. Almost all known species from underground waters belong to the Hydrobiidae. A neritimorph gastropod (*Neritilia* sp.) was reported from a freshwater well far from the seashore by Sasaki & Ishikawa (2001).

Terrestrial environments. Generally, the diversity on land is higher in the warmer, southwestern part of Japan than in the colder northeast. The species richeness is highest in the subtropical islands of the Ogasawara and the Ryukyu Islands. Most common terrestrial micromolluscs in Japan belong to the Cylophoridae and Diplommatinidae (both Caenogastropoda) and to the Helicarionidae (Stylommatophora).

Molluscs are common almost everywhere on vegetated land. Limestone areas often have an interesting specialized snail fauna. *Georissa shikokuensis* (Fig. 5C) and *Bensonella plicidens* (Fig. 15F) are examples of limestone-associated micro-landsnails. Most snails crawl on the ground, but attention should be also paid to tree-dwelling species. For example, *Parazoogenetes* (Fig. 15D) are attached to tree trunks both during active and resting periods. Some species are distributed closely along the sea-shore (*e.g.*, *Vallonia costata*: Fig. 15C).

In terrestrial environments, sorting from dead leaves is a standard method of sampling. Live specimens can be picked up by careful examination of leaves in the field, but it is not possible to collect all snails effectively. It is advisable to collect also dead leaves and sort them indoors, if any small snails are to be found. Collecting the soil below the leaf litter is not effective in most cases, because the specimens in that layer are often old empty shells.

Current problems and future topics

Compared to large-sized species, the study of micromolluscs is still at an early stage in Japan. Malacologists must survey various microhabitats more extensively, extend morphological study to little-known groups, pay attention to early ontogenetic stages, and accumulate new data on anatomy, DNA sequences and ecology. Fossils can never be overlooked in taxonomy. In addition, studies of introduced and endangered species will become increasingly important in the 21st century.

Basic taxonomy. The taxonomy of macromolluscs was well established in Japan during the days of Drs Kuroda and Habe. By contrast, basic taxonomy is substantially incomplete for micromolluscs. Major examples are found in the Rissoidae, Eulimidae, Triphoridae, Turridae and Pyramidellidae. Among non-marine or nearly non-marine families, the Assimineidae, Ellobiidae, Helicarionidae and Pisidiidae represent major problematic groups.

According to the estimations of various malacologists (Union of Japanese Societies for Systematic Biology 2002–2003), the number of undescribed species in Japan exceeds 1,400 compared to ca. 8,045 described species. However, this number might be still consirable an underestimate, especially for subtropical fauna (*cf.* Bouchet *et al.* 2002 for molluscan diversity in trocial region).

Little-studied groups. There are poorly studied molluscan families in Japan, and almost all are comprised of micromolluscs. Examples include the Skeneinae, Cingulopsidae, Eatoniellidae, Tornidae, Iravadiidae and Vanikoridae. Among the lower heterobranchs there are some little-known species in the Cimidae, Xylodisculidae, Murchisonellidae (= Ebalidae), Cornirostridae and Hyalogyrinidae. The Rissoellidae is apparently the least studied taxon in the intertidal zone, although it is common in temperate to warmer regions in Japan. Among bivalves, more attention should be paid to small-sized groups such as the Galeommatoidea and Condylocardiidae.

Confirmation of microhabitat. Collecting live material is an important first step in every field of biological study. Samples are easily collected if the animal is large enough and the habitat is well-known and easily accessible. However, in the case of micromolluscs, specimens are often unrecognizable in the field, and true microhabitats have not been well documented. Many species are still only known as dead shells. Finding live animals and describing the microhabitat of each species are significant steps in the study of micromolluscs.

Symbiosis. Some of the small-sized groups are now known to be symbiotic with various invertebrates. Examples include the Tornidae, Galeommatoidea (Lasaeidae, Montacutidae and Leptonidae) and Eulimidae, and these families encompass a large number of taxonomically difficult micromolluscs. Better knowledge of the ecology of these specialized groups is required.

Distinction of adult and subadult. It has been seldom acknowledged that the distinction between small adults and juveniles of larger species is essential in the identification of micromolluscs. This problem is serious when the shell does not show any sign of maturity, as is generally the case in bivalves. In contrast, many groups of caenogastropods thicken the apertural margin as adults, and the adult stage can thus be easily distinguished (Fig. 1C–F).

In the groups without distinct adult shell characters maturity can be directly verified by gamete histology, but this method is useful only in the breeding season. Adult size can be deduced by measuring the maximum size among samples in various seasons, but this method needs a large number of samples collected at different times. Adults of some small species can be readily discerned if eggs are brooded inside.

Identification of larvae. An understanding of the morphology of early ontogenetic stages cannot be neglected by any malacologist interested in micromolluscs. The larval shell (the protoconch or prodissoconch) is a very important conchological character, and its treatment requires knowledge of the larval stage.

In Japan the first comparative study of larval morphology was initiated by Habe (1944a–c) for marine gastropods and continued by Amio (1963) with work on gastropod oviposition and larval morphology. For bivalves, some others also produced similar works (*e.g.*, Drs Yataro Tanaka and Hiroshi Yoshida: see The Malacological Society of Japan 1979: 109, 114 for full listing), but available material was mainly limited to the species useful in commercial fisheries. Unfortunately the results of these earlier studies cover only a minute part of the more than 8,000 species of Japanese molluscs. Even now most of the larvae collected in the field (*e.g.*, Fig. 22) are almost completely unidentifiable at species or even family level.

Theoretically there are three possible methods to establish criteria for larval identification: (1) comparison between pre- and post-metamorphic stages, (2) direct identification by rearing larvae from eggs, (3) molecular-level identification using DNA sequences. Among these, (1) is indirect, and (2) and (3) are more reliable methods. Method (1) is often easiest but not always decisive, especially when similar species are distributed sympatrically. Method (2) is applicable only if the animal can be kept alive in an aquarium. Method (3) has not been widely adopted yet, but might be useful in the future. Molecular characters are especially important if the larvae of closely related species are hardly distinguishable morphologically (*e.g., Haliotis*: Hayashi 1983). However, all these methods have both merits and demerits. Therefore, a combination of all three seems to be the most reasonable approach.

Ontogenetic change. Mature and immature stages are similar in most species, but morphological characters can vary ontogenetically. In certain cases, juveniles have been regarded as a different species (see Fossaridae above). In some groups, the color pattern can change suddenly during growth. For instance, the shells of the Japanese species *Nipponacmaea gloriosa* (Habe, 1944) and *Lottia langfordi* (Habe, 1944) look quite different when comparison is made between specimens of 1–2 mm and those of larger sizes (Sasaki 2006a,c). In addition, in *N. gloriosa* the position of the apex greatly shifts before and after the shell attains ca. 0.6 mm in length (Sasaki 2006c). Without this knowledge we cannot even identify such common intertidal limpets at all stages of life history. Growth stages must be described for all other species to facilitate the identification of micromollusc samples.

Sexual dimorphism. Sexual dimorphism is a confusing aspect of morphological variation. In many groups of caenogastropods, the shells of females are often more swollen or larger. This is possibly because the pallial gonoduct in females occupies a larger space than in males. Similarly male-female differences may appear in micromolluscs.

One instructive example concerning sexual dimorphism is found in the taxonomy of Japanese *Tricolia*, in which males and females were once classified as separate species (see Tricoliidae above). The radula is also different between the two sexes in *Tricolia*, and a similar phenomenon is known in the Muricidae (Arakawa 1958; Fujioka 1984), although the latter is not a micromollusc. These cases suggest that malacologists must carefully consider male-female differences.

Comparative anatomy. Observing all possible characters is a fundamental principle in morphological studies, because systematic and phylogenetic implications are generally more evident if the number of available characters is larger. However, in the study of Japanese micromolluscs, observations have been made mostly at the level of conchology and radular description. For further improvement, anatomical study at the histological level is obviously required, especially in defining supraspecific taxa. In the studies of microgastropods, fine-scale work has been led by Drs Winston Ponder and Anders Warén (see above for a number of references in Caenogastropoda and lower Heterobranchia). Similar fine-scale work must also be carried out for micromolluscs in Japan.

Molecular phylogeny. Molecular phylogenetic analysis has progressively become a powerful approach in the construction of phylogenetic trees. One critical task in molecular analysis is obtaining sequences of rare taxa to achieve better taxon sampling. In most cases the missing taxa are micromolluscs. The importance of data from micromolluscs has been shown in the analysis of the Neritimorpha (Kano *et al.* 2002) and in the Vetigastropoda (Kano 2008) in Japan. Mitochondrial gene structure has been determined for *Ammonicera* (Kurabayashi & Ueshima, 2000a) and *Pupa* (Kurabayashi & Ueshima, 2000b) but not for other small-sized Japanese species. Similar work must also be performed for various groups (*cf.* Simison & Boore 2008 for review).

Fossil micromolluscs. The taxonomy of Cenozoic fossil micromolluscs is indispensable to the study of the Recent fauna, particularly in Japan. This can be seen by the fact that the names of paleontologists (*e.g.*, Yokoyama) frequently appear as the authors of valid scientific names of Recent species. However, the revision of fossil micromolluscs has been poorly attempted, with some notable exceptions (*e.g.*, Taki & Oyama 1954; Oyama 1973). Taxonomy must become more encompassing, both in neontology and paleontology.

Introduced species. The number of introduced species has increased and will continue to rise everywhere in the world. Some accidentally introduced species have disappeared after temporary stays, but others have spread explosively over wide areas. Such examples also exist among micromolluscs. For example, in Japan, the introduced pulmonate snail *Hawaiia minusucula* (Zonitidae: Fig. 15I) is rather common throughout temperate areas. The introduction of alien species may confuse the taxonomy of similar-looking domestic species. In marine molluscs, there is no case of clearly identified introduced micromolluscs so far in Japan, but malacologists must pay attention to that possibility.

Conservation. Numerous micromolluscs are already enumerated in the list of endangered species (red list: *e.g.*, Ministry of the Environment 2005). They are mostly non-marine, because relatively narrow distributions along with low dispersal capabilities can readily cause a reduction in population size and extinction. Snails on oceanic islands are the most typical case of endangered molluscs (*e.g.*, *Ogasawarana* and *Hirasea* on the Ogasawara Islands). Species in estuaries (*e.g.*, Assimineidae and Ellobiidae) are also generally threatened, because river banks have been heavily channeled with concrete in Japan. Micromolluscs in such a fauna should be examined before going extinct.

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