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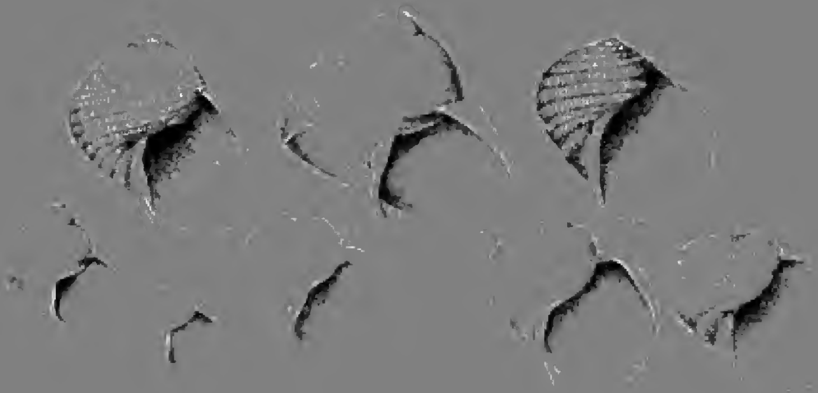
Evolution of *Janthina* and *Recluzia* (Mollusca: Gastropoda: Epitoniidae)

by

A. G. Beu



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Evolution of *Janthina* and *Recluzia* (Mollusca: Gastropoda: Epitoniidae)

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Abstract. Fossil and living neustonic gastropods referred previously to Janthinidae are revised and included in Epitoniidae. Species recognized in *Janthina* Röding, 1798 (= *Iodes*, *Iodina* and *Amethistina* Mörch, 1860, *Hartungia* Bronn, 1861, *Heligmope* Tate, 1893, *Violetta* Iredale, 1929, *Parajanthina* Tomida & Itoigawa, 1982, and *Kaneconcha* Kaim, Tucholke & Warén, 2012) are *J. typica* (Bronn), Messinian–early Piacenzian (latest Miocene–early late Pliocene), c. 7–3.0 Ma (New Zealand, southern Australia, Japan, Morocco, dredged off Brazil, Madeira, Gran Canaria I., Selvagem Grande I., and Santa Maria I., Azores); *J. krejcii* sp. nov., Zanclean (early Pliocene), c. 4.8–4.3 Ma (Santa Maria I.); *J. chavani* (Ludbrook), late Piacenzian–early Calabrian (latest Pliocene–early Pleistocene), 3.0–c. 1.7 Ma or later (New Zealand, southern Australia, Japan, mid-Atlantic ridge); *J. globosa* Swainson, living, and two late Pliocene–early Pleistocene records (Jamaica, Philippines); and *J. exigua* Lamarck, *J. janthina* (Linnaeus), *J. pallida* Thompson, and *J. umbilicata* d'Orbigny, all Holocene only. *Janthina* evolved from a benthic epitoniid resembling *Alora* during Messinian (late Miocene) time, and feeds mainly on colonial cnidarians (*Physalia*, *Velella*, *Porpita*). The extinction of *Janthina typica* and origination of *J. chavani* at 3.0 Ma (end of the Pliocene climatic optimum) potentially is useful for world Pliocene correlation. The two *Recluzia* species, *R. johnii* (Holten) and *R. lutea* (Bennett), feed on floating Minyadidae anemones. *Recluzia* has no fossil record and evolved independently during Holocene time from a benthic epitoniid resembling *Alexania* and *Surrepifungium*. Adaptation to a neustonic habit evolved twice in Epitoniidae. Twenty-two neotypes and six lectotypes are designated.

Keywords. Biostratigraphy; cosmopolitan; fossil record; neustonic gastropods; Pleistocene; Pliocene; phylogeny

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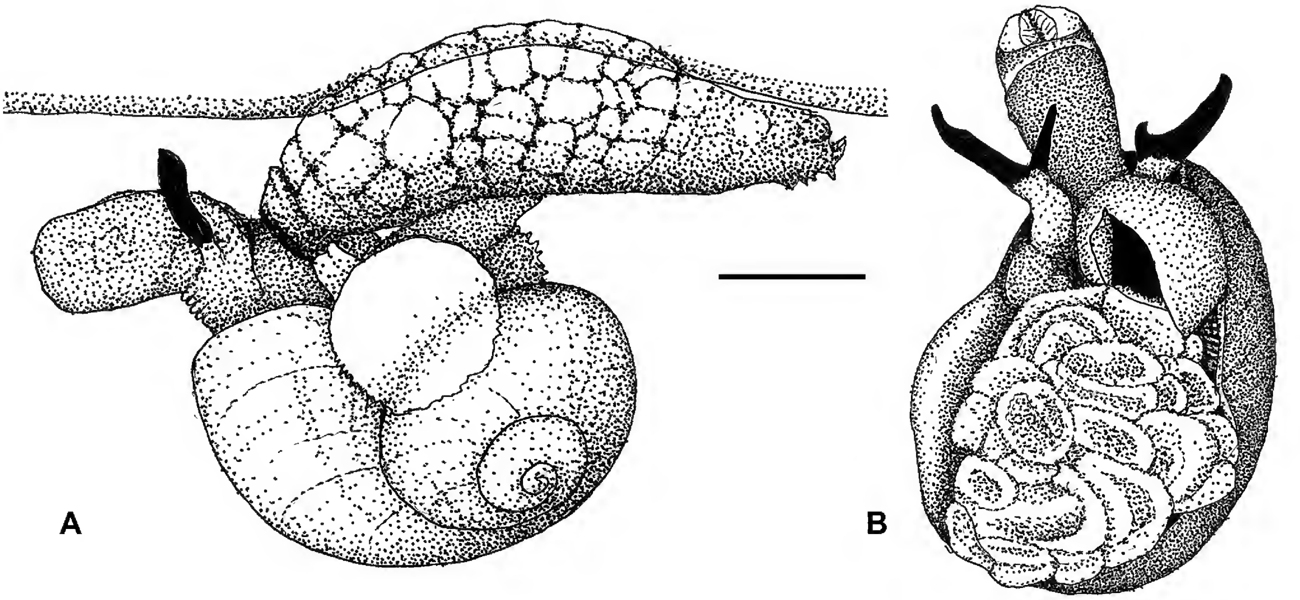

Figure 1. Living specimens of *Janthina janthina* (Linnaeus) in life position in an aquarium, suspended beneath their floats, redrawn from photographs in Wilson & Wilson (1956: pl. 1, figs 1–2) and Yonge & Thomson (1976: pl. 5, lower); bubbles in float shown schematically. *(A)* left (anatomically right) lateral view, showing float, attached to mesopodium and located against propodium (at left end of float); partially extended snout; black-tipped right cephalic tentacle, not fully visible here; smooth, almost circular right epipodium (centre); digitate posterior edge of left epipodium, at rear between shell and mesopodium; and rear end of float disintegrating. *(B)* dorsal (anatomically ventral) view of another specimen forming a new float bubble, showing odontophore and radula partly everted out of mouth at tip of snout; black-tipped, forked cephalic tentacles; cupped propodium with black lining, in process of enclosing an air bubble; shell (right edge); and epipodium (left edge; anatomically on right). Scale bar 10 mm.

Introduction

Janthina and *Recluzia* species are holoplanktonic gastropods, the only molluscs with relatively large, almost completely enclosing shells 20–40 mm in diameter that are members of the marine neustonic community (David, 1965; Cheng, 1975). They float at the surface of the open ocean suspended beneath a float constructed from bubbles of air coated with mucus. Consequently, all living species are cosmopolitan in temperate and tropical seas. Their calcitic shells are thin and brittle. The description of a brown outer teleoconch layer in *Janthina chavani* (Ludbrook, 1978) by Kaim *et al.* (2012: 428, figs 5C–D; identified as *Kaneconcha knorri* Kaim, Tucholke & Warén, 2012) demonstrates that the calcitic outer shell layer is only 25 µm thick, although the inner aragonitic layer can be up to 175 µm thick in some specimens. *Janthina* and *Recluzia* species float with the shell hanging spire-down, upside-down compared with benthic gastropods (Fig. 1). Some of the most accurate and useful drawings of living specimens of *Janthina janthina* (Linnaeus, 1758) and *J. globosa* (Swainson, 1821) were published by Okutani (1956), clearly illustrating the relationship to each other of the shell, epipodium, propodium and float. The other members of this small community of floaters at the interface of the sea and air are colonial cnidarians, including mainly the "Portuguese man-o-war" siphonophore *Physalia physalis* (Linnaeus, 1758) and the chondrophores *Porpita* and *Velella*, which form the main prey of *Janthina*; floating anemones of the family Minyadidae, which form the main prey of *Recluzia* (Abbott, 1968: 93, text-fig.); other floating anemones of the Abylidae (David, 1965: fig. 9); blue juvenile specimens of the fish *Nomeus gronovii* (Gmelin, 1789), which shelter within the tentacles of *Physalia* and feed on it, as well as on other jellyfish and plankton (the brown adults are demersal; Bailly, 2008); the nudibranch gastropod *Glaucus* (Batson 2003: 50), blue and free-floating, feeding on *Physalia*, *Porpita* and *Velella*, and the semi-neustonic nudibranch *Fiona pinnata* (Eschscholtz, 1831), creeping on chondrophores and other floating objects; small blue crabs of the genera *Planes* and *Pachygrapsus* found clinging to siphonophores, turtles, sea-snakes and other floating objects (Chace, 1951; Davenport, 1992; Fransen and Türkay, 2007; Pons *et al.*, 2011); and several species of stalked barnacles (Lepadidae) that attach to *Janthina* shells and other floating objects and one species, *Dosima fascicularis* (Ellis & Solander, 1786), which has a thin, translucent shell, forms a bubble float and floats independently at the sea surface. Some individuals of *D. fascicularis* share a common float up to 15 cm across (Cheng, 1975: 199, fig. 14). Barnacles of New Zealand, including Lepadidae, were revised by Foster (1979) and those of Australia were reviewed by Jones (2012); most Lepadidae are very widespread and common to both countries. One species of polychaete, *Hipponoe gaudichaudi* Audoin & Milne-Edwards, 1830, associates with neustonic animals and commonly shelters on *Dosima fascicularis* in the tropical Pacific (Cheng, 1975: 201). Some authors have used the term pleuston for this fauna (e.g., Savilov, 1969; Cheng, 1975), but the more general term neuston is preferred here.

Most obligate neustonic taxa are blue, an obvious protection at the sea surface. *Janthina* shells are bluish violet, counter-shaded, with a paler dorsal shell surface seen against the sky from under the living animal, and a darker ventral surface seen from above against the dark blue of the ocean. The cosmopolitan planktotrophic cerithioid gastropod *Litiopa melanostoma* Rang, 1829 (Litiopidae) is benthic but lives on floating *Sargassum* algae and on flotsam such as wood and pumice, so *Litiopa* is not part of the neuston, although it is rarely found in situations where it is not floating. Species of the isopod genus *Idotea* also cling to neustonic organisms, as well as to flotsam (Cheng, 1975: 201) and could be considered to be semi-neustonic in the same way as *Fiona* and *Litiopa* are. *Physalia*, *Porpita* and *Velella* are merely the most common and familiar of neustonic cnidarians. Hardy (1956: 114–122, fig. 31) described 10 other similar cnidarians occurring in British waters, although apparently none of them is cast ashore. Various small animals such as hydroids also are found attached to some *Janthina* shells. The water-strider insects, five species of the family Halobatidae (Herring, 1961) were included by David (1965: 99, fig. 3) in a category of their own, the epineuston, as they walk on the surface film of the ocean rather than being immersed in water. The species of *Glaucus* float upside-down at the sea surface buoyed by a bubble of gas in their stomach (Rudman, 1998: 1015). Their taxonomy was revised by Valdés & Campillo (2004) and Churchill *et al*. (2014). The "heteropods" (Pterotracheoidea; Thiriot-Quiévreux, 1973; Wall-Palmer *et al*., 2016) and "pteropods" (Thecosomata and Gymnosomata; Lalli & Gilmer, 1989; Newman, 1998) also are holoplanktonic oceanic gastropods, but they are much more highly specialized than *Janthina* and *Recluzia*. They have a highly modified shell or no shell at all, swim actively at various levels in the ocean, and are not part of the neuston. Smith (1998: pl. 24, fig. 4) illustrated a specimen of *Janthina janthina* (Linnaeus, 1758) in normal life position suspended beneath its float, feeding on the siphonophore *Physalia physalis*. The illustrated *Janthina* shell is covered densely with *Lepas* barnacles. This illustration conveys the appearance of the small neustonic community well.

Distribution. Like other neuston, *Janthina* and *Recluzia* float passively at the sea surface in mid-ocean. Early travellers described the enormous numbers of *Janthina* specimens found in mid-ocean in extensive but localized "rafts", e.g., "In lat. 2°53'S., long. 176°55'E., a remarkable white line was observed on the surface of the ocean … It proved to be an undulated line of *froth*, or scum, several yards in width, extending on either side as far as was visible by the naked eye, and accompanied by a heterogeneous assemblage of floating mollusks, small fish, crabs, other marine animals and oceanic birds. … *Janthinae*, or sea-snails, were the most abundant of the floating mollusks. Their number was immense; and their floats contributed greatly to the white appearance of the froth-line" (Bennett, 1840: 62–63; Italics original). Benson (1860) gave a very full account of abundant specimen of *Janthina* and a few specimens of *Recluzia* observed at sea and captured with towing nets, during a voyage from England to Calcutta in the sailing ship *Malcolm*. Among other descriptions, he noted that "As we approached the Tristan d'Acunha group, in the Southern Atlantic, we sailed for several days through a tract, from 30° S. lat. and 18° W. long, to 33° S. and 10° W., inhabited by a fine white and violet-coloured *Ianthina pallida*, Harvey, in company with a large variety of *I. exigua*" (Benson, 1860: 407; it is not clear that this was a single dense raft of specimens). Mörch (1860: 271, footnote) appended the following description: "M. Luwigson told me that, in the Chinese seas, he observed at a certain distance from the vessel something white … Examined closely, it was nothing but an enormous accumulation of Janthines …" (translation from French). Laursen (1953: 14) also quoted Simroth (1895) who recorded a "shoal" of *Janthina* specimens in the Atlantic 200 nautical miles across. *Janthina* specimens are familiar to most people only when cast ashore from time to time during prolonged on-shore winds. Wilson & Wilson (1956: 291–296) pointed out the close association between *Janthina* strandings in Cornwall and persistent, unusually strong westerly to north-westerly winds. The association also has always been obvious in New Zealand between persistent westerly winds and the stranding of *Janthina* specimens, accompanied by *Velella* and *Physalia*, along the west coast between Auckland (particularly Piha to Muriwai Beaches and western Awhitu Peninsula) and Wellington (particularly beaches along the Kapiti coast). The long, north-south-oriented western coasts of New Zealand and the southern coast of Australia provide excellent traps for neustonic animals in a region of predominantly westerly winds. Abbott (1974: 113) also stated that *J. janthina* is "common after certain easterly blows along the southeastern United States, especially from April to May". Risbec (1953: 194) also described specimens of *Janthina* cast ashore in New Caledonia after violent winds blowing in the same direction for a long time, perpendicular to the coast at Magenta Beach and Anse Vata. *Janthina* specimens become conspicuous when cast ashore because of their violet shells, and are known in English as "purple snails" or "violet snails". However, the yellow-brown shells of the two *Recluzia* species recognized here, *Recluzia johnii* (Holten, 1802) and *R. lutea* (Bennett, 1840), are much less common and conspicuous. Accounts of the stranding of specimens of *Janthina* and *Recluzia*, particularly along the southern and western coasts of Britain, including the Scilly Isles, but also in Australia, India, Japan, Kenya, New Caledonia, New Zealand, Spain, Sicily, and USA have been published by numerous authors (e.g., Grant, 1833; Dillwyn, 1840: 59; Jeffreys, 1867: 174; Smart & Cooke, 1885; Simpson, 1897; Russell & Kemp, 1932; Dakin, 1933; Ramanujam, 1935; Rogers, 1941; Fowler, 1946a, b, 1947, 1948, 1949; Habe & Tokioka, 1953; Risbec, 1953: 194; Wilson & Wilson, 1956; Wilson, 1958; Dakin, 1960: 251,

Figure 2 (facing page 123). Shells of the five living species of *Janthina* and two species of *Recluzia* recognized in this work; apertural views, and left lateral views showing outer lip sinus. *(A–F) Janthina janthina* (Linnaeus); A–B, D, GNS RM4442, two specimens, beach, Takou Bay, Northland, New Zealand; C, GNS WM15986, "bicolor" form, San Lourenço Beach, Santa Maria I., Azores, Atlantic; E, GNS RM6735, "bicolor" form, Ohope Beach, Whakatane, New Zealand; F, GNS WM15297, beach between Hutchinson Bluff and Rayner Point, Raoul I., Kermadec Islands. *(G–J) Janthina globosa* (Swainson); G, GNS WM15254, beach, Mauritius, Indian Ocean; H–J, GNS RM5321, two specimens, Muriwai Beach, West Auckland, New Zealand. *(K–L) Janthina pallida* Thompson, GNS WM15256, beach, Windy Harbour, Cape D'Entrecasteaux, southern Western Australia. *(M, O) Janthina exigua* Lamarck, GNS RM5626, Nukumaru Beach, Whanganui, New Zealand. *(N, Q) Janthina umbilicata* d'Orbigny, GNS RM5627, Nukumaru Beach, Whanganui, New Zealand. *(P, R) Recluzia johnii* (Holten), GNS WM17360, ventral and dorsal views; trawled in sediment, 130–180 m, Swain Reefs, SE Queensland, Australia (shortest specimen, last entry in Table 12). *(S–T) Recluzia lutea* (Bennett), GNS RM6748, beach, Great Exhibition Bay, Northland, New Zealand (from same sample as Figs 36M–P). Scale bar 10 mm, applies to all figures.

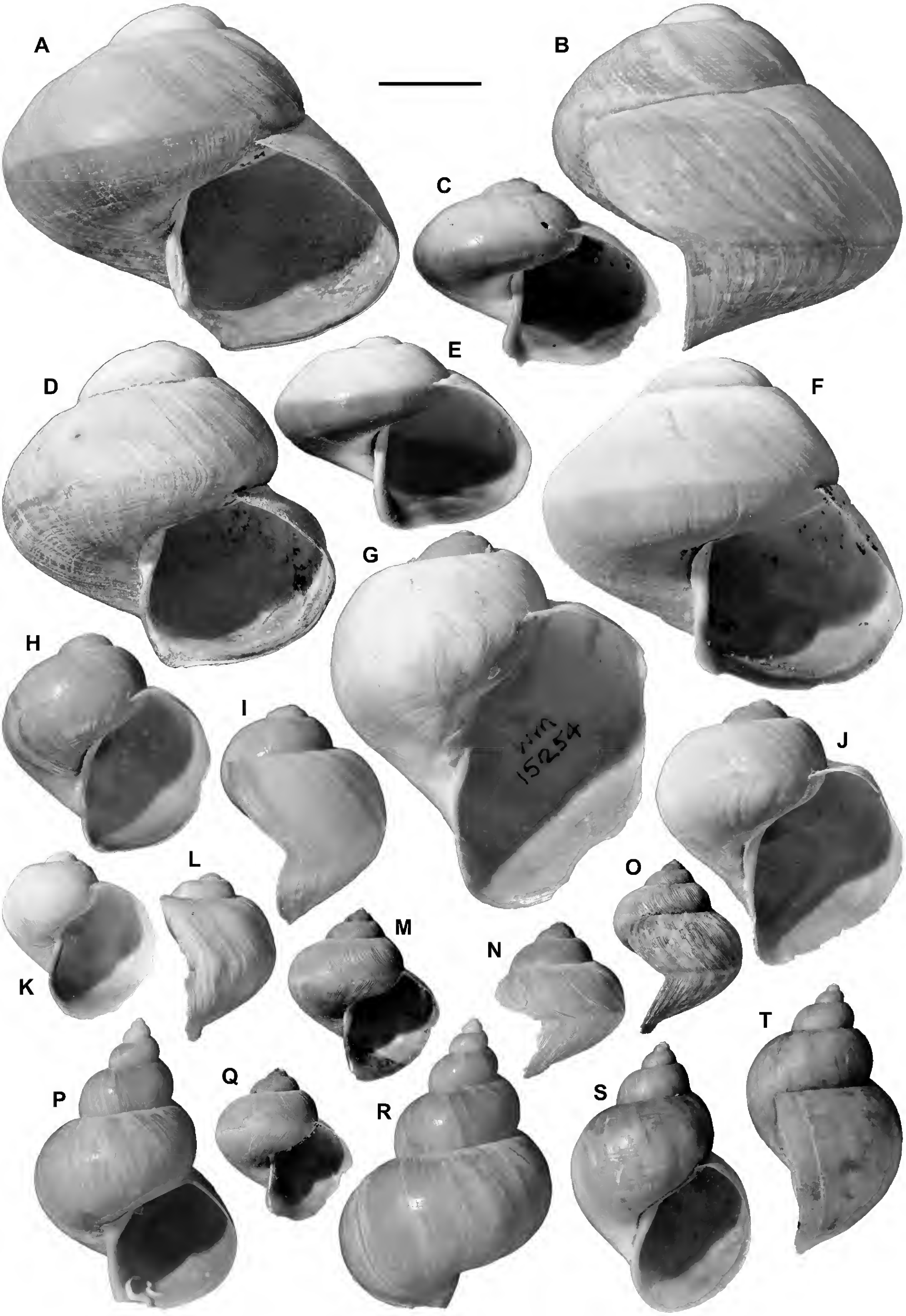

Figure 2. (See facing page 122 for caption).

pl. 63; Abbott, 1963; Bennett, 1966; Palazzi, 1979; Pinn, 1980; Turk, 1982; Turk & Humphreys, 1982; Boone, 1984; Colman, 1986; Komatsu, 1991; Thompson, 1991; Ueno *at al*., 1998; Light, 2003; Rolán & Trigo, 2003; Suzuki & Shiga, 2008; Okano & Wada, 2012; Riek, 2017). Gardiner & Cooper (1907: 46) described the neustonic fauna cast ashore at Diego Garcia Atoll, Chagos Archipelago, Indian Ocean: "… the shore behind being … sandy, the latter … having a piled-up ridge at high-tide level over a foot [30 cm] broad, formed of dead "Portuguese men-of-war" (*Physalia*) and the blue-shelled *Ianthina* …". Other accounts of the timing of strandings and other aspects of the neustonic community have been provided by David (1965), Bennett (1966: 47), Morton & Miller (1968: 472), Bingham and Albertson (1972), Cheng (1975), Lalli & Gilmer (1989) and Batson (2003: 61). Note, however, that Lalli & Gilmer's (1989: fig. 1d) illustration identified as *Recluzia* actually shows the cerithioid *Litiopa melanostoma*. The record of "*Recluzia* sp." as the most common gastropod epibiont on rafted pumice clasts collected along the east coast of Australia (Bryan *et al*., 2012: table 2) also was based on a species of *Litiopa*, probably *L. melanostoma* (Grove, 2014: fig. 2).

All seven living species of *Janthina* and *Recluzia* recognized here (Fig. 2) are more-or-less cosmopolitan in tropical and temperate seas, in winter minimum sea temperatures down to 10°C. However, *Janthina pallida* Thompson, 1840 has not been collected in New Zealand, eastern Australia, or the islands between (Lord Howe, Norfolk and Kermadec Islands) and seems to have a more limited distribution than the other *Janthina* species. *Recluzia johnii* also is a rare species recorded so far only from the tropical Indo-West Pacific province, and in recent times entirely from northeastern Australia. Wall-Palmer *et al*. (2016: fig. 6) presented a revised map of world zooplankton biogeographical provinces, based on those recognized by Oliver & Irwin (2008). Although these appear logical, they do not explain the distribution of such species as *J. pallida* and *Recluzia johnii. Janthina pallida* is absent from the south-western Pacific area of the circum-global warm-water region, although it occupies most or all of the rest of this region. Being larger, neustonic epitoniids presumably do not follow the same biogeographical patterns as zooplankton. The five *Janthina* species also vary significantly in their relative proportions in the fauna in some areas of the ocean. Savilov (1969: 318–403; page numbers refer to the translation) recorded numbers of specimens of *Janthina* species in RV *Vityaz* Pacific plankton samples; he did not report *Recluzia* species, implying that none were caught by RV *Vityaz*. His records make it clear that the details of relative numbers of *Janthina* species in different parts of the ocean are due to the limitation of some species to particular water masses, trade wind belts and current systems, simply as a result of passive drifting influenced by water motion and wind.

Late Neogene (almost entirely Zanclean, Piacenzian or Gelasian) fossils of *Janthina* are recorded here from Santa Maria Island in the Azores, other Atlantic islands (Gran Canaria, Madeira, Selvagem Grande), coastal Morocco, the mid-Atlantic ridge at 23°N 45°W, Jamaica, Japan, the Philippine Islands, New Zealand, southern Australia, and dredged offshore from Brazil, indicating that they had similarly wide oceanic distributions to most of the living *Janthina* species. Therefore, as was pointed out by Finlay (1931), Fleming (1953a), Beu (1979) and Beu & Maxwell (1990: 292), speciation within Pliocene *Janthina* species potentially provides a cosmopolitan biostratigraphical zonation based on readily identifiable macrofossils 20–40 mm in diameter. All *Janthina* species are regarded here as cosmopolitan in temperate and tropical seas, with no marked biogeographical patterns at present apart from the lack of *J. pallida* in the Southwest Pacific, and fossils are assumed to have had the same distribution.

Material and methods

The writer has tried for many years to understand the evolution and taxonomy of "Janthinidae". The excellent monograph by Laursen (1953) was a start towards this, but Laursen did not refer to type specimens, and had a relatively narrow focus on *Janthina* specimens captured during the *Dana* expeditions. Laursen (1953) also did not include fossils or *Recluzia* species, and so did not provide a basis for understanding the evolution of neustonic Epitoniidae. The potential wide biostratigraphical utility of pelagic, relatively large, readily identified fossil *Janthina* species was also an impetus for this research. The writer surveyed all literature on neustonic Epitoniidae, fossil and living, and examined the reported specimens wherever possible. However, this has not proven easy, as the present location of almost all of the critical fossil material reported in early works is unknown. Nevertheless, all known records of fossils are listed in detail below. Collections of Recent *Janthina* and *Recluzia* species in world museums listed below in "Abbreviations" also were examined as fully as possible over many years, when the opportunity allowed during visits for other research. These collections are very voluminous and records of Recent specimens are not listed here, other than generalized records of all species in Australia and New Zealand. For Australian museums, these lists record data collected many years ago (1971), before several of the collections were catalogued. They do not include precise locality data, but this seems of little significance in view of the cosmopolitan distributions of almost all *Janthina* and *Recluzia* species; the broader distribution is more important than precise details. New Zealand records include more details for NMNZ and GNS collections. The resulting knowledge of distributions, and particularly of ages of fossils, was compiled using as accurate data on biostratigraphy as possible, to derive an accurately dated evolutionary hypothesis useful for biostratigraphers as well as biologists. The time scale followed is that of Gradstein et al. (2012).

Present-day specimens are illustrated in colour in Figure 2. For all original photographs of fossils the specimens have been whitened with magnesium oxide before photography; a few photographs of significant unwhitened specimens from other sources also have been included. Small specimens were illustrated by scanning electron microscopy (SEM) where protoconchs were available (an FEI Quanta 450 ESEM in the Victoria University of Wellington microscopy unit, formerly Industrial Research Ltd., Lower Hutt). The external anatomy of living specimens has been clarified by many excellent colour photographs taken in aquaria of specimens found alive on beaches by Tony Healy (Sydney), Dimitris Poursanidis (Heraklion, Crete) and Denis Riek (Brunswick Heads, New South Wales) (Figs 4–7).

In preparing the systematic revision of *Janthina* and *Recluzia* species the writer had access to (1) the manuscript of a revision of living *Janthina* species commenced by Tom Iredale c. 1910, now kept in the Australian Museum, Sydney. Iredale evidently added to it in later years, and extracted the proposal of *Violetta* from it (Iredale, 1929). It reveals Iredale's thorough knowledge of early works on Mollusca and includes a number of obscure early species names. (2) Laursen's (1953) monograph, the most useful published work on living species of *Janthina*. (3) The online catalogue of North American Mollusca by Rosenberg (2017), Malacolog 4.1.1 (accessed 5 Jun 2012). (4) An online catalogue of Australian Mollusca prepared at the Australian Museum by P. Middlefart and co-workers, of which the section on Janthinidae was sent to the writer for comment by W. F. Ponder (17 Mar 2012). (5) W. F. Ponder's updated version of Charles Hedley's loose-leaf catalogue of published references to Australian Mollusca. This contains a few further references not noted in any other works. Many other papers also provided references to "Janthinidae" in earlier works. It is hoped that this combination has brought to light all published names in *Janthina* and *Recluzia*. However, none of these sources considered either fossils or the species-level taxonomy of *Recluzia*. As far as the writer is aware, research on fossils over more than 45 years has brought all fossil records to light, but the writer is keen to hear of any fossil records not included.

Janthina species have been illustrated in most identification guides and faunal surveys of living tropical and temperate marine Mollusca for more than 400 years, and it is obviously impossible to include all published references in the chresonymies here. The chresonymy lists below are nevertheless fairly extensive and include all monographs of *Janthina* (Reeve, 1858; Mörch, 1860; Küster, 1868; G. B. Sowerby II, 1882; Laursen, 1953), most other well-known reference works and recent identification guides on Mollusca, all specialized papers on "Janthinidae" the writer is aware of, and a reasonably exhaustive list of Australian and New Zealand literature on Mollusca. Mörch (1860) provided references to a large number of early works in which names are not available; these are not included here. He also listed many other early works with available names (although no further synonyms), many of which have not been included because the chresonymy lists already are extensive. Mörch (1860) also gave an extensive summary of published works on *Janthina* anatomy and biology, a lot if it now known to be incorrect. Most other faunal surveys of living molluscs and most identification guides would provide further chresonymy.

Illustrations of whole shells by light photography in the present work are all provided as far as possible at the same scale, enlarged uniformly by two, to allow ready comparison of specimens and species. A few small specimens have been illustrated at twice this magnification, and other small and juvenile specimens have been illustrated at higher magnifications by SEM.

Abbreviations: institutional acronyms

AMS	Australian Museum, Sydney, Australia.
AUGD	Geology Department, University of Auckland, New Zealand (now Geology Programme, School of Environment).
AWM	Auckland War Memorial Museum, Auckland, New Zealand.
GNS	GNS Science, Lower Hutt, New Zealand (formerly NZ Geological Survey).
MCZR	Museo Civico di Zoologia di Roma, Italy.
MFM	Mizunami Fossil Museum, Mizunami, Gifu Prefecture, Japan.
MHNB	Musée d'Histoire naturelle de Bordeaux, France.
MHNG	Musée d'Histoire naturelle de Ville de Genève, Switzerland.
MIGM	Museo do Instituto Geológico e Mineiro de Portugal, Lisbon, Portugal.
MNHN	Muséum national d'Histoire naturelle, Paris, France.
NHMUK	The Natural History Museum, London, United Kingdom.
NMB	Naturhistorisches Museum Basel, Switzerland.
NMNZ	Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand.
NMV	Museum Victoria, Melbourne, Australia.
OUGD	Department of Geology, University of Otago, Dunedin, New Zealand.
RGM	Naturalis Biodiversity Centre, Leiden, the Netherlands, paleontological collections.
SAMA	South Australian Museum, Adelaide, South Australia.
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany.
ULPGC	Departmento de Biología, Universidad de Las Palmas de Gran Canaria, Gran Canaria Island, Spain.
UPSZTY	Museum of Evolution, Uppsala University, Sweden.
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.
WAM	Western Australian Museum, Perth, Western Australia.
ZMB	Museum für Naturkunde, Berlin, Germany.
ZMUC	Universitets Zoologiske Museum, Copenhagen, Denmark.

Other abbreviations. M24/f123 (etc.)—fossil locality numbers in the New Zealand *Fossil Record Electronic Database* (FRED; http://www.fred.org.nz); map sheet number (e.g., M24) in New Zealand map series 260 (1: 50 000) followed by the locality number (e.g., f123) within that sheet. Truncated grid references, locating each locality to within 10 m on the same NZMS 260 sheet, are also cited here; 14-figure grid references and precise latitude and longitude for each New Zealand fossil locality can be found in FRED. *Fm*, formation (in the sense of lithological/stratigraphical unit), used in captions and diagrams; *ka*, thousands of years ago; *Ma*, millions of years ago; *MIS*, marine isotope stage, now a standard subdivision of Pliocene and Pleistocene time, defined by glacial-interglacial sea-level changes (Pillans *et al.*, 1998; Pillans & Gibbard, 2012; standard series of MIS: Lisiecki & Raymo, 2005). Routine abbreviations for specimen dimensions: *H*, height; *D*, width (maximum diameter, orthogonal to height); and *SH*, spire height.

Overview of classification

Epitoniidae traditionally has been interpreted as a family of benthic gastropods with tall, narrow, white shells, most of which have similar sculpture of prominent, widely spaced axial lamellae or ridges and, at most, weak spiral sculpture. They are well-known for parasitizing benthic cnidarians, mainly anemones and corals. However, this is a description of species of *Epitonium*. The illustrations in Weil *et al.* (1999) demonstrate that other benthic epitoniids can be brown, red-brown, yellow, or spirally banded brown and white, many are much shorter and wider than typical *Epitonium* species, many species are weakly sculptured or smooth, a few genera such as *Alora* H. Adams, 1861 and *Eglisia* Gray, 1842 have predominantly spiral sculpture, and many others have a combination of axial and spiral sculpture. The fine, closely spaced axial ridges on many *Janthina* species are closely similar to those of some finely sculptured *Epitonium* species, and it is the violet colour that sets *Janthina* species apart from *Epitonium* species strongly at first sight. As the violet colour is clearly an adaptation by *Janthina* to floating at the surface of the sea, the obvious first question about Janthinidae is whether the family is distinct from Epitoniidae. Nützel (1998: 89) assumed that Janthinidae is a distinct family and must be an "old" group of Ptenoglossa with a very poor fossil record. Robertson (2007a: 9) also speculated that a poor fossil record might have masked an earlier history, janthinids and epitoniids having a common ancestor. However, Churchill *et al.* (2011a: fig. 1) demonstrated that both *Janthina* and *Recluzia* are nested within Epitoniidae in a molecular phylogeny (Fig. 3A). Takano & Kano (2014) also demonstrated that *Janthina umbilicata* d'Orbigny, 1841 belongs in the same clade as Epitoniidae in a molecular phylogeny (Fig. 3B). All the writer's efforts over more than 40 years to understand the history of this group have demonstrated that the earliest neustonic epitoniid, *Janthina typica* (Bronn, 1861), appeared only during latest Miocene (Messinian) time, c. 7–6 Ma, and the genus *Janthina* apparently evolved from a benthic epitoniid and adopted the neustonic habit at that time. *Janthina* is found fossil in parts of the world where an extensive, diverse Neogene fossil record is preserved and *Janthina* commonly is stranded on beaches at present during persistent onshore winds. In Japan and New Zealand the earliest species, *J. typica*, appeared in small numbers in latest Miocene (Messinian) rocks, and occurs more commonly in early Pliocene (Zanclean) rocks. Supposed late Miocene (Messinian and even purportedly Tortonian) records from Santa Maria Island in the Azores have all been demonstrated to be Pliocene (early Zanclean, 5.3–4.3 Ma) through the reorganization of stratigraphy by Sibrant *et al.* (2015). No Miocene specimens are recorded from anywhere else, including Australia. The fossil record of *Janthina* is helped by its relatively good preservation potential, despite its thinness and fragility, because its outer shell layer is calcitic. An interior aragonitic layer is white and chalky in many fossils and thickest over the columella. The mineralogy of epitoniid shells has been studied little, but deserves more attention because of its potential significance for phylogeny. It is obvious from the excellent preservation of fossil specimens of *Cirsotrema* species in limestone that at least this genus has a calcitic shell. It seems likely that all epitoniids have a calcitic outer shell layer, although it is possible that some are entirely aragonitic, as are most other gastropods. The calcitic shells of *Janthina* and *Recluzia* are surely a reflection of their phylogeny. Distinction between *Janthina* and benthic Epitoniidae based on shell characters clearly is superficial; if *Janthina* species had white shells they likely would always have been classified as Epitoniidae.

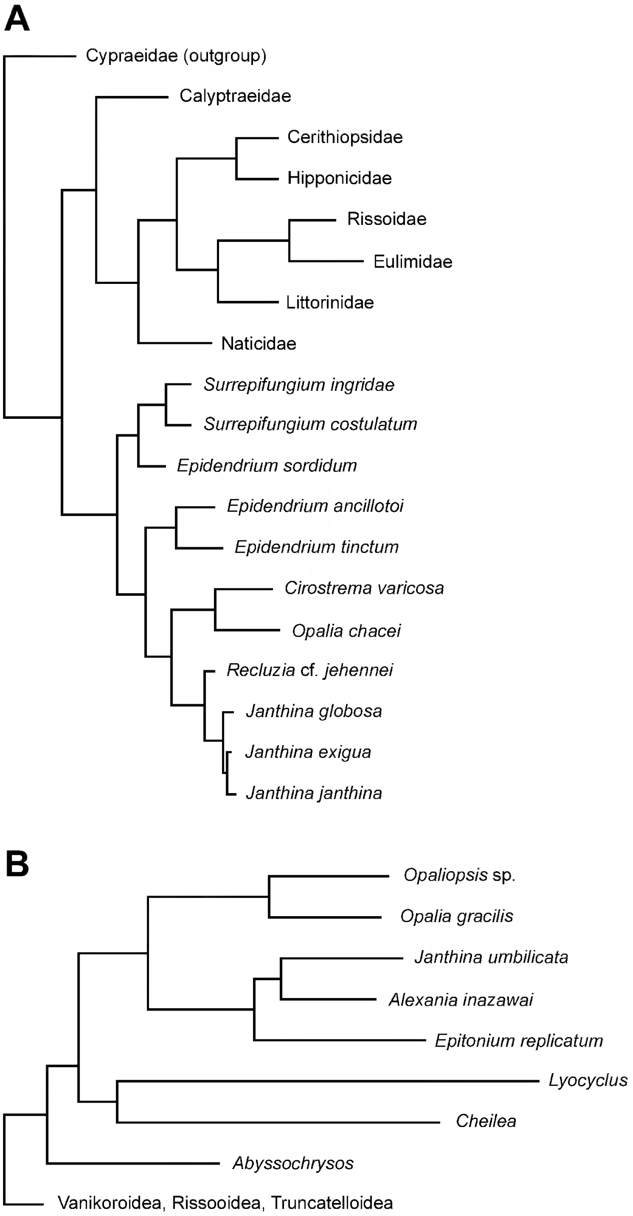

Figure 3. Previously published molecular phylogenies including *Janthina*, *Recluzia* and Epitoniidae. *(A)* "Bayesian phylogram of Janthinoidea and seven potential sister families. DNA sequence data come from four loci: mitochondrial 16S rDNA, nuclear 28S rDNA, Histone-H3, Histone-H4" (redrawn from Churchill *et al.*, 2011a: fig. 1A; name of one *Janthina* species corrected; probabilities etc. deleted), showing *Recluzia* and *Janthina* within Epitoniidae clade (benthic Epitoniidae: *Surrepifungium* to *Opalia*). *(B)* relevant part of diagram "Bayesian phylogeny of Vanikoroidea, Truncatelloidea and Rissooidea inferred from 5gGB alignment of 28S (D1–D7b), 18S, H3, 16S and COI genes" (redrawn from Takano & Kano, 2014: fig. 2; names corrected; probabilities etc. deleted). Epitoniidae (uppermost five taxa) includes *Janthina* on same branch as *Alexania*.

All benthic Epitoniidae that have been studied in detail are carnivores feeding on cnidarians, mainly anemones and scleractinian corals, but a few species feed on other

Table 1. Similarities and differences between benthic Epitoniidae, *Janthina* species and *Recluzia* species; based on Collin (2000: table 1), Churchill *et al*. (2011a: supplementary table S1) and AGB personal observation. Characters of unknown condition queried (?); the likely condition in *Recluzia* is stated where known.

character	benthonic Epitoniidae	*Janthina* species	*Recluzia* species
neustonic, with bubble float	no	yes	yes
feeding on (mainly)	benthic cnidarians	*Velella*, *Porpita*, etc.	minyadid anemones
shell calcitic	yes/no?	yes	yes
obvious periostracum	no/intritacalx	no	conchiolin
teleoconch axial ridges prominent	yes/no	yes/no	no
shell colour	white/brown	violet	yellow-brown
sinus in outer lip	no	yes	no
operculum in adult	yes	no	no
eyes in adult	obvious	minute	? (not obvious)
aphalic males	yes/no	yes	yes
cephalic tentacles	single	forked	single
epipodia	no	yes	no
unpaired labial gland	large	reduced	large
spermatozeugmata	yes	yes	?yes
protandrous hermaphroditism	yes	yes	yes
ptenoglossate radula	yes	yes	yes
divided radula and odontophore	yes	yes	yes
stylets in inner salivary glands	yes	no	yes
central tooth distinctive	yes/no	no	no
purple dye secreted	yes/no	yes	no
larval pigmented mantle organ	yes	yes	?yes
acrembolic proboscis	yes	no	no
cuticularized oesophagus	yes	yes	?yes
osphradial ridges	1 or 3	1 or 2	?
open pallial oviduct	yes	no	no
pairs of salivary glands	2	2	2
statocysts	yes	no	yes
egg capsules	small, linked	large, separate	large, separate
chalazae	yes	no	no
number of adult teleoconch whorls	5–20	3–5.5	4.5–7
juvenile stage associated with adult's egg mass or float	yes, on adult egg mass	no, juvenile has float	yes, on adult float

cnidarians (e.g., Robertson, 1963, 1970, 1981a; Bosch, 1965; Gittenberger, 2003; Gittenberger & Gittenberger, 2005). *Epidendrium reticulatum* (Habe, 1962) is an example of a benthic epitoniid species, tentatively assigned to *Epidendrium* by Nakayama & Hasegawa (2016: 21), that feeds on the plumulariid hydrozoan *Dentitheca habereri* (Stechow, 1909), which in turn lives attached to the anthozoan *Parazoanthus gracilis* (Lwowsky, 1913) (Habe, 1962; Nakayama & Hasegawa, 2016). *Janthina* and *Recluzia* appear merely to be epitoniids that feed on neustonic cnidarians, mainly the siphonophore *Physalia* and the chondrophores *Porpita* and *Velella* in the case of *Janthina* (e.g., Hardy, 1956; Ganapati & Subba Rao, 1959; Okutani, 1964; Palazzi, 1979; Rolán & Trigo, 2003) and "the rare floating anemone *Minyas*" in the case of *Recluzia* (Abbott, 1968: 93, text-fig.; Abbott, 1974: 114; Minyadidae, Cheng, 1975: 195; Robertson, 1997: 11; 2007a: 7) (note that *Actinecta* Blainville, 1830 has priority over the junior homonym *Minyas* Cuvier, 1817; Fautin *et al*., 2007; Fautin, 2013). The lack of a fossil record of *Recluzia* species indicates that *Recluzia* adopted the neustonic habit very recently, in geological terms. Although the most spectacular siphonophore, *Physalia*, has no fossil record (Harrington & Moore, 1956: 147), fossils convincingly similar to *Velella* are known from Devonian rocks and fossils similar to *Porpita* from Ordovician rocks (Harrington & Moore, 1956: 149–150). The origination of its main prey was not an impetus for the evolution of *Janthina*.

The most important consideration for the classification of *Janthina* and *Recluzia* is the phylogenetic significance of the synapomorphies that previously suggested the recognition of a separate family Janthinidae. Similarities and differences between benthic Epitoniidae, *Janthina* and *Recluzia* are listed in Table 1. *Janthina* and *Recluzia* species share with benthic Epitoniidae the ptenoglossan radula, aphalic males (also the case in some but not all benthic epitoniids), protandrous hermaphroditism, the radula and large odontophore being subdivided into two and used as an eversible grasping organ to pull large pieces of food into the gut (Graham, 1965: 336, fig. 5; see below), a hypobranchial gland secreting a purple dye (Robertson, 1983: 10; 2007a: 9) (although a purple secretion apparently is not produced by *Recluzia* species), a larval pigmented mantle organ, a cuticularized oesophagus, two pairs of salivary glands, stylets in the inner pair of salivary glands (in *Epitonium* and *Recluzia*, but not *Janthina*; Fretter & Graham, 1962: 260; Churchill *et al*., 2011a: supplementary table S1), and longitudinal ridges on the osphradium (although not as yet demonstrated in *Recluzia*). Further differences listed by Collin (2000: table

1) are that the pallial oviduct is open in benthic Epitoniidae but closed in *Janthina* and *Recluzia*, *Janthina* and *Recluzia* lack an operculum in the adult although it is present in the larva and in all benthic Epitoniidae, and statocysts are present in benthic Epitoniidae but absent in *Janthina* – although Churchill *et al.* (2011a) demonstrated that statocysts are present in *Recluzia*. Also, *Janthina* species have a whitish to pale blue body with subdivided (forked) and, in some specimens, black or at least black-speckled cephalic tentacles, shown well by Cheng (1975: fig. 11), Okutani (1956: text-figs 4–6, 8) and Wilson & Wilson (1956: pl. 1, fig. 2; Fig. 1B; Figs 4B–C, 5A, E) whereas the entire animal is yellow and the cephalic tentacles are single (undivided) in *Recluzia* species (Bennett, 1966: pl. 11, fig. 1; Churchill *et al*., 2011a: fig. 1B; Figs 6–7) and are undivided in benthic Epitoniidae. Exterior features of the animal of *Janthina* and *Recluzia* species are shown in Figs 4–7. The relatively well-known exterior anatomical characters of *J. janthina* are confirmed to be essentially identical in photographs of living animals of *J. globosa*, *J. pallida* and *J. umbilicata* illustrated here (Figs 5B–C, E). Some specimens of *J. janthina* have black or black-speckled cephalic tentacles and snout, as does the specimen of *J. pallida* illustrated here (Fig. 5B) but the photographs of *J. globosa* and some of those of *J. janthina* and other species published here (Figs 4B–C, E, 5A, E) show that they have subdivided tentacles, but they are translucent blue and at most a little darker than the rest of the animal tissue, although perhaps only when contracted; black speckling is far from uniform. The head and snout also are a little larger and more protruding in *Janthina* species than in *Recluzia* species, so *Janthina* species have evolved a sinus in the outer lip to accommodate the permanently protruding head and snout (or, more accurately, adapted an earlier, smaller sinus at the base of the lip), whereas a sinus is not required by *Recluzia*. *Recluzia* species and four of the five living species of *Janthina* also lay stalked egg capsules on the underside of their floats, rather than the more numerous, small, sand-agglutinated, linked egg capsules of benthic Epitoniidae. The egg capsules are simple, smooth, slightly club-shaped cylinders with hemispherical distal ends in both *Recluzia* species (Figs 6–7), but are ovate-triangular with the distal end wider than the proximal one and with small spines around the distal end in *Janthina* species (Laursen, 1953: figs 23, 27, 31, 37; Okutani, 1956: text-fig. 2). A further obvious difference is in the number of teleoconch whorls. This can range from as few as five to as many as 20 in benthic Epitoniidae (Weil *et al*., 1999: 118; 20 whorls in *Claviscala* "*kuroharai* Azuma, 1960", i.e., *C. terebralioides* Kilburn, 1975; Tsuchida, 2000: 329) whereas *Recluzia lutea* has 4.5–5.5 teleoconch whorls, *R. johnii* has 6–7, and *Janthina* species have only 3.5–5 teleoconch whorls. These distinctions from benthic Epitoniidae can all be understood as adaptations by *Janthina* and *Recluzia* to neustonic life suspended beneath a bubble float. Other characters important for classification are evaluated more fully below, in a review of the extensive previously published information on the biology and relationships of *Janthina* and *Recluzia*, amplified by new photographs of living specimens (Figs 4–7).

Review of biology of *Janthina* and *Recluzia*

Float and formation of bubbles. The two genera of neustonic Epitoniidae recognized here, *Janthina* and *Recluzia*, have been able to adopt a neustonic life because they float by means of a raft or float constructed from air bubbles coated with mucus that hardens on contact with seawater. The float is held in place against the mesopodium merely by a sheet of the same mucus. The animal must retain the float permanently to remain afloat, so the head, propodium and mesopodium remain permanently outside the shell. Wilson & Wilson (1956: 300, fig. 1) noted that the living animal floats with almost all of the animal and its float beneath the water surface, only a small part of the float protruding above the water-air interface (Fig. 1), but quite a light puff of air directed at the float "will make the snail scud along before it". Each float bubble is constructed by cupping air in the propodium and coating the bubble with mucus from the pedal mucus gland, which secretes mucus that hardens on contact with seawater. It is also the source of mucus attaching the float to the foot and egg capsules to the float (Laursen, 1953: fig. 4; Fretter & Graham, 1962: 115). The animal is able to form bubbles only while at the sea surface, in contact with air, and specimens that lose their float sink to the bottom and die. The foot must, therefore, remain outside the shell permanently to retain the float. Robertson (2007a: 4) claimed that "postlarval *Janthina* shells have never been recovered from deep-sea bottom sediments", but that is not correct. Simroth (1895: 7) listed specimens of *Janthina* dredged at considerable depths in the North Atlantic by the Plankton Expedition and Locard (1898) did the same for specimens dredged by the *Travailleur* and *Talisman*. Empty specimens have been dredged in small numbers offshore in deep water at numerous localities around northern New Zealand (material in NMNZ, listed under relevant species below). Also, nearly all the many fossils collected in New Zealand, southern Australia, Japanese and the Azores represent specimens that sank to the seabed on the continental shelf and were enclosed in sediment. The type material of *Kaneconcha knorri* Kaim, Tucholke & Warén, 2012 (= *Janthina chavani*) also was dredged buried in sediment in 3293–2827 m of water on the mid-Atlantic ridge (Kaim *et al*. 2012). In a remarkably similar case, the holotype of *Eunaticina abyssalis* Simone, 2014 (= *J. typica*) was dredged enclosed in sediment in 1500–1575 m in the South Atlantic off Itaúnas, Espiritu Santo State, Brazil. Obvious exceptions are the abundant specimens of *J. chavani* in Roe Calcarenite and Bridgewater Limestone in southern Australia and the excellent material of *J. typica* collected recently at La Esfinge, Gran Canaria

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Figure 4 (facing page 129). Living animals in aquaria. *(A) Janthina janthina* (Linnaeus) (centre) and *J. pallida* Thomson (left, and part of another float at right) together, showing different bubble sizes in floats, and *J. janthina* feeding on pink eggs of *J. pallida* beneath float; collected at Arina Beach, Heraklion, Crete. *(B) Janthina janthina*, collected on beach in northern New South Wales, Australia, clearly showing forked cephalic tentacles; *(C–E) Janthina janthina*, all data as for Fig. 4A; C, showing forked cephalic tentacles, lack of eyes, and teeth and odontophore protruding from mouth at end of extended snout; D–E, showing extended head and snout, odontophore visible in mouth, and partially expanded right epipodium lying over shell (*A, C–E*, reproduced with permission of Dimitris Poursanidis, Heraklion, Crete; *B*, reproduced with permission of Denis Riek, Brunswick Heads, New South Wales). Scale bars 10 mm.

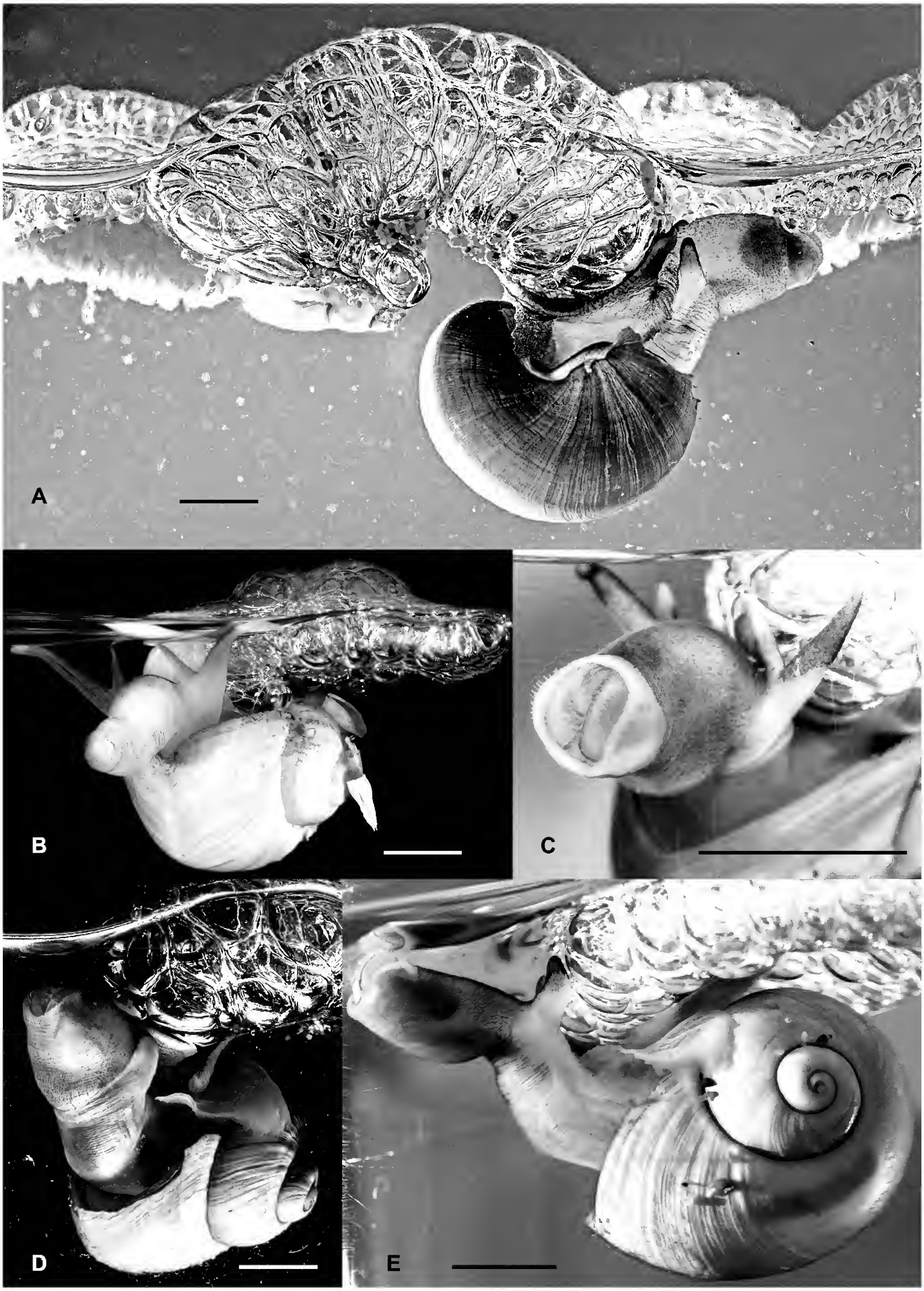

Figure 4. (See facing page 128 for caption).

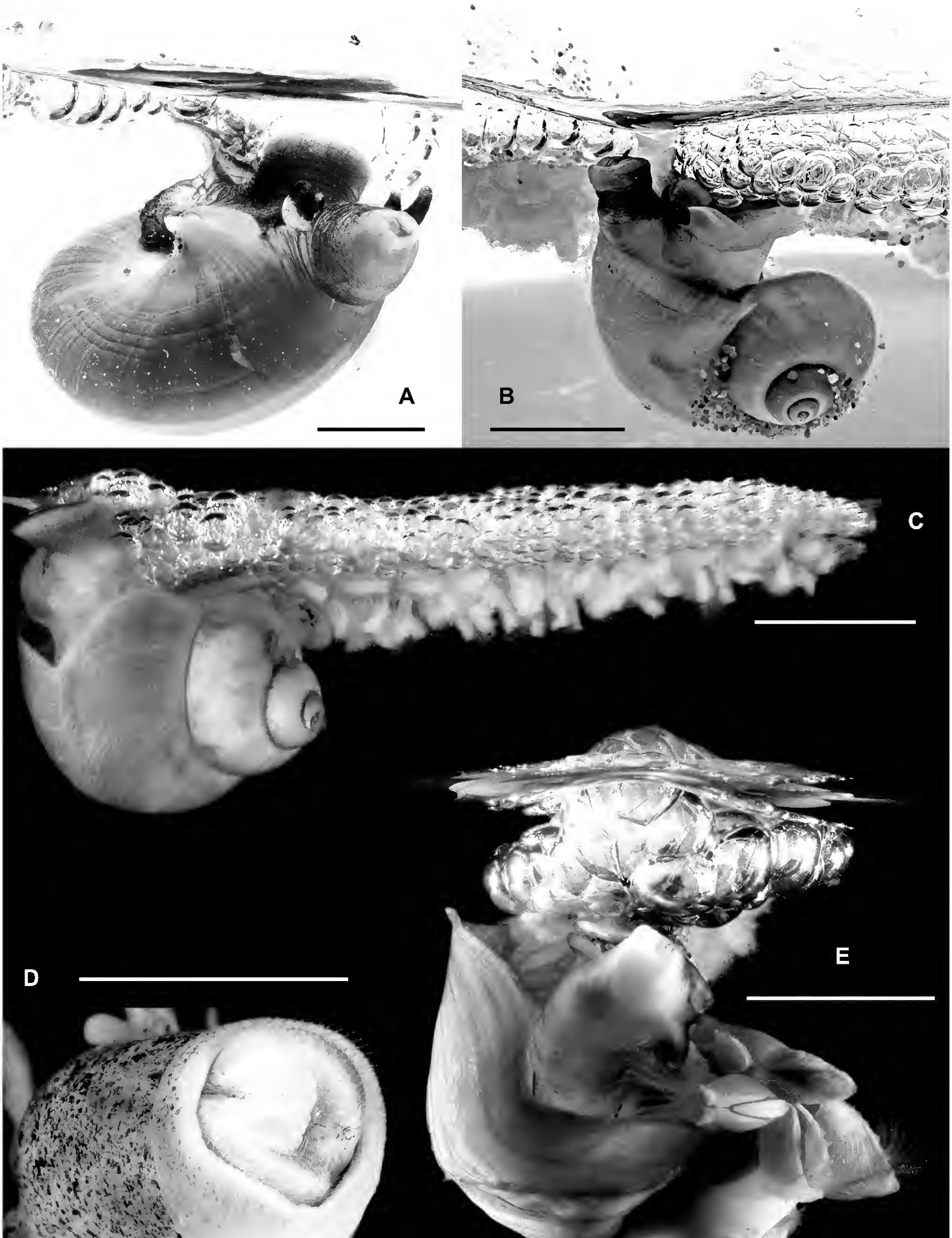

Figure 5. (See facing page 131 for caption).

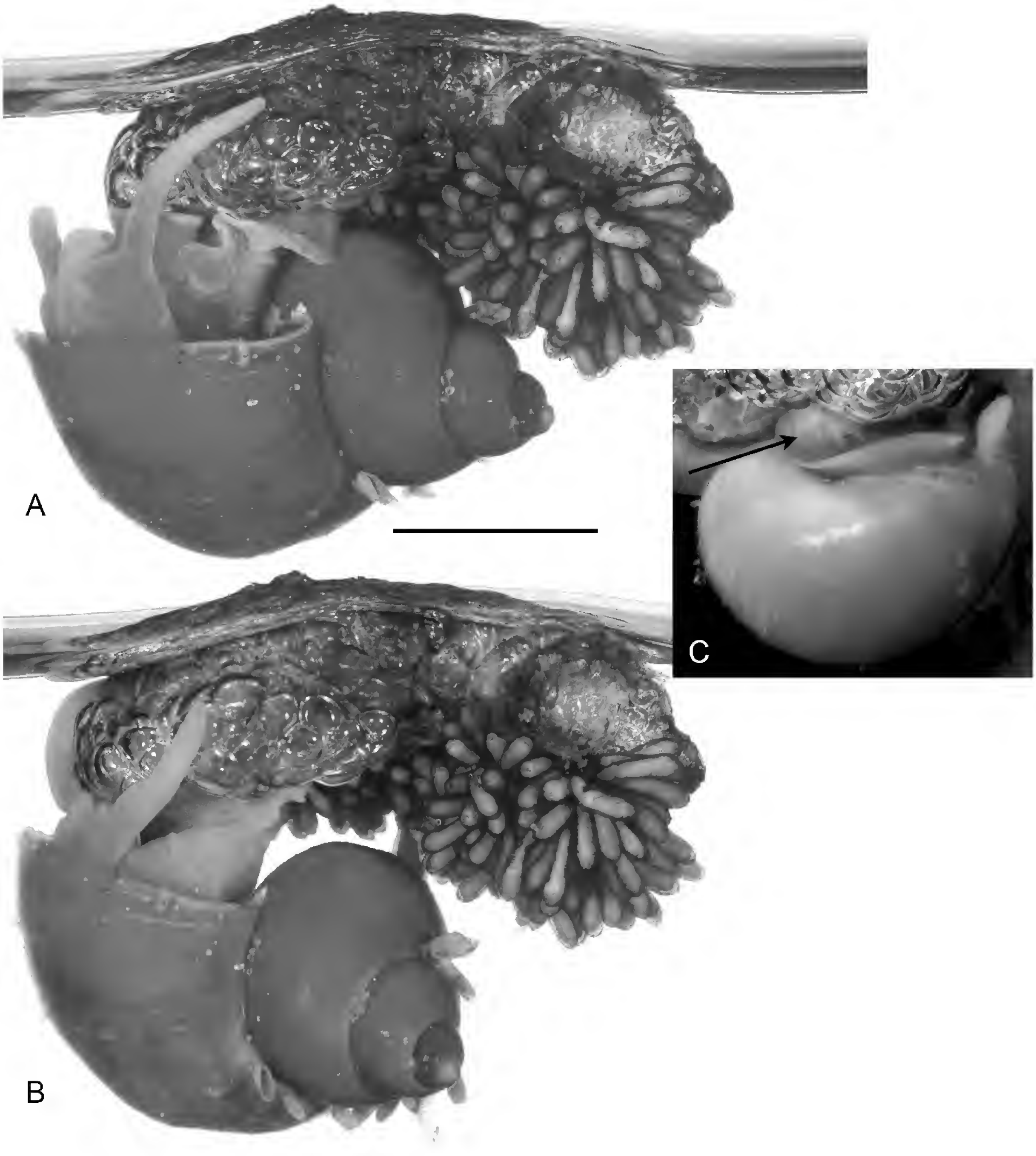

Figure 6. *Recluzia lutea* (Bennett), living animals in aquaria. *(A–B)* two views of same specimen, showing irregular float bubbles, and egg capsules beneath float; collected at Minnie Waters, near Lismore, New South Wales (reproduced with permission of Anthony Healy, Sydney). *(C)* specimen collected on beach in northern New South Wales, showing relatively large juvenile, presumably male specimen (arrowed) on foot of large female specimen, beneath female's float; located against blue *Physalia* specimen at right (reproduced with permission of Denis Riek, Brunswick Heads, New South Wales). Scale bar 10 mm, applies to all images.

Figure 5 (facing page 130). Living animals in aquaria. *(A) Janthina janthina* (Linnaeus), collected on Arina Beach, Heraklion, Crete, Mediterranean, showing partially contracted snout and forked cephalic tentacles, propodium between float and tentacles, snout resting in lip sinus, weak spiral grooves in base of shell, and small amount of ianthinin purple dye at right below snout. *(B) Janthina pallida* Thomson, all data as for Fig. 5A, showing float with pink egg capsules beneath, and snout partially expanded; part of float of another specimen visible at left. Faint spiral colour bands on this shell are unusual. *(C) Janthina umbilicata* d'Orbigny, collected on beach in northern New South Wales, Australia, showing long, narrow float as in *J. exigua* Lamarck, weakly expanded head and propodium (top left), and egg capsules beneath float. *(D) Janthina janthina*, all data as for Fig. 5C, odontophore and teeth visible in tip of expanded snout. *(E) Janthina globosa* (Swainson), all data as for Fig. 5C, showing float, anatomy essentially as in *J. janthina*, expanded head resting in lip sinus, forked cephalic tentacles partly visible, barnacles attached to *Janthina* shell, and pink eggs beneath float (*A–B*, reproduced with permission of Dimitris Poursanidis, Heraklion, Crete; *C–E*, reproduced with permission of Denis Riek, Brunswick Heads, NSW). Scale bars 10 mm.

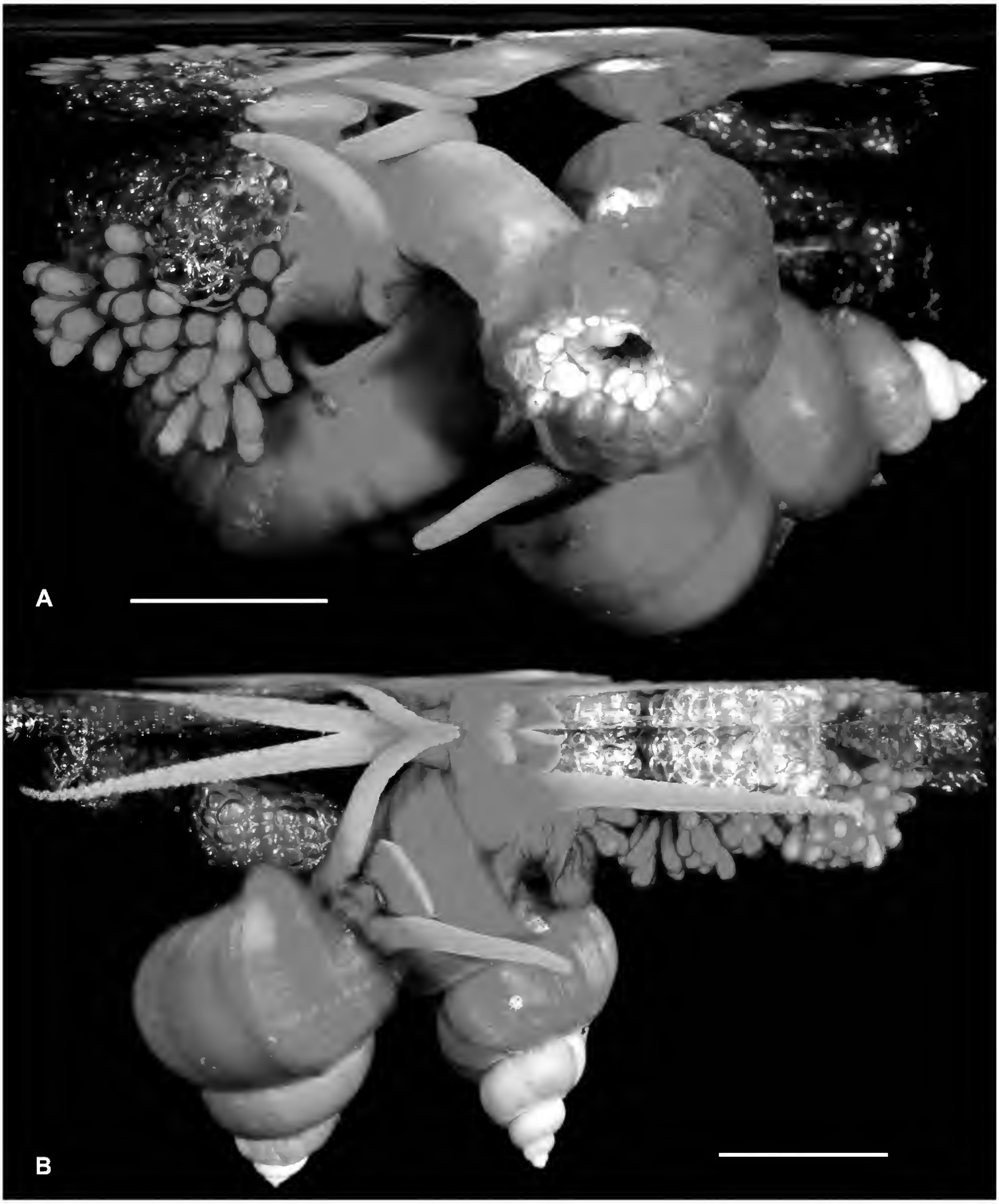

Figure 7. *Recluzia johnii* (Holten), two living animals in aquaria, collected on beach in northern New South Wales; specimens reflected on under-surface of water at top of images. *(A–B)* two views of the same two animals feeding on an *Actinecta* anemone (at upper right in Fig. 7A), showing similar characters to *R. lutea*, but taller shell and longer (more expanded?) cephalic tentacles; in Fig. 7B, anemone has been consumed (reproduced with permission of Denis Riek, Brunswick Heads, NSW). Scale bars 10 mm.

Island; these likely represent specimens blown ashore on a beach. The animal also cannot raise or lower itself in the water column as early authors thought, e.g., Swainson (1840: 31) described *Janthina* as having "a cellular organ attached to the belly, by which it floats on the surface of the ocean, or sinks to the bottom, at its own pleasure". Many authors have described and illustrated the animal of *Janthina* and the method of formation of bubbles by cupping air within the propodium, coating the bubble in mucus from the pedal mucus gland, and attaching bubbles to the float by pressing

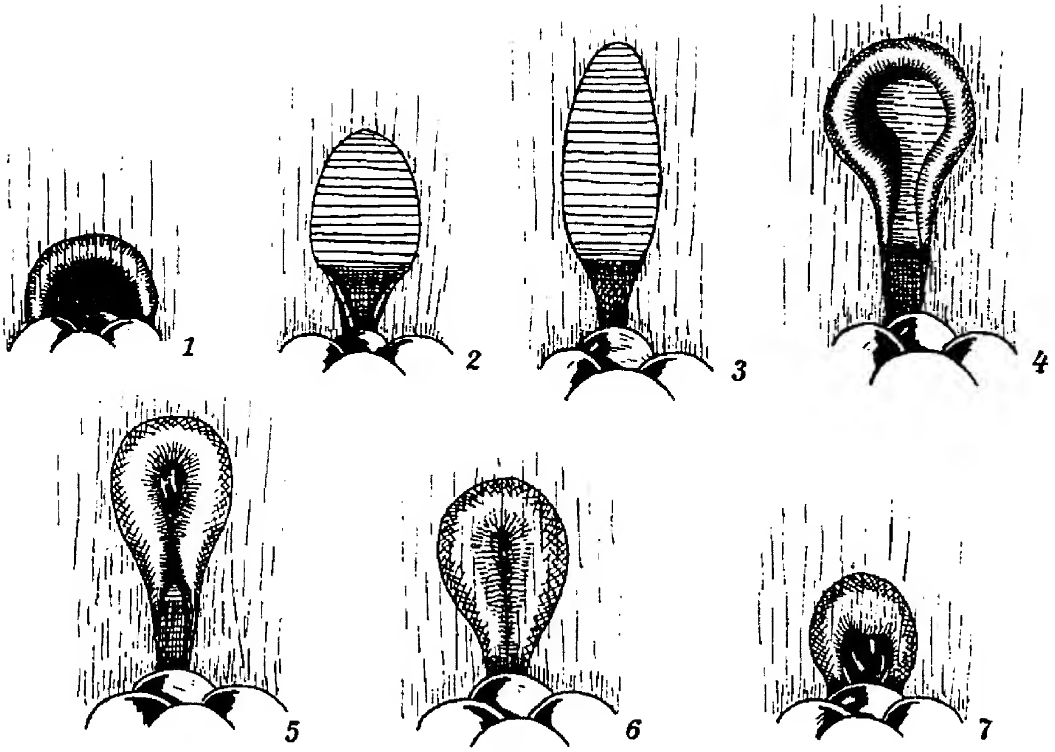

Figure 8. Bubble formation by *Janthina*; a sequence of schematic drawings of extension and contraction of the propodium, forming a bubble and adding it to the float; dorsal view. Presumably based on *Janthina janthina*; copy at published size of Fraenkel (1927: fig. 4); magnification unknown.

them against it while the mucus hardens (e.g., Forskål, 1775: 127–128; Bosc, 1802; Péron & Lesueur, 1807; Cuvier, 1808; most clearly by Coates, 1825, 1828; Eschscholtz, 1825: column 737; Quoy & Gaimard, 1825, 1832, vol. 1: 242; atlas, pl. 29, figs 1–8; Lesson, 1826; Rang, 1829: 196, pl. 5, fig. 3 [showing the shell of the brooding species *J. janthina* with egg capsules beneath the float, an impossible combination copied in several later manuals, e.g., Fischer, 1885: 774]; Grant, 1834; Lund, 1834a: 110, pl. 6, figs 23–26; Lund, 1834b; Bennett, 1834, 1840: 295–298; Costa, 1841; Delle Chiaje, 1841; Deshayes, 1843: 2–3; H. Adams & A. Adams, 1854: 86, pl. 69, figs 1–1a; Benson, 1860; Adams, 1862; Lacaze-Duthiers, 1865, 1866; Jeffreys, 1867: 174–189; Bouvier, 1886a, b, 1889; Simroth, 1895; Pruvot-Fol, 1925; Fraenkel, 1927; Thiele, 1929: 224–225; Laursen, 1953; Wilson & Wilson, 1956: 300; Okutani, 1956: text-figs 1–8; Fretter & Graham, 1962: 561–563; Bayer, 1963; Abbott, 1968: 92–93; Yonge & Thompson, 1976: 96, pl. 5, lower fig.; Lalli & Gilmer, 1982; Smith, 1998: 811–814; Light, 2003). Jeffreys (1867: 175) and other early authors referred to still earlier descriptions and illustrations by authors as early as Colonna (1616). Dollfus & Dautzenberg (1932: pl. 13, lower fig.) republished Colonna's (1616) plate, showing a clear illustration of a living *Janthina* animal with inverted shell, float, strongly protruding head and snout with forked cephalic tentacles, and protruding, subdivided odontophore and radula. The species illustrated is *Janthina globosa*, to judge from the evenly subspherical shell and the angular, protruding anterior end of the columella. Mörch (1860: 261–262) listed all descriptions of float formation known to him, including a still earlier one by Colonna (1606) and further descriptions and illustrations by early authors. He also listed reprints or translations of the excellent description by Coates (1825) in "Zoological Journ., vol. 3, p. 264. – Thompson. Ann. Philos. new ser. Vol. 10, p. 385. – Proceed. Bost. Journ. 1. 184. – Féruss. Bull. – Johnston Conchyl., p. 131" (Mörch, 1860: 262, footnote). The drawings by Fraenkel (1927: figs 3–4; Fig. 8) illustrate the formation and attachment of a bubble particularly clearly.

Wilson & Wilson (1956: pl. 1, figs 2–3), Bayer (1963: fig. 4) and Light (2003: figs 4–10) also illustrated bubble formation with photographs, although this subtle process is difficult to illustrate by this means. Yonge & Thompson (1976: 96) described bubble formation particularly clearly: "These surface-dwelling oceanic animals have a large float consisting of mucus-coated bubbles of air formed by the propodium which is raised, spoon-shaped, above the water surface to entrap an air bubble which, enclosed in mucus, is added to the base of the float below. The process takes under a minute and is repeated some ten times before a rest is taken. The compacted float is described as 'springy and dry'". One of the most thorough descriptions of *Janthina* anatomy and biology is by Simroth (1895: 5–26, pls 1–2). He listed six species collected by the Plankton Expedition, suggested two of them might be synonyms, and described their radulae, mantle cavity organs, tentacles and epipodia, foot, float and float formation, ontogeny, larvae and protoconchs. The early description by Delle Chiaje (1841: 104–110, pls. 67–68) is also thorough. Fretter & Graham (1962: 115) described the pedal mucus gland modifications clearly: "Across the anterior edge of the foot… runs a cleft marking the position of the anterior pedal mucus gland. Along the centre of the anterior half of the mesopodium … runs a groove into which the sole gland discharges mucus; this groove is called the funnel and posteriorly it ends in a transverse fold covered with smaller longitudinal grooves and rich in gland cells. It is here that air, trapped from the atmosphere, is covered with mucus to make the bubbles of the float". The *Janthina* float and its means of bubble formation are, therefore, among the most frequently described aspects of molluscan biology. They presumably attracted the attention of early naturalists because the bubble float is unique to *Janthina* and *Recluzia*, and living specimens of *Janthina* are obvious when a large number is cast ashore, forming a violet band on beaches.

An excellent photograph was published by Bennett (1966: pl. 11, fig. 1) and others were taken by Tony Healy (Figs 6A–B) of a living specimen of *Recluzia lutea*, and others have been taken of *R. johnii* by Denis Riek (Figs 7A–B). They show a relatively simple foot, with the float attached to the foot as in *Janthina*, and the undivided cephalic tentacles curled around the anterior end of the float and apparently aiding float retention in some situations. No epipodia can be distinguished in any photographs of living *Recluzia* specimens, and the head is a little smaller, proportionally, than those of *Janthina* species. The snout in Figs 6 and 7B also is seen to be much smaller than that of *Janthina* species. The float in these illustrations (Figs 6–7) is constructed of significantly smaller and more haphazardly arranged bubbles than those of *Janthina* species. This suggests the possibility that it is constructed in a different way from the float of *Janthina* species, but float construction has not been observed in *Recluzia*; a propodium presumably is required to form float bubbles. A propodium appears to be shown in Fig. 6A, behind the long tentacle and beneath the float, separated by a notch from the rest of the foot and its attached mucus sheet. Also, the left specimen in Fig. 7B can be seen applying an expanded part of its anterior to the shell of the right specimen. This structure lies beneath (posterior to) the snout and so is probably the propodium. Cephalic tentacles are single (not subdivided) in all illustrations of living *Recluzia* specimens. The anatomy of *Recluzia* clearly deserves further study. One of the living animals shown here (Fig. 6A) has an obvious sheet of mucus retaining the float, located between the float, the foot (mesopodium) and the lower part of the penultimate shell whorl. Churchill *et al.* (2011a: supplementary table S1) reported a mucus stalk retaining the float in *Recluzia*, but a sheet clearly is present in Fig. 6A, apparently removing one distinction between *Recluzia* and *Janthina*.

Other photographs of living *Janthina* specimens provided by Dimitris Poursanidis of specimens collected at Arina Beach, Heraklion, Crete, in the Mediterranean, and those by Denis Riek of specimens collected in northern New South Wales, Australia, all photographed in aquaria (Figs 4–7), reveal the external anatomical features of all *Janthina* and *Recluzia* species other than *J. exigua* (implying that *J. exigua* is a rare species in these areas). Specimens of *J. janthina* and *J. pallida* illustrated together (Fig. 4A) reveal the much larger, more randomly arranged float bubbles of *J. janthina* compared with the smaller, more uniform ones of *J. pallida*. Unusually bright pink egg capsules also are visible under the floats of specimens of *J. pallida*, whereas the egg capsules attached to some specimens of *J. globosa* (Fig. 5E) and *J. umbilicata* (Fig. 5C) are pale pink. The head views (Figs 4B–C, 5A, D) of *J. janthina* clearly show the forked cephalic tentacles, speckled with black in some specimens but paler to almost transparent in others, the protruding snout also speckled with black, the lack of obvious eyes and operculum, and the subdivided odontophore and radula, with teeth protruding from the mouth (Figs 4C, 5D). Lateral views of *J. janthina* (Figs 4D–E) also clearly show the triangular to almost circular right epipodium, with a serrated margin, and reveal its relationship to the rest of the foot. Epipodia are not visible in any other specimens, apparently because they were not in the correct orientation. The head-on view of *J. janthina* (Fig. 5A) clearly reveals the raised propodium, in front of the float but behind the cephalic tentacles. Some idea of the external anatomy of *J. pallida* is revealed by Figure 5B, although this specimen evidently did not expand from its shell as readily as *J. janthina* does. The illustrated specimen of *J. globosa* (Fig. 5E) is very similar to *J. janthina* in anatomy, although its head is extended rather than the snout; the forked cephalic tentacles are visible near the mouth. The large *Lepas* barnacles attached to the shell hide the area where an epipodium would have been expected. The specimen of *J. umbilicata* (Fig. 5C) is included to show its very long, narrow float closely resembling that of *J. exigua* (Laursen, 1953: fig. 1). These two species are closely similar in all characters other than the prominence and spacing of their exterior collabral sculpture. Several of these photographs (Figs 4B–C, 5A, E) reveal that the only obvious function of the sinus in the outer lip of the shell is to allow the head and snout to be maintained outside the anterior end of the shell, resting in the lip sinus. The lack of such a sinus in *Recluzia* species is shown in Figs 6–7 to result from the head and snout of *Recluzia* species being relatively smaller than in *Janthina* species, and not resting on the lip of the shell as they do in *Janthina* species.

Reproduction and larvae. Robertson (1981b) demonstrated protandrous hermaphroditism in an *Epitonium* species, and this is shared with many other epitoniids (Collin, 2000). Graham (1954) also reported that all male specimens he observed of *Janthina janthina* were markedly smaller than female specimens. Ankel (1930) reported the same size relationship in another species, probably *J. pallida*. However, Laursen (1953: 9–11) reported specimens in male, sterile and female phases, usually in increasing size order, although "the male and female individuals of presumably the same spat-falls are of the same size. Furthermore, there are in the material [examined by Laursen] sterile individuals, i.e. individuals which are neither in a male nor a female phase, and individuals which are both male and female" (Laursen, 1953: 9). Laursen (1953: fig. 2) illustrated the animal of a specimen of *J. pallida* with both male and female organs functioning simultaneously. A functional seminal duct is located on the wall of the mantle cavity, and a swollen oviduct full of eggs is attached to the same wall above the seminal duct. However, Laursen (1953: 11) also noted that in the majority of large specimens he dissected the seminal duct had disappeared and the oviduct, closely packed with eggs, occupied almost the entire body cavity. Wilson & Wilson (1956: 302) kept two large specimens of *J. janthina* from southern England alive in an aquarium, both "about the maximum size we saw". They reported that one shed packets of veligers whereas the other shed spermatozeugmata, indicating that large specimens can be either male or female. This is countered, however, by the observations on egg capsule occurrence by Okano & Wada (2012). They measured specimens in a mass stranding of *J. globosa* (Swainson, 1822) on the Sea of Japan coast, illustrating current and depleted capsules attached to some of the same floats, and determined that capsules were laid by all 41 specimens larger than 27.4 mm high in a collection of about 170 specimens (24%) ranging in height from 6.08–40.36 mm; i.e., all large specimens of *J. globosa* were female. It seems likely that a single cycle of protandry is normal in *Janthina* species, but is modified for unknown reasons in some specimens. The two published observations of young specimens of *Recluzia lutea*, by Colman (1986) and Churchill *et al.* (2011b), both reported small specimens, assumed to be males, located on the foot or float of a large adult female, implying that a single cycle of protandry also occurs in *Recluzia* species. The specimen of Churchill *et al.* (2011b: figs 1A–B) is in a photograph by Denis Riek taken in northern New South Wales, repeated here (Fig. 6C). The same physical relationship is confirmed by now dry specimens collected alive on a beach in northern New Zealand, in which several larval shells are preserved in dried mucus material attached to larger shells (see below under *R. lutea*; Fig. 37). This implies, however, that the production of a mucous string and single-bubble "proto-float" by juvenile specimens of *Janthina* species (Simroth, 1895; Churchill *et al.*, 2011b) did not evolve in *Recluzia*. Churchill *et al.* (2011b) recognized that this is a further significant distinction between the genera *Janthina* and *Recluzia*. Further research clearly is desirable on the life cycle and reproductive strategies of neustonic Epitoniidae.

Protoconchs. Simroth (1895: fig. 3) and Robertson (1971: pls 5–6) illustrated larval shells of several *Janthina* species attached to their teleoconchs at an angle to the teleoconch coiling axis. Albany (1940) also pointed out that the protoconch of *Janthina* is inclined to the coiling axis of the teleoconch. Richter & Thorson (1975: 136) also illustrated shells of veligers, demonstrating that they are very similar to the protoconchs of planktotrophic benthic Epitoniinae. Lalli & Gilmer (1989: fig. 6) illustrated the larval shell of an unidentified *Janthina* species with a unique rectangular projection on the outer lip resembling that of a classic neogastropod sinusigera larva, although the projection is not as long or strongly hooked as in a sinusigera. Fretter & Graham (1962: 402, fig. 211), Robertson (1976: 217–219, figs 4–5), Collin (2000: fig. 20), Gittenberger & Gittenberger (2005) and many other authors have described the numerous, small, sand-agglutinated egg capsules linked together by elastic threads (chalazae) of benthic Epitoniidae and contrasted them with the larger capsules attached to the underside of the float in *Janthina* and *Recluzia*. Robertson (1976) also commented that although *J. janthina* is ovoviviparous (i.e., it broods its eggs in the oviduct) while all four other *Janthina* species are oviparous, the late larval stages of all five species are planktotrophic veligers, as is the case for *Recluzia lutea* and presumably *R. johnii*. Robertson (1983: 10) also pointed out the similarity between the protoconch microsculpture of *Epitonium* and *Janthina* "first shown by Richter and Thorson" (1975: 136). Protoconchs examined for this report show that the *Janthina* protoconch is slightly shorter than those of most benthic Epitoniidae, but this appearance is the result partly of a truly slightly shorter larval shell (Robertson, 1971: fig. 22; 2007a: 8, text-fig.) and partly of the high angle of the coiling axis of the protoconch to that of the teleoconch in some species, so that the protoconch is enclosed slightly in the teleoconch. Protoconchs are particularly inclined at a high angle in specimens of *J. janthina* examined (Figs 32A–D) but are inclined at only a slight angle in *J. exigua*, *J. globosa* and *J. umbilicata* (Figs 30A–B, 34C, F, H), whereas the protoconch is parallel to the teleoconch coiling axis in *Recluzia lutea* (Figs 37B–F). Protoconchs of *J. pallida* and *R. johnii* were not available for examination. Rolán & Trigo (1973: fig. 3) illustrated that of *J. pallida* well, demonstrating that it is almost parallel to the coiling axis of the teleoconch, but is unusually short, only c. 2 whorls protruding from the teleoconch apex. They commented that "it is not possible to see how many whorls are present, because the lowest part is covered by the teleoconch" (Rolán & Trigo, 1973: 56). The obvious but fine, narrow, axial grooves and weak spiral grooves, with weak, rectangular deviations of the axial grooves where they are crossed by the spiral grooves, shown in Robertson's (1971, figs 18–19, 22) illustrations of *Janthina* larval shells, are also visible in all protoconchs of *Janthina* species and *R. lutea* examined here. The protoconch of *J. typica*, type species of *Hartungia*, has not been available despite a careful search of available well-preserved material, notably New Zealand material and that from the Roe Calcarenite in southern Australia. As noted below under the type material of *Eunaticina abyssalis* Simone, 2014 (= *Janthina typica*), its supposed protoconch illustrated by Simone (2014: figs 10I–J) is the corroded apex of the *Janthina* teleoconch, rather than the protoconch. The protoconch of *J. typica* cannot be evaluated as yet. *Recluzia lutea* has a protoconch closely similar to that of *Janthina* species in shape and sculpture, but has one fewer whorls. All *Janthina* and *Recluzia* protoconchs examined have a protoconch I of just over one smooth whorl, with an obvious but narrow terminal groove. That of *Janthina* species examined (counted in *J. exigua* and *J. janthina*) has a protoconch II of 3.2 whorls (Figs 32B, 34C, F), whereas protoconch II of *R. lutea* consists of only 2.2 whorls (Fig. 37B).

Spermatozeugmata. Graham (1954) described the reproductive anatomy of *Janthina janthina*, based on the specimens collected in Cornwall by Fowler (1946a, b). He provided details of the anatomy, and again reported fertilization by the spermatozeugmata described by Ankel (1930). All adults Graham examined were protandrous hermaphrodites and lacked a penis when in the male phase. This is equally true of all adult males observed since, so the large swimming spermatozeugmata provide the means of transferring sperm between individuals. Egg capsules and spermatozeugmata of *Janthina* were described also by Müller (1863), Baldasseroni (1916) and Ankel (1926, 1930), among others. Collin (2000: table 1) when describing the anatomy and development of *Nitidiscala tincta* (Carpenter, 1865) pointed out that spermatozeugmata are produced by Epitoniidae, Janthinidae, Cerithiopsidae and Triphoridae, among the families included in Ptenoglossa by some authors. Spermatozeugmata were described also in benthic Epitoniidae by Bulnheim (1962, 1968), Melone *et al.* (1978, 1980) and McDermott (1981). Nishiwaki & Tochimoto (1969) described two distinct sizes of spermatozeugmata, both present in two species of *Epitonium*. Healy (1994) and Robertson (2007b) also described the incidence of spermatozeugmata in families Epitoniidae, Janthinidae, Cerithiopsidae and Triphoridae, but Healy (1994) pointed out that those of Cerithiopsidae and Triphoridae are strongly distinct from those of Epitoniidae and Janthinidae. Once again, spermatozeugmata have not been reported in *Recluzia* species, but presumably they are present, as males of *Recluzia* species also lack a penis. This again reflects the need for further research on this rare genus. Identical spermatozeugmata provide another character common to benthic and neustonic Epitoniidae.

Egg capsules and brooding. *Recluzia* species and most species of *Janthina* secrete egg capsules attached to the underside of their bubble float by hardened mucus that forms a short stalk at the narrow end of the capsule. The

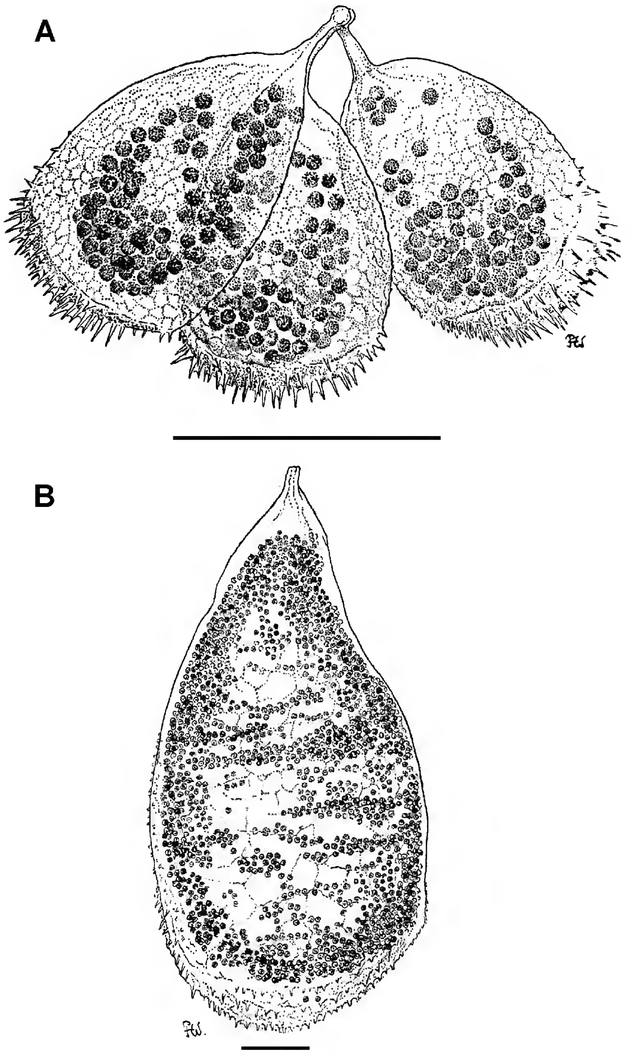

Figure 9. *Janthina* egg capsules. *(A) Janthina umbilicata* d'Orbigny (copy of Laursen, 1953: fig. 27). *(B) Janthina globosa* (Swainson) (copy of Laursen, 1953: fig. 31, reduced). Scale bars 1 mm.

egg capsules of *Janthina* species are ovate-triangular and translucent, with fine spines around the exterior of the wider, convex, distal end (Simroth, 1895: pl. 1, figs 24–26; Laursen, 1953: figs 23, 27, 31, 37; Okutani, 1956: text-fig. 2; Rolán & Trigo, 1973: figs 4–5; Fig. 9), so they resemble the egg capsules of neogastropods. The capsules of *Recluzia* species have not been described in detail previously. The capsules of both *R. lutea* and *R. johnii* are shown by the illustrations by Bennett (1966: pl. 11, fig. 1), Churchill *et al.* (2011b: figs 1B–C) and here (Figs 6–7) to be significantly simpler than those of *Janthina*, without spines, slightly brownish dull yellow in colour, more opaque and a little longer and narrower than those of *Janthina*, and cylindrical with a hemispherical distal end.

The exception is *Janthina janthina*, which broods its eggs to the veliger stage in the oviduct, releasing veligers into the sea. The description by Wilson & Wilson (1956: 302; see paragraph below) of the release of veligers by *J. janthina* expressly mentioned the release of packets, which almost immediately opened to release individual veligers. Cross-sections of oviducts of *J. janthina* shown by Laursen (1953: figs 5–7) closely resemble those of *J. exigua* (Laursen, 1953: fig. 3). This implies that at least some remnant of capsule formation is retained in *J. janthina*; eggs evidently are enclosed in capsules before release in all species, and ephemeral transparent capsules enclosing the veligers are retained in *J. janthina*. The egg capsules of most *Janthina* species and, in *J. janthina*, packets of veligers are released on the left (inhalant) side of the mantle cavity, as the right side is blocked by the right epipodium (Wilson & Wilson, 1956; Fretter & Graham, 1962: 563; Bayer, 1963: 460) and simply by the shell. The egg capsules of neustonic Epitoniidae contrast strongly with the long chains of many small, roughly spherical to tetrahedral, sand-agglutinated egg capsules joined by chalazae that are produced by benthic Epitoniidae (e.g., Bennett, 1966: pl. 9, fig. 2; pl. 10, figs 1–2; pl. 11, fig. 1; Robertson, 1983, 1994; Pastorino & Penchaszadeh, 1999; Gittenberger & Gittenberger, 2005). McDermott (1981) described the elongate, cylindrical but still linked, rough-surfaced capsules of *Epitonium rupicola* (Kurtz, 1860). The capsules of *Janthina* and *Recluzia* are not linked by chalazae, an obvious adaptation to life attached to a bubble float, as long chains of egg capsules would be impractical for neustonic gastropods. The chalazae of benthic Epitoniidae are tough, elastic mucus threads secreted by the pedal mucus gland, rather than being secreted by any structure in the oviduct (Bennett, 1966; Robertson, 1983: 6; Gittenberger & Gittenberger, 2005: figs 264–299). Therefore, there is no difference in origin or composition between the bubble float of *Janthina* and *Recluzia* and the chalazae of benthic Epitoniidae; their pedal mucus glands merely are adapted to secrete differently shaped products. Formation of a bubble float is an unexpected adaptation for an epitoniid, but it does not provide a radical character that precludes the classification of *Janthina* and *Recluzia* in Epitoniidae. Indeed, Churchill *et al.* (2011a: 802) viewed the bubble float of *Janthina* and *Recluzia* as a modified epitoniid egg mass, providing a helpful perspective on the evolution of the floating habit.

Wilson & Wilson (1956: 302) described the shedding of larvae by *Janthina janthina*. They reported that "In the later part of the day after [the *Janthina* specimens were collected], one animal shed singly at intervals at least thirty-six dark brown cylindric pellets, [each] about 1/10 in. [2.5 mm] long … They fell to the bottom of the container … and quickly disintegrated, releasing a number of fully developed veliger larvae with brownish purple shells, swimming with a bilobed velum. Twenty or more were in each packet, varying from 100 to 230 µm across the shell at its maximum width. … As a prelude to the shedding of a packet the propodium was withdrawn from its normal resting position appressed to the base of the float, and was furled up and twisted from side to side. … Extrusion was so rapid that it could be missed … from between the bottom of the foot and the gills a "little bullet" suddenly shot upwards and out over the (morphologically) left-hand side of the shell, that which is not covered by the epipodium … Several packets were seen shortly after emergence and there was no doubt that they came out from this side. … [T]he next day, when it was less active … a small number of veligers emerged singly at their own pace". The larvae were neither geotaxic nor phototaxic, but gyrated actively over the bottom of the container. Bayer (1963: 460) similarly described the ejection of a pellet about 3 x 4 mm, which fell to the bottom of the dish, and after about five minutes disintegrated to form a small heap of larvae that dispersed rapidly.

The normal gastropod action of passing egg capsules out through the oviduct and mantle cavity (although on the opposite side from usual), observed by Wilson & Wilson (1956) and Bayer (1963: 460), demonstrates that Laursen's (1953: 11) description of capsules passing through a supposed duct through the centre of the foot muscle was incorrect. The pedal mucus funnel (Fretter & Graham, 1962: 115) is an adaptation to neustonic life that produces mucus for the formation of float bubbles, for attaching the float to the mesopodium, and for attaching egg capsules to the float. The lack of epipodia presumably allows *Recluzia* species to attach their egg capsules to the float in the normal gastropod manner through the right side of the mantle cavity. Robertson (1983) and Collin (1997: 429, footnote) also pointed out that benthic Epitoniidae share hydrophobic larval shells with heterobranchs, and Robertson (2007a) noted that they are shared with *Janthina*.

Lack of operculum and obvious eyes. *Janthina* and *Recluzia* species lack an operculum in the adult, whereas it is present in all benthic Epitoniidae. This is another adaptation to a neustonic life attached to a bubble float, because the head and foot must remain permanently outside the shell to retain the float, and an operculum is redundant. An operculum is present in the veliger of *Janthina* (Fraenkel, 1927: fig. 7; Risbec, 1953: fig. 1.15; Fretter & Graham, 1962: 563; Fig. 10) and presumably in *Recluzia*, although *Recluzia* veligers have never been studied. Adult *Janthina* and *Recluzia* specimens also lack obvious pigmented eyes, although as the veliger larva of *Janthina* has eyes as well as a pigmented mantle organ ("Farbdrüse"; Simroth, 1895; Fraenkel, 1927: fig. 7), the lack of obvious eyes in the adult is presumably another adaptation to neustonic life; prey is literally "bumped into" while floating passively. Also, several observers have commented on the sensibility of the *Janthina* animal to movement of the observer, so it evidently has organs for detecting light and motion, e.g., "the expanded animal when in a glass jar could perceive our near approach and would contract into the shell" (Wilson & Wilson, 1956: 301). Bayer (1963: 460) also noted that "Although lacking eyes, [*Janthina*] *janthina* must be extremely sensitive to small variations in illumination. When resting quietly with head extended, they invariably withdrew into their shells upon the approach of any object from above, and it was not necessary for a shadow to fall across the animals. The reaction took place readily in low, indirect illumination but was more pronounced in brighter light". So it is not surprising that Thiele (1928: 75) described small rudimentary eyes in *Janthina*. Fretter & Graham (1962: 562) also described two "minute eyes … each with a lens, lying ventral to the cerebral ganglia under the muscles of the body wall posterior to the base of [each] tentacle". However, these minute eyes have not been observed (or, probably, looked for) in *Recluzia* species.

Radula and subdivided buccal mass. Many authors have described the radula of *Janthina* and noted that it is indistinguishable from that of benthic Epitoniidae (e.g., Lovén, 1847: 190, pl. 3; Troschel, 1875; Thiele, 1928; Laursen, 1953: figs 16–18, 24, 33, 39; Fretter & Graham, 1962, 1982; Bayer, 1963: fig. 4; Graham, 1965; Palazzi, 1979; Pinn, 1980; Robertson, 1983, 2007a; Roberts, 1992; Nützel, 1998). Rolán & Trigo (2003: figs 11–14) illustrated the radula of *J. pallida* particularly clearly, showed its subdivision into two "arms", which are extremely narrow and quite long in this species, and described each arm as a "hemiradula". Some species can be distinguished by minor tooth shape differences (Laursen, 1953: figs 16, 24, 28, 33, 39; Roberts, 1992). Pruvot-Fol (1952) suggested that the *Janthina* radula is [i.e., presumably all ptenoglossan radulae are] not comparable with the radulae of other gastropods, but consist of modified jaw plates. However, this has not been accepted, partly because distinct jaw plates resembling those of other caenogastropods are also present in all ptenoglossans (e.g., Graham, 1965; Rolán & Trigo, 2003: figs. 7–10). Based on the specimens that had been studied by Bayer (1963), Graham (1965: 324) described the feeding of *Janthina janthina*: "… the snout is extended and the buccal cavity then turned inside out through the mouth to form a pre-oral proboscis-like structure carrying the radula at its tip, and with the point of entry to the oesophagus from the buccal cavity exposed on its surface as an apparent mouth. During this eversion the odontophore spreads laterally so as to stretch the subradular membrane and erect all the radular teeth; on withdrawal it collapses and the teeth fold down on to the surface of the subradular membrane: it is this which is the main feeding process of the mollusc and it forms a mechanism for grasping the whole or rasping a part of the body of the prey". Graham (1965) went on to describe the action of this mechanism and its anatomy in detail; he noted that the odontophore consists of "two palmate pads united only at their posterior base" (Graham, 1965: 324). Robertson (1983: 9) commented that Graham (1965) described the anatomy of the buccal mass of *Janthina* "in exquisite detail", and "much of what Graham (1965) wrote about *Janthina* is applicable to *Epitonium*". Graham's (1965, fig. 5) brilliant illustrations of the everted odontophore and radula of the *Janthina* are repeated here (Fig. 11). A similarly detailed illustration of the anterior alimentary tract and subdivided buccal mass of *Epitonium clathrus* (Linnaeus, 1758) was provided by Fretter & Graham (1962: 163, fig. 101), but it appears quite different because the buccal mass is retracted, rather than everted as in Graham's (1965) illustrations. The two halves of the odontophore and radula are spread apart to form a retractile grasping organ in the same way in both *Janthina* and benthic Epitoniidae; all ptenoglossan odontophores and radulae are essentially identical and function in the same way (Graham, 1965: 338). The protruding, deeply subdivided odontophore is a characteristic feature that can be seen clearly in many published drawings of living *Janthina* animals, as early as

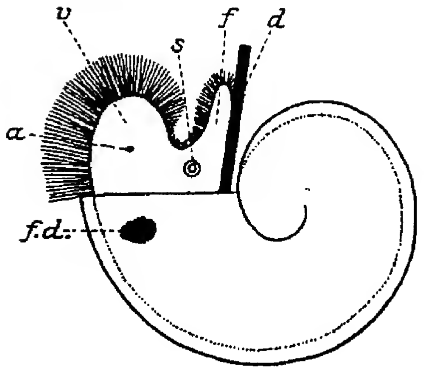

Figure 10. Living early veliger larva of a *Janthina* species; copy of Fraenkel (1927: fig. 7; described as semi-schematic). Abbreviations: *a,* eye; *d*, operculum; *f*, foot; *f.d.*, pigmented mantle organ; *s*, statocyst; *v*, velum. Magnification unknown.

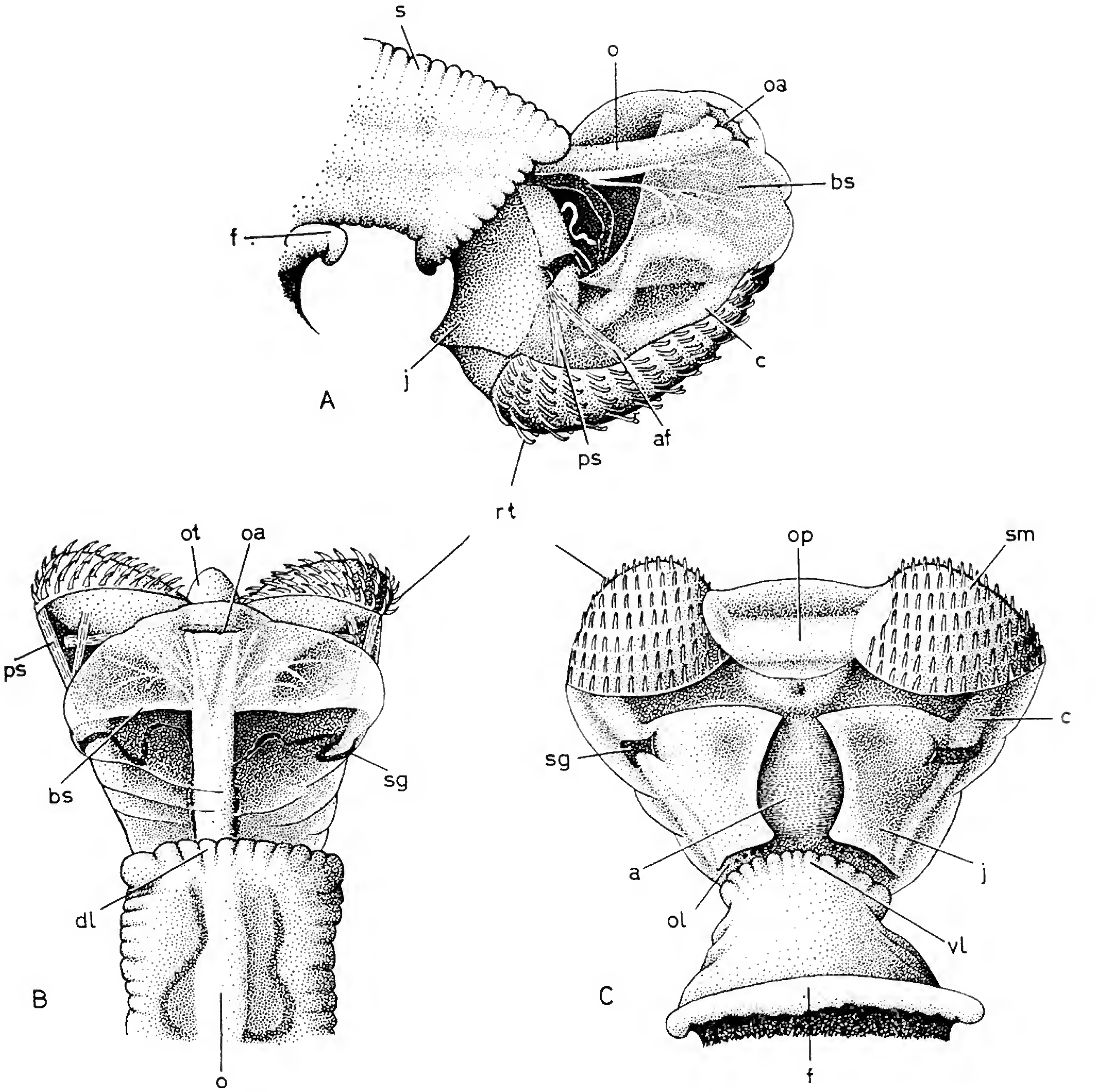

Figure 11. *Janthina janthina* (Linnaeus), everted radula and odontophore in feeding position; enlarged copy of Graham (1965: fig. 5). *(A)* right lateral view; *(B)* dorsal view; *(C)* ventral view. Abbreviations: *a*, anterior transverse muscle; *af*, accessory flexor muscle of the cartilage; *bs*, buccal septum; *c*, cartilage; *dl*, dorsal lip; *f*, anterior edge of foot; *j*, jaw; *o*, oesophagus; *oa*, opening of oesophagus on dorsal surface of extrovert; *ol*, opening of labial gland; *op*, outer posterior transverse muscle; *ot*, tip of odontophore; *ps*, protractor muscle of subradular membrane; *rt*, radular tooth; *s*, snout; *sg*, salivary gland; *sm*, subradular membrane; *vl*, ventral lip. Scale bar 10 mm.

Colonna (1616; reprinted by Dollfus & Dautzenberg, 1932: pl. 13, lower fig.). The radulae of *Recluzia* species have not been described in detail, and are not visible protruding through the mouth in living specimens in the same way as *Janthina* radulae do, but presumably are identical to those of *Janthina* and benthic Epitoniidae. Feeding and prey are discussed further below.

Epipodia. Photographs of the external anatomy of a living *Janthina janthina* animal in its normal life position, inverted beneath the float, were published in black-and-white by Wilson & Wilson (1956: pl. 1, fig. 1–2; Fig. 1) and again in colour by Yonge & Thompson (1976: pl. 5, lower). A drawing based on the first of these photographs was also published by Pinn (1980: fig. 5). Drawings showing similar details were published also by Okutani (1956: text-figs 1–10). These photographs, Okutani's (1956) drawings, and further side views of the head of *J. janthina* published here (Figs 4D–E) clearly show the protruding snout (short and contractile, but not an eversible proboscis) and forked cephalic tentacles, the propodium, the mesopodium to which the float is attached, and the colourless, translucent epipodium of the right side. Another epipodium on the left is not visible in this view, although its posterior edge is shown in Fig. 1A and a contracted left epipodium of *J. janthina* is visible in Fig. 5A. The drawings by Okutani (1956: text-figs 9–10) are the only ones the writer is aware of that reveal a pair of almost identical epipodia, right and left, linked across the centre so they comprise one deeply embayed structure, with finely digitate margins. The right epipodium (Fig. 1A, centre) is subcircular with finely digitate edges when fully expanded, and when resting on the shell extends down to cover the top of the last shell whorl and part of the surface of the penultimate whorl below the aperture. Its relationship to the rest of the foot is shown well in Figs 4D–E. Another good photograph by Wells & Bryce (1986: 61) shows the epipodium less clearly. Another was used as the cover illustration for *Journal of Molluscan Studies* vol. 77, but shows the base of the shell rather than a spire view, so epipodia are not visible. Another view published by Batson (2003: 107) shows a specimen of *J. janthina* with its propodium extended, evidently in the process of adding a bubble to its float, but the epipodia are out of focus. Anderson (2007: 48) also published a good photograph of a living specimen of *J. janthina*, showing the float excellently, including its degenerating outer end and *Lepas* barnacles attached to the shell, but again epipodia are not visible. Anderson (2007: 48) described the float as “quite firm, reminding me of … plastic bubble wrap”. Another excellent photograph of *J. janthina* by Dimitris Poursanidis included in a “creatura-blog” by Crew (2014) clearly shows the expanded snout with slightly protruding odontophore, the black-speckled, subdivided cephalic tentacles, the separate propodium between the float and the tentacles, and a contracted left epipodium (Fig. 5A). The function of the epipodia seems not to have been determined, although Thiele (1892: 580, pl. 23, fig. 2) described and compared *Janthina* epipodia. Wilson & Wilson (1956: 301) suggested that the right epipodium helps control the passage of water through the mantle cavity. Wilson & Wilson (1956: 301) also noted that “when the animal is alive the shell is very slippery”, so one possible function of the epipodia is to secrete mucus over the external surface of the shell. This would help it to avoid both predators and epifauna. A problem with this interpretation, though, is that in photographs of living specimens (Figs 5D–E) the epipodia scarcely touch the shell. Certainly, the epipodia are held virtually motionless. No observers during the last century have confirmed the suggestions of early writers that the epipodia aid movement of the animal with swimming motions, in the same manner as pteropod “wings”. Mörch (1860: 263) discussed the various opinions published up until that time on the function of the epipodia (he did not provide references to most of these opinions, but most are fairly obvious among the references in the present report). He stated that Blainville and Rang considered them to be “appareil natatoire”, i.e., swimming apparatus, and Quoy & Gaimard (1832: 244) stated that they helped a little with locomotion carried out largely by the foot. Johnston also regarded the epipodia as governing the animal’s movements, but d’Orbigny (1841) rejected these assertions. Grant also stated (correctly, as is now known) that the epipodia do not move at all, although slight motion to rest against the shell or lie free above it must be possible if the epipodia secrete mucus over the shell exterior.

No epipodia are visible in any illustrations of living specimens of *Recluzia* species, in the excellent photograph published by Bennett (1966: pl. 11, fig. 1), in those by Churchill *et al.* (2011a: fig. 1B; 2011b: figs 1B, G), or in Figs 6–7. Epipodia apparently are not present in *Recluzia* species. If their functions in *Janthina* include the secretion of mucus over the shell surface, the persistent pale brown conchiolin periostracum of *Recluzia* possibly serves the same protective function. A periostracum is not obvious in any *Janthina* specimens the writer has observed and it is apparently very ephemeral in *Janthina* species.

Ianthinin purple dye. Robertson (2007a: 9) stated that the purple dye of *Janthina* is very different from the “Tyrian purple” of muricoidean neogastropods, as muricoidean purple dye is secreted by a different gland, has a different composition, is in solution, and is an anaesthetic used to help capture prey. In contrast, *Janthina* purple dye is finely particulate, and Robertson thought it was used in defence. However, Ganapati & Subba Rao (1959) described a specimen of *Porpita* collected with a specimen of *Janthina* (*J. pallida*?) attached to its underside. Secretion of purple dye by the *Janthina* specimen caused the *Porpita* animal to remain motionless and distended while *Janthina* preyed upon it. This seems to indicate that the dye has an anaesthetic effect in *Janthina*, besides its camouflaging and antagonistic effects. Wilson & Wilson (1953: 301–302) also reported observations made by P. M. David on RV *Discovery II* on *Janthina* specimens collected at sea: “Several … *Velella* were taken with small *Ianthina* attached to the under surface … apparently browsing on the *Velella*; the latter seemed to be lifeless … It was observed that the *Ianthina* exuded their purple dye periodically (fairly frequently) while feeding, and it seems possible the dye may be used to anaesthetize the *Velella*”. Similar accounts of feeding apparently involving anaesthesia were provided by Hardy (1956) and Rolán & Trigo (2003). *Janthina pallida*, in particular, has been reported by several authors to relinquish its float and creep on specimens of *Velella* or *Porpita* while browsing on the chondrophore, forming another float when only the *Velella* skeleton remains (Ganapati & Subba Rao, 1959; Bayer, 1963: 458) [Bayer (1963: 458) pointed out that the account by Ganapati & Subba Rao (1959) actually described a capsule-laying species, not *J. janthina* as they thought]. Bennett (1966: 47, pl. 10, fig. 3) noted of specimens observed in the North Pacific: “by the time the ship reached 127°31'W, it was found that almost all [*Velella*] animals caught had from one to five small *Janthina pallida* Thompson, feeding on the undersuface among the tentacles”. Most specimens of *J. pallida* collected near the Kuroshio Current by the *Vityaz* also were attached to *Velella* floats, on which they had been feeding (Savilov, 1969). Most notably, Palazzi (1979) recorded 280 specimens of *J. pallida*, ranging from small juveniles to 21 mm high, collected on the beaches of Terrasini, Sicily, on 7–8 Mar 1979, of which 253 (90.4%) were still attached to and feeding on specimens of *Velella* when collected. Giannuzzi-Savelli *et al.* (1999: 56, 57, fig. 101) also published photographs of specimens of *J. pallida* feeding on the underside of specimens of *Velella*, again aided by the anaesthetic effects of ianthinin purple dye.

Allan (1934) gave a popular account of “Tyrian purple” and its sources, recording several muricids, “sea hares” (*Tethys*), *Janthina* and benthic Epitoniidae as secreting purple dye, without distinguishing the types of dye they produce. Moseley (1877a: 13–14, pl. 2, figs 15a–c) named janthinid dye "ianthinin", and published three analytical spectra. Comfort (1961: 313) stated that "several older authors assume that [the dye of *Janthina*] is identical with *Murex* purple (6-6'-di-bromoindogotin), to which it bears no resemblance, either in spectral absorption or solubilities". Comfort (1961) stated that ianthinin is distinct from all other described molluscan pigments, and is also distinct from the blue colouring chemical of its prey, *Velella*. Therefore, if the violet colouring of *Janthina* is extracted from *Velella* and *Porpita*, as in the nudibranch *Fiona* (Willan, 1979), it evidently is modified by *Janthina* after ingestion; it seems more likely that the purple dye is independent of that of its prey. The yellow-brown shell and yellow animal of *Recluzia* species and the lack of reports of a purple dye in this genus indicate that *Recluzia* does not secrete ianthinin. However, the secretion of purple dye is well-known in some benthic Epitoniidae (Allan, 1934: 151; Robertson, 1983: 10; 2007a: 9). This is presumably another character of phylogenetic significance, requiring investigation in *Recluzia* and its possible parent genus *Alexania*.

Feeding and prey. The discussion above of the use of ianthinin dye as an anaesthetic leads to more general consideration of the prey of *Janthina* and *Recluzia*. Photographs sent by Dimitris Poursanidis of specimens collected at Arina Beach, Heraklion, Crete, and kept together in a glass container show specimens of *J. janthina* feeding on the eggs of *J. pallida*. Risbec (1953: 201) reported small entire *Janthina* shells and numerous fragments in the alimentary tract of *Janthina* specimens he studied. He noted that he had verified the "cannibalism" of these species many times, but he had never found any cnidarians in the digestive tract of the specimens he collected in New Caledonia. Laursen (1953) reported copepods, the "water-strider" insect *Halobates*, barnacle plates (*Lepas*), and *Janthina* radulae and small shells in the gut of *Janthina*, so evidently *Janthina* eats anything it comes in contact with. However, all direct observations of feeding by *Janthina* species have reported *Velella* and/or *Porpita* as the main prey, and beach strandings of *Janthina* almost invariably are accompanied by abundant specimens of *Physalia*, *Velella* and/or *Porpita*, and in warmer waters by the other cosmopolitan members of the neustonic community. Presumably Risbec (1953) did not observe siphonophores because soft-bodied cnidarians disintegrate rapidly in the gut. Abbott (1968: 93, text-fig.; Abbott, 1974: 114), Cheng (1975: 195; Minyadidae) and Robertson (1997: 11, 2007a: 7) stated that *Recluzia lutea* preys on the floating sea anemone *Minyas* (i.e., *Actinecta*). Specimens of *Recluzia johnii* photographed in northern New South Wales by Denis Riek (Fig. 7A) also were observed feeding on large brown *Actinecta* anemones. Minyadidae comprises two genera and five species of anemones that float by means of a chitinous float secreted by their foot disc (Daly *et al*., 2007: 134). Cairns *et al*. (2009) recorded two species of oceanic Minyadidae from New Zealand waters (*Actinecta viridula* (Quoy & Gaimard, 1833); *Oceanactis rhodactylus* Moseley, 1877b). The more common "wandering anemone" *Phlyctenactis tuberculosa* (Quoy & Gaimard, 1833) (Powell, 1951: 7, fig. 13, as *P. retifera*) was also placed in Minyadidae by Fautin (2013), although *Recluzia* evidently does not feed on this coastal species, which occurs in New Zealand at least as far south as Cook Strait (Powell, 1951: 7; AGB pers. obs.). At least these two oceanic species presumably occur also in Australia, explaining the occurrence of their predator *Recluzia* in the Australasian region. A specimen of *R. lutea* photographed in northern New South Wales (Fig. 6C) is located against a specimen of *Physalia*. Churchill *et al*. (2011a: fig. 1B) illustrated the same living specimen of *R. lutea* said to be "feeding on the cnidarian *Physalia physalis*", but the photographer, Denis Riek (Brunswick Heads, NSW, pers. comm. 12 Nov 2015) stated that he did not observe the *Recluzia* specimen feeding on the *Physalia* specimen; they merely were located together in an aquarium. Previous authors have not reported *Recluzia* preying on siphonophores, but *Recluzia* is so rare that its habits have been reported by very few authors. It is possible that, like *Janthina* species, it feeds on any animals it comes in contact with, but all direct observations report it feeding only on Minyadidae.

Independent evolution of the neustonic habit in *Janthina* and *Recluzia*

In the writer's opinion, *Janthina* and *Recluzia* very likely adopted the pelagic habit, feeding on neustonic cnidarians, independently from distinct benthic epitoniid ancestors. *Recluzia* has no fossil record. It also has less extreme adaptations to a neustonic life than those of *Janthina*, with a taller spire, i.e., a more nearly "normal" narrow epitoniid teleoconch shape, and an almost smooth, yellow-brown rather than violet shell. It is assumed to be yellow-brown mainly because it is constructed of uncoloured calcite, but also possibly in part because it preys on the brown floating anemone *Actinecta* (Abbott, 1968: 93, text-fig.; Abbott, 1974: 114; Minyadidae, Cheng, 1975: 195; Robertson, 1997: 11, 2007a: 7) rather than the blue chondrophores *Velella* and *Porpita* and the blue siphonophore *Physalia* that form the predominant prey of *Janthina*.

The differences listed in Table 1 and ages derived from the fossil record (described below) indicate that *Janthina* evolved late in Miocene time, c. 7–5.5 Ma, from a short, wide, finely axially sculptured and rather coarsely spirally sculptured benthic epitoniid similar to *Alora* H. Adams, 1861 (type species *Trichotropis gouldii* A. Adams, 1857; Recent, eastern Pacific; Keen, 1971: 436, fig. 669; Gittenberger & Gittenberger, 2012: figs 1, 3–8). *Alora gouldii* reaches 38 mm in height (Weil *et al*., 1999: 144, fig. 439) and is similar to *Janthina* species in its short shape and coarse sculpture. The inner lip also curls over the narrow umbilical chink enough to close it, and closely resembles that of *Janthina* species. However, *Alora gouldii* is significantly taller and narrower than *Janthina* species. Other benthic Epitoniidae that resemble *Janthina* shells in shape include:

1 *Globiscala bonaespei* (Barnard, 1963: 104, fig. 17b) from bathyal depths off Cape Point, South Africa (Weil *et al*., 1999: 54, fig. 139). *Globiscala bonaespei* resembles *Janthina janthina* in shell shape because of its rather weakly inflated whorl sides and base and, consequently, angled periphery and weakly trochiform shape. Its sculpture is also a combination of fine axial lamellae and low, narrow, closely spaced spiral cords.

2 Other species of *Globiscala* de Boury (1909) (type species *Scalaria bullata* G. B. Sowerby II, 1844, Recent, Indo-West Pacific; Weil *et al.*, 1999: 54, fig. 140).
3 *Sagamiscala* Masahito, Kuroda & Habe in Kuroda *et al.* (1971: 258) (type species *Sagamiscala globosa* Masahito, Kuroda & Habe, 1971, Recent, Japan; Weil *et al.*, 1999: 124, fig. 394).
4 *Librariscala* Kilburn (1985: 302) (type species *Scalaria millecostata* Pease (1861), Recent, Indo-West Pacific).

The sculpture of *Alora* is most similar to that of early *Janthina* species, with fine axial ridges and more prominent spiral cords. Keen (1971: 436) recorded the presence of a "dull buff" periostracum (an intritacalx?) in the type species of *Alora*, *A. gouldii*, and Weil *et al.* (1999: 144) described it as "The shell is white underneath a thin buffy periostracum". The protoconch of illustrated *Alora* species (Bouchet & Warén, 1986: figs 1227–1228) is of lecithotrophic epitoniine type, relatively short and inflated, with very fine, closely spaced spiral and axial sculpture, and does not resemble that of *Janthina* species in detail. If *Janthina* evolved from *Alora*, it did so before *Alora* lost planktotrophy. DeVries (2007) described a middle Miocene species of *Alora* from Peru, confirming that *Alora* pre-dated the evolution of *Janthina*. However, *Alora teresmonile* DeVries, 2007 has a taller spire and much finer and closer spiral sculpture than any *Janthina* species. Some North Pacific species previously referred to *Alora* were revised by Nakayama & Hasegawa (2016); some were transferred to *Epidendrium* (Epitoniidae) and one to the genus *Tuba* (Mathildidae, Heterobranchia). *Alora tenerrima* (Dautzenberg & Fischer, 1896) (Bouchet & Warén, 1986: 542, fig. 1251) is perhaps the benthic epitoniine most closely resembling *Janthina typica*. It is relatively short and has few (c. 10), widely spaced spiral cords and uniform, fine axial ridgelets similar to those of *Janthina* species over the entire teleoconch surface. Viewing the bubble float of *Janthina* and *Recluzia* species as a modified epitoniid egg mass (Churchill *et al*., 2011a) shows how the change from a benthic to a neustonic mode of life might have occurred rapidly through a relatively minor mutation.

In contrast, the complete lack of any fossil record implies very recent adoption of the neustonic habit by *Recluzia* species, presumably by very similar modifications of the pedal mucus gland and egg mass. The bright yellow animal tissue suggests that *Recluzia* possibly evolved from a benthic epitoniid similar to *Surrepifungium* Gittenberger & Gittenberger, 2005 or *Epidendrium* Gittenberger & Gittenberger, 2005, which have similar bright yellow tissues. However, shell character similarity makes it seem more likely that *Recluzia* evolved from a smooth brown epitoniid similar to *Alexania* Strand, 1928. Comparison of molecular sequences should resolve these possibilities. Robertson (1997) illustrated a specimen of *Alexania floridana* (Pilsbry, 1945) found in Texas, and commented that *Alexania* is "conchologically … the epitoniid equivalent of the janthinid genus *Recluzia* …" (Robertson, 1997: 11). The name *Alexania* has had a complex nomenclatural history. Its synonyms include *Alexandria* Tomlin, 1926, type species *Alexandria natalensis* Tomlin, 1926, Recent, South Africa; junior homonym of *Alexandria* Pfeffer (1881: 63; Echinoidea); *Problitora* Iredale (1931: 216), type species *Amauropsis moerchi* A. Adams & Angas, 1864, eastern Australia; *Tomlinula* Strand (1932), unnecessary new name for *Alexandria*; *Habea* Kuroda, 1943, type species *Habea inazawai* Kuroda, 1943; and *Stenacme* Pilsbry, 1945, type species *Stenacme floridana* Pilsbry, 1945 (Robertson & Oyama, 1958; Robertson & Habe, 1965). Robertson (1997) suggested that there is only one widespread species of *Alexania*, *A. natalensis* (= *Amauropsis moerchi*, *Habea inazawai* and *Stenacme floridana*) although a spirally colour-banded second species, *A. callizona* (Habe, 1961) (Okutani, 2000: pl. 170, fig. 118) is recognized in Japan. Hayase *et al.* (2015: 111, pl. 5, figs 1a–d) illustrated specimens of *A. inazawai* (i.e., *A. natalensis*) collected alive feeding on anemones under boulders at Maeshima Island, Mikawa Bay, Aichi Prefecture, Japan. Abbott (1974: 124) noted that *Alexania* preys on the benthic anemone *Aiptasiomorpha luciae* (Verrill, 1898) (*Diadumene luciae*; Habe, 1943; Okutani, 2000: 343), introduced from Southeast Asia and occurring widely in eastern USA. *Alexania* reaches a smaller adult size (shell rarely more than 10 mm high) and has a slightly shorter and wider teleoconch shape than adult *Recluzia lutea*, and has a shallower suture and an adult operculum (Habe, 1943; Pilsbry, 1945). Its dark brown colour indicates that the shell likely is calcitic. Habe (1943) described and illustrated the creeping animal with operculum, radula, veliger larva, undivided cephalic tentacles, and egg capsules of *Habea inazawai* (i.e., *A. natalensis*). The numerous small egg capsules are bound together by elastic threads (Habe, 1943: 65). An unusual feature is the thin, smooth mantle lobes riding up over both sides of the shell as far as the spire apex (Habe, 1943: fig. 2; Okutani, 2000: pl. 170, bottom right fig.; Riek, 2017, living animal of "*Alexania moerchi*" illustrated), explaining the smooth teleoconch exterior. These mantle lobes resemble the epipodia of *Janthina* species closely, but presumably superficially. Robertson (1997: 11) noted that "*Alexania* and *Recluzia* are brown transitional shell forms. The anatomy, like the ptenoglossate radula, is also similar …". Takano & Kano (2014: figs 1–2; Fig. 3B) also found *Alexania inazawai* to be the most nearly related to *Janthina* of the four species of benthic Epitoniidae they included in their molecular analysis. Both *Alexania* and *Janthina* were included in the same clade as *Epitonium*, and *Opalia* and *Opaliopsis* species belong in a second clade of Epitonioidea (Nystiellinae?; *Opaliopsis* Thiele, 1928 is now accepted as an earlier synonym of *Nystiella* Clench & Turner, 1952; Kilburn, 1985: 259; Brown & Neville, 2015: 13; but *Opalia* H. Adams & A. Adams, 1853 has always been classified in Epitoniinae and species of *Opalia* certainly have the type of protoconch usually regarded as diagnostically epitoniine). More taxa evidently need to be included in molecular comparisons to resolve these relationships. It is feasible that *Recluzia* evolved recently from the benthic epitoniid *Alexania*, adapting to preying on floating anemones rather than benthic ones. Churchill *et al.* (2011a) interpreted the distinctions between *Recluzia* and *Janthina* (Table 1) as indicating that *Recluzia* evolved earlier and was ancestral to *Janthina*, and consequently *Recluzia* is not as fully adapted to neustonic life as *Janthina* is. However, the fossil record indicates that the opposite interpretation is much more likely; *Recluzia* and *Janthina* adopted a neustonic life independently, evolving from distinct ancestors. *Janthina* adopted neustonic life late in Miocene time. In contrast, *Recluzia* adopted neustonic life very recently, apparently late in Holocene time, and so

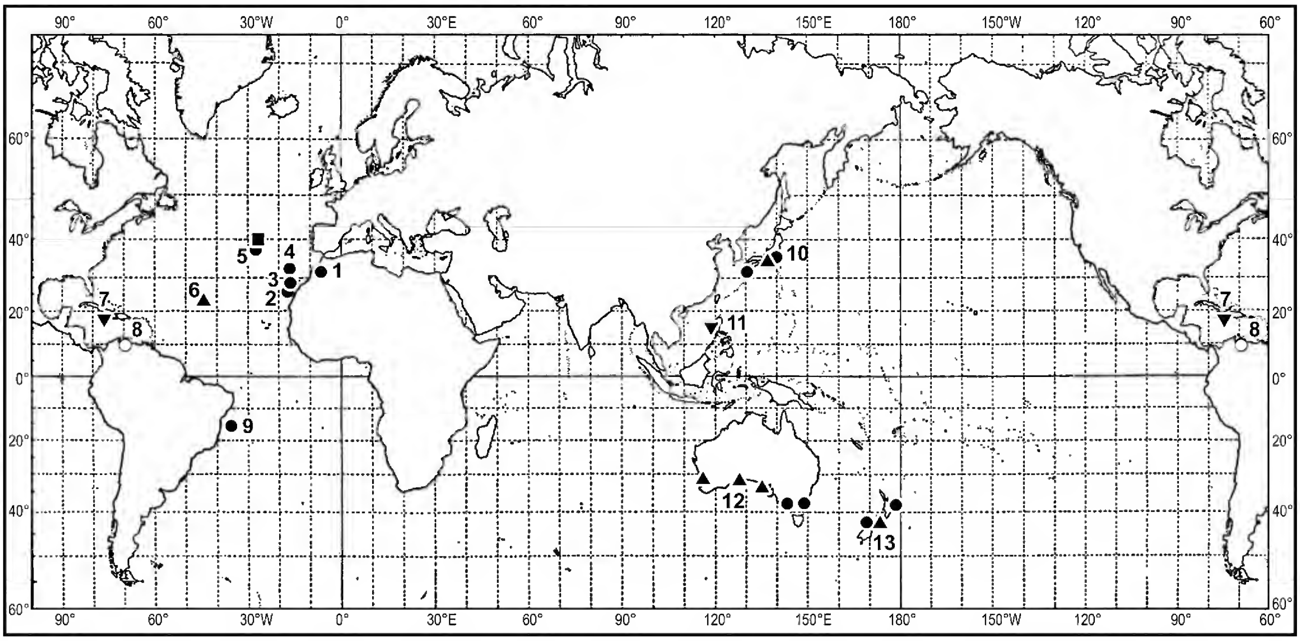

Figure 12. World late Miocene–early Pleistocene fossil localities for *Janthina* species, and purported fossil record of *Recluzia*. Symbols: ▲, *Janthina chavani*; ▼, *Janthina globosa*; ■, *Janthina krejcii*; ●, *Janthina typica*; ○, incorrect fossil record of *Recluzia*. Localities: *(1)* Fouarat, near Casablanca, Morocco (*J. typica*; type locality of *Acrybia chouberti* Chavan); *(2)* La Esfinge, Gran Canaria, Canary Islands *(J. typica)*; *(3)* Selvagem Grande I. *(J. typica* or possibly *J. chavani)*; *(4)* São Vicente, Madeira *(J. typica* or possibly *J. chavani)*; *(5)* Santa Maria I., Azores (type locality of both *J. typica* and *J. krejcii* sp. nov.); *(6)* Kane Megamullion, mid-Atlantic Ridge (*J. chavani*; type locality of *Kaneconcha knorri* Kaim, Tucholke & Warén); *(7)* Bowden, Jamaica *(J. globosa)*; *(8)* Casa Cantaure, Paraguana Peninsula, Venezuela (incorrect early Miocene record of *Recluzia*); *(9)* dredge station off Itaúnas, Espiritu Santo, Brazil (*J. typica*; type locality of *Eunaticina abyssalis* Simone); *(10)* SE Japan *(J. typica* and *J. chavani)*; *(11)* Anda, Cabarruyan I., Luzon, Philippines *(J. globosa)*; *(12)* southern Australia *(J. typica* and *J. chavani)*; *(13)* northern and southwestern New Zealand *(J. typica* and *J. chavani)*. More detailed localities in the Atlantic islands, New Zealand, southern Australia and Japan are shown on succeeding maps.

has not evolved as many adaptations to neustonic life as *Janthina* has. With the passage of time, predation pressure could have enhanced the protective violet coloration of the shell of *Janthina*, again implying that, lacking protective coloration, *Recluzia* likely is the more recent adopter of the neustonic habit.

The neustonic habit and the necessary modification of the pedal mucus gland to allow it to form a bubble float rather than chalazae, along with other adaptations to neustonic life such as the lack of an operculum and the laying of modified egg capsules on the underside of the float, provide the only distinctive characters of *Janthina* and *Recluzia*. These characters seem to be of ecological significance rather than phylogenetically informative, as was also concluded by Lalli & Gilmer (1989: 22–23). There seems to be no reason to regard *Janthina* and *Recluzia* species as anything other than neustonic Epitoniidae and, as noted above, this has been demonstrated from molecular sequences by Churchill *et al.* (2011a) and Takano & Kano (2014). It is concluded that *Janthina* and *Recluzia* are epitoniids that independently have adopted neustonic life, feeding on distinct prey, *Janthina* on mixed prey but mainly on *Physalia*, *Velella* and *Porpita*, and *Recluzia* species mainly (entirely?) on minyadid anemones. This is separate from the question of whether Nystiellinae Clench & Turner (1952: 336) should be recognized at family-group level (Nystiellidae: Nützel, 1998: 90, 128), a question to be resolved by molecular comparisons. *Janthina* and *Recluzia* share the weakly sculptured protoconch of planktotrophic taxa assigned to Epitoniinae rather than the prominently axially ribbed protoconch of planktotrophic taxa assigned to Nystiellinae.

The fossil record

To establish accurate time ranges in order to date the evolutionary history of neustonic Epitoniidae, it is important to establish the localities and their ages where fossils of *Janthina* have been recorded. The writer is not aware of fossils of *Recluzia*; the one putative but incorrect record is shown in Figure 12, which shows the areas of the world where *Janthina* fossils have been recorded. Localities in the Atlantic islands, New Zealand, southern Australia and Japan are shown in more detail on succeeding maps.

The succession on Santa Maria Island. The small Santa Maria Island (17 km E–W, 6 km N–S; Fig. 13) is the oldest and south-easternmost of a complex chain of volcanic islands forming the Azores, in the eastern North Atlantic. It is important for the present report because the island is the type locality of the stratigraphically earliest and earliest-described fossil *Janthina* species, *J. typica* (Bronn, 1861). The stratigraphy of Santa Maria Island was mapped and described by several earlier authors, notably Hartung (1861), Zbyszewski *et al.* (1961), Zbyszewski & da Veiga Ferreira (1962a) and Serralheiro & Madeira (1993). Helpful descriptions were also provided by Krejci-Graf *et al.* (1958) and Krejci-Graf (1961). Santa Maria is unique among Azores islands in having Pliocene (Zanclean) and, it was thought until recently, small areas of latest Miocene (Messinian and even possibly Tortonian) limestone and fossiliferous tuffaceous lenses interbedded between the lava flows. All other Azores islands are younger, and have no marine fossils. The localities on Santa Maria Island where limestone and other sedimentary lenses crop out were mapped in detail

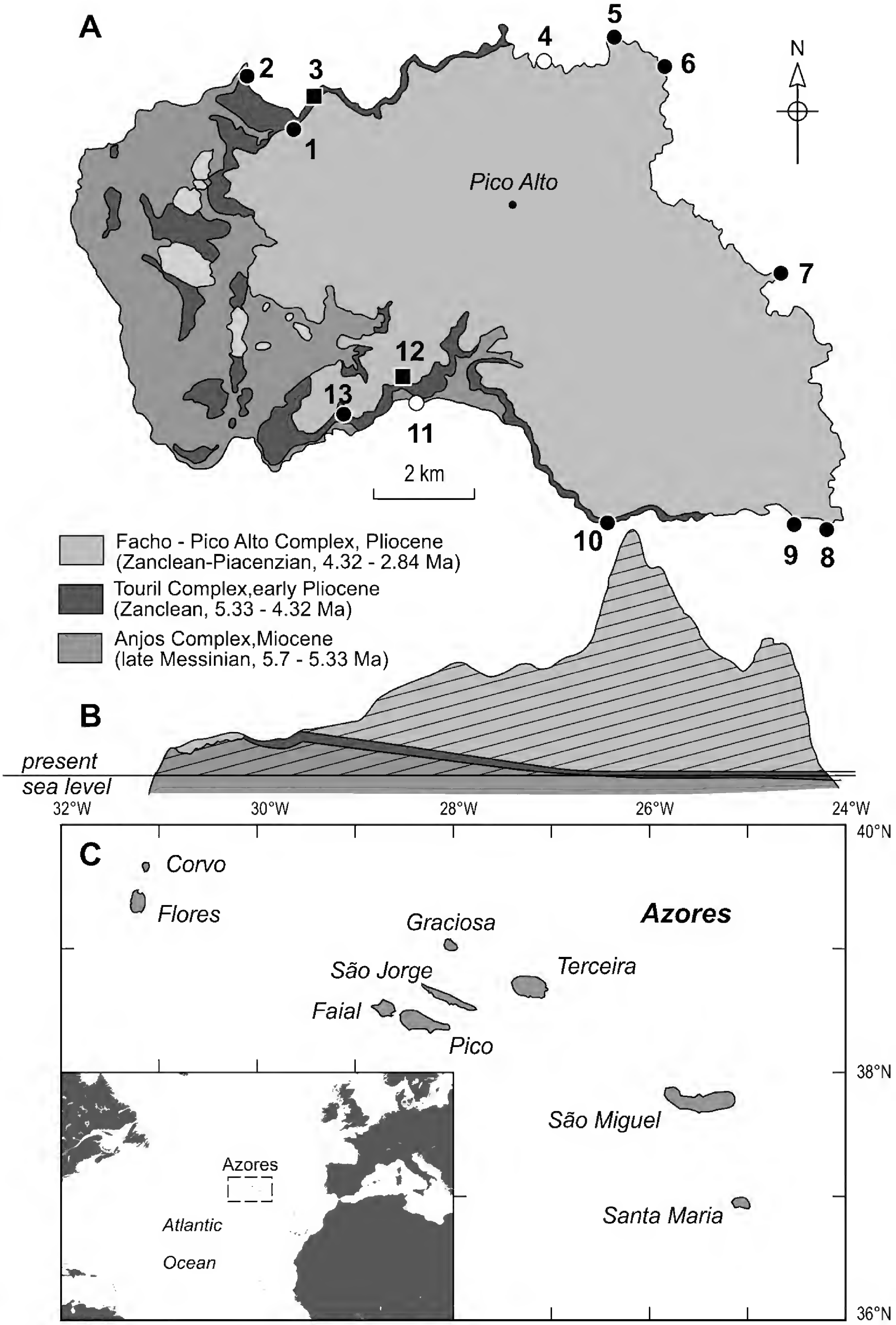

Figure 13. Fossil localities on Santa Maria Island, Azores, based on da Veiga Ferreira (1961: fig. 1), Madeira *et al.* (2011: text-fig. 1) and Sibrant *et al.* (2015: fig. 2). Several other Pleistocene (MIS 5e) localities mapped along south coast by Ávila *et al.* (2015a: fig. 1) are not shown. *(A)* geological map and legend, with fossil localities; *(B)* semi-diagrammatic east-west cross-section, showing dips on lava flows schematically; vertical exaggeration × 20; modified slightly from Sibrant *et al.* (2015: fig. 6B) to allow Touril Complex to crop out at sea level around east coast. *(C)* location of Santa Maria Island in the Azores (Madeira *et al.*, 2011: text-fig. 1). ■, Pliocene localities with *Janthina krejcii* sp. nov.; ●, Pliocene localities, some of which have yielded *Janthina typica*; ○, Pleistocene (MIS 5e) localities (most not shown). Localities: *(1)* Cré (no *Janthina* records); *(2)* Ponta dos Frades (no *Janthina* records); *(3)* Pinheiros (probably *J. krejcii*, identification uncertain); *(4)* Lagoinhas (MIS 5e); *(5)* Ponta do Norte (locality of *Janthina typica* neotype); *(6)* Ponta dos Matos *(J. typica)*; *(7)* Ponta das Salinas *(J. typica)*; *(8)* Ponta do Castelo *(J. typica*; includes also late Pleistocene, MIS 5e); *(9)* Pedra-que-pica (no *Janthina* records; includes also late Pleistocene, MIS 5e); *(10)* Ponta do Malbusca (no *Janthina* records; includes also late Pleistocene, MIS 5e); *(11)* Prainha (MIS 5e); *(12)* Miradouro de Macela (type locality of *Janthina krejcii* sp. nov.); *(13)* Figueiral *(J. typica)*.

Table 2. Fossil localities on Santa Maria Island, Azores, with latitude and longitude, and historical changes of name; from Madeira *et al*. (2011: table 1) and Ávila *et al*. (2015a: table 1); Ponta dos Matos and Miradouro de Macela not included. Most localities mapped on Fig. 13A.

outcrop name	age	location	earlier names
Cré	Zanclean	37°0'03.76"N 25°08'10.78"W	Bocca do Cré, Forno do Cré, Furna da Cré, Casa da Cré, Escarpa da Cré, Pedreira dos Frades
Pedra-que-Pica	Zanclean + 5e	36°55'48.6"N 25°01'31.5"W	—
Ponta do Malbusca	Zanclean	36°55'46.10"N 25°04'08.14"W	Forno da Cré, Furna da Cré, Boca da Cré, Ponta da Piedade
Ponta do Castelo	Zanclean + 5e	36°55'43.7"N 25°00'59.3"W	Ponta da Maia
Ponta dos Frades	Zanclean	37°0'41.67"N 25°08'44.68"W	—
Ponta das Salinas	Zanclean	36°58'22.97"N 25°01'43.38"W	Feiteirinhas, Feteirinha
Ponta do Norte	Zanclean	37°0'57.76"N 25°03'50.80"W	—
Pinheiros	Zanclean	37°0'21.45"N 25°07'48.87"W	Pinheiras
Figueiral	Zanclean	36°56'53.82"N 25°07'40.31"W	—
Prainha	MIS 5e	36°57'06.8"N 25°06'47.1"W	Praia Formosa
Lagoinhas	MIS 5e	37°0'47.05"N 25°04'58.23"W	—
Vinha Velha	MIS 5e	36°55'53.0"N 25°01'53.2"W	—
Ichnofossils cave	Zanclean + 5e	36°56'02.2"N 25°04'26.8"W	—

by da Veiga Ferreira (1961) in a paper concerned mainly with limestone resources. A helpful list of the main fossil localities, their locations including latitude and longitude, and their historical changes of name was provided by Madeira *et al.* (2011: table 1) (Table 2). The record of name changes is helpful because some names (e.g., Forno da Cré) have been used for different localities on opposite coasts of the island, and some names used commonly in early accounts do not appear on modern maps (e.g., Feiteirinhas; now known as Ponta das Salinas). This follows the standard European practice of assigning a unique semi-formal name to each fossil locality, rather than recording fossils from a site identified by a map grid reference or GPS position, as is normal in, for example, Australia and New Zealand. Ávila *et al.* (2015a: fig. 1, table 1) identified a total of 20 named fossil localities on Santa Maria Island, several of them for the first time. Several sedimentary lenses in the Touril Complex contain a diverse shallow-water molluscan fauna. Earlier authors up to da Veiga Ferreira (1952, 1955) and Zbyszewski & da Veiga Ferreira (1962a, b) relied on pectinid biostratigraphical correlation with mainland Europe to date the succession as "Vindobonian", or in modern terms Langhian, Serravallian and Tortonian Stages (middle and late Miocene) (M. Harzhauser, Naturhistorisches Museum Wien, pers. comm. 24 Sep 2014). Krejci-Graf *et al.* (1958) used foraminiferans and Janssen *et al.* (2008) used pteropods to date the Touril Complex as early Pliocene (Zanclean). Younger Pliocene lava peaks rise above the Touril Complex in the eastern half of the island, to Pico Alto (590 m). Fossiliferous Last Interglacial (MIS 5e, c. 120–130 ka) beach deposits crop out behind the beach at Prainha, west of Praia on the south coast, at Lagoinhas on the north coast (Garcia-Talavera, 1990; Ávila *et al.*, 2002, 2009, 2015a, 2015c), and at several newly identified localities along the south coast (Ávila *et al.*, 2015a: fig. 1, table 1; Ponta do Castelo, Pedra-que-pica, Vinha Velha, Pedrinha da Cré, Ichnofossils cave, Praia do Calhau), indicating that no uplift has occurred during the last 120 ka. Previous studies of the ages of lavas (Abdel-Monem *et al.*, 1975), geomagnetic polarity stratigraphy (Feraud *et al.*, 1984) and strontium isotope dates (Kirby *et al.*, 2007) indicated a Tortonian–Messinian (late Miocene) age for the lowest, oldest lavas (Anjos Complex) and for the lowest part of the Touril Complex, which consists of fossiliferous marine limestone, conglomerate, calcarenite and claystone interbedded with lava flows and pyroclastic material. The upper part of this succession is Zanclean (early Pliocene). The Touril Complex at Ponta do Costelo was described as deposited as storm-generated deposits (tempestites) by Meireles *et al.* (2013). The Pliocene marine fossils have been studied over many years (Bronn, 1861, 1862; Mayer, 1864a, b; Berkeley Cotter, 1892, 1953; da Veiga Ferreira, 1952, 1955; Zbyszewski & da Veiga Ferreira, 1962b; Kirby *et al.*, 2007; Madeira *et al.*, 2007, 2011; Ávila *et al.*, 2015a, b, d).

Janthina typica previously has been thought to occur in Messinian and Zanclean rocks on Santa Maria Island, and the writer assumed that *J. krejcii* sp. nov. occurs higher in Zanclean rocks. *Janthina krejcii* sp. nov. is described below from the Miradouro de Macela, on the road descending from Almagreira to Praia. It likely occurs also at Pinheiros, a short distance northeast of Cré, as Mayer (1864: 63) recorded a specimen of "*Janthina hartungi*" without spiral folds from Pinheiros. Therefore, it is possible that *J. krejcii* occurs more widely on Santa Maria Island than the writer is aware of. Unfortunately, *J. krejcii* has not been recorded from anywhere other than Santa Maria Island, suggesting that either *Janthina* fossils have not been collected from this precise age of rocks elsewhere, or it was a restricted Atlantic species.

Understanding of the ages and stratigraphical relationships of Santa Maria Island has been revolutionized recently by Sibrant *et al.* (2015). They carried out high-precision Potassium-Argon dating of volcanic rocks and studied the stratigraphical relationships of volcanic complexes. They recognized an initial shield volcano, now dated at 5.7–5.33 Ma (latest Messinian), comprising the Anjos Complex, without fossiliferous marine interbeds, and making up the western third of the island. This is overlain at a low angle, with the contact dipping eastwards, by the Touril Complex,

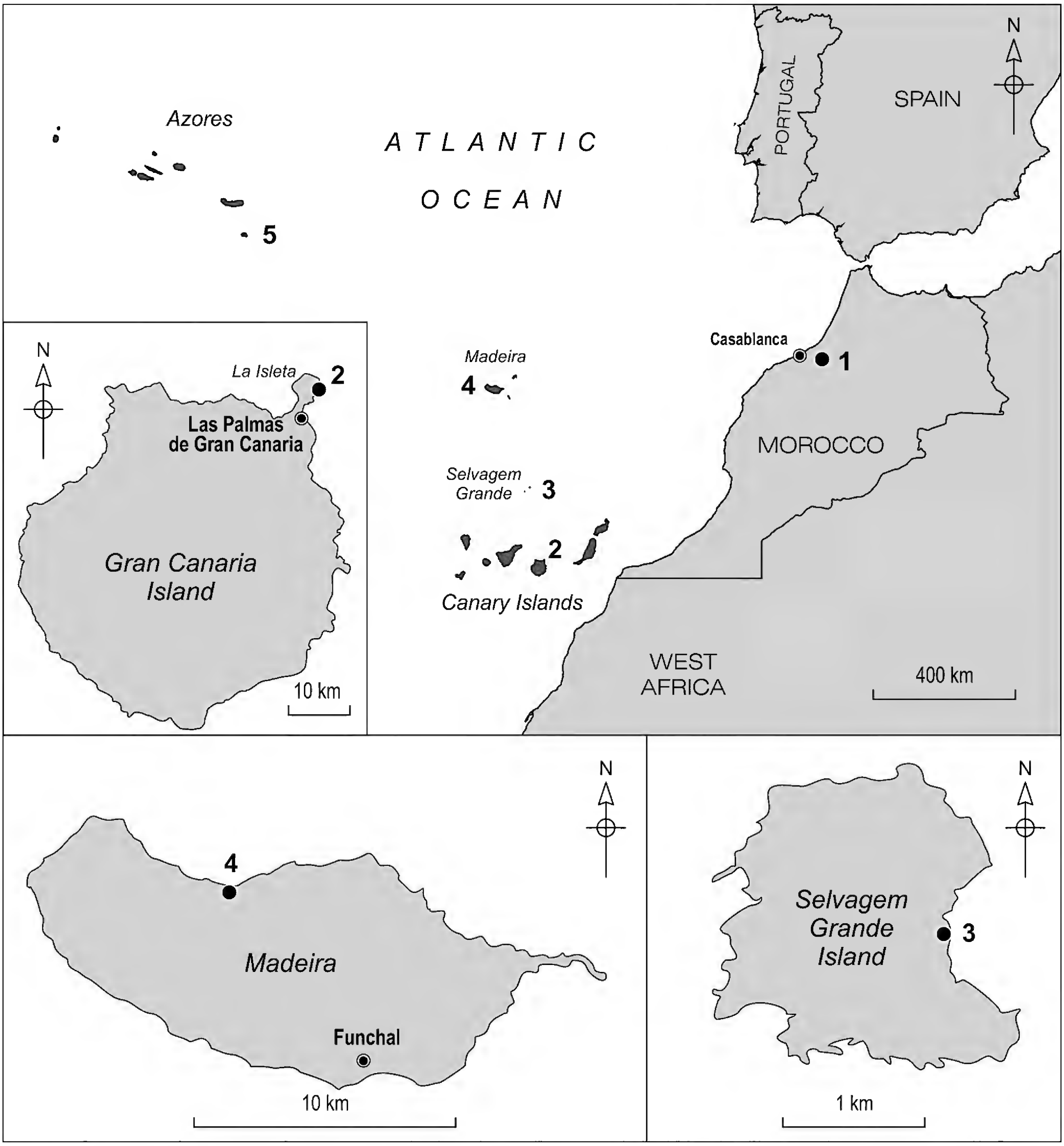

Figure 14. *Janthina* fossil localities in the eastern Atlantic, showing location of Morocco, Madeira, the Canary Islands, Selvagem Grande Island, and the Azores Islands. ● *Janthina typica* (possibly including other *Janthina* species at Madeira and Selvagem Grande I.). Localities: *(1)* Fouarat, Morocco *(J. typica*, type locality of *Acrybia chouberti)*; *(2)* La Esfinge, on La Isleta, Gran Canaria, Canary Islands *(J. typica)*; *(3)* Selvagem Grande I. *(J. typica* or possibly *J. chavani)*; *(4)* São Vicente, Madeira *(J. typica* or possibly *J. chavani)*; *(5)* Santa Maria I., Azores (type locality of both *Hartungia typica* and *Janthina krejcii* sp. nov.).

an intermediate volcano-sedimentary succession formed during 5.33–4.32 Ma (early Zanclean). The Touril Complex includes all the marine sedimentary rocks on the island other than late Pleistocene deposits. The Touril Complex is overlain in turn by a younger shield volcano, the Facho-Pico Alto Complex, formed during 4.32–3.94 Ma (late Zanclean), again without marine interbeds. Younger "parasitic" cones ceased erupting at only 2.84 Ma in the area of the Facho-Pico Alto Complex. This new dating indicates that all records of marine fossils from Santa Maria Island are early Zanclean in age (5.33–4.32 Ma), including the type localities of both *Janthina typica* and *J. krejcii* sp. nov. Figure 13 shows the new interpretation of Santa Maria Island stratigraphy by Sibrant *et al.* (2015). All Pliocene fossil localities (including those that have not yielded fossil *Janthina* specimens) and a few of the main late Pleistocene fossil localities are superimposed, but several of the newly recorded Pleistocene localities along the south coast are not shown.

Other Atlantic islands: Madeira, Selvagem Grande, Gran Canaria. *Janthina typica* has been recorded from three other eastern Atlantic islands (Fig. 14): at São Vicente on the main island of Madeira, at La Esfinge on Gran Canaria, Canary Islands, and at Selvagem Grande, a small island between the Canary Islands and Madeira (Krejci-Graf *et al*., 1958: 336; Meco *et al*., 2015, 2016). Mayer (1864a, b: 63) rather casually recorded *Janthina hartungi* from São Vicente, on the north coast of Madeira. Mayer's (1864a, b: 63) text about *J. hartungi* concluded with the statement that of the six specimens he had available, three typical ones originated from Feiteirinhas (i.e., Ponta das Salinas), one from Ponta dos Matos, another without spiral folds ("Reifen") from Pinheiros (all localities on Santa Maria Island) and another showing only traces of spiral folds from São Vicente, Madeira. He also noted that traces of purple coloration were visible on the specimen from São Vicente. The writer is not aware of any other mention of fossil *Janthina* specimens from Madeira. The description of weak spiral folds suggests the possibility that the specimen from Madeira is *J. chavani*, or even possibly *J. krejcii* sp. nov. Unfortunately, like all other early fossils, the location of any of the specimens recorded by Mayer is unknown, other than the poor modelling clay impression reported below from Ponta dos Matos, Santa Maria Island, which is possibly the basis of Mayer's record from that locality.

Miocene fossils were first reported from the very small Selvagem Grande Island (2 x 1.7 km) by Böhm (1898). He reported three species of neritid gastropods and a euloxid bivalve, apparently representing a well-preserved aragonitic fauna. He did not record *Janthina*. Joksimowitsch (1911: fig. 6) provided a map of Selvagem Grande showing a single small locality for Miocene marine fossils near the centre of the bay on the east coast. Gagel (1911: fig. 1) provided a very similar map, showing "Lager der miocänen Fossilien" in the same locality. Gagel (1911: pl. 11) also showed a profile of Selvagem Grande viewed from the east, with geological formations indicated. His unit H, "Lager der miocänen Fossilien (+ 98 m)", overlies the main volcanic rocks and underlies thin units of (in ascending order) "Kalksand mit Foraminiferen", "Aschentuffe", further tuffs, and further thin basalt flows. Again, macrofossils are shown as exposed in only a small area at the top of basalt cliffs near the centre of the profile. Joksimowitsch (1911: fig. 7) showed an almost identically labelled profile of Selvagem Grande, identifying unit H as "Fossilienfundort". The map and profile were provided to both Joksimowitsch and Gagel by Dr A. C. de Noronha, a medical doctor in Funchal. Gagel (1911: 409) provided a brief list of fossils from this locality present in the museum in Funchal (with spelling corrected here): *Littorina neritoides*, *Gibbula schmitzi*, *Janthina hartungi*, *Pleuroploca* (*Fasciolaria*) sp.?, *Purpura sismondae*, *Nerita martiniana*, *N. selvagensis*, *N. connectens*, *Cerithium rugosum* and *Tectarius* cf. *nodulosus*. Several of these species had been named only slightly earlier by Joksimowitsch (1911). Apart from this, Gagel (1911) described only volcanic rocks.

The description of the Selvagem Islands by Joksimowitsch (1911: 52–95, pls 1–3) was much more concerned with fossils than with igneous rocks, assigning the fossils to *die zweite Mediterranstufe* (the second Mediterranean Stage), equivalent to the current Langhian and early Serravallian Stages, middle Miocene; M. Harzhauser, Naturhistorisches Museum Wien, pers. comm. 24 Sep 2014). Harzhauser *et al*. (2003: 325–326) described the long succession of miscorrelations that led to the wide usage of the stage names *I und II Mediterranstufe* in Europe. Joksimowitsch (1911) provided excellent illustrations of large *Spondylus* specimens, suggesting that most of his fossils from Selvagem Grande were calcitic, unlike the aragonitic ones reported by Böhm (1898). Joksimowitsch (1911: 74, 94) recorded "*Janthina hartungi* Mayer" from Selvagem Grande, mentioning that Mayer (1864) had recorded this species also from Santa Maria and from São Vicente, Madeira. Modern age assignments have not been provided for the localities at São Vicente and Selvagem Grande, to the writer's knowledge. Judging from the succession on Santa Maria Island, both localities likely are Zanclean in age. It would be very helpful for *Janthina* phylogeny to examine specimens of *Janthina* from São Vicente and Selvagem Grande, to identify them and determine their ages.

Recently, Meco *et al*. (2015: 61, figs Appendix 4A–B; 2016) recorded and illustrated a bedding plane exposing abundant specimens of *Janthina typica* at La Esfinge, just north of Las Palmas de Gran Canaria, on the east coast of La Isleta, at the north-eastern tip of Gran Canaria, Canary Islands. The enlarged view of specimens in outcrop (Meco *et al*., 2015: fig. Appendix 4A) shows a relatively low spire and spiral folds present on the sutural ramp. Specimens from this locality have also been loaned to the writer by Joaquín Meco (ULPGC), confirming their identification as *J. typica* (Figs 25N, Q–R, T). Nearby ^{40}Ar/^{39}Ar dates on an underlying lava flow provide a maximum age for the *Janthina* specimens of 4.20±0.18 Ma, late in Zanclean time (Meco *et al*., 2015).

The succession in New Zealand. The interpretation here differs a little from those published earlier by Beu & Maxwell (1990: 292, pl. 37a–b), Beu & Darragh (2001: 25, 27) and Beu & Raine (2009: BM292). The New Zealand Plio-Pleistocene time scale was summarized by Beu *et al*. in Cooper (2004: 197–228), and is shown here in Figs. 16, 17 and 22. The most recently updated international time scale (Gradstein *et al*., 2012) did not change ages in the Neogene part of the column, and the latest re-calibration (Raine *et al*., 2015) merely lowered the base of the Waipipian Stage to 3.7 rather than 3.6 Ma, with no other changes. In New Zealand (Figs 15–16), *Janthina typica* (=*Turbo postulatus* Bartrum, 1919) was first reported from Kaawa Creek, a richly diverse shallow-water locality of Opoitian (Zanclean) age on the west coast of the North Island south of Waikato Heads, southwest Auckland. Most of the fauna at this locality was described by Laws (1936a, b, 1940a). Finlay (1931) pointed out that "*Turbo*" *postulatus* and the "Australian" species *Heligmope dennanti* Tate, 1893 constitute one species of *Janthina*. *Janthina typica* is moderately common and unusually well-preserved at Kaawa Creek. The Kaawa Formation is well dated by Mollusca, Foraminifera and other fossils (Beu & Maxwell, 1990: 271), but is an isolated occurrence of marine rocks that does not provide an age context for dating the evolution of *Janthina*. This is also true of many other isolated occurrences in New Zealand, as in most other regions.

Although it is uncommon in most areas of New Zealand other than at Kaawa Creek, *Janthina typica* occurs rarely in Kapitean (Messinian) rocks near East Cape and at a few other Kapitean localities in the Gisborne district (Figs 15A). It also occurs very widely, scattered in Opoitian (Zanclean)

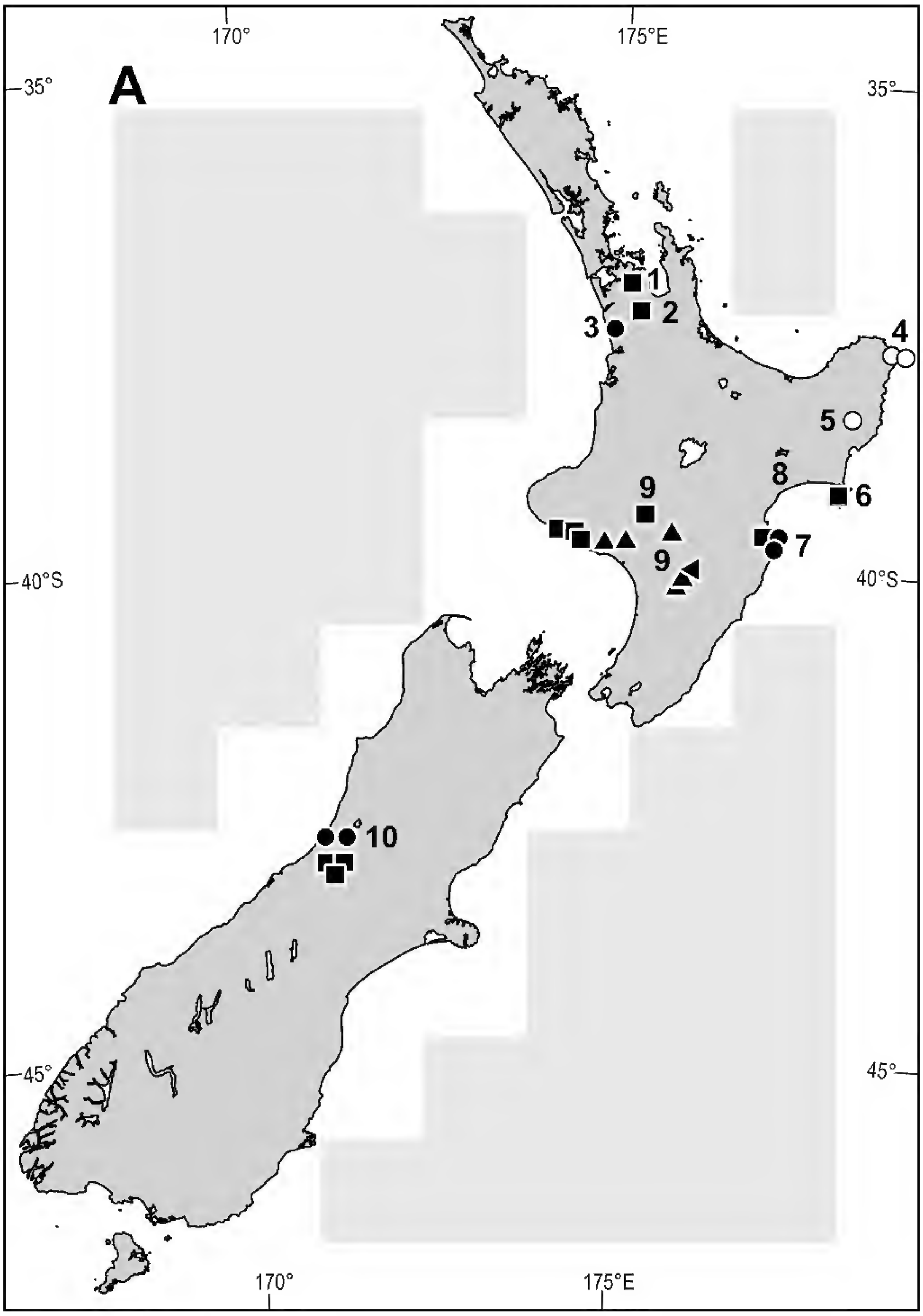

Figure 15. *Janthina* fossil localities in New Zealand. Symbols: ▲, *Janthina chavani*, Gelasian–early Calabrian (Nukumaruan New Zealand Stage, 1.63–2.4 Ma); ◀, *Janthina chavani*, late Piacenzian–early Gelasian (Mangapanian New Zealand Stage, 2.4–3.0 Ma); ■, *Janthina typica*, early Piacenzian (Waipipian New Zealand Stage, 3.0–3.7 Ma); ●, *Janthina typica*, Zanclean (Opoitian New Zealand Stage, 3.7–5.3 Ma); ○, *Janthina typica*, Messinian (Kapitean New Zealand Stage, 5.3–7.2 Ma). — *(A)* Main islands of New Zealand, showing general locations of areas in Figs 15B–D. Localities: *(1)* Otahuhu well, Auckland *(J. typica)*; *(2)* Pukekohe *(J. typica)*; *(3)* Kaawa Creek, SW Auckland *(J. typica*, type locality of *Turbo postulatus)*; *(4)* East Cape *(J. typica)*; *(5)* Waimata Road, inland from Tolaga Bay *(J. typica)*; *(6)* Mahia Peninsula *(J. typica)*; *(7)* Cape Kidnappers *(J. typica)*; *(8)* Gisborne–northern Hawke's Bay (detailed localities shown in *B*); *(9)* South Taranaki coast–Whanganui Basin (see detail in *C*); *(10)* Westland (see detail in *D*); ... [caption continued on next pages, pp. 148–149].

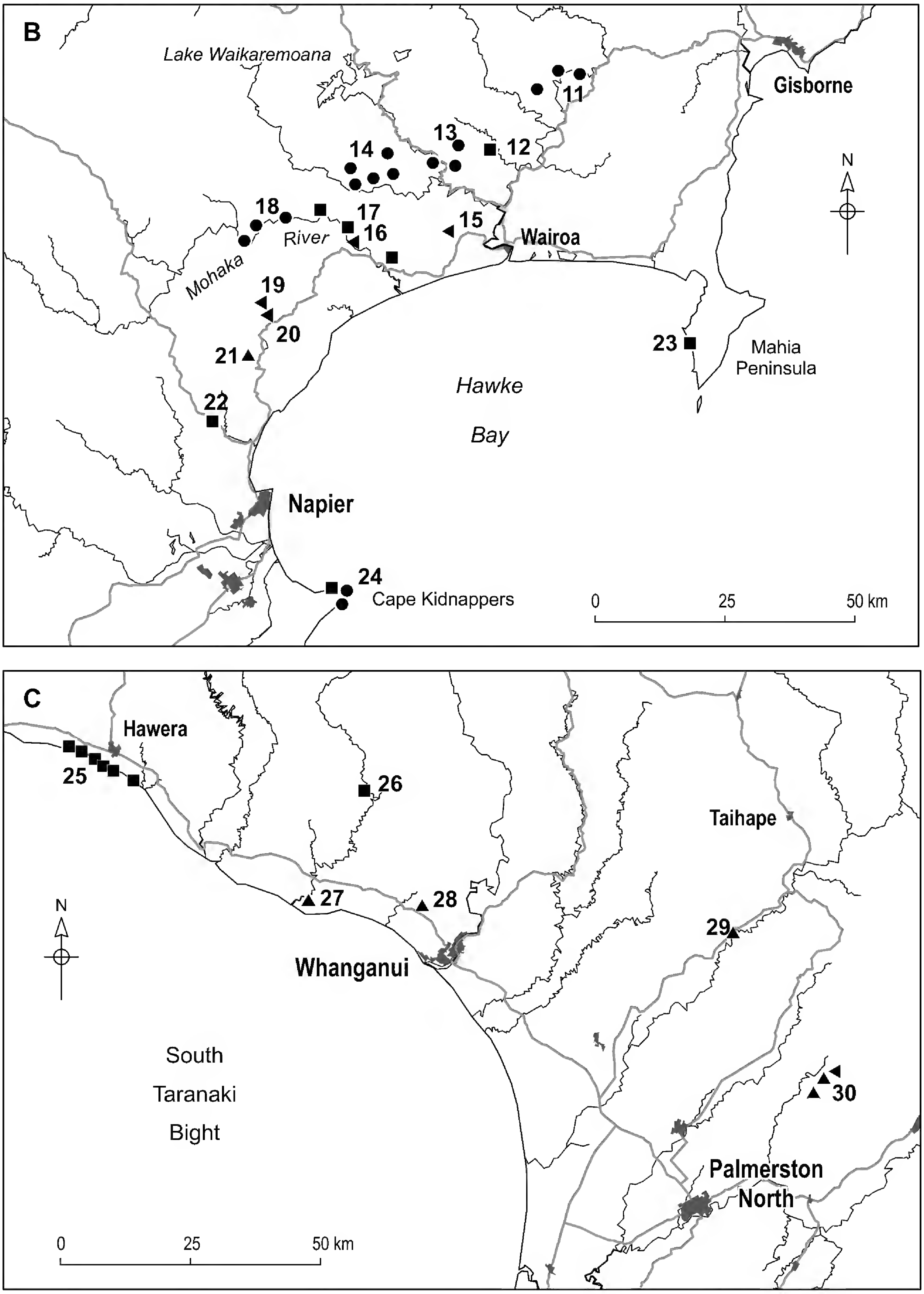

Figure 15 (continued) ... *(B)* Localities in northern and central Hawke's Bay, New Zealand; only the more significant ones identified individually: *(11)* Hangaroa area, Tiniroto–Gisborne highway *(J. typica)*; *(12)* Te Reinga Falls, Wairoa River *(J. typica)*; *(13)* upper Wairoa Syncline *(J. typica)*; *(14)* Waiau River–Cricklewood Road area, Wairoa Syncline *(J. typica)*; *(15)* lower Cricklewood Road *(J. chavani)*; *(16)* Mangapanian sandstone, Mohaka River *(J. chavani)*; *(17)* Waipipian mudstone underlying sandstone, Mohaka River *(J. typica)*; *(18)* Waipipian and Opoitian localities on upper Mohaka River *(J. typica)*; *(19)* Matahorua Road, Tutira *(J. chavani)*; *(20)* Pohokura Road, Tutira *(J. chavani)*; *(21)* Darkies Spur Road, west of Devil's Elbow, which is on Highway 2 north of Napier (youngest record of *J. chavani* in Hawke's Bay); *(22)* Esk Valley *(J. typica)*; *(23)* Kopuni Stream, Mahia Peninsula *(J. typica)*; *(24)* Cape Kidnappers *(J. typica)*. — *(C)* Localities in Whanganui Basin and South Taranaki, New Zealand: *(25)* Manaia Beach–Hawera coast, ... [caption continued on next page]

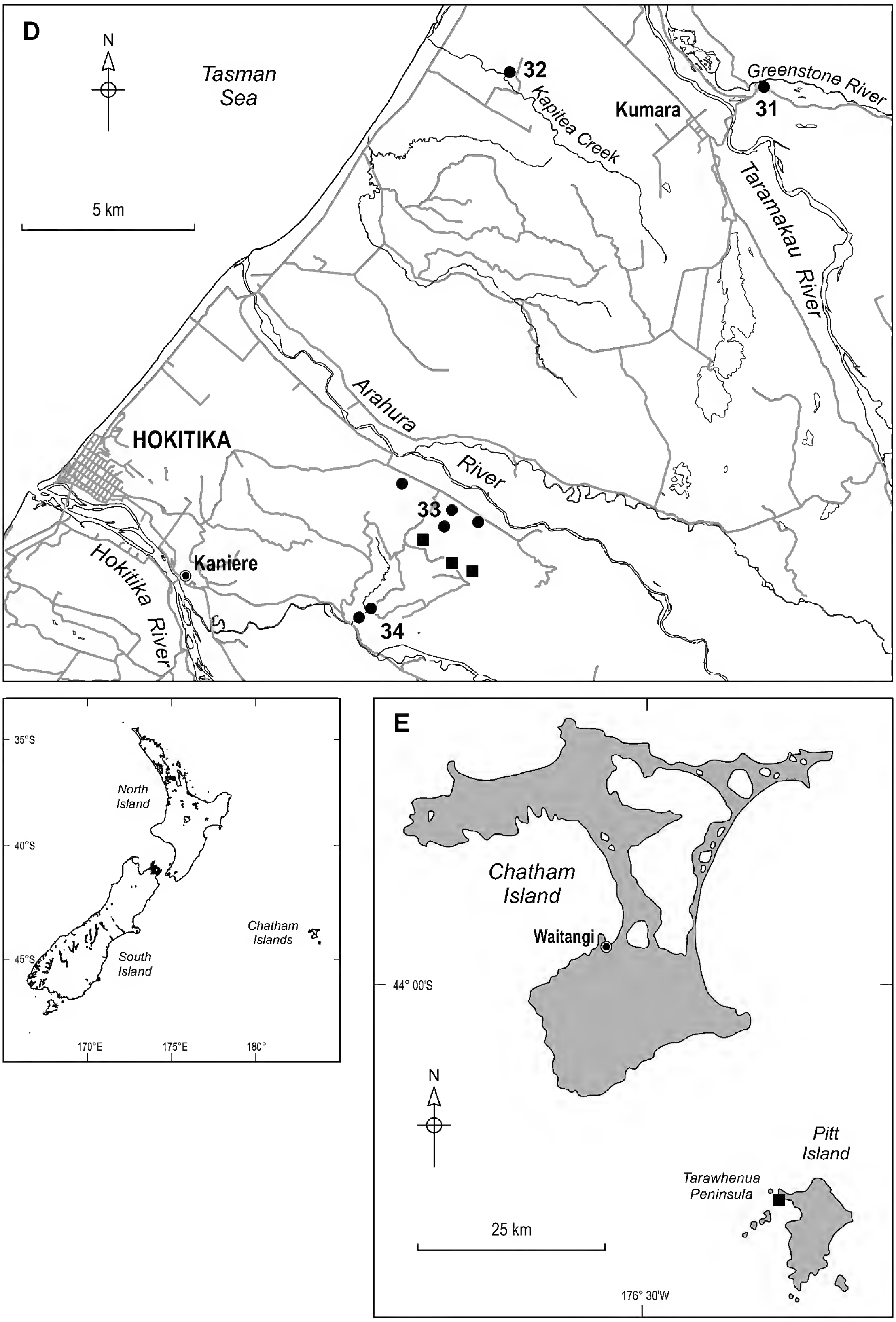

Figure 15 (continued) ... South Taranaki *(J. typica)*; *(26)* Ngamatapouri, Waitotara Valley *(J. typica)*; *(27)* Nukumaru Limestone, Waitotara, W of Whanganui *(J. chavani)*; *(28)* youngest New Zealand locality, Tewkesbury Fm, shellbed with Vinegar Hill Tephra (MIS 61, 1.75 Ma), Brunswick Road, W of Whanganui *(J. chavani)*; *(29)* Highway 1 uphill from Makohine Stream, Ohingaiti, Rangitikei Valley *(J. chavani)*; *(30)* Te Ekaou Stream area, Pohangina Valley *(J. chavani)*. — *(D)* Localities in Westland, New Zealand (several roads shown are logging tracks): *(31)* Greenstone–Kumara Road *(J. typica)*; *(32)* Kapitea Creek *(J. typica)*; *(33)* Greek's Creek and nearby streams, S side of Arahura Valley *(J. typica)*; *(34)* McKay's Creek, Kaniere *(J. typica)*. — *(E)* Chatham Islands, New Zealand, showing the one *Janthina* fossil locality on Tarawhenua Peninsula, Pitt Island *(J. typica)*. Small map shows relationship of Chatham Islands to New Zealand.

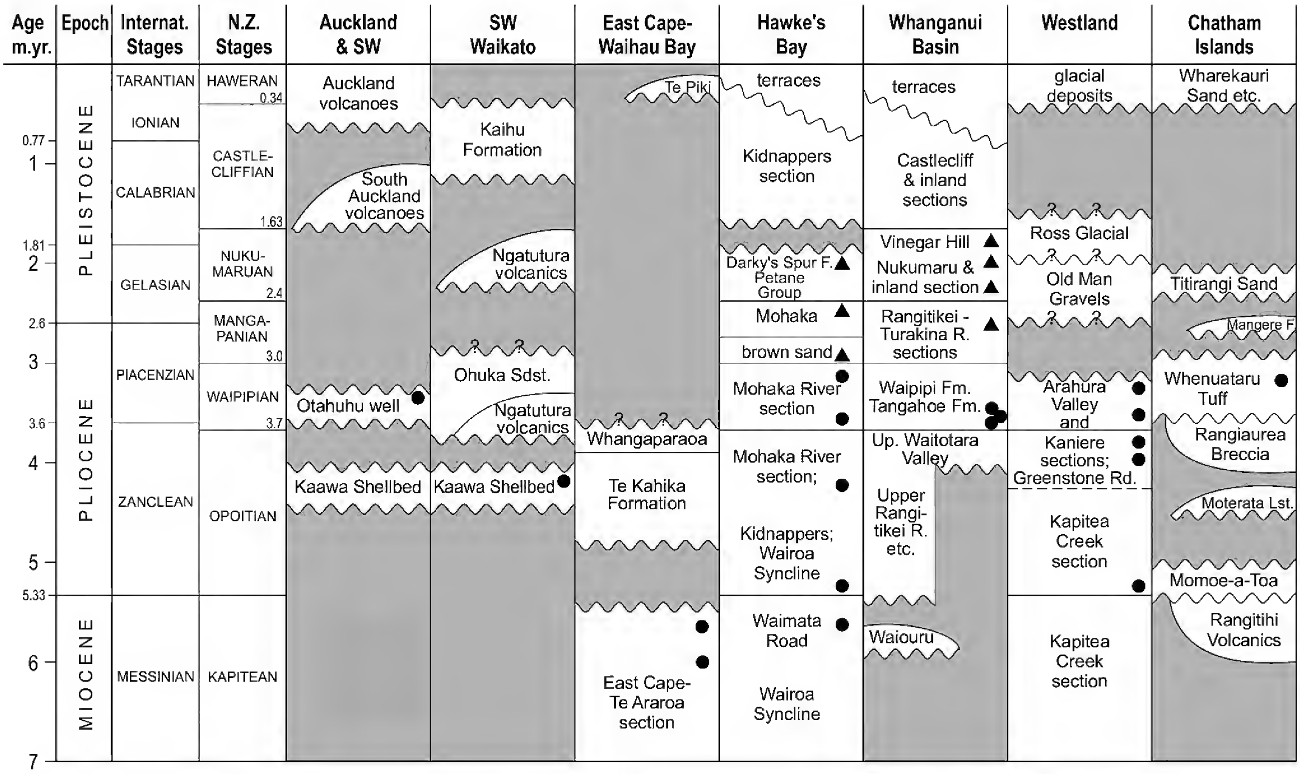

Figure 16. Stratigraphical position of *Janthina* fossil localities in New Zealand. Stratigraphy greatly simplified. Symbols: ▲ *Janthina chavani*; ● *Janthina typica*. Grey tone = stratigraphical hiatus.

rocks in northern Hawke's Bay and Westland. It is also common, although poorly preserved and somewhat crushed, in Opoitian mudstone forming the main cape promontory at Cape Kidnappers, Hawke's Bay. It also occurs widely, but scattered in small numbers, in Waipipian (early Piacenzian) rocks in northern Hawke's Bay, along the South Taranaki coast of Whanganui Basin, and in the Kaniere-Arahura district and on the Greenstone-Kumara Road in Westland, with a single record from the Chatham Islands (which lie 850 km east of the central South Island). The Wairoa Syncline in northern Hawke's Bay reveals a particularly thick succession of late Miocene–early Pleistocene rocks, 9 km thick, between the outlet of Lake Waikaremoana and the coast at Wairoa. The most significant succession for dating *Janthina* evolution is exposed along the Mohaka River, in a long, continuously exposed section through the Wairoa Syncline succession upstream from the Mohaka River road and rail bridges. Unfortunately, no complete stratigraphical column has been compiled for the Mohaka River Opoitian–Waipipian section between Willow Flat and Highway 2 (c. 25 km of continuous exposure along the river, 17 km in a straight line, entirely through gently and consistently dipping Pliocene rocks). Partial columns and maps of the stratigraphy in this region were provided by Hornibrook (1981), Scott *et al.* (1990), Cutten (1994), Bland *et al.* (2004) and Kamp *et al.* (2006), and the geology of the wider region was mapped by Lee *et al.* (2011). The writer collected from the Mohaka River section by boat with N. de B. Hornibrook and T. L. Grant-Taylor during February 1982. A good specimen of *Janthina chavani* was collected from the thin, richly fossiliferous Mangapanian brown-weathering sandstone bed 3 km upstream from the road bridge (GS13079, W19/f031), whereas the underlying thick Opoitian and Waipipian mudstone unit contains sparse specimens of *J. typica* wherever it was examined. Importantly, a specimen of *J. typica* was observed, but not collected, 1 m below the top of the Waipipian mudstone unit immediately underlying the Mangapanian sandstone formation. This identifies the Waipipian–Mangapanian Stage boundary (mid-Piacenzian, 3.0 Ma) as the date of replacement of *J. typica* by *J. chavani*. *Janthina chavani* occurs rarely at a few other localities in Mangapanian (late Piacenzian–early Gelasian) and Nukumaruan (Gelasian–earliest Calabrian) rocks in Hawke's Bay and Whanganui Basin. Exposures of similarly young rocks further south in Marlborough-North Canterbury have not yielded specimens of *Janthina*. The New Zealand succession demonstrates a late Kapitean–Waipipian (late Messinian–early Piacenzian) time range for *J. typica* and a Mangapanian–Nukumaruan (late Piacenzian–early Calabrian) time range for *J. chavani*, with an age of 3.0 Ma for the extinction of *J. typica* and origination of *J. chavani*.

The Pliocene–Pleistocene boundary is now placed at the base of the Gelasian Stage (2.59 Ma; Gibbard *et al.*, 2010) in MIS 103 (Lisiecki & Raymo, 2005: fig. 4; Pillans & Gibbard, 2012: fig. 30.4). Based on correlations by Naish *et al.* (1998) and Carter & Naish (1998, 1999) this boundary, identified by the Gauss–Matuyama geomagnetic polarity reversal, is now recognized within the upper part of the succession included within the Mangapanian Stage in Whanganui Basin. It lies between the Parihauhau Shellbed and the overlying Te Rama Shellbed in Fleming's (1953b: 125–126) description of Whanganui Basin stratigraphy and paleoecology. Late Mangapanian, Nukumaruan and younger strata are now all classified as Pleistocene. Therefore, *Janthina chavani* extends well into the expanded Pleistocene in New Zealand.

The succession in Whanganui Basin (Fleming, 1953b; Fig. 17) is complex stratigraphically because much of it was deposited in less than 50 m of water during the Plio-

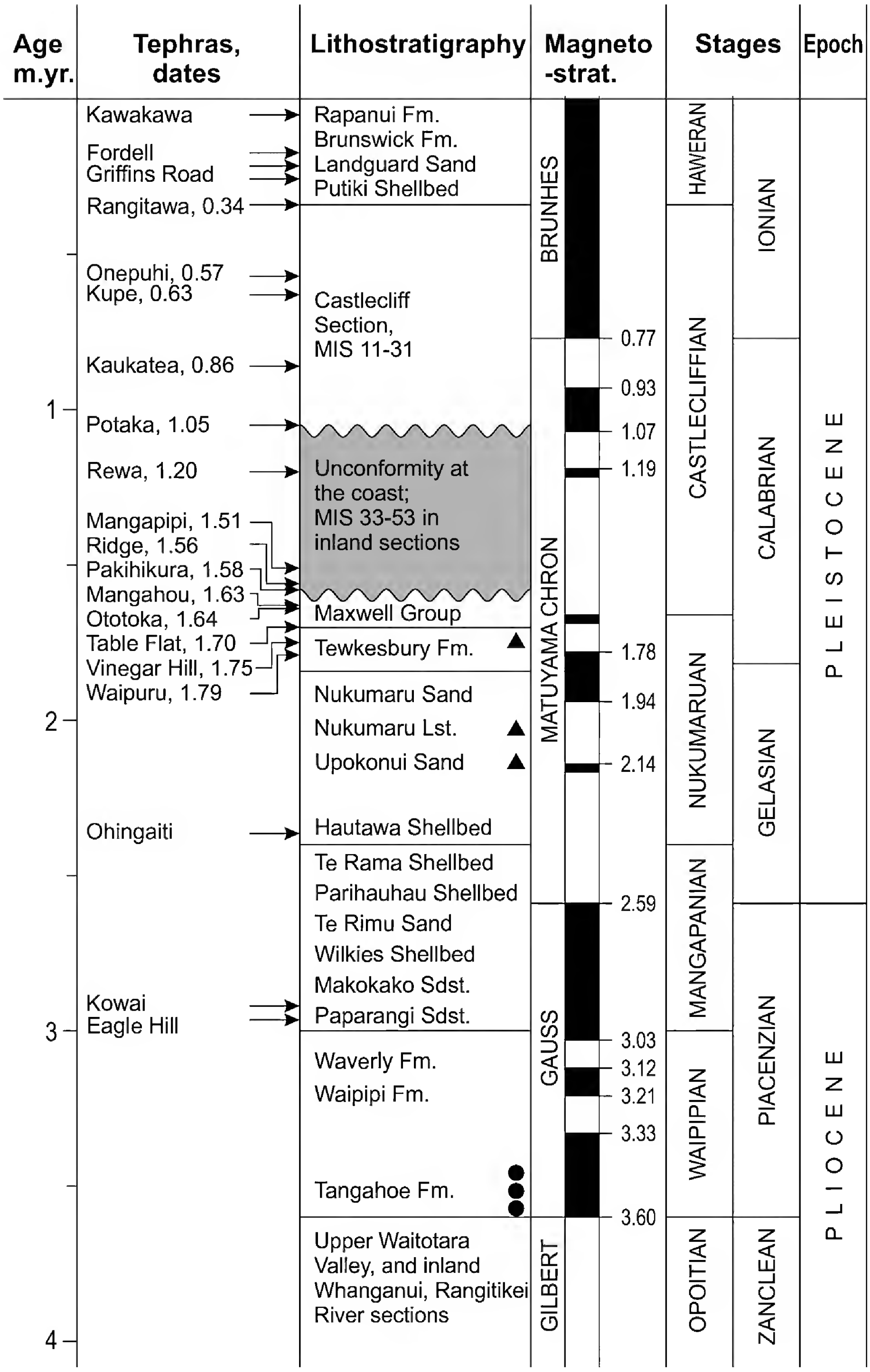

Figure 17. Stratigraphical column of Pliocene–Pleistocene rocks in Whanganui Basin, New Zealand, showing precisely dated positions of *Janthina* fossils. Stratigraphy simplified from Carter and Naish (1998, 1999), most lithological details not shown; tephras from Pillans *et al.* (2005). Symbols: ▲ *Janthina chavani*; ● *Janthina typica*. Grey tone = stratigraphical hiatus.

Pleistocene 41-ka glacial-interglacial sea-level fluctuations (Naish *et al.*, 1998; Pillans *et al.*, 1998). Sea level oscillated by c. 50 m during the earlier 41-ka cycles and by up to 130 m during the 100-ka cycles of the last 800,000 years, so the sea retreated from the basin during all glacial periods. Consequently, almost all Mangapanian and younger glacial periods are represented by unconformities in this basin. The succession consists of many cyclically deposited thin formations with strongly distinct lithologies and sharp boundaries, deposited during interglacial periods. Opoitian–Waipipian rocks in inland sections, particularly those exposed along the Whanganui, Turakina and Rangitikei Rivers, were deposited in slightly deeper water and are less obviously cyclical. The basin is only gently deformed, and the succession is exposed well in many river sections and along the coast. It contains many dated silicic tephras (Alloway *et al.*, 1993; Pillans *et al.*, 2005; Fig. 17) which, along with geomagnetic polarity stratigraphy (e.g., Seward *et al.*, 1986, Kamp & Turner, 1990, Turner & Kamp, 1990, Turner *et al.*, 2005; Fig. 17) and detailed analyses of

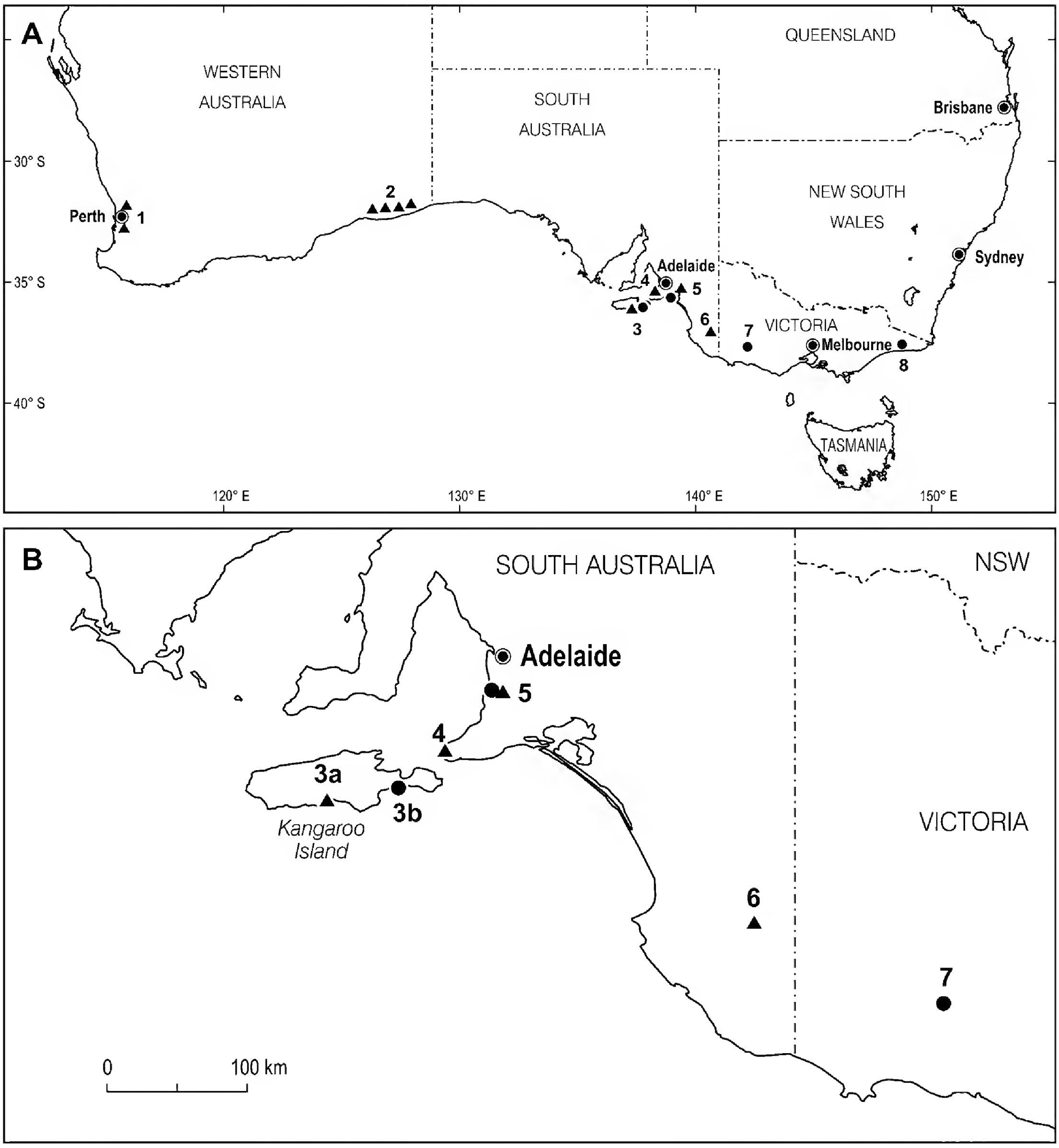

Figure 18. *Janthina* fossil localities in southern Australia. Symbols: ▲ *Janthina chavani*; ● *Janthina typica*. *(A)* general map of southern Australia; *(B)* localities in southeastern South Australia and western Victoria. Localities: *(1)* "lower" Ascot Fm in wells, Perth Basin *(J. chavani)*; *(2)* Roe Calcarenite, Roe Plain *(J. chavani*, type locality of *Hartungia dennanti chavani)*; *(3)* Point Ellen Fm, Vivonne (3a) *(J. chavani)* and unnamed limestone, Table Rock (3b) *(J. typica)*, south coast of Kangaroo Island; *(4)* Point Ellen Fm, Cape Jervis, Fleurieu Peninsula *(J. chavani)*; *(5)* Hallett Cove Sandstone, Hallett Cove, Adelaide *(J. typica* and *J. chavani)*; *(6)* Bridgewater Limestone, Naracoorte *(J. chavani)*; *(7)* Grange Burn Fm, Grange Burn and Muddy Creek, near Hamilton *(J. typica*, type locality of *Heligmope dennanti)*; *(8)* Jemmys Point Fm, Bunga Creek, E Gippsland *(J. typica)*.

sequence stratigraphy (e.g., Abbott & Carter, 1994, 1999; Kamp & McIntyre, 1998; Abbott *et al.*, 2005) have allowed precise correlation with the international Plio-Pleistocene succession (Naish *et al.*, 1998; Carter & Naish, 1998, 1999; Cooper, 2004; Raine *et al.*, 2015). This provides a precisely dated record of the time range of *Janthina chavani* in New Zealand. The basinal succession from the Mangapanian Stage upwards was summarized by Naish *et al.* (1998: figs 2, 4) and a highly simplified version is shown here (Fig. 17). The entire succession consists of a 5 km-thick pile of Zanclean–Ionian (Opoitian–Haweran) marine rocks.

Other Mangapanian (late Piacenzian–earliest Gelasian) records of *Janthina chavani* in New Zealand are sparse, and consist mostly of single specimens. A few fragments were collected at one locality along Cricklewood Road in northern Hawke's Bay. A few poor specimens were collected from brown-weathered sandstone between conglomerate beds on Pohokura and Matahorua Roads, west of Lake Tutira, Hawke's Bay. Material in the Department of Geology, University of Otago reported by Carter (1972) from the Komako area, Pohangina Valley, easternmost Whanganui Basin, includes a specimen from latest Mangapanian rocks and three from the immediately overlying basal Nukumaruan beds, laterally equivalent to Hautawa Shellbed in the Rangitikei and Turakina River successions.

The Nukumaruan (late Gelasian–early Calabrian) youngest records of *Janthina chavani* in New Zealand are also mostly of single specimens. One robust specimen was collected by C. A. Fleming from the lowest lens of Nukumaru Limestone on the Waitotara coast, west of Whanganui (Fleming, 1953b: 139). This formation was labelled "not resolved" stratigraphically by Abbott *et al.* (2005: fig. 3), i.e., it is significantly older than MIS 77, the oldest MIS stage recognized in the analysis by Abbott *et al.* (2005), but younger than the Pliocene-Pleistocene boundary in MIS 103. Darkies Spur Formation on Darkies Spur Road, west of Devil's Elbow, c. 30 km north of Napier, Hawke's Bay (Haywick & Henderson, 1991; Haywick *et al.*, 1991, 1992; Haywick, 2004) has yielded one specimen and a fragment (Figs 28I, K). Several specimens were collected by D. Cowe (Greytown) from a thin shell lens within "undifferentiated Upper Okiwa Group" (Fleming, 1953: 133–136) between Tuha Sand and Ohingaiti Sand in a road cut on Highway 1 uphill from Makohine Stream, 2 km south of Ohingaiti, Rangitikei Valley (one specimen in GNS; Figs 28B, E, H). The youngest record of *Janthina chavani* in New Zealand lies within early Calabrian (Pleistocene) rocks: one incomplete specimen from a shellbed enclosing Vinegar Hill Tephra (MIS 61, 1.75 Ma; Pillans *et al.*, 2005: 79, figs 5A, 11), within Tewkesbury Formation (late Nukumaruan) on Brunswick Road, Kai Iwi Valley, west of Whanganui (locality illustrated in colour by Townsend *et al.*, 2008: fig. 35). The stratigraphical positions of Whanganui Basin specimens are shown in Fig. 17.

New Zealand successions are important for indicating an abrupt, apparently punctuational speciation event when *Janthina chavani* (Mangapanian and Nukumaruan New Zealand Stages, late Piacenzian–early Calabrian) originated from *J. typica* (Kapitean, Opoitian and Waipipian New Zealand Stages, late Messinian–early Piacenzian) at 3.0 Ma. The one post-Nukumaruan fossil record of *Janthina* in New Zealand is a Holocene specimen of *J. janthina* from Table Cape, Mahia Peninsula (see below under *J. janthina*). Thick, younger, normal marine successions crop out extensively in New Zealand, in Nukumaruan successions throughout Hawke's Bay and Wairarapa district, in the Castlecliffian succession at Cape Kidnappers, Hawke's Bay, and in the Nukumaruan–Castlecliffian successions in Whanganui Basin and North Canterbury. They record complex glacial-interglacial sequences deposited during the last 1.63–0.3 Ma (Fleming, 1953b; Naish *et al.*, 1998). However, apart from the one Holocene specimen, *Janthina* fossils have not been recorded from rocks younger than MIS 61. There is no reason to assume that *Janthina chavani* became extinct at 1.75 Ma, however. The lack of specimens probably simply results from sea temperatures being too cool around New Zealand to be inhabited by *Janthina*, particularly during glacial stages. The sparseness of *Janthina* fossils younger than Waipipian might also have resulted partly from a lack of persistent onshore winds after 3.0 Ma. This conceivably resulted from sheltering of basins in eastern New Zealand from prevailing westerly winds as a result of changing paleogeography, e.g., late Pliocene–Pleistocene uplift of the central mountain ranges, rather than from a lack of *Janthina* specimens in the seas around New Zealand.

The succession in southern Australia. Successions from which fossil *Janthina* specimens have been collected occur widely but sparsely across southern Australia (Figs 18–19). The relative ages of all these formations, other than those on Kangaroo Island, South Australia, were summarized by Darragh (1985) and refined by Beu & Darragh (2001: fig. 6), based on pectinid biostratigraphy. However, correlation with international stages is less precise than in New Zealand.

Janthina typica (= *Heligmope dennanti* Tate, 1893) was first recorded by Tate (1893) from Grange Burn Formation (Zanclean) at "MacDonald's bank", on Muddy Creek, near Hamilton in western Victoria. The fauna at this locality forms the basis of Darragh's (1985: 106) molluscan assemblage XVI (Kalimnan Australian Stage). *Janthina typica* also occurs in the same formation nearby at Grange Burn, a tributary of Muddy Creek. It also occurs uncommonly at one locality (road cutting at Bunga Creek, Princes Highway) in Jemmys Point Formation near Lakes Entrance in Gippsland, easternmost Victoria, within the same Kalimnan molluscan assemblage XVI (Zanclean). It is surprising that *J. typica* does not occur more widely in Jemmys Point Formation, which is richly fossiliferous and crops out extensively around Lakes Entrance in Gippsland. *Janthina* fossils similarly are absent from Cameron Inlet Formation (Pliocene) and the overlying Memana Formation (early Pleistocene) on Flinders Island, Bass Strait, again despite highly diverse faunas and extensive outcrop and collecting. As with the more southern New Zealand outcrops, eastern Victorian and Bass Strait localities presumably were either too cool for *Janthina* to occur or lay outside areas where water movements or wind carried *Janthina* specimens into shallow water.

Ludbrook (in Milnes *et al.*, 1983: 23) cautiously recorded "what may be *Hartungia dennanti dennanti*" (i.e., *Janthina typica*) among poorly preserved molluscs collected from an unnamed early Pliocene limestone unit overlying Kingscote Limestone at Table Rock, near Point Reynolds, south coast of Kangaroo Island, South Australia. The only other record of *J. typica* from Australia is in Tate's type material from Hallett Cove Sandstone, Adelaide. One incomplete specimen among the syntypes of *H. dennanti* from Hallett Cove is *J. typica*, with an evenly subspherical shape, a low spire, and prominent spiral folds over the entire exterior. Tate's two other syntypes from Hallett Cove Sandstone are *J. chavani*. Parkin (1969: 220, fig. 115) provided a photograph of the coastal exposure near Blanche Point, on the coast south of Adelaide, showing "Hallett Cove Sandstone, upper bed of ?Pleistocene limestone over a lower bed of Pliocene sand". The two species evidently are segregated stratigraphically at Hallett Cove, late Piacenzian–Gelasian specimens of *J. chavani* occurring higher in the section than early Piacenzian specimens of *J. typica*. It seems likely that Hallett Cove Sandstone spans at least the central part and perhaps all of the Piacenzian Stage. Marine successions in Victoria have not yielded *J. chavani*.

Bridgewater Limestone, a complex series of late Pliocene–Pleistocene–Holocene marginal marine units deposited during interglacial high-stands, crops out extensively south-westwards from Naracoorte to the present coastline in southeastern South Australia (Sprigg, 1952; Murray-Wallace *et al.*, 2001; Blakemore *et al.*, 2015). It includes unusual thin (5–10 cm thick), laterally continuous, strongly cemented limestone beds with concentrations of huge specimens of *Janthina chavani* covering large bedding-plane exposures in some lime quarries near Naracoorte, alternating with thicker unconsolidated sand beds barren of macrofossils. This was observed by the writer and T. A. Darragh (Museum Victoria) at Henske's Quarry, Elderslie Road, 2.6 km southeast of Naracoorte. Here *Janthina chavani* is abundant in a few thin

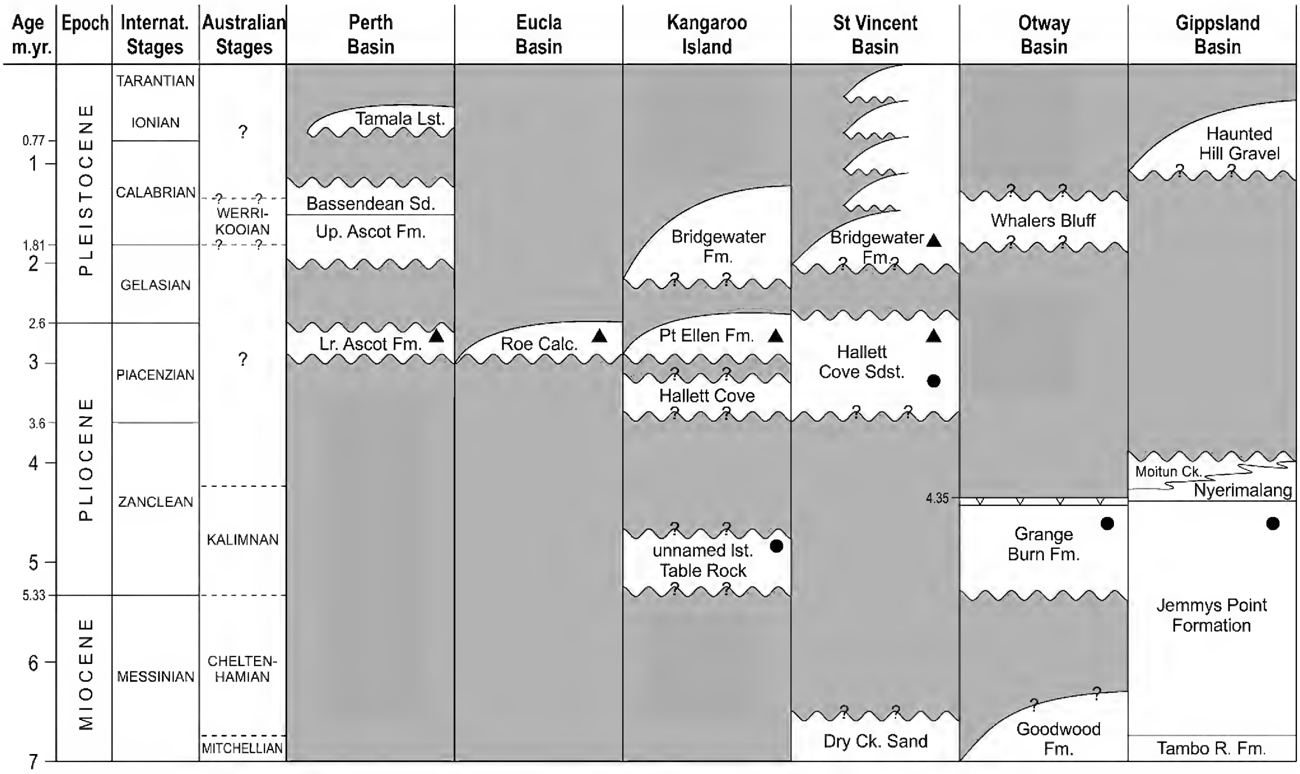

Figure 19. Stratigraphical position of *Janthina* fossil localities in southern Australia, modified from Beu and Darragh (2001: fig. 6). Bridgewater Limestone Fm shown diagrammatically; on mainland southern Australia it probably represents every interglacial high-stand from at least 2 Ma to MIS 3. Symbols: ▲ *Janthina chavani*; ● *Janthina typica*. Grey tone = stratigraphical hiatus.

limestone layers in overburden above the quarried Gambier Limestone (Longfordian, Aquitanian, early Miocene). A thin block of limestone c. 1 m^2 containing abundant *J. chavani* was also observed at the quarry office. Bridgewater Limestone usually has been mapped as Pleistocene in age. The Dismal dune ridge, the oldest dune ridge east of Mount Gambier in south-easternmost South Australia, was deposited during MIS 23 (middle Pleistocene; Blakemore *et al*., 2015, and references therein) and the ridges extend up to MIS 3 (latest Pleistocene) at the present coast (Blakemore *et al*., 2015). The oldest ridge west of the Kanawinka Fault scarp further north at Naracoorte, the Naracoorte dune ridge (Sprigg, 1952: fig. 17a, and geological map) has been dated by aminostratigraphy and thermoluminescence dating at c. 800 ka (late Calabrian, Pleistocene) (Murray-Wallace *et al*., 2001), although it would have been judged to be late Piacenzian–Gelasian from its content of *J. chavani*. Possibly the date has been affected by diagenesis. If not, this date indicates that *J. chavani* has a fossil record in southeastern South Australia that is very much younger than anywhere else. Other excavations into dune ridges likely would reveal further *Janthina* fossils. Parallel older dune ridges extend further north-eastwards into south-western Victoria and further inland in South Australia, and it is conceivable that they will reveal a detailed evolutionary history of *Janthina* species. However, water temperature would be significant again here; the Naracoorte ridge of Bridgewater Limestone evidently was influenced by the warm Leeuwin Current, which transported *Janthina* specimens from Western Australia eastwards into South Australia. Similarly warm temperatures would have to have affected South Australia during other interglacial periods for *Janthina* fossils to occur in other dune ridges.

Roe Calcarenite (type formation of *Janthina chavani*; Ludbrook, 1978) in southeastern Western Australia contains abundant, beautifully preserved specimens of *J. chavani* in weakly consolidated sand. Large collections from Roe Calcarenite are present in several Australian museums. Correlations by Beu & Darragh (2001: fig. 6) suggested an early Piacenzian age for Roe Calcarenite, but in view of current knowledge of *Janthina* time ranges in New Zealand, the age is now known to be late Piacenzian (3.0–2.59 Ma). James *et al*. (2006) and James & Bone (2007) described the outcrop, stratigraphy, lithology, and environment of deposition of Roe Calcarenite. James *et al*. (2006: table 1, fig. 6) also reported strontium isotope ratios indicating a Pliocene–early Pleistocene age. However, the surprisingly large age range of 4.45–1.17 Ma indicates diagenetic alteration of aragonite in many shells, as the real age range is now known to be 3.0–2.59 Ma. James & Bone (2007) recognized two members. The lower member, consistently 1 m thick, comprises uniform, mostly structureless, unconsolidated, bivalve-gastropod-*Marginopora* rudstone or floatstone, with a biofragmental grainstone matrix containing some quartz grains. The large warm-water foraminifer *Marginopora* is abundant throughout. The upper member is more variable in thickness, distribution and lithology than the lower member, and in many exposures is severely cemented by soil carbonates. The fine-grained biofragmental grainstone contains few identifiable molluscs. The contact between the members is gradational in a few places, but a burrowed unconformity separates them in most places, and a thin bed of finely laminated grainstone separates them in a few places. The total observed thickness of the formation is 3 m (James & Bone, 2007: fig. 6). Deposition took place on a very shallow carbonate platform at the head of the Great

Australian Bight. The lower member accumulated during a period of sea-level rise, in no more than 10 m of water, on shallow near-shore beds of the seagrass *Amphibolis*, during a period slightly warmer than at present. The upper member was deposited during a period of regression in a series of adjacent intertidal sand flat, beach, and supratidal lacustrine environments. The abundant specimens of *Janthina chavani* are all from the lower member and represent rafts of specimens cast ashore during periods of persistent onshore winds. They probably lost their floats through wave action and were deposited a short distance from the beach. All specimens observed are spectacularly well-preserved, although a few are slightly incomplete and none retains the protoconch. Roe Calcarenite evidently was deposited under the influence of the warm Leeuwin Current and its fauna includes several species of, for example, Cypraeidae and Volutidae that live further north in Western Australia at present. The faunas of Jemmys Point, Memana and Cameron Inlet Formations in Gippsland and Bass Strait reveal much lower water temperatures at their times of deposition than those affecting Roe Calcarenite, apparently at least partly explaining their lack of *Janthina* fossils.

An important Australian record for confirming the time ranges of *Janthina* species is the abundant material of *Janthina chavani* recorded from Point Ellen Formation at Point Ellen, Vivonne, Kangaroo Island, and in a small remnant of the same formation at Cape Jervis, southern tip of the Fleurieu Peninsula, on mainland South Australia opposite Kangaroo Island (Ludbrook in Milnes *et al*., 1983: 28; Ludbrook, 1983: 45, figs 3h–j; Ludbrook, 1984: 232, figs 57o–p). Ludbrook (1983, 1984) correlated Point Ellen Formation directly with Roe Calcarenite because *J. chavani* is abundant in both units, but in no others. Therefore, she dated it as early Pleistocene, the age she assigned to Roe Calcarenite (Ludbrook, 1978). However, now that Roe Calcarenite is recognized as late Piacenzian (late Pliocene), no other formations on Kangaroo Island are dated as late Pliocene, and no other indicators of an early Pleistocene age are present in Point Ellen Formation, it is concluded here that Point Ellen Formation also is late Piacenzian in age. As the underlying unnamed Pliocene limestone at Table Rock contains specimens identified cautiously by Ludbrook (in Milnes *et al*., 1983: 23) as "what might be" *Hartungia dennanti dennanti* (i.e., *J. typica*), this succession helps confirm the age ranges of *Janthina* species determined in New Zealand.

Thanks to the life-long devotion of the late George Kendrick (formerly of WAM), several complete specimens and many recognisable fragments of *Janthina chavani* also have been collected from cuttings from water wells in the Perth Basin in Western Australia. They are limited to the "lower" Ascot Formation, of late Piacenzian age, and have not been collected from the overlying "upper" Ascot Formation. Mallett (1982) reported a late Pliocene form of the diagnostic early Pleistocene index foraminifer *Globorotalia truncatulinoides* (d'Orbigny) from the "Jandakot beds", i.e., "lower" Ascot Formation, in wells around Jandakot in the Perth Basin, in samples supplied by Kendrick (base Pleistocene was defined at that time at 1.81 Ma, rather than the present 2.59 Ma). James *et al*. (2006: 414) used amino acid racemization ratios to correlate the "lower" Ascot Formation with the Roe Calcarenite, a correlation that seems reasonable from their containing the same *Janthina* species. However, the several late Pliocene deposits in widely separated areas of southern Australia each likely represent a short period of late Pliocene time, and possibly each was deposited during a single interglacial period. This includes "lower" Ascot Formation around Perth, Roe Calcarenite, Point Ellen Formation, and the laterally equivalent Norwest Bend Formation in the Murray River succession. There is ample time for them all to have subtly different ages during this period when shallow-water sedimentation was dominated by 41-ka sea-level cyclicity. Hallett Cove Sandstone was deposited during at least two distinct 41-ka cycles, and Bridgewater Limestone clearly was deposited during many or all 41-ka and 100-ka cycles during the last 2 m yrs. Australian successions help confirm a Messinian–early Piacenzian age range for *J. typica* and a late Piacenzian–Gelasian age range for *J. chavani*, with origination of *J. chavani* at c. 3.0 Ma. However, apart from in Bridgewater Limestone, *Janthina* fossils have not been recorded from marine rocks younger than late Piacenzian in southern Australia. Aminostratigraphy indicates that Bridgewater Limestone containing *J. chavani* extends up to at least late Calabrian in age. Bridgewater Limestone dune ridges in the region extending from inland of Naracoorte southwest to the coast of South Australia southeast of Robe potentially could provide a detailed history of the evolution and time ranges of the younger species of *Janthina*.

The succession in Japan. Rather few fossil specimens of *Janthina* have been collected in south-eastern Japan (Figs 20–21). *Hartungia elegans* Tomida & Nakamura, 2001 was based on specimens with spiral folds over the entire teleoconch. These specimens are interpreted here as having a low, wide, medially keeled shape and a flattened spire as a result of severe post-mortem compaction, and are reidentified as *Janthina typica*. *Hartungia elegans* was recorded from Senhata Formation, Miura Group, at Okumotona, Chiba Prefecture, Boso Peninsula, near Tokyo, Honshu, and from Tano Formation, Miyazaki Group, at Tano, Miyazaki Prefecture, Shikoku. Both localities were assigned to planktonic foraminiferal zone N17 (late Miocene, late Tortonian–mid-Messinian) (Tomida & Itoigawa, 1986: 116, fig. 1; Tomida, 1989; Ozawa & Tomida, 1992; Nakamura *et al.*, 1999; Tomida & Nakamura, 2001). Some of the Japanese material identified as *Parajanthina* or *Hartungia japonica* Tomida & Itoigawa, 1982, of latest Miocene–early Pliocene age (late Messinian–Zanclean, planktonic foraminiferal zones N18–20; Hilgen *et al*., 2012: fig. 29.10) also has spiral folds over the entire teleoconch, including the sutural ramp. This material, also, is reidentified here as less severely compressed specimens of *J. typica*: Tamari Formation, Sagara Group, zones N18–19, late Messinian–early Zanclean, at Tamari, Kakegawa City, Shizuoka Prefecture (Tomida & Itoigawa, 1982: 62, fig. 1B); Abina Formation, Kakegawa Group, Shimokurasawa, Kakegawa City, Shizuoka Prefecture, and Ukari Formation, Kakegawa group, at Nito, Kakegawa City (Nobuhara, 1993; Nobuhara *et al*., 1995); and Osozawa Member of Akebono Formation, Shizukawa Group, also zone N18, at Osozawa, Yamanashi Prefecture (Tomida, 1996). The youngest material identified as *H. japonica*, from planktonic foraminiferal zones N21–22 (late Piacenzian–Calabrian and younger; Hilgen *et al*., 2012: fig. 29.10) has weaker spiral sculpture, lacking folds on the sutural ramp, and although most specimens are relatively

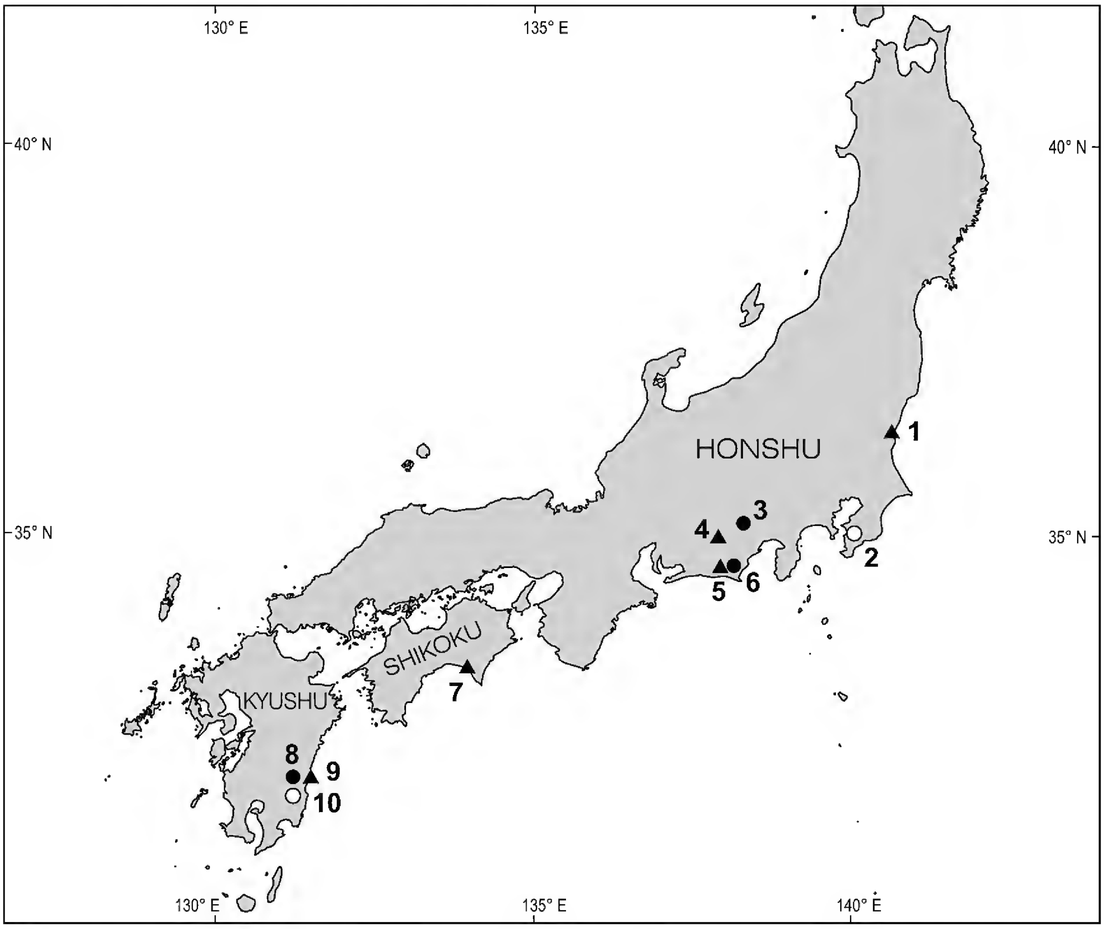

Figure 20. *Janthina* fossil localities in Japan. Symbols: ▲ *Janthina chavani*; ● Pliocene records of *Janthina typica*; ○, late Miocene records of *Janthina typica*. Localities: *(1)* Hatsuzaki, Hitachi City, Ibaragi Prefecture, Honshu; Hitachi Fm, Gelasian *(J. chavani)*; *(2)* Okumotona, Chiba Prefecture, Honshu; Senhata Conglomerate, Messinian *(J. typica)*; *(3)* Osozawa, Yamanashi Prefecture, Honshu; Osozawa Member of Akebono Fm, Zanclean *(J. typica)*; *(4)* Iida, Shizuoka Prefecture, Honshu; Dainichi Fm, Gelasian *(J. chavani*, type locality of *Parajanthina japonica)*; *(5)* Tombe and Nito, Kakegawa City, Shizuoka Prefecture, Honshu; Hijikata Fm, early Calabrian *(J. chavani)*; *(6)* Tamari, Kakegawa City, Shizuoka Prefecture, Honshu; Tamari Fm, Zanclean *(J. typica)*; *(7)* Tonohama, Kochi Prefecture, Shikoku; Ananai Fm, Gelasian *(J. chavani)*; *(8)* Shimoyamaji, Saito City, Miyazaki Prefecture, Kyushu; Tsuma Fm, early Zanclean *(J. typica)*; *(9)* Hioki, Miyazaki Prefecture, Kyushu; Takanabe Fm, late Piacenzian *(J. chavani)*; *(10)* Tano, Miyazaki Prefecture, Kyushu; Tano Fm, Messinian *(J. typica*, type locality of *Hartungia elegans)*.

small (immature), the few relatively large shells also have taller spires than the older material. This material is reidentified here as *J. chavani*: Hitachi Formation, Hatsuzaki Group, zone N21, at Hatsuzaki, Hitachi City, Ibaragi Prefecture (Tomida & Itoigawa, 1989: 125, fig. 1; Noda *et al*., 1995); Ananai Formation, Tonohama Group, also zone N21, at Tonohama, Kochi Prefecture (Tomida & Kitao, 2002: 159, fig. 1); Dainichi Formation, Kakegawa Group, also zone N21, at Higashigumi, Iida, Shizuoka Prefecture (type locality of *Parajanthina japonica*; Tomida & Itoigawa, 1982: 61, fig. 1A); Dainichi Formation, Kakegawa Group, at Nito, Kakegawa City, Shizuoka Prefecture (Nobuhara *et al*., 1995); and Hijikata Formation, Kakegawa Group, lowermost zone N22, late Gelasian–Calabrian, at Tombe, Kakegawa City, Shizuoka Prefecture (Tomida & Itoigawa, 1984: 111, pl. 31, fig. 2a, b). Tomida *et al*. (2013: 60, figs 1, 3A–D) recorded another strongly sculptured specimen of *J. typica* from Tsuma Formation, Miyazaki Group, at Shimoyamaji, Saito City, Miyazaki Prefecture, Kyushu, a locality referred to planktonic foraminiferal zone N18 (early Zanclean, basal Pliocene). However, the two specimens recorded by these authors from higher in Miyazaki Group, from Takanabe Formation at Hioki, near the coast of Miyazaki Prefecture (Tomida *et al*., 2013: figs 1, 3E–L) have more exert spires and have weaker spiral sculpture on the sutural ramp than *J. typica*, and are also reidentified here as *J. chavani*. They were correlated with a position low in planktonic foraminiferal zone N21 (late Piacenzian).

Japanese successions are dated with respect to Blow's (1969) planktonic foraminiferal "N" zones, which were correlated rather imprecisely to the international Neogene stages by Hilgen *et al*. (2012: fig. 29.10). Japanese correlations of Blow zones also differ slightly from those of Hilgen *et al*. (2012). Briefer and more precisely correlated planktonic foraminiferal zones were established by Wade *et al*. (2011), but have not been adopted in Japan. Although obscured a little by relatively imprecise correlation with the European stage succession, the record of *Janthina* in Japan seems to match that in New Zealand and southern Australia. *Janthina typica* is recorded from late Messinian and Zanclean rocks and *J. chavani* is recorded from late Piacenzian, Gelasian and early Calabrian rocks in Japan. So far, there

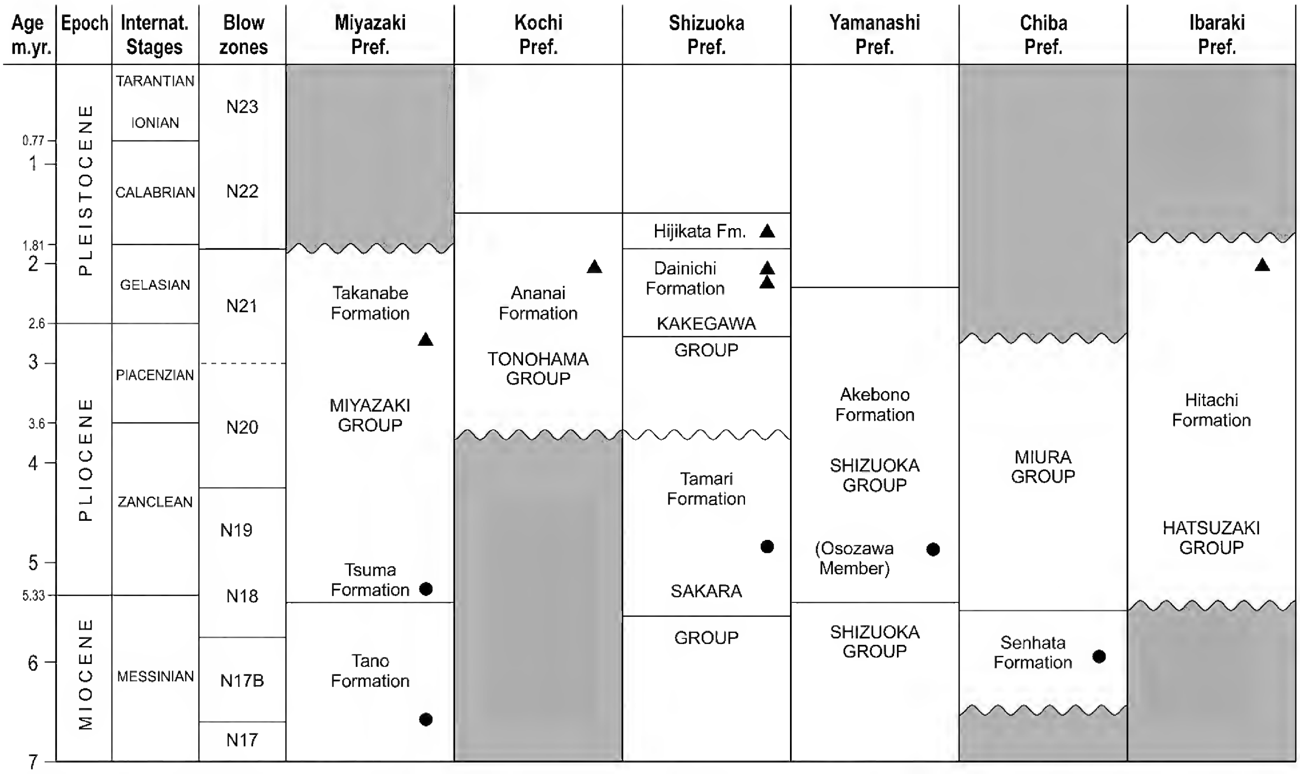

Figure 21. Stratigraphical position of *Janthina* fossil localities in Japan. Symbols: ▲ *Janthina chavani*; ● *Janthina typica*. Grey tone = stratigraphical hiatus; not all stratigraphical units are identified.

seem to be no records of *Janthina* from early Piacenzian rocks in Japan. Apart from this, the Japanese succession helps to confirm the origination of *J. chavani* during Piacenzian time, at around 3.0 Ma. As in New Zealand, many thick, well studied, younger Japanese successions record complex glacial-interglacial sequences over quite large areas in Japan (e.g., Ito, 1998), but very few *Janthina* fossils have been recorded from them. Possibly both successions lay within water too cool to be inhabited by *Janthina* at that time. Nevertheless, the thick Japanese Pleistocene marine successions potentially provide one of few locations where the later evolution of *Janthina* might be revealed.

An interesting interpretation of the Japanese succession was provided by Tomida *et al.* (2013: 62): "The Late Neogene eustatic curves of Malmgren and Berggren … show major rises in global sea level at c. 6.8 Ma (N17a), 5.7 Ma (N17b), 5–3.8 Ma (N18–19), 3–2.6 Ma (N20–lower 21), and 2.0–1.8 Ma (upper N21). Our field studies of Late Neogene molluscan faunas in Japan have shown the clear correspondence between stratigraphic levels with warm-water faunas and the times of major eustatic sea level rises … Additional study has shown that *Janthina* occurs in all major Neogene transgressions. All these facts support the idea that vigorous, warm currents flowed along the Pacific coast of Kyushu in the earliest Pliocene (N18), and in the latest Pliocene (lower N21)". Occurrences of *Janthina* in Japan are interpreted as related to incursions of the tropical Kuroshio Current rather than with periods of onshore winds, although both likely occurred simultaneously to record the occurrence of *Janthina*.

Overview of time ranges. None of the successions described above establishes the full evolutionary history of *Janthina*, for the following reasons:

1. No succession is known that records the extinction of *Janthina chavani* or its replacement by a later species such as *J. janthina*;
2. No succession records the evolution of a living *Janthina* species, although isolated Piacenzian or Gelasian sites in Jamaica and the Philippine Islands indicate that *J. globosa* had evolved before *J. chavani* became extinct;
3. Only the succession at Santa Maria Island includes *Janthina krejcii*;
4. The writer is not aware of any other successions that would clarify this evolutionary history further, with the possible exception of Bridgewater Limestone in south-eastern South Australia and south-western Victoria. Bridgewater Limestone extends both much older (well back into the Pliocene) and much younger (up to MIS 3) than the fossils recorded here from Naracoorte (Sprigg, 1952; Murray-Wallace et al., 2001; Blakemore et al., 2015) and potentially could reveal the full evolutionary history of *Janthina*.

The gently uplifted successions around southern Australia include beautifully preserved, abundant fossil material of *Janthina*. Bridgewater Limestone, Point Ellen Formation and Roe Calcarenite record the gentle lapping of the sea onto a tectonically passive margin, where the neustonic fauna was cast ashore in abundance, and preserved during late Pliocene–Pleistocene sea-level high-stands. Little else has happened since, other than gradual slight uplift, and cementation of calcareous beds through pedogenic processes in the case of Bridgewater Limestone. Unlike tectonically active areas such as Japan and New Zealand, almost no younger rock has ever been deposited on these units, and their fossils are well-preserved and undeformed. In contrast, tectonically active margin sequences in New Zealand and Japan have longer but much less well-preserved *Janthina* successions, resulting from a combination of their oceanic positions and strong late Neogene tectonism. Despite the very much poorer preservation of fossils, largely due to a combination of cementation of the rock and crushing during compaction, these longer successions are important for dating the evolutionary history of *Janthina*. Even in these active locations, young uplifted successions do not record any of the living *Janthina* species, probably merely because late Pliocene–Pleistocene temperatures fell too low for *Janthina* to occur in these northern and southern locations. Occurrences in Japan, southern Australia and northern New Zealand likely reflect periods influenced by warm currents, as well as onshore winds. Other occurrences of *Janthina* fossils, notably at Santa Maria Island in the Azores, at other Atlantic islands, Jamaica, in the Philippines, and on the mid-Atlantic ridge add usefully to the record of neustonic epitoniid evolution. A few other records might be expected in future from such localities as the Philippine Islands or Italy where young rocks and active tectonism provide suitable conditions for the preservation of *Janthina* fossils in warm locations. Fossils from Madeira and Selvagem Grande Island also need to be investigated. Occasional chance records like those from off Brazil and at Kane Megamullion on the mid-Atlantic ridge will also result from deep-sea dredging and possibly from coring, but fossils of *Janthina* are common on land only in New Zealand, Japan and, in particular, along the southern coast of Australia.

Coeval with the time range of *Janthina chavani*, *J. globosa* had evolved by Piacenzian–Gelasian time and is recorded from two widely separated localities, in Jamaica and the Philippine Islands (see below under *J. globosa*). Unfortunately, the ages of these localities are not closely constrained within Piacenzian–Gelasian time, and the relationship of these specimens of *J. globosa* to the evolution of *J. chavani* is unknown. The main speciation event of potential biostratigraphical utility identified here within *Janthina*, when *J. chavani* replaced *J. typica* abruptly throughout the world ocean, possibly was brought about by cooling at the end of the Pliocene climatic optimum. The climatic optimum was identified by Dowsett *et al.* (2013) as mid-Piacenzian, occupying 3.2–3.0 Ma. The earliest record of *J. globosa* at about this time might also not be a coincidence.

Based on the stratigraphical successions described above, time ranges of the species of *Janthina* are:

1. *Janthina typica*: latest Miocene–early late Pliocene (Messinian, Zanclean and early Piacenzian Stages), Kapitean, Opoitian and Waipipian New Zealand Stages; c. 7–3.0 Ma; time of first appearance poorly constrained, possibly nearer 6 than 7 Ma.
2. *Janthina chavani*: late Pliocene–early Pleistocene (late Piacenzian–early Calabrian Stages); Mangapanian New Zealand Stage and most of the Nukumaruan New Zealand Stage; upper limit uncertain, extending well into the expanded Pleistocene, to at least MIS 61 (1.75 Ma, early Calabrian). In the Mohaka River section, northern Hawke's Bay, New Zealand, *J. chavani* succeeded *J. typica* at the Waipipian–Mangapanian Stage boundary, at 3.0 Ma in mid-Piacenzian time, and the *Janthina* succession on Kangaroo Island, South Australia, appears to correlate directly with this; 3.0–c. 1.7 Ma (probably significantly younger, c. 1 Ma?, in Bridgewater Limestone in SE South Australia), upper limit not constrained.
3. *Janthina krejcii* sp. nov.: early Pliocene (Zanclean), recognized definitely so far only on Santa Maria Island, Azores. Possibly a restricted Atlantic species, but more likely limited to a time range not represented in other rocks containing fossil neustonic Epitoniidae; c. 4.8–4.3 Ma at the type locality.
4. *Janthina globosa*: Late Piacenzian or Gelasian–present-day; earliest appearance poorly constrained.
5. *Janthina janthina*: Reported fossil only from Holocene rocks in New Zealand, and from late Pleistocene–Holocene core-top samples in the Red Sea (Janssen, 2007a, b), the eastern Mediterranean (Janssen, 2012: 25) and probably the Cariaco Basin, Venezuela (Jung, 1975); present day.
6. All other *Janthina* and *Recluzia* species have no fossil record.

The successions described above are summarized in Fig. 22 to provide correlations of *Janthina* species time ranges with international stages, biostratigraphical zonations and geomagnetic polarity stratigraphy.

Evolutionary history

Because of the almost cosmopolitan ranges of all living *Janthina* species in water warmer than 10°C, it is assumed here that all earlier species also were cosmopolitan in the same temperature range. It is also assumed that the fossils represent a single clade, and that all extinct species have now been recognised. Obviously, the addition of further species would alter the phylogeny significantly. The stratigraphical successions described above demonstrate that the earliest neustonic epitoniid was *Janthina typica*. This species occurs in the Touril Complex on Santa Maria Island (Zanclean, 5.33–4.32 Ma) and in the latest Miocene (Kapitean, Messinian) and early to early late Pliocene (Opoitian–Waipipian; Zanclean–early Piacenzian) in New Zealand. The same time range is confirmed, less precisely, in Australia and Japan; Japanese late Miocene records probably extend a little earlier than New Zealand ones. *Janthina typica* has evenly rounded whorls and a moderately and consistently low spire, similar in size and shape to the widespread "garden snail" *Cornu aspersum* (Linnaeus, 1758). It has a lower spire and fewer whorls than *C. aspersum*, with prominent spiral folds in the shell wall, uniform fine axial ridgelets over the entire teleoconch, and an obvious, small, semicircular sinus in the base of the outer lip. *Janthina typica* was succeeded abruptly at 3.0 Ma by *J. chavani*, which ranges through late Pliocene–Pleistocene (late Piacenzian–Calabrian) rocks. Specimens of *J. chavani* have a taller, flatter sutural ramp and most specimens have weaker spiral folds than in *J. typica* and at least the uppermost two spiral folds on the sutural ramp of *J. typica* are suppressed in *J. chavani*. In other characters it is almost identical to *J. typica*, except that larger specimens have taller spires than smaller ones, much more obviously than in *J. typica*. On Santa Maria Island a previously undescribed species, *Janthina krejcii* sp. nov., apparently replaced *J. typica* relatively high in the Touril Complex, although its time range elsewhere demonstrates that *J. typica* continued on and did not become extinct at the origination of *J. krejcii*. The type locality, at the lookout (Miradouro de Macela) on the road from Almagreira to Praia, is at a similar elevation to the locality at Cré described by Janssen *et al.* (2008), where pteropods confirm a Zanclean

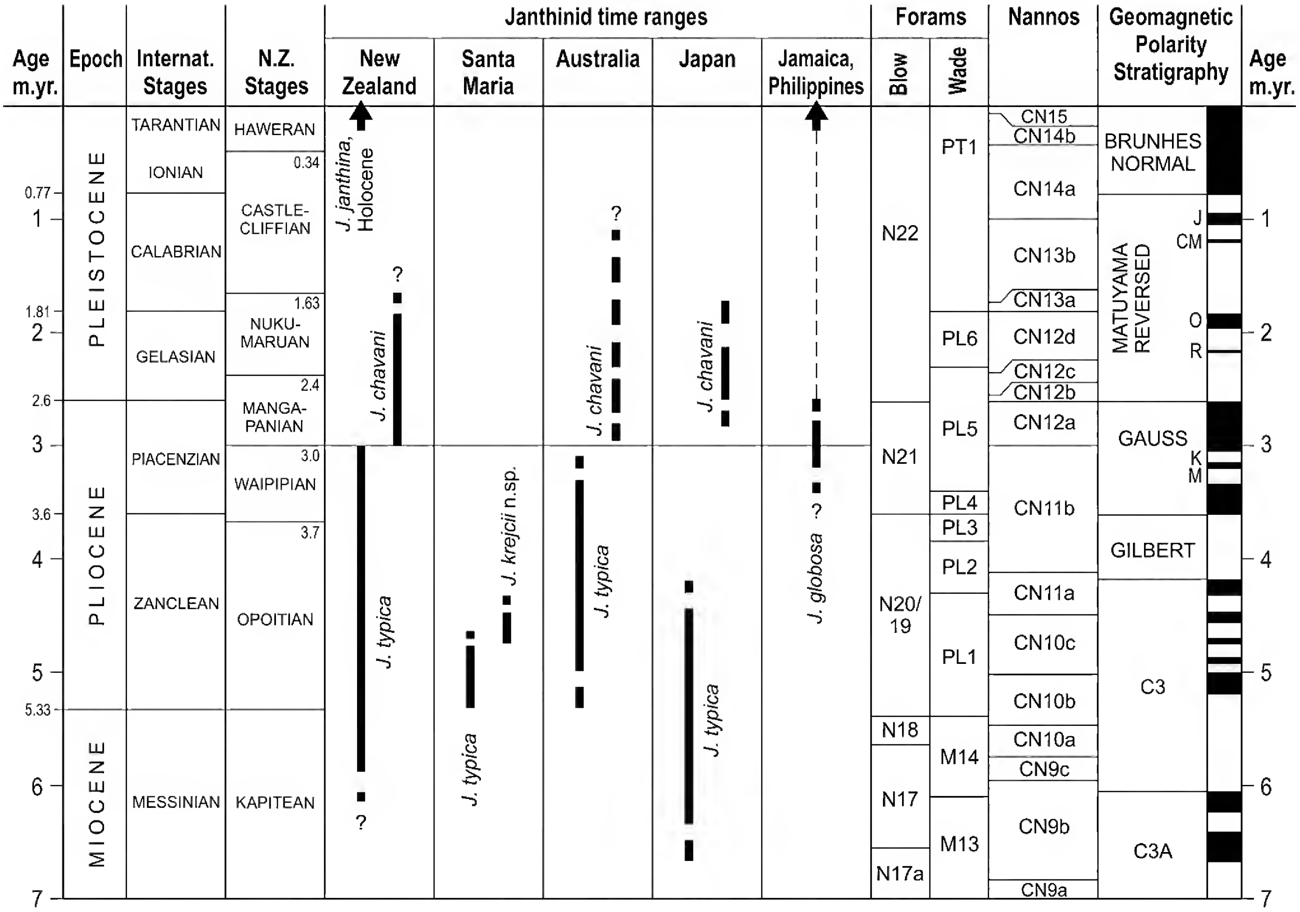

Figure 22. Stratigraphical positions and ages of world *Janthina* fossil localities, correlated with biostratigraphical zonations and geomagnetic polarity stratigraphy (normally magnetized intervals in black, reversed intervals in white). Planktonic microfossil zones (based on Blow, 1969; Wade *et al*., 2011; Okada and Bukry, 1980: "Nannos") and geomagnetic polarity stratigraphy all from Gradstein *et al*. (2012).

age. *Janthina krejcii* probably also occurs at Pinheiros, a short distance northwest of and at the same elevation as Cré. Apparently *J. krejcii* is more widespread than the present data indicate, and its time range is poorly constrained. *Janthina krejcii* has evenly rounded whorls, prominent, fine, straight axial ridgelets, and a very low spire similar to that of juvenile specimens of *J. typica* and *J. janthina*, but it completely lacks spiral folds. It possibly evolved from *J. typica* abruptly through a heterochronic process. *Janthina chavani* is not recorded from the Atlantic islands (although it possibly occurs at Madeira) so the complete evolutionary succession cannot be examined in any one locality or area. This leaves several possible phylogenies to be evaluated.

Coevally with *Janthina chavani*, *J. globosa* is recorded from two widely separated Piacenzian or Gelasian localities. The two early records of *J. globosa* lie near the equator in the central tropics in both main oceans: Luzon, Philippine Islands, in the Indo-West Pacific, and Jamaica in the Atlantic. In contrast, Pacific records of *J. chavani* lie in higher latitudes to the north and south of the one fossil record of *J. globosa*. Although this latitudinal segregation does not hold in the Atlantic, it gives the impression that *J. chavani* was limited in the Pacific to more temperate areas during late Piacenzian time, both north and south of the tropics, while *J. globosa* occupied the central tropics. This possibly could represent the type of zonal distribution described by Savilov (1969) for living species. However, neustonic epitoniids, and especially the species extending up to the living fauna, are recorded from far too few fossil localities as yet to able to evaluate the significance, if any, of this distribution.

Phylogeny. It is accepted here that *Recluzia* evolved during Holocene time independently of other neustonic Epitoniidae, recently enough to have no fossil record. The major question remaining is the phylogeny of the species formerly included in the genera *Janthina* and *Hartungia*. In evaluating the several possible phylogenies of *Janthina* species allowed by the history of fossils described above, a few key similarities and character changes are significant phylogenetic indicators. As recorded below under *J. chavani*, the most important of these is the great similarity between *J. chavani* and *J. janthina*. These two species are similar in having the outer lip sinus limited to the base of the lip, or occupying mainly the lower limb of the lip in the case of *J. janthina*. The sinus is symmetrical, with its centre in the centre of the outer lip in all other living *Janthina* species. *Janthina janthina* and *J. chavani* are also similar in their great variation in shell shape, most large specimens tending to be taller and narrower than small (young) ones—moderately so in the case of *J. janthina*, but strongly so in the case of *J. chavani*, although shell shape is highly variable in both species. Weak spiral grooves in the shell wall also occur below the periphery in many specimens of *J. janthina* (Figs 2A, D, 4A, 5A), similar to but much weaker than the folds of *J. chavani*, although

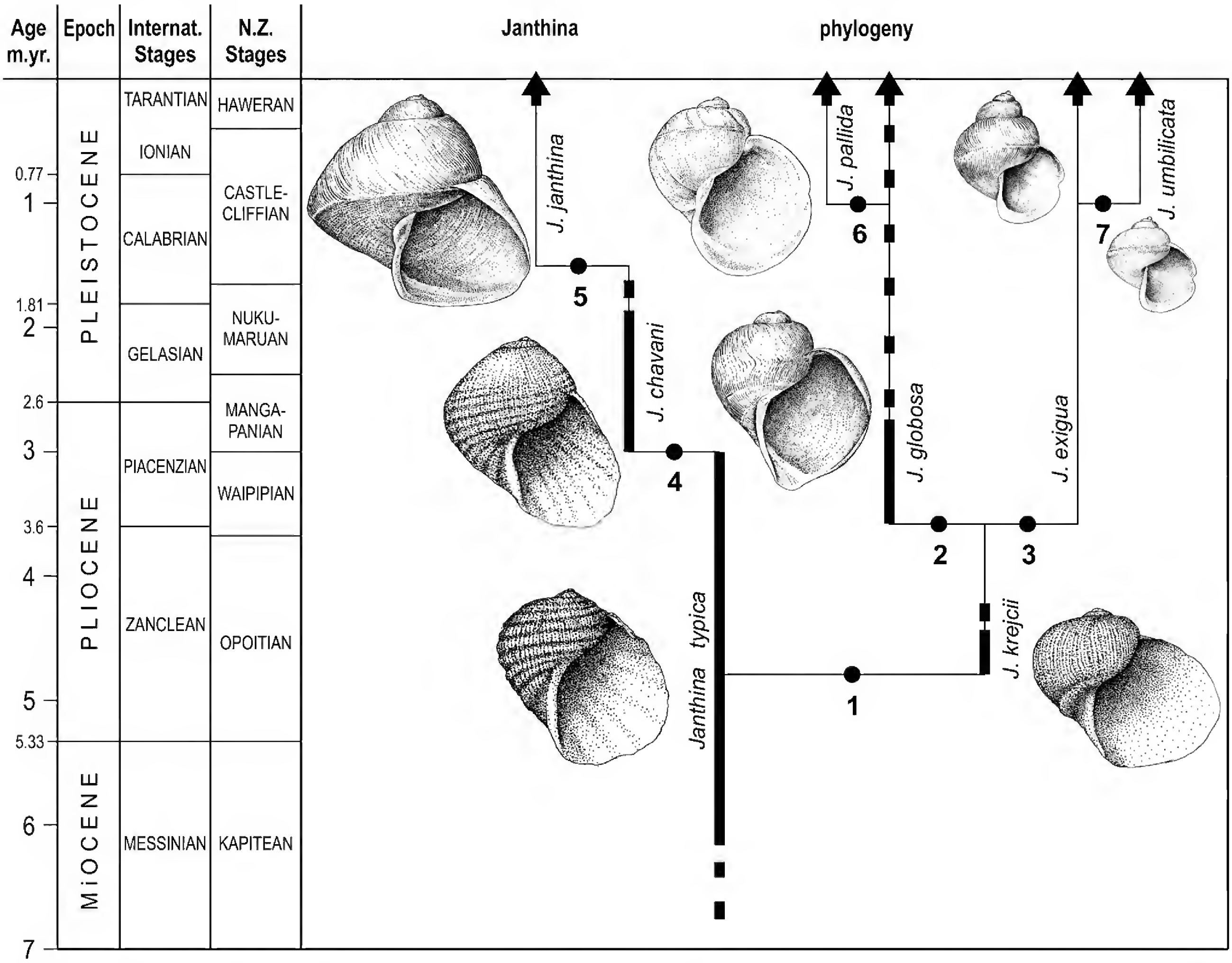

Figure 23. Suggested phylogeny of *Janthina* species. Bold lines = recorded time ranges; thin lines = suggested phylogeny. Evolutionary changes at nodes: *(1)* loss of spiral folds; retention of low-spired juvenile shape in adult, apparently heterochrony; *(2)* loss of axial riblets; increase in spire height; sinus migrated up outer lip; *(3)* retention of axial riblets; decrease in size; increase in spire height; sinus migrated up outer lip; *(4)* weakening of spiral folds; heightening and flattening of sutural ramp; increase in spire height allometry; *(5)* loss of spiral folds; adoption of trochiform shape; sinus migrated up outer lip; adoption of brooding?; *(6)* expansion of aperture into evenly oval, flared lip; shallowing of outer lip sinus; *(7)* greatly decreased prominence of and spacing between axial riblets (drawings not to scale; uppermost five drawings from Laursen, 1953: figs 14, 22, 26, 30, 36).

it should be noted that similar spiral grooves also occur in some specimens of *J. globosa* (Fig. 2G). The sutural ramp of *J. chavani* also is taller and less strongly convex than in *J. typica*, i.e., with a straighter outline, possibly to be interpreted as the beginning of development of the trochiform shape characteristic of *J. janthina*. These similarities indicate that the most likely ancestor of *J. janthina* is *J. chavani*. The evolution of *J. janthina* would have involved further weakening of the spiral folds, reduction of the axial ridgelets to only the earliest 1–1.5 spire whorls, widening of the outer lip sinus and progression of its apex higher up the lip, further weakening of the convexity of upper and lower whorl surfaces to generate the trochiform shape, and some reduction of the variability in spire height and its allometric increase with growth. Presumably it also involved the evolution of egg brooding, although of course it is not possible to know when brooding evolved.

The second key phylogenetic indicator is the retention of prominent axial sculpture by the *Janthina exigua-J. umbilicata* species pair and its loss from the *J. globosa-J. pallida* species pair. The presence of prominent axial sculpture—essentially fine, closely spaced *Epitonium* sculpture—over the entire teleoconch exterior indicates that the *J. exigua-J. umbilicata* species pair originated from one of the extinct *Janthina* species before the genus lost axial sculpture, but after it lost prominent spiral folds. Identical axial sculpture is unlikely to have evolved again after it was lost. *Janthina exigua* apparently originated during Zanclean–early Gelasian time, presumably from *J. krejcii*, the one fossil species with axial ridgelets covering the exterior, but with no spiral folds. It is assumed to have been the parent species in this pair because its coarse axial sculpture is identical to that of *J. typica* and *J. krejcii*, and it seems more likely that the finer sculpture of *J. umbilicata* was derived from that of *J. exigua* than the other way around. The main character changes in the evolution of *J. exigua* would have been a reduction in size, a very marked increase in spire height, and the development of a much wider, deeper sinus with its apex in the centre of the outer lip.

The *Janthina globosa-J. pallida* species pair also lacks spiral folds, but differs further from all earlier *Janthina* species in also lacking axial ridgelets. As *J. globosa* had evolved by at least Piacenzian–early Gelasian time, it likely also evolved from *J. krejcii*, the Zanclean species without spiral folds. *Janthina pallida* is assumed to be a daughter species that originated from *J. globosa*. The evolution of *J. globosa* would have required a moderate increase in spire height, increase in whorl convexity, loss of all axial ridgelets, and development of a wider, deeper sinus with its apex in the centre of the outer lip, although the sinus is significantly shallower than that of *J. exigua*. If the suggested phylogeny is correct, it implies that the progression of the outer lip sinus from a narrow feature at the base of the lip to occupying the entire height of the outer lip, with its centre in the middle of the lip, evolved twice; it took place in descendants of both *J. chavani* and *J. krejcii*. This lends some doubt to the suggested phylogeny, and its significance will not be clear until the function(s) of the sinus are clear.

The four living *Janthina* species that lay eggs enclosed in capsules clearly fall into two pairs of closely similar species. *Janthina globosa* and *J. pallida* resemble each other much more closely than either does the other pair of similar species, *J. exigua* and *J. umbilicata*. It is feasible that each pair of species resulted from the origination of a daughter species from the parent species as a result of geographical isolation, i.e., "standard" allopatric speciation, within an enclosed area such as the Mediterranean Sea. This possibly was aided by their occurrence in isolated neuston "rafts" (e.g., Bennett, 1840: 63; Dakin, 1933; Savilov, 1969). Subtle genetic differences likely result between "rafts", and could have led to genetic drift and speciation during isolation as a result of Plio-Pleistocene glacial-interglacial sea-level fluctuations. Sympatric speciation as a result of ecological change across an ecotone, such as a sharp temperature gradient, is another possible explanation (e.g., Johannesson *et al*., 2010; Krug, 2011; Bowen *et al*., 2013). These species are all so similar in most characters that their inclusion in the single genus *Janthina* seems reasonable. The suggested phylogeny of *Janthina* is shown in Figure 23.

The loss of spiral folds is a significant event in the evolution of *Janthina*. Spiral folds are the character by which Bronn (1861) separated *Hartungia* from *Janthina*. It could be interpreted as indicating that *J. krejcii* was the earliest species of a separate genus *Iodina* Mörch, 1860, which evolved from *Janthina* during Zanclean time. *Iodina* would include the species now identified as *Janthina krejcii, J. exigua*, *J. globosa*, *J. pallida* and *J. umbilicata*. *Janthina* would then include only *J. typica*, *J. chavani* and *J. janthina*. However these species are classified, there is no doubt that *Hartungia* is a synonym of *Janthina* if the proposed phylogeny approaches reality. At present the phylogeny of *Janthina* species is so little understood and all species are so similar that it is preferable to retain all species in *Janthina*. While the suggested phylogeny is plausible, it is of course based solely on morphology and should be tested, including evaluating the recognition of *Iodina*, by comparing molecular sequences. It would be preferable if all living *Janthina* and *Recluzia* species were compared with as many benthic species of Epitoniidae as possible, including species of *Alora*, *Surrepifungium* and *Alexania*.

Systematic revision

Gastropoda
Epitonioidea Berry, 1910 (1812)

Epitoniidae Berry, 1910 (1812)

Scalariidae Lamarck, 1812.
Janthinidae Lamarck, 1822.
Recluziidae Iredale & McMichael, 1962, not available; Bouchet & Rocroi, 2005: 72, 254.

Epitoniinae Berry, 1910 (1812)

Janthina Röding, 1798

Janthina Röding, 1798: 75. Type species (by tautonymy): *Helix janthina* Linnaeus, 1758 (*H. janthina* cited in synonymy of *Janthina violacea* Röding, 1798); Recent, cosmopolitan.
Ianthina Lamarck, 1801: 427. Incorrect subsequent spelling of *Janthina* Röding, 1798 (many later authors used this incorrect spelling).
Janthinus Montfort, 1810: 214. Incorrect subsequent spelling of *Janthina* Röding, 1798.
Zanthina Fischer von Waldheim, 1823: 236. Incorrect subsequent spelling of *Janthina* Röding, 1798.
Ametistina Schinz, 1825a: 586 (suppressed under ICZN Opinion 989, 1972).
Hyanthina Porro, 1841: 87. Incorrect subsequent spelling of *Janthina* Röding, 1798.
Achates Gistel, 1848: 169 (unnecessary substitute name for *Janthina*); Mörch, 1860: 277. Type species (automatically that of the substituted name): *Janthina violacea* Röding, 1798 (= *Helix janthina* Linnaeus, 1758).
Ametistina H. Adams & A. Adams, 1854: 86 *(nomen nudum)*.
Amethystina Chenu, 1859: 118 *(nomen nudum)*.
Iodes Mörch, 1860: 273. Type species (by subsequent designation, Tryon, 1887: 34): *Iodes britannica* "Leach" Forbes & Hanley, 1852 (= *Helix janthina* Linnaeus, 1758).
Iodina Mörch, 1860: 282. Type species (by subsequent designation, Tryon, 1887: 34): *Janthina exigua* Lamarck, 1816; Recent, cosmopolitan.
Amethistina Mörch, 1860: 282; section of nominotypical subgenus of *Janthina*; attributed by Mörch to "Schintz". Type species (by subsequent designation, Tryon 1887: 34): *Janthina pallida* Thomson, 1840; Recent, cosmopolitan.
Hartungia Bronn, 1861: 110. Type species (by monotypy; combined description of a new genus and species): *Hartungia typica* Bronn, 1861; early Pliocene (Zanclean), Santa Maria Island, Azores; late Messinian to early Piacenzian, cosmopolitan.
Jantina Weinkauff, 1873: 66. Incorrect subsequent spelling of *Janthina* Röding, 1798.
Jodes Marschall, 1873: 122. Incorrect subsequent spelling of *Iodes* Mörch [*ex* Leach ms], 1860.
Jodina Marschall, 1873: 122. Incorrect subsequent spelling of *Iodina* Mörch, 1860.
Eligmope Dennant, 1889: 48 (*nomen nudum*).
Heligmope Tate, 1893: 328. Type species (by monotypy): *Heligmope dennanti* Tate, 1893 (= *Hartungia typica* Bronn, 1861).
Amethystina Pallary, 1920: 56. Incorrect subsequent spelling of *Amethistina* Mörch, 1860.

Violetta Iredale, 1929: 279. Type species (by original designation): *Janthina globosa* Swainson, 1822; Pliocene–Recent, cosmopolitan.

Parajanthina Tomida & Itoigawa, 1982: 60. Type species (by original designation): *Parajanthina japonica* Tomida & Itoigawa, 1982 (= *Hartungia dennanti chavani* Ludbrook, 1978); late Pliocene–early Pleistocene, cosmopolitan.

Kaneconcha Kaim, Tucholke & Warén, 2012: 427. Type species (by original designation): *Kaneconcha knorri* Kaim, Tucholke & Warén, 2012 (= *Hartungia dennanti chavani* Ludbrook, 1978).

Remarks. The name *Iodes* was first introduced as a *nomen nudum* by Gray (*ex* Leach ms) (1847a: 269) (Oct) and Gray (1847b: 148) (Nov) in the synonymy of *Janthina*. Its original rank was a subgenus of *Janthina*; the name was attributed by Mörch (1860) and Tryon (1887) to Leach. The name *Janthina britannica* was first introduced in synonymy (of *Janthina communis* Lamarck, 1822, i.e., *J. janthina*), but was made available under ICZN Art. 11.6.1 by its use as a valid name, e.g., by Mörch (1860: 273). Tryon (1887: 34) included the single species "*Ianthina britannica* Leach" in "*Iodes* (Leach) Gray, 1847", but it is not clear that this was intended to be a type species designation, as he stated that "The following sections of Mörch have very slight value", and that he was merely assigning a single species to each section. Nevertheless, it is the one published type species designation the writer is aware of. The same type species question applies also to *Iodina* Mörch, 1860 and *Amethistina* Mörch, 1860. Cossmann (1925: 158) also designated *Janthina exigua* as the type species of *Iodina*, and on the same page also designated *J. pallida* as the type species of "*Amethistina* Schinz 1825 (fide Moerch, 1860)" and so is taken here to have designated *J. pallida* as the type species of *Amethistina* Mörch, 1860.

Bronn (1861) compared his species *Hartungia typica* with *Janthina* species, and although he did not use a family-group heading, he expressly included it in Janthinidae. The Atlantic fossil species revised here were also referred to *Janthina* by Mayer (1864a, b). Finlay (1931) was the first to realize that *Turbo postulatus* Bartrum, 1919 belongs in *Heligmope* Tate, 1893 and that *Heligmope* is a genus of Janthinidae. Recognition that *Hartungia* Bronn, 1861 is an earlier name for *Heligmope* Tate, 1893 and that *Hartungia* belongs in the Janthinidae must be credited to Chavan (1951). The writer was informed by C. A. Fleming that Chavan's (1951) brief paper inspired Fleming's (1953a) research. Chavan (1951) regarded *Hartungia* as a subgenus of *Acrybia* H. Adams & A. Adams, 1853. Chavan thought *Acrybia* was the valid synonym of *Bulbus* Brown, 1839, because the name *Bulbus* had been used earlier by Humphrey (1797). Cossmann (1925: 159) had come to the same conclusion and ranked *Heligmope* Tate, 1893 as a subgenus of *Acrybia*, so Chavan (1951) was following Cossmann's classification, although Cossmann (1925) did not mention the name *Hartungia*. However, Humphrey's (1797) work is non-binominal and all names introduced in it are unavailable (ICZN Opinion 51, 1912), which leaves *Bulbus* Brown, 1839 as an available name. *Bulbus* is a genus of Naticidae, mainly distributed in the boreal region. Dell (1990: 153) discussed the genus *Bulbus*, treated *Acrybia* as a junior synonym, and recorded three Antarctic species. Fleming's (1953a) brief list of species related to *Hartungia typica* and suggestion that they provided a novel means of Pliocene correlation provided the initial impetus for the present work.

A significant difficulty with Laursen's (1953) otherwise excellent monograph of *Janthina* is his failure to identify type specimens. Laursen illustrated Linnaeus's (1758) syntypes of *Helix janthina* in Uppsala, Sweden, and in the Linnean Society's collection in London, but although he recognized that two species are represented he did not designate an unequivocal lectotype. Laursen also did not mention any type material of any other species names. Therefore, a major emphasis of the present work has been to stabilize the nomenclature by identifying all possible available names with particular species by finding or designating type specimens, particularly for the early-proposed names that could be referred to any of several species. Twenty two neotypes and six lectotypes are proposed in this report to identify names unambiguously, to avoid future confusion about which names apply to which species. An Appendix (p. 208) lists the new type designations in the present work. As all revised species are at present or are assumed to have been formerly cosmopolitan neustonic species in temperate and tropical seas, the usual requirement that neotypes should come from as near as possible to the original type locality is considered to be unimportant in this case. Also, some type specimens have debated localities (e.g., *Recluzia rollandiana* Petit de la Saussaye, 1853—from western Mexico or from New Caledonia?). Designating a suitable neotype of the appropriate species was deemed more critical than matching the original type locality for cosmopolitan *Janthina* and *Recluzia* species.

The teleoconch of *Janthina* is characterized by its violet colour, its more-or-less equidimensional heliciform shape, its fine axial teleoconch sculpture (present in only some of the living species, but in all extinct species) resembling that of finely sculptured *Epitonium* species, and its sinus in the outer lip. Differences between *Janthina*, *Recluzia* and benthic Epitoniidae are listed in Table 1. In the fossil species *J. typica*, *J. krejcii* and *J. chavani* the sinus is small and located at the base of the outer lip, semicircular in most specimens, although a little wider in some specimens of *J. chavani*. It generates a spiral fold parallel to the inner lip, wider than the other spiral folds on the rest of the surface. In contrast, in most living species the sinus is V-shaped and occupies the entire width of the outer lip, with its apex at the centre of the lip, and does not generate any swelling of the shell surface. The sinus is shallow in *Janthina janthina* and more obvious in the basal limb of the lip than adapically, and is very shallow in *J. pallida*, but it is deeper, wider and more prominent in the other living species, particularly in *J. exigua* and *J. umbilicata*. Photographs of living specimens (Figs 4B–C, 5A, E) reveal that the (main?) function of the sinus is to accommodate the head and snout as they protrude permanently from the shell. In a species that cannot retract its head at any time, as it must protrude (with the mesopodium) to retain the bubble float, the sinus accommodates the protruding head. However, the much narrower and more basal lip sinus of the extinct species *J. typica*, *J. krejcii* and *J. chavani* suggests that the sinus originally had a different function, possibly to allow the extrusion of egg capsules. The axial sculpture and the closely similar protoconch are characters in common with benthic Epitoniidae. *Janthina* essentially contains short, wide, violet, neustonic species of *Epitonium* that have undergone mutations of the pedal mucus gland and propodium enabling them to form mucus bubbles, attach them to each other to form a float, lay relatively large egg capsules attached to the float rather than chalazae-linked small capsules, and all the other necessities of the neustonic habit. The minor shape and sculptural characters used by, e.g., Mörch (1860) and Iredale (1929) to distinguish genera or subgenera within *Janthina* are regarded here as merely species characters. The groups segregated by Mörch (1860) were treated as sections of *Janthina* by Thiele (1929: 225), but have been used by few other authors. Whether the adult lays egg capsules or broods its eggs in the oviduct also is a developmental difference, of no phylogenetic significance (Bouchet, 1990).

Included species. Species included here in *Janthina* are listed and revised in their order of appearance in the stratigraphical record.

1 *Janthina typica* (Bronn, 1861) (= *Janthina hartungi* Mayer, 1864, *Heligmope dennanti* Tate, 1893, *Turbo postulatus* Bartrum, 1919, *Acrybia (Hartungia) chouberti* Chavan, 1951, *Hartungia elegans* Tomida & Itoigawa, 2001, *Eunaticina abyssalis* Simone, 2014), late Miocene–early late Pliocene (Messinian–early Piacenzian), Azores, Madeira, Selvagem Is., SW Atlantic, Morocco, New Zealand, southern Australia, Japan; presumably formerly cosmopolitan.

2 *Janthina krejcii* sp. nov., Pliocene (Zanclean), Santa Maria I., Azores; presumably formerly cosmopolitan.

3 *Janthina chavani* (Ludbrook, 1978) (= *Parajanthina japonica* Tomida & Itoigawa, 1982, *Kaneconcha knorri* Kaim, Tucholke & Warén, 2012), late Pliocene–early Pleistocene (late Piacenzian–Calabrian), southern Australia, New Zealand, Japan, mid-Atlantic ridge; presumably formerly cosmopolitan.

4 *Janthina globosa* (Swainson, Jan 1822) (= *J. prolongata* Blainville, Aug 1822), Piacenzian/Gelasian–present day, cosmopolitan in warm seas; Piacenzian–Gelasian fossils from Jamaica and Luzon, Philippines.

5 *Janthina janthina* (Linnaeus, 1758) (30 synonyms), one Holocene fossil in New Zealand, many reported from core tops in the Mediterranean Sea and the Cariaco Basin, Caribbean; living, cosmopolitan in warm seas.

6 *Janthina exigua* Lamarck, 1816, living only, cosmopolitan in warm seas.

7 *Janthina pallida* Thomson, 1840, living only, almost cosmopolitan in warm seas; not recorded from New Zealand or eastern Australia.

8 *Janthina umbilicata* d'Orbigny, 1841, living only, cosmopolitan in warm seas.

Taxa not included. The following taxa have been included in Janthinidae by earlier authors, but are excluded here from Epitonioidea:

1 Röding (1798: 75–76) included six species in *Janthina*, first section, "Elevata", and a further nine species and four varieties in a second section, "Depressiuscula". The second section obviously has nothing to do with *Janthina* as used now, as most names refer to Gmelin (i.e., mostly Linnaeus) *Helix* species (*H. pomatia*, with two varieties; *H. scalaris*, *H. ligata*, *H. jamaicensis*, *H. picta*) and three are *nomina nuda*. Four of the six names in section Elevata also are *nomina nuda*, none of which has been referred to again to the writer's knowledge (*J. singularis*, *J. turbinoidea*, *J. limbata*, *J. pellucida*). The fifth name, *J. cytherea*, refers to Chemnitz (1786: pl. 123, fig. 1063), a basal view of a small blue-grey shell on a plate showing terrestrial snails, so this is an available but probably unidentifiable name.

2 *Janthina alba* Anton, 1838: Anton (1838: 50) noted that the specimen he described as *Janthina alba* might really be a young specimen of *Helix pisana*. Dr K. Schniebs (Senckenberg Naturhistorische Sammlung Dresden, pers. comm. 23 Feb 2016) stated that Anton's own copy of his catalogue has a hand-written note by Anton: "It is *Helix pisana* Mllr. juv.", so this name is a synonym of *Theba pisana* (Müller, 1774), Helicidae. A type specimen is not present in Dresden.

3 *Kaiparathina* Laws, 1941: Laws (1941) presumably composed this generic name because he thought the shallow sinus in the outer lip of the early Miocene type species indicated that it is related to *Janthina* (*K. praecellens* Laws, 1941, Pakaurangi Point, Kaipara Harbour, New Zealand; Otaian New Zealand Stage, 21.7–18.7 Ma, late Aquitanian–early Burdigalian). He did not refer the genus to a family, apparently deliberately, although he compared it with some of the characters of *Heligmope* (i.e., *Hartungia*; synonymized here with *Janthina*). This small (height 3.2 mm), thick, aragonitic shell with a nacreous inner layer was referred to the Trochidae by Beu (1973) because a nacreous inner shell layer is plesiomorphic for Vetigastropoda, particularly Trochoidea and Turbinoidea (Williams *et al*., 2010). This position was confirmed by Marshall (1993) when he described five living Southwest Pacific species, recorded fossils as old as early Eocene, and referred the genus to Margaritinae Kaiparathini. Williams (2012: 589) placed *Kaiparathina* in family Trochidae, subfamily Kaiparathininae Marshall, 1993.

4 *Edithais pehuensis* (Marwick, 1926: 319, pl. 73, figs 6, 8), late Miocene (Tongaporutuan New Zealand Stage, Tortonian); referred to *Lippistes* Montfort, 1810 by Marwick (1926), to *Heligmope* by Finlay (1931: 5) following a suggestion by J. Marwick, and to *Hartungia* by Fleming (1953a; 1966: 49, pl. 90, figs 948, 950), Tomida & Nakamura (1981) and Tomida & Kitao (2002). However, it was referred to *Concholepas* Lamarck, 1801 by Beu (1970) and to the cosmopolitan muricid genus *Edithais* Vermeij, 1998 by Vermeij (1998). This unusual shell with an isostrophic spire and regular, low, wide spiral cords has a general resemblance to *Janthina typica*, but the enlarged spiral ridge bordering the wide umbilical hollow fades out before the aperture, i.e., it is not generated by a sinus in the lip, the axial ridges are low, wide and widely spaced, and the spire is below the top of the aperture. The similarity is increased by its thin, dark brown, calcitic outer layer over a thicker aragonitic inner layer, but this is seen also in many other muricids. Holotype (still the only known specimen): GNS TM4494, mid-Tongaporutuan New Zealand Stage (mid-Tortonian, late Miocene, c. 9 Ma), Okoke Road, 1.2 km west of Pehu trig. station, Waitara district, North Taranaki. *Edithais*, Family Muricidae.

5 *Janthina cimbrica* Sorgenfrei (1958: 176, pl. 32, fig. 110), Arnum Formation, Denmark (Miocene), from a depth of 55 m in a well at Glejbjerg. This minute (H 1.68, D 1.37 mm) evenly inflated shell with sculpture of microscopic cancellate lirae does not belong in Epitoniidae. It is a larval shell, type species of *Mioseguenzia* Nordsieck (1973) (*nomen nudum*), recognized as cypraeacean by Quinn (1983: 727, 744) following comments by P. Bouchet, and referred to *Cypraea* by Janssen (1984: 195). Janssen (1984: pl. 8, figs 7–8) illustrated very similar protoconchs of Cypraeidae from Winterswijk-Miste, the

Netherlands (middle Miocene). *Cypraea* (*sensu lato*), Family Cypraeidae.

6 *Janthina primigenia* Seguenza (1867: 18, figs 1a–3) and *J. delicata* (Philippi, 1844) var. *subangulosa* Seguenza (1867: 19), Pliocene, Messina, Sicily. In a review of Seguenza's types remaining in the University of Florence, Bertolaso and Palazzi (2000: 34, figs 54–55) illustrated type material of *Janthina delicata* var. *subangulosa*, and concluded that it is a synonym of *Torellia delicata* (Philippi, 1844). Evidently no type material remains of *J. primigenia*; many of Seguenza's types were destroyed in the Messina earthquake. The small size (D c. 8 mm), low, wide shape, numerous narrow whorls and simple, close, fine spiral sculpture revealed in Seguenza's illustrations show that these names do not refer to species of *Janthina*; both are assumed to refer to *Torellia delicata* (Philippi, 1844). *Torellia,* Family Capulidae.

7 Shuto (1969: 98, pl. 6, figs 15–18) recorded *Janthina janthina* from latest Miocene rocks of Panay Island, Philippine Islands. His illustrations show a small, smooth, low-spired shell with a narrowly open umbilicus, evenly inflated whorls without the peripheral angulation of *J. janthina*, a straight acline outer lip, and a large (width 3.25 mm) low protoconch of less than one whorl, so it is clearly a direct-developing species; apparently based on a juvenile specimen of a terrestrial pulmonate snail.

8 Sherborn (1922–1933) listed four further names in *Janthina* based on Palaeozoic fossils. Mörch (1860: 272) also listed several Palaeozoic genera that he thought might be related to living pelagic gastropods, including pteropods and heteropods: *Platyschisma*, *Raphistoma*, *Scalites*, and several species of *Murchisonia* and *Pleurotomaria*. This list was repeated by Tryon (1887). In view of suggestions of a poorly known pre-late Miocene fossil record (Nützel, 1998: 89) it is important to record that all these Palaeozoic fossils are now referred to superfamilies Murchisonioidea or Pleurotomarioidea and have no relationship to Epitonioidea. The species listed by Sherborn are all Carboniferous:

  a *Janthina glabrata* (Phillips).—McCoy in Griffith (1842: 19); *Pleurotomaria glabrata* Phillips (1836: 228), Pleurotomarioidea.

  b *Janthina helicoides* (Phillips).—McCoy in Griffith (1842: 19); *Pleurotomaria helicoides* (J. Sowerby) in Phillips (1836: 228); *Ampullaria helicoides* J. Sowerby (1826: 40), Pleurotomarioidea.

  c *Janthina issedon* Verneuil in Murchison *et al*. (1845: 341, pl. 23, figs 5a–b); *Scalites issedon* (Verneuil) in d'Orbigny (1850: 121); *Scalites* was referred to Raphistomatidae (Pleurotomarioidea) by Knight *et al.* (in Moore 1960: 201).

  d *Janthina ovoidea* (Phillips).—McCoy in Griffith (1842: 19); *Pleurotomaria ovoidea* Phillips (1836: 228), Pleurotomarioidea.

Nomina nuda. Several names proposed in *Janthina* were not accompanied by descriptions or illustrations and remain *nomina nuda*. They are listed here with comments, and are not included in any of the synonymies below.

1 *Janthina subsinuosa* Bronn: Bronn (1826: 328) merely listed this name. Presumably based on a Recent Mediterranean species of *Janthina*, but unrecognisable; not *J. exigua*, which is listed on the same page.

2 *Janthina vulgaris* Grant: Grant (1833: 14) recorded large numbers of *Janthina* "*vulgaris* Lam." and *Velella* cast ashore at Whitsand Bay, near Land's End, Cornwall. No description or reference accompanied the name. Gray later published the name *J. vulgaris* in several places, but it remained a *nomen nudum* until validated by Gray (1850: 101), referring to earlier illustrations by Lister, "Forskael", Cuvier, Lesueur, and Quoy [& Gaimard] as referring to this species. These references demonstrate that Gray (1850) intended to use the name *J. communis* (= *J. janthina*) rather than *J. vulgaris*; he used the name *J. communis* for the same Quoy & Gaimard illustration earlier in the same work (Gray 1850: 9; referring to Lister, Quoy [& Gaimard, 1833, pl. 29, figs 1–2] and "Forskael"), and there is no voucher material bearing the name *Janthina vulgaris* in NHMUK.

3 *Janthina bifida* "Nuttall": Jay (1839: 68) listed this name without any indication or description, other than the locality "Wahoo" (Oahu, Hawaii) and it has never been made available.

4 *Ianthina rotundata* (Leach ms) Dillwyn and *Ianthina mediterranea* (Jeffreys ms) Dillwyn: Dillwyn (1840: 59) included in a section "Zoological memoranda" the following statement: "1824, July—many thousand shells of *Janthina*, of which some retained the animals alive, and skeletons of the Medusa Velella and of the Medusa Navicula were thrown on the shores of Oxwich Bay—the weather was remarkably hot at the time. A few of these *Janthina*, which had before at different times been washed up in the same bay, received from Dr Leach his MS name of *J. rotundata*; and Mr Jeffreys informs me, that among the multitude which now covered the shore, he detected a few shells of *J. mediterranea* mixed with them" [Italics added]. Smart & Cooke (1895: 298) also gave an account of strandings in the Scilly Isles under the name "*Ianthina rotundata* Leach", presumably referring to *J. janthina*, although again there is no way of telling which species they intended. They noted: "Occasionally driven on shore from the westward, on the beaches facing south-west. The Scillonians have an idea that they come in at fixed periods of about seven years. The South Wales fishermen about Tenby have the same belief. … Occasionally they have occurred in such numbers that hundreds might have been collected at once". The main other mention of these *nomina nuda* the writer is aware of is by Locard (1898: 1), who listed "[*Janthina*] *rotundata*, Leach, 1840. *In* Dillwyn, *Contr. Hist. Swans*., p. 59" in the synonymy of *J. communis*. Laursen (1953) also included *J. rotundata* Dillwyn in the synonymy of *J. janthina*, but did not mention *J. mediterranea.* Some later authors have listed *J. rotundata* Leach as a *nomen nudum* in the synonymy of *J. janthina*, but the writer is not aware of any means of determining which species were intended by these names.

5 *Iodes angulatus* and *Iodes norrisii* Leach: Gray [*ex* Leach ms] (1847a: 269) published a list of names of British Mollusca, including the *nomina nuda Iodes angulatus* and *Iodes norrisii.* In Gray's editorial introduction to Leach (1852: x) (Petit, 2012: 94, note 29), Gray stated that *Iodes angulatus* Leach is "*Ianthina vulgaris* Lam." (*nomen nudum*, presumably intended for *J. communis* Lamarck, = *J. janthina*), but did not identify *Iodes norrisii*.

6 *Janthina striata* Montrouzier: Montrouzier (1860: 115) listed this name after his description of *J. capreolata* (Montrouzier, 1860: 114, pl. 11, fig. 4) without providing any description or indication for *J. striata*, and the name has never been made available.

7 *Janthina bipartita* Tenison Woods: Tenison Woods (1878:

44) included in a list of Tasmanian shells the three names *Ianthina exigua* Lamarck, *Ianthina communis* Lamarck, and *Ianthina bipartita* "Gray?". No description, locality or other comments followed the last name, and the writer knows of no other mention of it.

8 *Janthina nicobarica* "Reeve": Laursen (1953: 16) mentioned after the synonymy of *J. janthina* that specimens in ZMUC are labelled "*Janthina nicobarica* Reeve". He had also seen the name attributed to Röding. It was also listed by Rosenberg (2017) in the synonymy of *J. janthina*, attributed to Laursen. However, it was not made available by any authors, and remains a *nomen nudum*.

Janthina typica (Bronn, 1861)

Figs 24–25

Hartungia typica Bronn, 1861: 119, pl. 19, figs 3a–d; Bronn, 1862: 32 (in part); Fleming, 1953a: 135; Veiga Ferreira, 1955: 6, 8; Beu & Maxwell, 1990: 292, 411, pl. 37a–b; Tomida, 1996: pl. 33, figs 3a–4; Maxwell in Spencer *et al.*, 2010: 245.

Janthina hartungi Mayer, 1864a: 242, pl. 6, figs 41a–c; 1864b: 62, pl. 6, figs 41a–c; Berkeley Cotter, 1892: 285; Joksimowitsch, 1911: 80, 94; Gagel, 1911: 409; Berkeley Cotter, 1953: 100; Veiga Ferreira, 1955: 9–10.

Heligmope dennanti Tate, 1893: 329, pl. 7, figs 5–5a; Finlay, 1931: 1.

Turbo postulatus Bartrum, 1919: 100, pl. 7, fig. 14.

Acrybia (Heligmope) dennanti (Tate).–Cossmann, 1925: 161, pl. 4, figs 11–12; pl. 9, fig. 3 (copy of Tate, 1893: pl. 7, fig. 5).

"Turbo" postulatus Bartrum.–Bartrum & Powell, 1928: 141, pl. 25, figs 6–7; Marwick, 1931: 28, 43.

Heligmope postulatus (Bartrum).–Finlay, 1931: 1; Laws, 1940b: 38; Marwick, 1948: 6, 8; Law, 1950: 7, faunal list.

Janthina (Hartungia) typica (Bronn).–Wenz, 1940: 815; Tomida *et al.*, 2013: 60, figs 3A–D only (not figs 3E–L).

Bulbus (Heligmope) denanti [sic] (Tate).–Wenz, 1941: 1036, fig. 2967.

Acrybia (Hartungia) chouberti Chavan, 1951: 135, fig. 1; Lecointre, 1952: 114; Choubert, 1965: 49; Brébion, 1973: 50.

Hartungia chouberti (Chavan).–Fleming, 1953a: 135; Ludbrook, 1978: 122, pl. 12, figs 17–19.

Hartungia dennanti (Tate).–Fleming, 1953a: 135; Darragh, 1970: 166; Ludbrook, 1973: 256, pl. 28, figs 93–94; Darragh, 1985: 106.

Hartungia postulata (Bartrum).–Fleming, 1953a: 135; Schofield, 1958: 252; Marwick, 1965: 10, table 4; Fleming, 1966: 49.

Janthina typica (Bronn).–Krejci-Graf *et al.*, 1958: 336 (in part); Zbyszewski *et al.*, 1961: 15; Zbyszewski & Veiga Ferreira, 1962: 219, 222, 224, 227–228, 273; Beu & Raine, 2009: BM292; Meco *et al.*, 2015: 61, figs Appendix A–B.

Hartungia sp.–Wilkins, 1963: 58; Tomida & Itoigawa, 1984: 112; Tomida, 1989: 96; Ozawa & Tomida, 1992: 428.

Hartungia dennanti dennanti (Tate).–Ludbrook, 1978: 122, pl. 12, figs 15–16.

Parajanthina japonica Tomida & Itoigawa, 1982: 60, pl. 19, figs 1a–c (in part only).

Parajanthina sp.–Tomida & Itoigawa, 1982: 62, pl. 19, figs 2–3.

Hartungia sp. A.–Nakamura *et al.*, 1999: pl. 2, figs 17a–b.

Hartungia elegans Tomida & Nakamura, 2001: 217, figs 2.1a–e, 2.2a–e.

Eunaticina abyssalis Simone, 2014: 586, figs 10E–K.

Type material. *Hartungia typica*, location of any original type material unknown; extensive enquiries over more than 40 years have brought none to light. Bronn's introduction to his descriptions of the fossils of Santa Maria Island in Hartung (1861: 116) reads: "In the spring of 1858 I received from Hartung a collection of hand specimens of Tertiary limestone with fossil shells for investigation and determination, which he had collected on Santa Maria. A year later I received another similar consignment, which Mr Drouet from Toyes had gathered at the same time as Mr Hartung, but which contained no other species than the first. I give here the results of my research" (translated from German by T. A. Darragh, Museum Victoria, pers. comm. 10 Nov 2015). Bronn had only one specimen of *Hartungia typica* (Bronn, 1861: 129, table 3) so the "contained no other species" statement makes it certain that the holotype belonged to the German geologist Hartung rather than to Drouet. Bronn's fossil collection was originally in the University of Heidelberg, but was purchased by Louis Agassiz (Cleevely, 1983: 68) and is now in Paleontology, Museum of Comparative Zoology, Harvard University. However, it does not include any Azores material (K. Boss, Museum of Comparative Zoology, pers. comm. 18 May 1983). Possibly the Azores material described by Bronn was returned to the collectors, Hartung and Drouet. In view of the acquisition by Mayer of the material in Heidelberg described by Bronn (see below under *Remarks*) it is also possible that all Bronn's Azores material was sent to Mayer and never returned, but again, it is not present in Mayer-Eymar's collection in NMB. The location of any Azores material formerly belonging to Hartung also is unknown.

Janthina hartungi, again no original material known. Mayer-Eymar's collection (in NMB) includes only NMB Po.6227, two poor, small (shell fragment c. 11.5 mm wide) impressions in modelling clay from the same cavity in the rock at Santa Maria Island, identified by Mayer-Eymar as *Janthina hartungi*, and labelled "Ponta dos Matos, S. Maria". This impression of a partial spire bears weak axial ridges and vague, low spiral folds (Fig. 24M), indicating that it is indeed a very poor partial mould of a *Janthina* species similar to *J. typica*, but Mayer's (1864a, b: pl. 6, fig. 41) illustrations of a complete shell (Figs 25D–F) cannot have been based on it. Mayer (1864a, b: 63) recorded a specimen from "Ponta dos Mattos" (sic), but the modelling clay impression is not identifiable to species and is not considered to be type material. Again, the location of the specimen Mayer's illustration was based on is unknown. Therefore, a neotype is required for both *Hartungia typica* and *Janthina hartungi*, unequivocally to establish the application of these names to the present species. To find any genuine well-preserved Santa Maria Island specimens of *Janthina typica* in modern collections or to re-collect specimens at Santa Maria Island proved very difficult. The writer visited Santa Maria Island with Bernard Landau in February 1998, but localities near sea-level in the Touril Complex were all inaccessible (during winter) through either severe wave action or their location at the foot of inaccessible cliffs. None was found in the overgrown remnants of the limestone quarry at Figueiral, although pectinids were common. The one well-preserved specimen from Santa Maria Island referable to *Janthina typica* that the writer is aware of is a very small one, MIGM1312. This specimen (Figs 24A–C) is here designated the neotype of both *Hartungia typica* Bronn, 1861 and *Janthina hartungi* Mayer, 1864. It is from "Farolim da Ponta

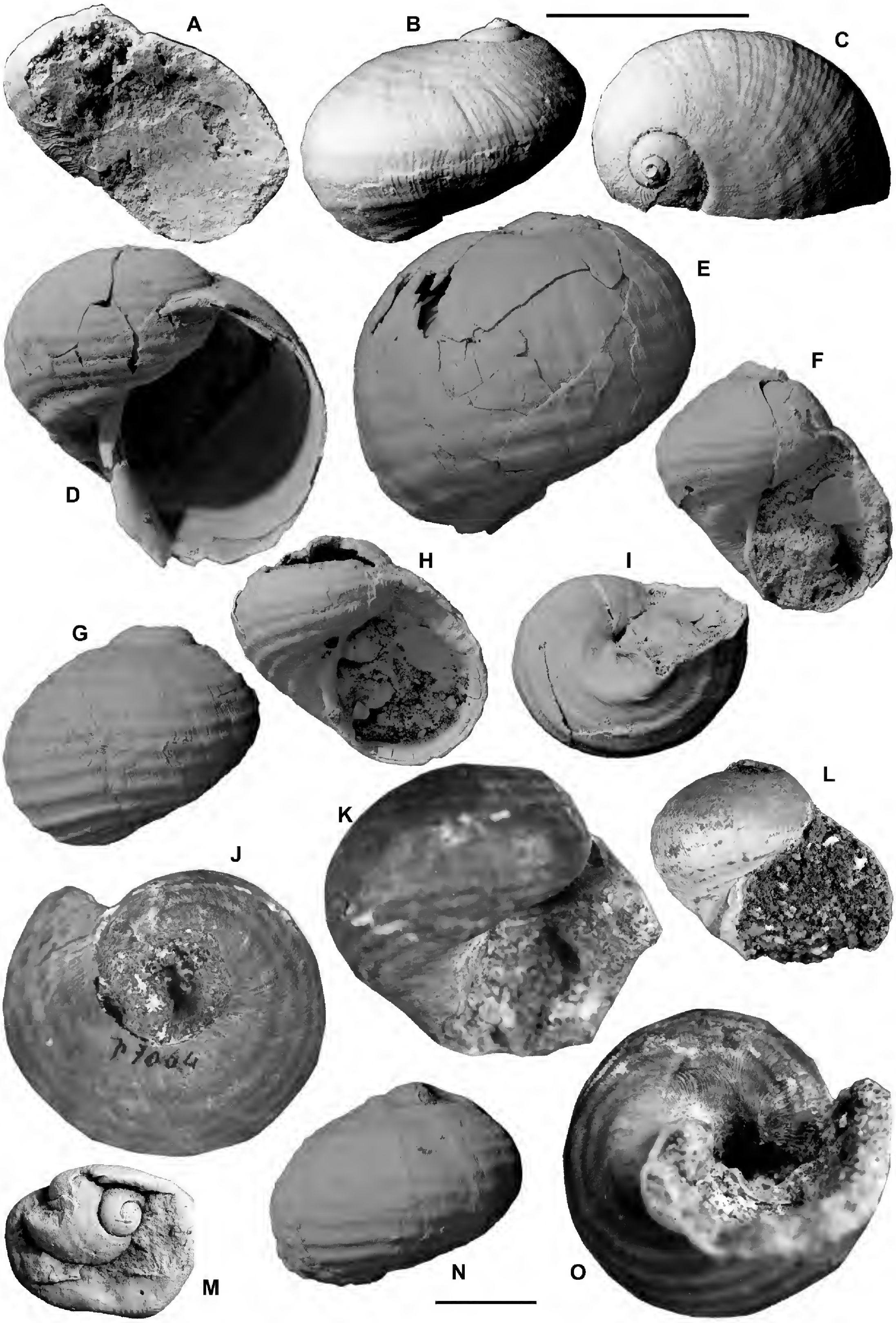

Figure 24. Specimens of *Janthina typica* (Bronn), all except A–C enlarged uniformly. *(A–C)* neotype designated here of *Hartungia typica* Bronn, 1861 and *Janthina hartungi* Mayer, 1864, MIGM1312, Farolim da Ponta do Norte (North Point Lighthouse), Santa Maria I., Azores, Zanclean (photos by C. Marques da Silva). *(D, E)* neotype designated here of *Turbo postulatus* Bartrum, AUGD G5721, Kaawa Creek, SW Auckland, New Zealand, Opoitian (Zanclean). *(F–I)* 2 specimens, Kaawa Creek, SW Auckland, Opoitian (Zanclean); F, I, GNS TM4670; G–H, GNS TM4671. *(J, K, O)* holotype of *Acrybia (Hartungia) chouberti* Chavan, Service Géologique du Maroc, Rabat, Morocco, P7064; unwhitened photos from Rabat sent by N. H. Ludbrook (see also Ludbrook 1978: 122, pl. 12, figs 17–19, at half this scale); Fouarat, E of Casablanca, Morocco, Zanclean. *(L)* abraded specimen, DBUA-F-428, University of the Azores, Ponta Delgado, Azores; from Ponta do Castelo, SE tip of Santa Maria I., Azores, Zanclean, coll. S. Ávila, 15 Sep 2006 (photo by S. Ávila). *(M)* NMB Po.6227, *ex* Mayer-Eymar collection; possible type material of *Janthina hartungi* Mayer, modelling clay impression from natural cast in rock, Ponta dos Matos, Santa Maria I., Azores, Zanclean. *(N)* GNS GS12289, E branch Greeks Creek, Arahura Valley, Westland, New Zealand, Waipipian (early Piacenzian). Scale bars 10 mm; upper bar applies to Figs 24A–C, lower bar applies to all other figures.

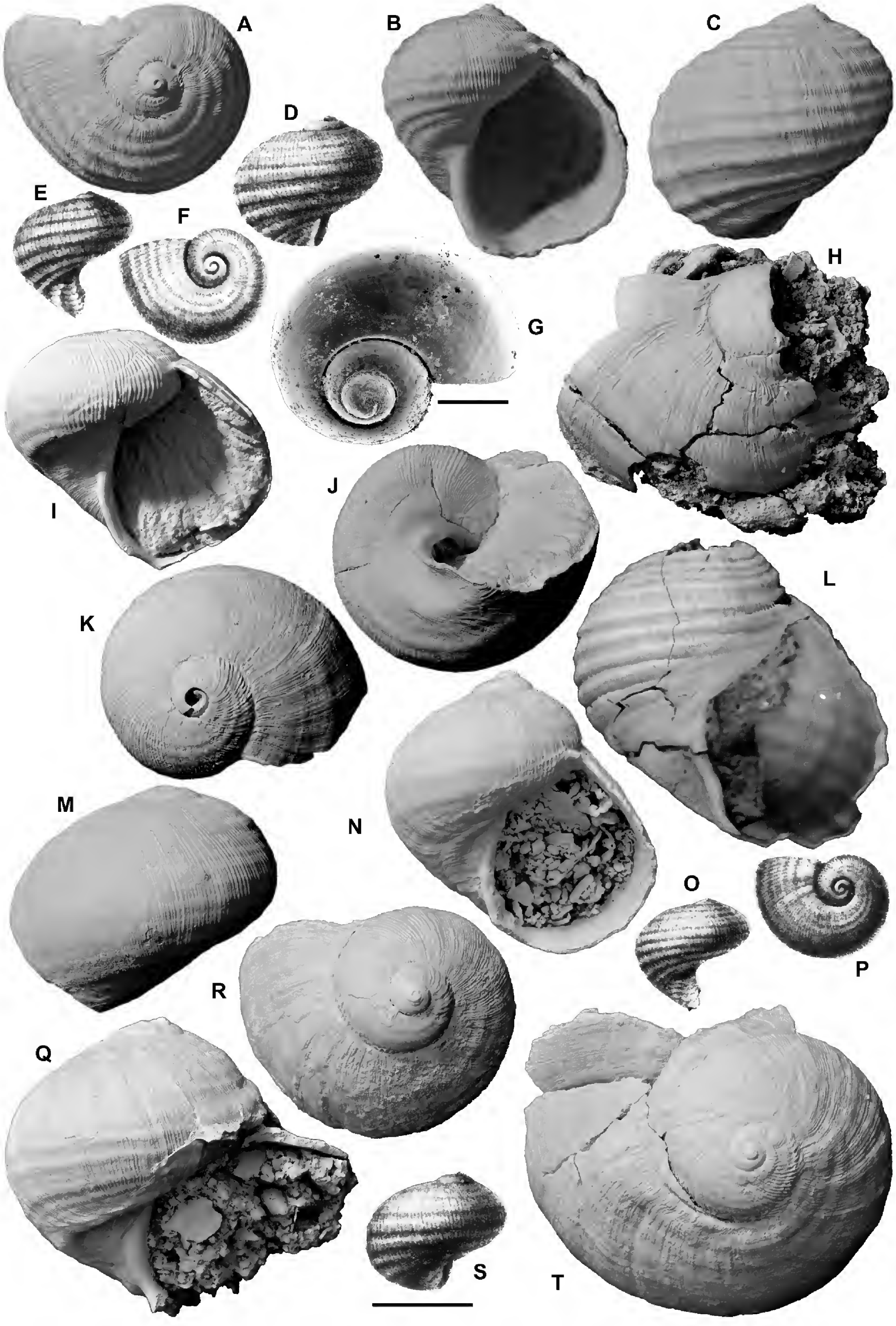

Figure 25. Specimens of *Janthina typica* (Bronn). *(A–C)* GNS WM7656, Grange Burn Fm, Kalimnan (Zanclean), Muddy Creek, near Hamilton, Victoria, Australia; i.e., from type locality of *Heligmope dennanti* Tate. *(D–F)* copy of Mayer's (1864: pl. 6, figs 41a–c) illustrations of *Janthina hartungi,* Santa Maria I., Azores, Zanclean; slightly enlarged from published size, H 19, D 22 mm (photos by D. L. Homer). *(G, I–K, M)* weakly sculptured specimen, MNHN IM.2000-27158, holotype of *Eunaticina abyssalis* Simone, *Marion Dufresne* cruise MD55 stn 45-CB79, 1500–1575 m, off Itaúnas, Espiritu Santo State, Brazil, SW Atlantic, probably Zanclean; G, SEM, apical 2.5 teleoconch whorls, showing outer calcitic layer removed; I–K, M, apertural, ventral, apical and posterior views. *(H)* GNS GS12164, fragment, Whenuataru Tuff (Waipipian, early Piacenzian), Tarawhenua Peninsula, Pitt I., Chatham Islands; oblique latero-dorsal view. *(L)* SAMA T1494A, lectotype designated here of *Heligmope dennanti* Tate, Grange Burn Fm, Kalimnan (Zanclean), Muddy Creek, near Hamilton, Victoria, Australia (photo by D. L. Homer). *(N, Q, R, T)* ULPGC LE20151–2, Universidad de Las Palmas de Gran Canaria, Canary Islands; largest two of six specimens from La Esfinge, Gran Canaria, Canary Islands, Zanclean; N, R, LE20152; Q, T, LE20151, broken outer lip partially retained in sediment. *(O, P, S)* copies of Bronn's (1861: pl. 19, figs 3a–d) illustrations of the holotype of *Hartungia typica*; Santa Maria I., Azores, Zanclean; at published size, H 18, D 22 mm (photos by D. L. Homer). Scale bars: Fig. 25G = 500 µm; Figs 25D–F and 25O–P, S are copies of published figures, approx. natural size; lower scale bar, 10 mm, applies to all other figures.

do Norte" (North Point Lighthouse), Santa Maria Island. Ponta do Norte is now clearly understood to be in early Zanclean Touril Complex, following the reinterpretation by Sibrant *et al.* (2015). Unfortunately, the apertural side of the neotype is poorly preserved, the specimen evidently having been attached to the outcrop by this side, but the specimen definitely has spiral folds and fine axial ridges over the entire teleoconch, and has a low spire as in all other small specimens of *J. typica*.

Heligmope dennanti, five syntypes in SAMA Tate type collection; SAMA T1494A–B, two syntypes, "Miocene", Muddy Creek, near Hamilton, western Victoria (Grange Burn Formation, Kalimnan Australian Stage, Zanclean, early Pliocene; Beu & Darragh, 2001: fig. 6); SAMA T1515A–C, three syntypes, Hallett Cove Sandstone (Piacenzian), labelled "Miocene, Hallett's Cove, St Vincent Gulf", coast south of Adelaide, South Australia. The specimens from Grange Burn Formation (T1494A–B) are both well-preserved specimens of *Janthina typica*. In contrast, one of those from Hallett Cove Sandstone (T1515B) is a small, incomplete shell probably assignable to *J. typica*, with a low spire and obvious spiral folds all over, whereas the other two (T1515A, C) are more complete specimens with no spiral folds on the sutural ramp. They are identified as *J. chavani*, despite Ludbrook's (1978: 122) misgivings about their identity. As noted above under "Biostratigraphy", the specimen of *J. typica* presumably is from the lower, early Piacenzian part of the formation, whereas the specimens of *J. chavani* presumably are from the overlying late Piacenzian–Gelasian part of the formation. Tate's two Muddy Creek syntypes were illustrated by Ludbrook (1973: pl. 28, figs 93–94) in an unusual oblique dorso-lateral view necessitated by their still being glued to Tate's tablet. A lectotype designation is necessary because two species are present among Tate's syntypes. Tate's figured syntype, SAMA T1494A (Fig. 25L) from Grange Burn Formation at Muddy Creek, Victoria, is much the larger of the Muddy Creek syntypes and is here designated the lectotype of *Heligmope dennanti*. The paralectotype T1494B is a juvenile specimen. The lectotype has the spire tip missing, but both Muddy Creek specimens have obvious, prominent spiral folds over the entire teleoconch and are conspecific with the neotype of *Hartungia typica*.

Turbo postulatus, holotype basal fragment not found in AUGD (N. Hudson, AUGD pers. comm. 24 Sep 2012). The specimen selected by Bartrum & Powell (1928: 141, pl. 25, figs 6–7) as the "neotype", AUGD G5721 (Figs 24D–E) is here again designated the neotype of *Turbo postulatus*, although it had no status as a neotype in 1928, as the original type material was still available (ICZN Article 75.1). Both specimens are from Kaawa Creek, coast south of Waikato Heads, southwest Auckland, North Island, New Zealand (Opoitian New Zealand Stage, Zanclean, early Pliocene; Cooper, 2004: fig. 13.1). Material of *Janthina typica* from this site is rather fragile and tends to disintegrate through the calcite outer layer flaking off the aragonite inner layer, and the neotype has been reassembled recently by N. Hudson (AUGD), so presumably the holotype fragment disintegrated many years ago. A neotype is required to establish that the name applies to *J. typica* rather than supplanting *J. chavani*, which occurs at several other New Zealand localities. The neotype is an unusual, highly inflated, subspherical specimen with a short spire, relatively weak spiral folds, a strongly and evenly inflated last whorl, and a particularly prominent major fold generated by the sinus in the outer lip, but agrees with other material of *J. typica* in having spiral folds over the entire surface. Other specimens from Kaawa Creek (e.g., Figs 24F–I) are closely similar to specimens from Grange Burn Formation at Muddy Creek, Victoria (Figs 25A–C, L) and the neotype of *Hartungia typica* in shape and sculpture, and there is no doubt that the Kaawa Creek population falls within the variation of *Janthina typica*.

Acrybia (Hartungia) chouberti, holotype in G. Lecointre collection, Service Géologique du Maroc, Rabat, Morocco, P7064 (Ludbrook, 1978: 122, pl. 12, figs 17–19; Figs 24J–K, O), not seen; plaster casts in Paléontologie collection, MNHN, and GNS WM7327. The type locality in Morocco was described by Chavan (1951) as "Aïn Sebaa, cuttings from well 10 … in sandstone, with *Semicassis* cf. *laevigata* (Defr.), *Gryphaea forskali* (Chemn.), *Balanus perforatus* Brug. Holotype …; two fragments; one internal mould" (translation from Chavan, 1951: 136). However, the cast in GNS (WM7327) bears the locality label "Dar bel Hamri". The locality was described by Chavan (1951: 135) as "from the series of l'Oued Fouarat", and is known in most works on Moroccan Plio-Pleistocene stratigraphy (e.g., Arambourg, 1969) as Fouarat. Fouarat was located on the map by Lecointre (1963: 22) a few kilometres east of Casablanca. The holotype was said by Chavan (1951: 135) to be "a little taller than wide", but his illustration of the holotype (Chavan, 1951: fig. 1) shows a specimen that is slightly wider than it is tall, although with the spire apex missing. He stated the dimensions as "height: 32 to 34 mm; width: 30 mm" (Chavan, 1951: 136), but his drawing, stated to be enlarged x 1.75, provides dimensions of H 30, D 32 mm, so possibly Chavan accidentally reversed the dimensions. The unwhitened photographs sent to Ludbrook (1978: pl. 12, figs 17–19) from Rabat, Morocco, were sent in turn to the writer by N. Ludbrook (Figs 24J–K, O) and show again that it is a specimen of *Janthina typica* with unusually numerous, prominent, narrow spiral folds on the sutural ramp, similar to those of the lectotype of *Heligmope dennanti* (Fig. 25L).

Parajanthina japonica is included below under *Janthina chavani* (Ludbrook, 1978). *Hartungia elegans*, holotype in Department of Earth Sciences, Nagoya University, ESN2687, from Tano Formation (late Miocene, late Tortonian–early Messinian, planktonic foraminiferal zone N17) at Tano, Miyazaki Prefecture, near the east coast of Kyushu, Japan (Tomida & Nakamura, 2001: 217, fig. 1a); one paratype MFM111029, from Senhata Formation, Miura Group (late Miocene, also zone N17) at Motona, Chiba Prefecture, east side of Tokyo Bay, Boso Peninsula, Honshu, Japan (Tomida & Nakamura, 2001: 217–218, fig. 1b); not seen. These specimens have obvious spiral folds all over and are interpreted here as severely dorsoventrally to obliquely compressed internal moulds of *Janthina typica*; several similar specimens have been collected in New Zealand.

Eunaticina abyssalis, holotype MNHN IM.2000-27158 (only known specimen; Figs 25G, I–K, M) from *Marion Dufresne* cruise MD55 (BRESIL) station 45-CB79, 19°01'59.9916"S 37°47'59.9964"W, 1500–1575 m, off Itaúnas, Espiritu Santo State, Brazil, SW Atlantic, collected by P. Bouchet, B. Métivier and J. Leal, 25 May 1987. The holotype was said by Simone (2014: 587) to be in "compact blocks (no living specimen)", and is a Pliocene fossil specimen of *Janthina typica* enclosed in weakly lithified cream limestone ("globigerina ooze") dredged from the sea floor. Examination of the holotype, loaned by P. Bouchet and V. Héros (MNHN 16 Sep 2015) left no doubt that this specimen is a weakly sculptured specimen of *J. typica* with a low spire and low spiral folds and fine, closely spaced axial ridges all over. It has now been cleaned further and whitened before photography, revealing its sculpture more clearly. The smooth, polished "protoconch" illustrated by Simone (2014: figs 10I–J) is actually the apical spire whorls of the *Janthina* teleoconch (Fig. 25G); the protoconch is missing. The narrow spiral gap between whorls on this smooth apex demonstrates that the 25 µm-thick calcitic outer layer has been dissolved from the first c. 2.5 teleoconch whorls, revealing the smooth, lightly polished aragonite infilling of the original calcitic shell and leaving a polished surface lower than the outer surface of the rest of the teleoconch. Weak impressions of the spiral and, to a lesser extent, axial ridges on the exterior of the calcitic teleoconch remain on the aragonitic shell. Matrix from within the aperture of the holotype was examined for calcareous nannofossils by Denise Kulhanek (International Ocean Drilling Program Office, College Station, Texas) and Claire Shepherd (GNS; pers. comm. 15 Oct 2015). They reported that nannofossils are difficult to interpret because of overgrowth or dissolution of many specimens; the remobilized carbonate presumably caused the weak lithification of the sample. *Reticulofenestra* is dominant and small *Gephyrocapsa* specimens are present, but not large ones, indicating an age greater than 1.73 Ma. This is consistent with the holotype being a Pliocene fossil rather than a present-day specimen.

Other material examined. **Santa Maria Island**: Touril Complex (Zanclean), Ponta do Castelo, SE tip of island, Zanclean (DBUA-F-428, University of the Azores, Ponta Delgado, Azores Islands, Portugal; 1 specimen, collected by S. Ávila, 15 Sep 2006; photographs sent by S. Ávila, 02 Oct 2012; Fig. 24L). This specimen is abraded and incomplete, but nevertheless is a relatively large specimen confirming the occurrence of *Janthina typica* at more than one locality on Santa Maria Island.

Gran Canaria Island: La Esfinge, a short distance north of Las Palmas de Gran Canaria, east side of La Isleta, NE Gran Canaria, Canary Islands, material reported by Meco *et al*. (2015, 2016) (ULPGC LE20151–LE20156, 6 specimens loaned by Joaquín Meco, ULPGC; Figs 25N, Q–R, T). As noted above, nearby ^{40}Ar/^{39}Ar dates on an underlying lava flow provide a maximum age for the *Janthina* specimens of 4.20±0.18 Ma, late in Zanclean time (Meco *et al*., 2015).

About 120 specimens from localities in Australia and New Zealand: **Australia: Victoria:** Grange Burn Formation (Kalimnan, Zanclean), Muddy Creek, near Hamilton, W Victoria (NMV P26906, 1; P26908–9, 2; P40662, 1; P40663, P40667, 3; P316445, 1; P316449, 1; P406640, P406645, 5; GNS WM7656, 1); Lower Jemmys Point Shellbed (Kalimnan, Zanclean), road cutting SW side of Bunga Creek, Princes Highway, near Lakes Entrance, E Victoria (Wilkins, 1963: 58; NMV P22612, Wilkins's spec., 1 fragment; P26905, 1; P40666, 1). **South Australia:** Hallett Cove Sandstone, Hallett Cove, coast south of Adelaide, one of Tate's syntypes (SAMA T1515C, with spiral folds all over, here early Piacenzian).

New Zealand: Kapitean (Messinian): East Cape: first cutting E of Awatere River mouth, East Cape (NMNZ M043211, 1 incomplete); 250 m NE of lighthouse, East Cape (AUGD10194, Z14/f0127, grid ref. Z14/994775; 1). **Gisborne district:** Waimata Rd, 16 km W of Tolaga Bay (GS1357, Y17/f7477, grid ref. Y17/604021; 2 poor moulds, severely compressed).

Opoitian (Zanclean): SW Auckland: Kaawa Creek, coast S of Waikato Heads (GS996, GS5513, R12/f8518, 11; R13/f7020, R13/f7022, R13/f7027, R13/f7033, R13/f7051, R13/f7056, R13/f7057, R13/f7059, R14/f7062, grid ref. R13/646085, GNS and mainly in AUGD, many; Figs 24F–I; OUGD unnumbered, pres. C. R. Laws, 1). **Gisborne district:** Waihora Valley, Te Karaka, Gisborne (Marwick, 1931: 43) (GS870, Y17/f7462, grid ref. Y17/364961; 1 poor mould). **Hawke's Bay:** Mangawhero Stream (GS1543, W19/f7462, grid ref. W19/831408; 6); Waikaremoana Rd, road cut 30 km from Wairoa (GS1544, W19/f7566, grid ref. W19/810464; 1); Waikaretaheke River 1 km S of junction with Waiau River (GS1555, W19/f7472, grid ref. W19/793441; 2); Waikaremoana Rd, road cut 27 km from Wairoa (GS1556, W19/f7473, grid ref. W19/709446; 1); Cricklewood Rd, 0–1200 m E of Waiau Rd (GS1557, W19/f7474, grid ref. W19/661402; 1); beneath white tephra, Waiau River, 200 m from Mangaone Stream (GS1561, W19/f7477, grid ref. W19/665418; 3); junction Waiau River and Pakihiwi Stream (GS1567, W19/f7516, grid ref. W19/708424; 1); Cricklewood Rd, 2.4 km E of Mohaka–Putere Rd (GS1580, W19/f7486, grid ref. W19/618401; 1); Waihi Stream 400–800 m upstream from Waihi homestead (possibly Kapitean; GS2063, W19/f7492, grid ref. W19/694499; 1); Hangaroa–Tiniroto Rd 5 km SSW of Hangaroa (GS2852, X18/f7488, grid ref. X18/099650; 1); Parikanapa Rd (GS8030, X18/f9624, grid ref. X18/104593; 3); Opoiti Limestone, Mangapiopio Stream (GS8041, X18/f9627, grid ref. X18/034645; 1); Putere Rd (GS8154, W19/f7617, grid ref. W19/615403; 1); Mohaka River below Willow Flat bridge (GS8182, W19/f8573, grid ref. W19/520370; 1 poor mould); road SW of Willow Flat (GS8213, W19/f8582, grid ref. W19/506352; 1); 1 km E of Ardkeen hall, Frasertown–Waikaremoana Rd (GS8273, W19/f7675, grid ref. W19/812434; 1); Ruakituri River road (GS11313, X18/f081, grid ref. X18/951592; 1); Hangaroa Bluffs, Tiniroto–Gisborne Rd (GS11466, X18/f7553, grid ref. X18/100659; 1 fragment); siltstone between Kidnappers shelter hut and Cape Kidnappers (GS10855, W21/f8584, grid ref. W21/607657; 16 poor); bay S side of Cape Kidnappers (GS10856, W21/f8585, grid ref. W21/611648; 2 poor). **Westland:** Kapitea Creek, base of Opoitian section (GS12487, J32/f9774, grid ref. J32/562409; 1 poor); road cut, Greenstone–Kumara Rd (GS3046, J32/f9146, grid ref. J32/634410; 1; GS11557, J32/f9809, grid ref. J32/634410; c. 15 small specimens in one block); Greeks Ck., S side Arahura Valley (GS2875, J33/f7075, grid ref. J33/511258; 2); C. S. Almond's (1980) collections from Arahura–Kaniere district in OUGD (topographically lower localities along S side of Arahura Valley are Opoitian; higher ones in the same streams are Waipipian): first left bank tributary Arahura River (J33/f051, grid ref. J33/549382; 1); Fraser Creek (J33/f008, grid ref. J33/540286; 1; J33/f092, grid ref. J33/540287; 1); McKay's Ck., Kaniere (J33/f021B, grid ref. J33/515261; 2; J33/f024C, grid ref. J33/513261; 1); Greeks Ck., Arahura (J33/f035, grid ref. J33/546284; 1, crushed; J33/f036D, grid ref. J33/545283; 1; J33/f047, grid ref. J33/542283; 1).

Waipipian (early Piacenzian): Auckland: Otahuhu well (GS3528, R11/f7014, grid ref. R11/755698; 1, in C. R. Laws collection; Marwick, 1948: 6; Laws, 1950: 7, listed from 3 beds in Otahuhu well faunal list); Mouldy's farm, Pukekohe (GS3611, R12/f7001, grid ref. R12/752493; 1; Marwick, 1948: 8). **Hawke's Bay:** limestone, mouth of Kopuni Stream, W coast of Mahia Peninsula (GS11476, X20/f7559, grid ref. X20/277142; 1); Te Reinga Falls, Wairoa River (GS1541, X18/f9477, grid ref. X18/021539; 1); near base of Waipipian section, Mohaka River (GS13930, W19/f062, grid ref. W19/545366; 1); Mohaka River, *Mesopeplum crawfordi* (Hutton, 1873b) locality at "second flat" (GS13931, W19/f066, grid ref. W19/599369; 1 poor); Esk Valley (GS683, V20/f8474, grid ref. V20/423949; 1); Black Reef, Cape Kidnappers (OUGD8242, W21/f8544, grid ref. W21/604657; 1 fragment). **South Taranaki:** Manaia Beach, end of Rainie Rd (GS875, Q21/f6492, grid ref. Q21/117792; 2); Ngamatapouri, Waitotara Valley (GS1166, R21/f8497, grid ref. R21/670793; 1); Waingongoro River mouth (GS1172, Q21/f6494, grid ref. Q21/123792; 2). **Westland:** conglomerate at top of E branch, Greek's Creek, Arahura Valley (GS12289, J33/f066, grid ref. J33/547283; 1; Fig. 24N); C. S. Almond's collections in OUGD: E branch Greeks Ck. (J33/f066, grid ref. J33/547283; 1). **Chatham Islands:** Whenuataru Tuff, near NW end of Tarawhenua Peninsula, Pitt I., Chatham Islands (GS12164, CH/f025B, 1 fragment; Fig. 25H).

The only other specimens observed in world museums are the neotype of *Janthina typica*, the type material of *Heligmope dennanti*, the neotype of *Turbo postulatus*, and the holotype of *Eunaticina abyssalis*, all listed above under "Type material".

Distribution. The type material of *Janthina typica* was recorded by Zbyszewski & Veiga Ferreira (1962b: 273) from Pinheiros and Feiteirinhas (i.e., Ponta das Salinas), Zanclean localities on Santa Maria Island. Specimens also were recorded from "Feiteirinhas, Ponta dos Matos, Pinheiros, Praia" by early authors, summarized by Berkeley Cotter (1892: 285), but presumably all specimens from Praia are from close to the Miradouro de Macela and are actually *J. krejcii* sp. nov. It is also possible that all specimens from Pinheiros are *J. krejcii*. The neotype of *J. typica* is from

Ponta do Norte; also seen from Ponta do Castelo. The writer has seen no material from Pinheiros or from Feiteirinhas (currently known as Ponta das Salinas). *Janthina typica* also has been recorded recently from La Esfinge, on La Isleta, north-eastern Gran Canaria, Canary Islands, with photographs confirming the identification (Meco *et al*., 2015: 61, fig. Appendix 5A; six examined specimens listed above). *Janthina typica* is also recorded from Selvagem Grande Island, north of the Canary Islands (Gagel, 1911; Joksimowitsch, 1911) and from São Vicente on the north coast of Madeira (Mayer, 1864a, b; Krejci-Graf *et al*., 1958: 336). However, the stratigraphy and age at these sites has not been described in modern times and these records possibly refer to *J. chavani*. The type material of *Acrybia chouberti*, from a well a short distance east of Casablanca, Morocco, is the sole record from another eastern Atlantic locality. The holotype of *Eunaticina abyssalis* (Simone, 2014: 586) is a specimen of *J. typica* found *in situ* in rock dredged in 1500–1575 m off Espiritu Santo State, Brazil, SW Atlantic, in a case remarkably parallel to that of the earlier-described species *Kaneconcha knorri* (see below under *J. chavani*). In Japan, *Janthina typica* is recorded from relatively few late Miocene–Pliocene (Messinian–early Piacenzian) localities along the Pacific coast of Honshu, Shikoku and Kyushu Islands. In Australia, *Janthina typica* is uncommon and occurs at one locality in Jemmys Point Formation near Lakes Entrance in eastern Victoria, in Grange Burn Formation at Muddy Creek, western Victoria, possibly in the unnamed early Pliocene limestone overlying Kingscote Limestone on Kangaroo Island, and a single specimen is recorded from the lower part of Hallett Cove Sandstone on the coast southwest of Adelaide. In New Zealand, it occurs rarely in Messinian (Kapitean) rocks along the coast between East Cape and Te Araroa and in the Gisborne district, the northernmost locations where latest Miocene rocks are recorded in New Zealand. It also is moderately common at Kaawa Creek, SW Auckland and at Cape Kidnappers, Hawke's Bay (both Opoitian, Zanclean), and occurs widely but uncommonly in Zanclean rocks in N Hawke's Bay (22 localities) and Westland (10 localities). Schofield (1958: 252), based on identifications by C. A. Fleming, also recorded a specimen of "*Hartungia postulata* Bart." from GS3611, R12/f7541, bank near Glasson's Creek, north of the Waiuku–Runciman main highway, Auckland, in a re-collection of GS3611, originally listed by Marwick (1948: 8). Localities in northern Hawke's Bay were listed (in part) by Marwick (1965: table 4) and mapped (by GNS collection numbers) on the geological map in Marwick (1965), although the sole discussion in the text (Marwick, 1965: 10) incorrectly referred to "*Hartungia postulata*" as one of the species first appearing in the Opoitian Stage. Whitten (1973) also recorded Waipipian specimens from South Taranaki between Inaha Stream and Hawera, not seen, in AUGD. Whitten (1973) described 23 new members of Tangahoe Formation, but recorded *Janthina typica* (as *Hartungia postulata*) from three members only: Whareroa Shellbed (one locality, Q21/f6639), Ohawe Sandstone (three localities, Q21/f6553, f6627, f6631, plus an earlier record from Hawera: Laws 1940b), and Waingongoro Member (five localities, Q21/f6613, f6615–f6618). These localities are listed by Whitten (1973, Appendix I) as: Waingongoro Member: Q21/f6613, grid reference Q21/108792, 150 m E of Inaha Stream mouth; Q21/f6615, grid ref. Q21/109792, 175 m E of Inaha Stream mouth; Q21/f5616, grid ref. Q21/109792, between the two previous localities; Q21/f6617, grid ref. Q21/111792, 325–375 m E of Inaha Stream mouth; Q21/f6618, grid ref. Q21/112792, 450 m E of Inaha Stream mouth; Ohawe Sandstone: Q21/f6553, grid ref. Q21/134789, SE end of Ohawe Beach; Q21/f6627, grid ref. Q21/156776, mouth of small stream 1.1 km NW of Waihi Beach; Q21/f6631, grid ref. Q21/167768, mouth of Waihi Stream; Q21/f6639, grid ref. Q21/214746, Whareroa Shellbed, 250–450 m NW of small stream near Hawera rifle range. So in Waipipian (early Piacenzian) rocks it occurs in S Auckland (three localities), N Hawke's Bay (nine localities), the Whanganui-S Taranaki coast (11 localities), the Kaniere-Arahura district, Westland (three localities) and the Chatham Islands (one locality, on NW Pitt Island). These widely separated Atlantic, Japanese, Australian and New Zealand localities indicate that *J. typica* had a cosmopolitan distribution in tropical and temperate seas, just as living *Janthina* species do.

Dimensions. See Table 3.

Table 3. Dimensions of *Janthina typica*. Stage abbreviations: *Wo*, Opoitian New Zealand Stage (Zanclean, 5.3–3.7 Ma); *Wp*, Waipipian New Zealand Stage (early Piacenzian, 3.7–3.0 Ma).

locality	height	diam.	NSF	H/D
Janthina typica neotype, Santa Maria Is.†	15.4	19.3	13	0.79
Acrybia chouberti holotype*	30+	32	—	—
Turbo postulatus neotype, G5721	31.75	32.1	12	0.99
Hartungia elegans holotype (distorted)*	19.1+	29.8	—	—
Eunaticina abyssalis holotype*	20.6	26.6	(12)	0.77
Australian specimens				
SAMA T1494A, *H. dennanti* lectotype	30.4	28.9	10	1.05
SAMA T1494B, paralectotype	17.5	19.0	10	0.92
NMV P28906, Muddy Creek	+	+	12	—
NMV P26906, Muddy Creek	+	24.5	9	—
NMV P26908, Muddy Creek	27.8	29.3	9	0.95
NMV P26909, Muddy Creek	24.2	25.0	10	0.97
NMV P40662, Muddy Creek	19.5	21.0	8	0.93
NMV P40663, Muddy Creek	25.3	25.2	9	1.00
NMV P40666, Muddy Creek	30+	29.8	9	1.01
NMV P40667, Muddy Creek	29.5	29.8	9	0.99
NMV P316445, Muddy Creek	26.5	30.8	9	0.86
NMV 406640, Muddy Creek	23.2	25.2	10	0.92
GNS WM7656, Muddy Creek	24.7	24.8	9	1.00
NMV P40668, Bunga Ck, Gippsland	19.8	24.8	11	0.79
NMV P27905, Bunga Ck, Gippsland	17.9	22.2	9	0.81
New Zealand specimens				
GS5513, Kaawa Ck, SW Auckland, Wo	25.0+	23.1	11	1.08
GS5513, Kaawa Creek	26.0	25.3	10	1.03
GS5513, Kaawa Creek	31.4+	31.7	11	0.99
GS5513, Kaawa Creek	22.8+	24.7	11	0.92
AUGD, Kaawa Creek	26.0	23.1	9	1.13
AUGD, Kaawa Creek	21.9	23.3	9	0.94
AUGD, Kaawa Creek	23.1	22.7	11	1.02
AUGD, Kaawa Creek	22.9	22.0	9	1.04
AUGD, Kaawa Creek	17.3	18.5	9	0.94
AUGD, Kaawa Creek	23.6	28.2	9	0.84
AUGD, Kaawa Creek	23.6	23.4	10	1.01
AUGD, Kaawa Creek	40.7	38.4	11	1.06
AUGD, Kaawa Creek	31.6	31.8	10	0.99
AUGD, Kaawa Creek	35.6	37.2	10	0.96
AUGD, Kaawa Creek	31.8	31.3	10	1.02
GS875, Manaia Beach, S Taranaki, Wp	26.3	29.5	9	0.89
GS1172, Waingongoro R mouth, Wp	29.3	29.0	11	1.01

+ incomplete
* dimensions from original publications
† dimensions supplied by C. Marques da Silva, Lisbon
diam. diameter
NSF number of spiral folds

Diagnosis. Teleoconch moderately large (to c. 40 mm wide), whorls evenly convex; most specimens heliciform throughout growth, spire consistently low; completely covered with fine, closely spaced axial ridges; 8–12 evenly convex spiral folds per whorl (9 or 10 on most specimens) over entire teleoconch surface, as prominent on sutural ramp as elsewhere. Outer lip sinus relatively small, narrow, semicircular, located at base of lip, generating lowermost, wide spiral fold parallel to columella. Protoconch not seen.

Original description. Bronn's (1861: 119–120) original description of *Hartungia typica* reads: "*Hartungia typica* n. g. sp. [new genus and species]. A very delicate thin and also *Ianthina*-like shell, filled with rock, 18 mm high and 22 mm wide, with three whorls, which (as in *I. communis*) [i.e., *Janthina janthina*] form a flatly arched upper side and of which the first two [whorls] are only 5 mm in height. In contrast, the wide ovate aperture measures 17 mm in height and 15mm in width, while its complete lower edge (as in *I. nitens* Menke) [i.e., *Janthina globosa*] wraps around vertically towards the base. In the same way the umbilicus is not open, but is just in the form of a narrow chink behind the inner lip, which lies conspicuously on the penultimate whorl, as in the said species. The dense fine and elegant vertical striation also recalls it [presumably referring to *Janthina exigua*], but does not form a re-entrant sinus in the middle of the outer lip as in *Ianthina*, but is straight there; in contrast, further down opposite the end of the umbilical chink, [the striation] bends in on a spiral rib [to form] a somewhat insignificant small arch [sinus]. However, what distinguishes this gastropod immediately from all known *Ianthina* species and would better accord with *Narica* are 8 flat, broadly rounded spiral cords, which extend down along the outermost convexity of the last whorl, remaining somewhat distant from the suture and even more from the umbilicus, and [of] which the fourth, without forming a keel, is situated furthest towards the outside and scarcely exceeds its upper and lower neighbours in strength. The height of two spiral cords conforms to the width of 6–7 vertical striations. Thus this species is distinguished from *Ianthina* by the form of the sinuosity and the sculpture of the shell, with which it stands closely in a family and seems to form its own genus, which we name after the indefatigable explorer of the west European islands. This genus probably has some similarity in shape and lip sinus with *Neritoma* Morris from the Portland beds, but *Neritoma* is bi-sinuate, somewhat thick-shelled and not umbilicate, behind the inner lip somewhat canal-forming, the growth lines simple. The shell seems too thin for the early whorls of a *Magilus* and the aperture too regular" (slightly modified translation from German by T. A. Darragh, NMV, pers. comm. 12 Nov 2015).

Remarks. Bronn (1861: 119–120) compared *Hartungia typica* with "*Ianthina*" species in several places in his description, stating that it "stands closely in a family" with *Janthina*, and clearly regarded *Hartungia* as a new genus of Janthinidae. He appreciated that *H. typica* is similar to living *Janthina* species, differing in its small basal sinus and the presence of spiral folds. Mayer (1864: 62) later redescribed the same species in *Janthina*, apparently changing the species name to maintain the association with the collector, Georg Hartung.

Mayer's (1864b: i–ii) foreword explained that Bronn had died, and so Hartung asked Mayer "in the autumn of 1861" to describe the fossils collected by Reiss at Madeira and Porto Santo. On examining the fossils he found they had a lot in common with those described by Bronn in the works by Hartung and Reiss on the Azores. Therefore, he thought the whole assemblage should be written up together, and asked Hartung and Reiss to help arrange a loan of Bronn's material from the University of Heidelberg. "With the greatest willingness Professors Blum and Pagenstecher immediately fulfilled my wish, sending me the material able to be found, and so in the first half of the last winter I could attend to my expanded task" (translation from German by T. A. Darragh, NMV, pers. comm. 12 Nov 2015). This statement suggests that some of Bronn's material already could not be traced in 1861. Mayer (1864: 62) listed the description of *Hartungia typica* by Bronn (1861: 119, pl. 19, fig. 3) in a chresonymy below the species heading for *Janthina hartungi*, along with the listing of *H. typica* by Bronn in Reiss (1862: 32). So it is clear that he renamed Bronn's species, although he did not state a reason for doing so. He also compared *Janthina hartungi* with *J. communis* (i.e., *J. janthina*) and with *J. capreolata* Montrouzier (i.e., *J. exigua*). He stated the dimensions as "Alt. 19, lat. 22 mill.", only subtly different from the dimensions of 18 mm high and 22 mm wide provided by Bronn (1861: 119). The list of material at the end of the description makes it clear that Mayer had actual shells before him, as he said the six examples he had included three typical ones from Feiteirinhas (i.e., Ponta das Salinas), another from "Ponta dos Mattos" (presumably the modelling clay impression in Fig. 24M), one without spiral folds from Pinheiros and one with weak folds from São Vicente (Madeira). The lack of an express statement of a type specimen suggests that Mayer regarded all these as type material of *J. hartungi*. Mayer's and Bronn's illustrations are particularly similar, including the unusual lateral view of the angular columellar base. As Mayer had Bronn's material before him, the very similar illustrations (Mayer's: copied as Figs 25D–F; Bronn's: copied as Figs 25O–P, S) likely are different artist's drawings of the same specimen. In view of the brittleness of *Janthina* fossils, this material possibly has disintegrated over the intervening years.

Janthina typica is characterized by its moderately large size, reaching about 40 mm in diameter and 38 mm in height, although most specimens are 25–35 mm in diameter; its consistent, more-or-less equidimensional, heliciform shape, with a moderately low spire; the few, rapidly expanding teleoconch whorls; the low, thin, closely spaced axial ridgelets covering the entire teleoconch surface, about 1 mm apart over the periphery of large specimens; the quite prominent, evenly convex spiral folds with equally wide, evenly concave interspaces that also cover the entire teleoconch surface, 8–12 on the last whorl (most specimens have 9 or 10 folds), visible on spire whorls as well as on the last whorl; and its relatively small, semicircular sinus in the outer lip, situated at the base of the lip against the columella base. In most specimens, the sinus generates a particularly prominent, wide spiral ridge parallel to the other spiral folds and to the columella and the inner lip of the aperture, higher and wider than the normal spiral folds, although this basal fold is not obviously differentiated in a few specimens. The whorl outline is regularly and strongly convex on most specimens, although a few large shells develop a slightly to quite strongly concave sutural ramp over the last half-whorl. Some of these develop a thickened, smoothly rounded lip edge over the concave area, whereas the lip edge is simple and thin in all other specimens. Traces of the axial ridgelets are visible on almost all specimens, but they are much better preserved on some than on others, and on well-preserved specimens from Kaawa Creek, southwest Auckland, New Zealand (Opoitian, Zanclean) and, in particular, on specimens from Grange Burn Formation (also Zanclean) at Muddy Creek, near Hamilton in western Victoria, Australia, quite high, thin lamellae are preserved. The protoconch has not been observed, despite careful searching of all available material. A supposed protoconch on the holotype of *Eunaticina abyssalis* (Simone, 2014: 586, figs 10I–J) is actually the broken and corroded apex of the *Janthina* teleoconch (Fig. 25G). The teleoconch of *J. typica* is thin, brittle and calcitic, apart from an interior white aragonitic layer, most obvious on the columella, and chalky in many specimens. Most freshly exposed specimens also have a distinctive pale brownish coloration, reflecting their calcitic composition. Because of the calcitic composition, even small, pale brown fragments of shell bearing axial ridgelets are diagnostic of *Janthina* in many Pliocene outcrops. Finlay (1931: 5) claimed that a few New Zealand specimens still showed "traces … of the characteristic dark bluish-violet colour", but the writer has not observed colour on any specimens, and other New Zealand paleontologists consulted also have not observed it. The diagnostic spiral folds are widest and most prominent at the periphery in most specimens, and grade into lower, narrower and more closely spaced ones on the sutural ramp and on the base, except for the wide one generated by the sinus, which on most specimens is almost twice as wide as one peripheral fold.

Considerable variation is observed in most characters. The spire is significantly lower in small than in large specimens, as in *Janthina chavani* and *J. janthina*, although the weak allometrical growth in spire height observed in *J. chavani* is not obvious in *J. typica*. The two specimens observed from Santa Maria Island and the drawings published by Bronn (1861: pl. 19, fig. 3) and Mayer (1864a, b: pl. 6, fig. 41) show specimens that would not be surprising to find among samples collected in New Zealand or southern Australia. The six specimens observed from the material of Meco *et al.* (2015, 2016) from La Esfinge, Gran Canaria Island (Figs 25N, Q–R, T) are rather fragile, but most are well-preserved, with low to moderately high spires and relatively weak sculpture, but are not as weakly sculptured as the holotype of *Eunaticina abyssalis* (Simone, 2014) and provide a good basis for understanding the variation that might be expected in the Santa Maria Island population. The two smallest specimens from Gran Canaria are internal moulds, lacking shell. The total range of variation is no greater than is observed between widely separated populations of living *Janthina* species. Some consistent differences are observed between Australian and New Zealand collections, attributed solely to differences in preservation. Specimens from Grange Burn Formation (Kalimnan Australian Stage, Zanclean) at Muddy Creek and its tributary Grange Burn, near Hamilton, western Victoria, Australia (Figs 25A–C, L) are easily removed from weakly consolidated sediment and are much the best-preserved in the world. However, the material from La Esfinge, Gran Canaria Island, and the neotype of *Hartungia typica* are reasonably well-preserved. Almost all others observed have the axial ridgelets abraded to some extent, and most others are at least a little distorted—some dramatically so. Fine details are more consistently preserved in southern Australian than in New Zealand material, and most New Zealand specimens from localities other than Kaawa Creek are slightly to severely crushed. The few New Zealand Messinian specimens are all either very poorly preserved internal moulds of crushed shells or are very incomplete. Most Japanese specimens also are crushed and many are internal moulds only, although a few are excellently preserved (e.g., Tomida & Itoigawa, 1982: pl. 19, figs 1–3; Tomida & Kitao, 2002: fig. 2). Specimens from the Azores, Canary Islands, Japan, Australia and New Zealand are so similar that there is little doubt they are conspecific, displaying less variation than is observed in the living population of *Janthina janthina*.

Chavan's (1951: 135, fig. 1) pen drawing of the holotype of *Acrybia* (*Hartungia*) *chouberti* illustrated the sculpture diagrammatically. The identity of this specimen was resolved when Ludbrook (1978: pl. 12, figs 17–19) published photographs of Chavan's holotype (Figs 24J–K, O) rather than of the poor plaster casts available previously, although the specimen has not been whitened before photography and focus is not ideal. The casts in MNHN and GNS are of a specimen with almost no sculpture, likely made from the paratype internal mould mentioned by Chavan rather than from the holotype. Ludbrook's (1978: pl. 12, figs 17–19) illustrations reveal that the holotype has prominent spiral folds all over, including unusually prominent ones on the sutural ramp, and falls within the range of variation of *Janthina typica*. Ludbrook (1978: 121) cautiously concluded that "while there may be good reason to suspect that the Australian and New Zealand material is identifiable at the species level with the Azores *Hartungia typica* and its synonym *Janthina hartungi*", she thought that could not be confirmed because of the lack of authentic Azores material for comparison. Now that this has been resolved, the writer sees no reason to doubt that fossil *Janthina* species had the same cosmopolitan geographical ranges as living *Janthina* species, and that *Heligmope dennanti*, "*Turbo*" *postulatus*, *Acrybia chouberti*, *Hartungia elegans* and *Eunaticina abyssalis* are all synonyms of *Janthina typica*.

It is unfortunate not to retain Georg Hartung's name. He collected the fossils described by Bronn (1861) and some of those described by Mayer (1864a, b). Pinto & Bouheiry (2007) provided an account of Hartung's research in the Azores, Madeira and Canary Islands and his extensive collaboration with Charles Lyell.

Time range. Messinian–early Piacenzian (latest Miocene–early late Pliocene); c. 7–3.0 Ma, to judge from its range in New Zealand (Kapitean–Waipipian Stages; Messinian–early Piacenzian; Cooper, 2004: fig. 13.1). This time range is confirmed less precisely in Japan and southern Australia.

Janthina krejcii sp. nov.

Figs 26A–N

Hartungia typica Bronn.–Bronn, 1862: 32–33 (in part misidentified as *H. typica* Bronn, 1861).
Janthina typica (Bronn).–Krejci-Graf *et al.*, 1958: 336, pl. 3, fig. 6, pl. 4, fig. 11 (misidentification).

Type material. Holotype SMF10135a (Figs 26A–B, D–E), with two paratypes SMF10135b–c (Figs 26C, F–H), labelled "Azoren, Santa Maria, Wegknick [road bend] bei Praia, K. Krejci-Graf," 23 April 1955, in SMF. The type locality is the upper, seaward-directed hairpin bend on the road descending from Almagreira to the beach at Praia, Santa Maria Island, illustrated by Krejci-Graf *et al.* (1958: fig. 4) (a lower, landward-directed hairpin bend is in the underlying volcanic rocks). The writer visited the pale grey outcrop labelled "*Janthina* find-point alongside the collectors" in fig. 4 of Krejci-Graf *et al.* (1958) with Bernard Landau on 28 Feb 1998, but found no calcareous fossils. The matrix proved non-calcareous, and is not datable by microfossils; it lacks Foraminifera, Radiolaria, calcareous nannofossils and dinoflagellate cysts. Evidently Krejci-Graf's party sampled a last small pocket of calcareous rock, probably between volcanic blocks at the base of the outcrop. However, a new lookout, the Miradouro de Macela, was being constructed during Feb 1998 to overlook the beach at Praia, at the seaward extremity of the bend, across the road and behind the photographer in Krejci-Graf *et al.*'s (1958: fig. 4) photograph. The soft, fawn, non-calcareous, tuffaceous sandstone in the foundations of the lookout was found to contain numerous moulds of *Janthina krejcii* sp. nov. Ten of these are here designated as paratypes (GNS WM18973; the two most complete illustrated, Figs 26I–N), and three others are incomplete. Colom (in Krejci-Graf *et al.*, 1958: pls 5–6) illustrated planktonic foraminiferans in a sample from quarries near Figueiral on the south side of Pico do Facho, near the Miradouro de Macela, including *Globoconella puncticulata* (Deshayes, 1832), *Hirsutella* cf. *margaritae* (Bolli & Bermudez, 1965) and *Globigerinoides sacculifer* (Brady, 1877) (reidentified by M. Crundwell, GNS, pers. comm. 17 Sep 2012), a diagnostic Zanclean fauna. The age of the type locality of *Janthina krejcii* has not been determined in detail but, as it is at a similar elevation to the quarries sampled by Krejci-Graf *et al.* (1958) and the Cré locality described by Janssen *et al.* (2008), is likely to be a similar age within Zanclean time. Only the type material has been observed.

Distribution. The writer has seen specimens of *Janthina krejcii* sp. nov. only from the type locality and the outcrop across the road from it, at the lookout (Miradouro de Macela) on the road descending from Almagreira to Praia, Santa Maria Island, Azores Islands. Bronn (in Reiss, 1862: 33) noted that one of his specimens of *Janthina typica* from near Praia was crushed but lacked spiral folds, so his material seems to have included a specimen of *J. krejcii* sp. nov. from the type locality. He discussed whether it might be a distinct species, but concluded this was individual variation. As with all other relevant early collections, the present location of Reiss's material is not known to the writer. Mayer (1864: 93, 101) also recorded a single specimen of "*Janthina hartungi*" from Praia, but as it is not mentioned in the list of material following his description (Mayer, 1864: 63), he presumably merely repeated Bronn's record. However, Mayer (1864: 63) also recorded a specimen of "*Janthina hartungi*" without spiral folds from Pinheiros, a locality a short distance northeast of Cré, Santa Maria Island. As the writer has not seen material from Pinheiros, it is possible that *J. krejcii* sp. nov. occurs more widely on Santa Maria Island than the present record indicates.

Dimensions. See Table 4. Most paratype moulds are too incomplete or too distorted to measure. The largest fragmentary paratype in WM18973 is 34 mm wide, but is compressed significantly; a maximum diameter of c. 32 mm is likely.

Diagnosis. Teleoconch moderately large, short and wide (D/H 1.2–1.35), spire very low to almost flat, whorls evenly convex; completely covered with fine, straight, acline axial ridges, but without obvious spiral sculpture. Outer lip straight, acline; sinus small, moderately deep, semicircular to weakly V-shaped, situated at base of lip.

Description. Teleoconch moderate-sized for genus, reaching c. 32 mm in diameter and 25 mm in height, wide (D/H 1.2–1.35), very low-spired, with c. 3.5 evenly and strongly convex teleoconch whorls; without obvious spiral sculpture. Spire little elevated above last whorl; suture appressed. Axial sculpture of many closely spaced, straight, thin, acline, low lamellae with flat-bottomed interspaces, extending from suture to umbilical hollow over entire teleoconch, c. 1 mm apart at periphery on last whorl. Aperture large, tall, almost vertical, with thin lips; columellar area and umbilical hollow poorly preserved in all material, apparently similar to those of *Janthina typica* and *J. chavani*. Outer lip sinus against base of columella, moderately large, semicircular to weakly V-shaped as in *J. chavani*, visible in only two paratype moulds in WM18973. Protoconch not seen.

Remarks. *Janthina krejcii* sp. nov. resembles *J. typica* and *J. chavani* in its uniform sculpture of fine, closely spaced, straight axial ridges over the entire teleoconch and in its semicircular to shallowly V-shaped outer-lip sinus situated at the base of the lip. However, it differs from them both in its consistently very low to almost flat spire, so that width is significantly greater than height in all specimens, and in its complete lack of obvious spiral sculpture. It also reaches a markedly smaller maximum diameter than *J. chavani*, although similar in width to *J. typica*. Were only K. Krejci-Graf's original specimens available they might be thought aberrant specimens of *J. typica*, but all 10 reasonably complete moulds and several additional fragments from the Miradouro de Macela (GNS WM18973) are consistent with Krejci-Graf's specimens in their low spire and in completely lacking spiral folds. With 15 consistent specimens available, it must be concluded that this is a previously unrecognized species of *Janthina*.

Table 4. Dimensions of *Janthina krejcii* sp. nov.

locality	height	diameter	D/H	H/D
holotype SMF10135a	23.0	30.8	1.34	0.75
paratype SMF10135b	20.7	27.0	1.30	0.77
paratype SMF10135c	16.8	22.6	1.35	0.74
paratype GNS WM18973	22.6	26.8	1.19	0.84
paratype GNS WM18973*	24.4	23.8	0.98	1.03
paratype GNS WM18973	21.4	25.2	1.18	0.85

* Distorted.

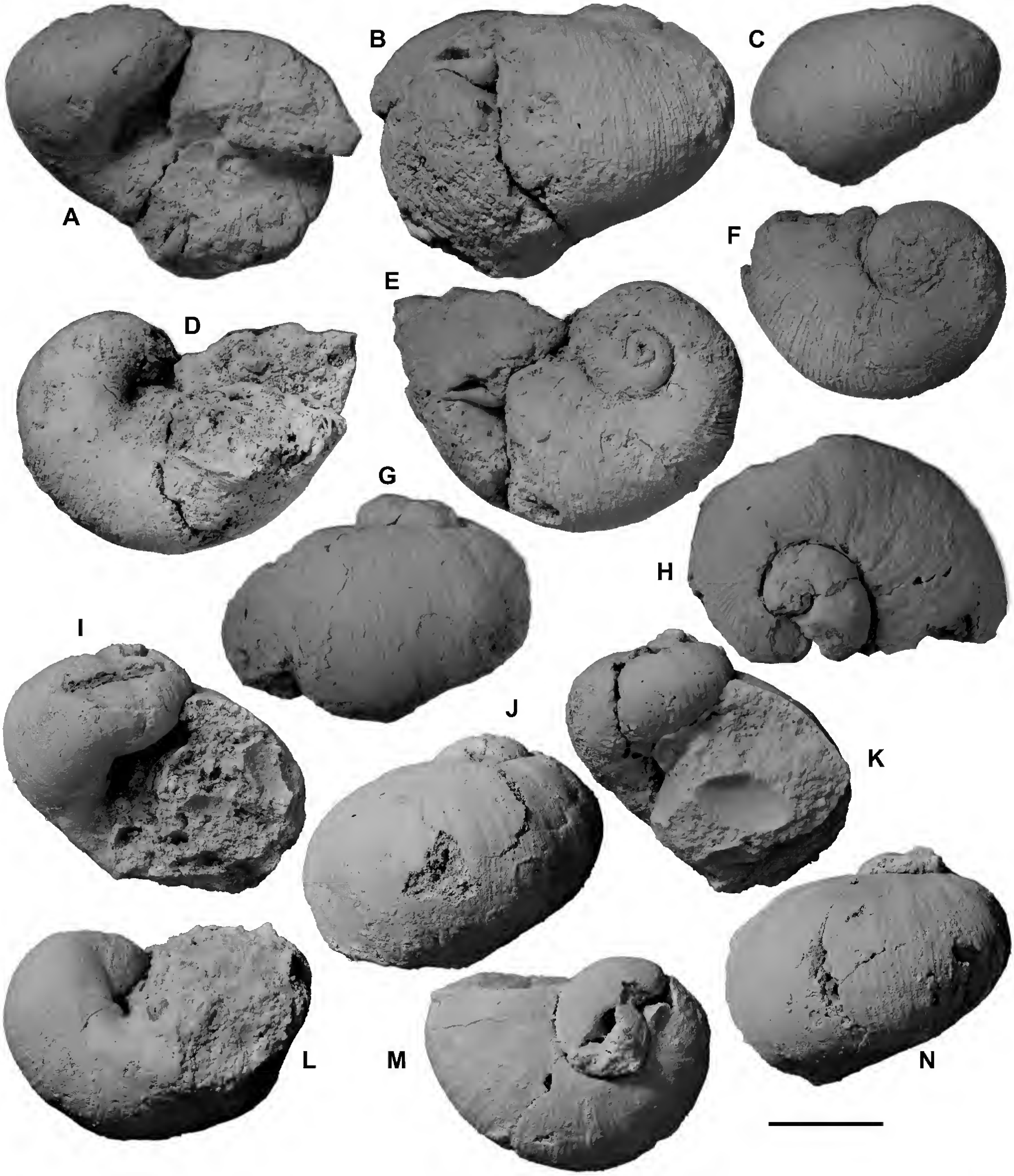

Figure 26. Specimens of *Janthina krejcii* sp. nov., all from Miradouro de Macela, road descending from Almagreira to Praia, Santa Maria I., Azores, Zanclean. *(A–B, D–E)* holotype, SMF10135a; C, F, paratype, SMF10135c; G–H, paratype, SMF10135b; all from road cut opposite Miradouro de Macela, coll. K. Krejci-Graf. *(I–N)* 2 paratype moulds, GNS WM18973, sandstone in foundations of Miradouro de Macela. Scale bar 10 mm.

Apparently *J. krejcii* sp. nov. occurs also at Pinheiros, a short distance NW of Cré, Santa Maria Island, but this locality requires re-collecting. It is not clear as yet whether *J. krejcii* sp. nov. represents a restricted Atlantic species or, as seems more likely, it happened to live during a late Zanclean time interval that is otherwise not represented by facies suitable for the preservation of *Janthina* fossils. It is intermediate between *J. chavani* and the living *Janthina* species in having consistent axial ridges but lacking spiral folds. Only the collection of *J. krejcii* at further localities will clarify its time and geographical ranges and its position in the phylogeny of *Janthina* species.

Etymology. The new species is named in honour of Dr Karl Krejci-Graf, formerly of Universität Frankfurt am Main, who collected the type material and advised the present writer about its locality.

Time range. Zanclean, c. 4.8–4.3 Ma; the older limit is poorly constrained, but the upper limit on Santa Maria Island cannot be younger than 4.32 Ma (Sibrant *et al*., 2015).

Janthina chavani (Ludbrook, 1978)

Figs 27–28

Heligmope postulatus (Bartrum).–Fleming, 1953b: 139 (misidentification).

Hartungia postulata (Bartrum).–Carter, 1972: 306, 321 (misidentification).

Hartungia typica typica (Bronn).– Johnstone *et al*., 1973: 14; Quilty, 1974a: 308; Quilty, 1974b: 29 (misidentification by A. Beu & G. Kendrick pers. comm.).

Hartungia dennanti chavani Ludbrook, 1978: 119, pl. 12, figs 1–14; Ludbrook, 1983: 45, figs 3h–j; Ludbrook, 1984: 232, figs 57o–p; Kendrick *et al*., 1991: 424, 436.

Parajanthina japonica Tomida & Itoigawa, 1982: 60, pl. 19, figs 1a–c; Ogasawara, 2002: 545 (in part).

Hartungia japonica (Tomida & Itoigawa).–Tomida & Itoigawa, 1984: 112, pl. 31, figs 1a–2b; Tomida & Itoigawa, 1989: 126, pl. 23, figs 1a–2d; Noda *et al*., 1995: 83, figs 11.7a–d; Nobuhara et al., 1995: 39, figs 3.2a–b; Tomida & Kitao, 2002: 158, figs 2.1a–2c; Ogasawara, 2002: 394, 545.

Hartungia chavani (Ludbrook).–Kendrick in Tomida & Itoigawa, 1984: 112, pl. 31, figs 3a–5b; Beu & Maxwell, 1990: 411; Maxwell in Spencer *et al*., 2009: 245.

Hartungia sp.–Nobuhara *et al*., 1995: 38, figs 3.1a–b.

Kaneconcha knorri Kaim, Tucholke & Warén, 2012: 247, figs 3A–E.

Janthina (*Hartungia*) *typica* (Bronn).–Tomida *et al*., 2013: 60, figs 3E–L only (in part misidentified).

Type material. *Hartungia dennanti chavani*, holotype WAM69.300c, with six figured and numerous unfigured paratypes in WAM, Geological Survey of Western Australia, and Geological Survey of South Australia (listed by Ludbrook, 1978: 120; WAM and GSSA material observed); from Roe Calcarenite (late Pliocene; Beu & Darragh, 2001: 31, fig. 6), pits c. 50–125 km W of Eucla, Roe Plain, southeastern Western Australia. As noted above, although Beu & Darragh (2001: fig. 6) suggested an early Piacenzian age, correlation with successions in New Zealand now indicates a late Piacenzian age for Roe Calcarenite. Ludbrook (1978: 120) also recorded specimens from water wells beneath Perth, Western Australia, from Plio-Pleistocene Bridgewater Limestone in the region around Naracoorte, South Australia, and from Reedy Wells, Culburra, South Australia (the last not seen; from Bridgewater Limestone near Mount Gambier).

Parajanthina japonica, holotype MFM110004, from Dainichi Sand (late Pliocene, Piacenzian, upper part of planktonic foraminiferal zone N21), Higashigumi, Iida, Shizuoka Prefecture, Honshu, Japan (Tomida & Itoigawa, 1982: 61); not seen.

Kaneconcha knorri, holotype (Figs 28A, D, G) in Institute of Paleobiology, Polish Academy of Sciences, Warsaw, ZPAL Ga.16/1, with six incomplete paratypes, ZPAL Ga.16/2–7, from *Knorr* dredge station 180-2-26, 23°23'N 45°23'W, Kane Megamullion, east flank of Adam Dome, mid-Atlantic ridge, 3293–2827 m (mapped by Kaim *et al*., 2012: fig. 1). The writer has seen photographs of only the holotype, which is a slightly crushed specimen of *Janthina chavani*. Although it has weak spiral folds on the weakly convex sutural ramp, it is identified as *J. chavani* partly because the matrix was dated by calcareous nannofossils by M.-P. Aubry (the leading expert on nannofossil biostratigraphy; in Kaim *et al*., 2012) as zone NN16B, 2.5–2.8 Ma (late Piacenzian–earliest Gelasian, latest Pliocene–earliest Pleistocene). Kaim *et al*. (2012: 427–429, figs 5C–D) mentioned that although six other specimens were collected, they are all fragmentary. They described two shell layers (both now replaced by calcite) in a paratype fragment, and suggested that the outer, dark brown later 25 µm thick is a periostracum preserved by replacement with calcite. The inner layer, 175 µm thick over the columella, is milky white homogeneous calcite. However, reidentification of this shell as *J. chavani* demonstrates that the outer layer is the brown calcite outer shell layer (violet in life), only 25 µm thick, whereas the inner white layer is the original aragonite inner layer. In most specimens from other localities the inner layer apparently is not so thick.

Other material examined. **Australia: South Australia:** Two paralectotypes of *Heligmope dennanti,* from Hallett Cove Sandstone, coast east of Hallett Cove, south of Adelaide (see above under *H. dennanti*; SAMA T1515A, B); Geological Survey of South Australia, Bridgewater Limestone (Piacenzian–Calabrian?), Kanawinka Fault scarp, Naracoorte, SE South Australia (GSSA F87/65, 2; photographs sent by N. H. Ludbrook); cliffs S of car park, Point Ellen, Vivonne, Kangaroo Island, South Australia, grid ref. Vivonne 970138 (locality PL3173, NMV P316448, 22); thin cemented beds in Bridgewater Limestone (late Piacenzian–Calabrian?) at top of Henske's Quarry, Elderslie Road, 2.6 km SE of Naracoorte, SE South Australia, grid reference Hynam 793085 (locality PL3249, NMV P318105, 20, in small limestone blocks, collected by T. A. Darragh and A. G. Beu; also block of specimens c. 1 m^2 observed at quarry office); Naracoorte quarries, SE of Naracoorte, South Australia (clearly from Henske's Quarry; NMV P316446, 1). **Western Australia: Roe Plain:** Roe Calcarenite (late Piacenzian), district around Hampton microwave repeater tower, Roe Plain, 48–126 km W of Eucla Motel, SE Western Australia, suites in several museums (WAM.71-1438a–g, 7; WAM.69-298, 1; WAM.69-300a–z, 26; WAM.69-301a–d, 4; WAM.69-299a–d, 4; WAM.59-305, 1; WAM.69-302a–c, 3; WAM.69-303, 1; WAM.70-2156a–c, 3; WAM.69-297a–f, 6; WAM.67-778a, b, 2; WAM.69-306, 1; WAM.69-304, 1; NMV P26917, 2; P316447, 18; P322322, 1, Fig. 27I; GNS WM14468, 10, Figs 27A–H, 28C, F, J); Madura Cave, Roe Plain (WAM.62-50, 1; WAM.63.44, 1). **Perth Basin:** "lower" Ascot Formation, water wells in Perth Basin, collected over many years by G. W. Kendrick (Kendrick in Quilty, 1974b: 29; Kendrick *et al*., 1991: 424, 436), all in WAM; most lots consist of one specimen or fragment: 30 m, Vale's bore, Evelyn St, Gosnell's, Perth (WAM.70-2615); Redcliffe primary school bore, Perth (WAM.69-292, WAM.69-293, WAM.69-294); Geological Survey of Western Australia bore Gnangara no. 21, W Bullsbrook, Perth (WAM.68-179, many fragments); Kowalski's bore, corner Bullfinch & Balfour Streets, Gosnell's, Perth (WAM.69-296).

New Zealand: Mangapanian (late Piacenzian–earliest Gelasian): **Hawke's Bay:** Cricklewood Road (GS12515, W19/f020, grid ref. W19/798357; 4 fragments); brown sandstone 3 km upstream from road bridge, Mohaka River (GS13079, W19/f031, grid ref. W19/634313; 1, now fragmentary); Matahorua Road, Tutira (GS12508, V19/f011, grid ref. V19/481224; 1); sandstone between conglomerate beds, Pohokura Road, Tutira (GS12507, V20/f018, grid ref. V20/444168; 2 fragments). **Whanganui Basin:** basal conglomerate of Komako Formation, Te Ekaou Stream, Pohangina Valley (OUGD, OU8037, T23/f6565, grid ref. T23/576173; 1; Carter, 1972).

Nukumaruan (Gelasian–earliest Calabrian): **Hawke's Bay:** Darkies Spur Formation, road cut, Darkies Spur Road, Arapaoanui Valley, c. 30 km N of Napier (GS11225, V20/f8002, grid ref. V20/407104; 1 + fragment; Figs 28I, K). **Whanganui Basin:** Komako Formation, Pohangina Valley (Carter, 1972: 306, 321), Makawakawa Stream (OUGD, OU7597, T23/f6516, grid ref. T23/594099; 1); Konewa Stream (OUGD, OU7668, T23/f6548, grid ref. T23/595201; 1); Te Ekaou Stream (OUGD, OU8125, T23/f6563, grid ref. T23/574175; 1); Hautawa Shellbed, Te Ekaou Stream, Dept. of Earth Sciences, University of Waikato (T23/f060, grid ref. T23/577174;

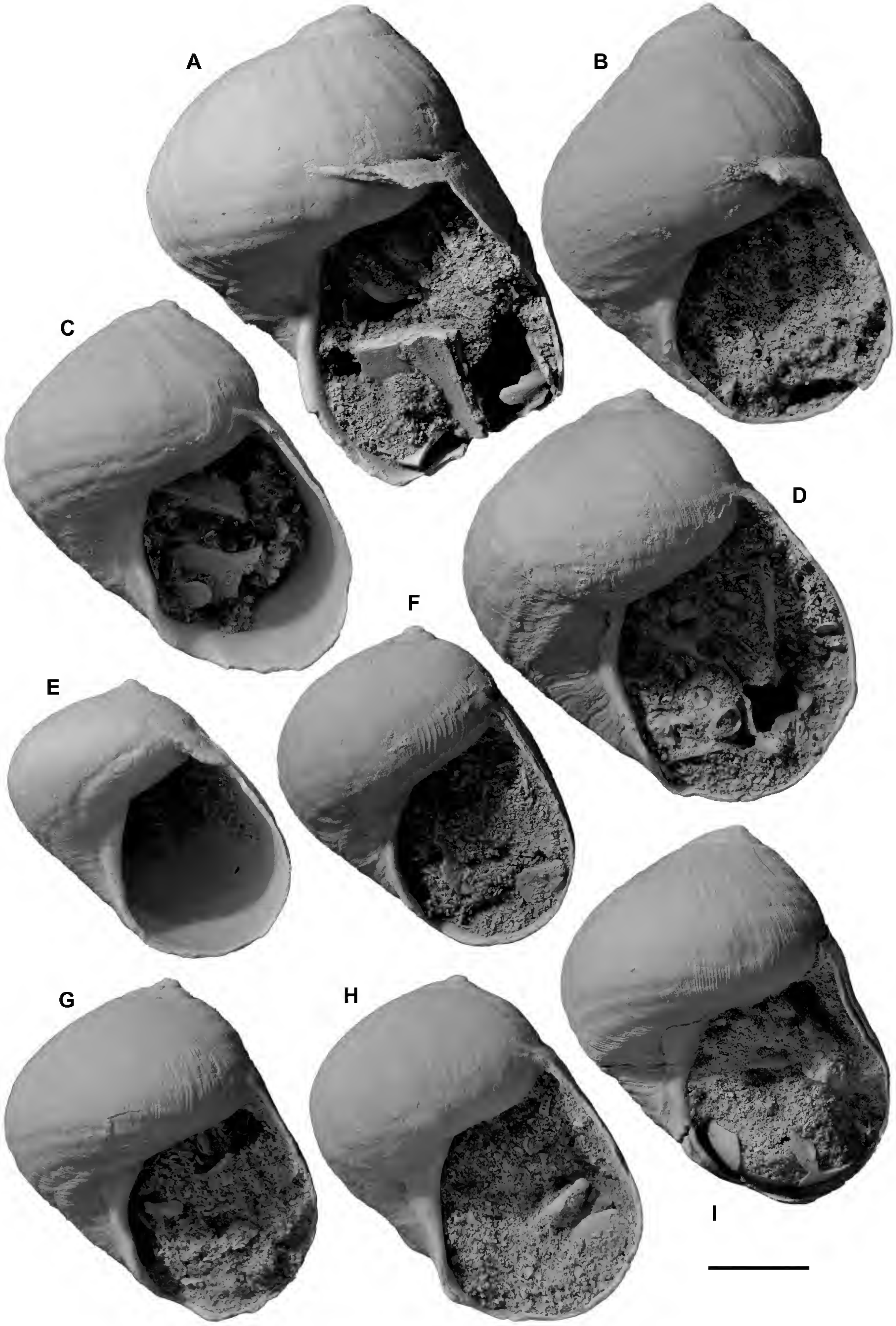

Figure 27. Specimens of *Janthina chavani* (Ludbrook); all from the type formation, Roe Calcarenite, late Piacenzian; Roe Plain, SE Western Australia. *(A–H)* GNS WM14468, 16 km W of Madura; *I*, NMV P322322, 88 km W of Eucla Motel. Scale bar 10 mm.

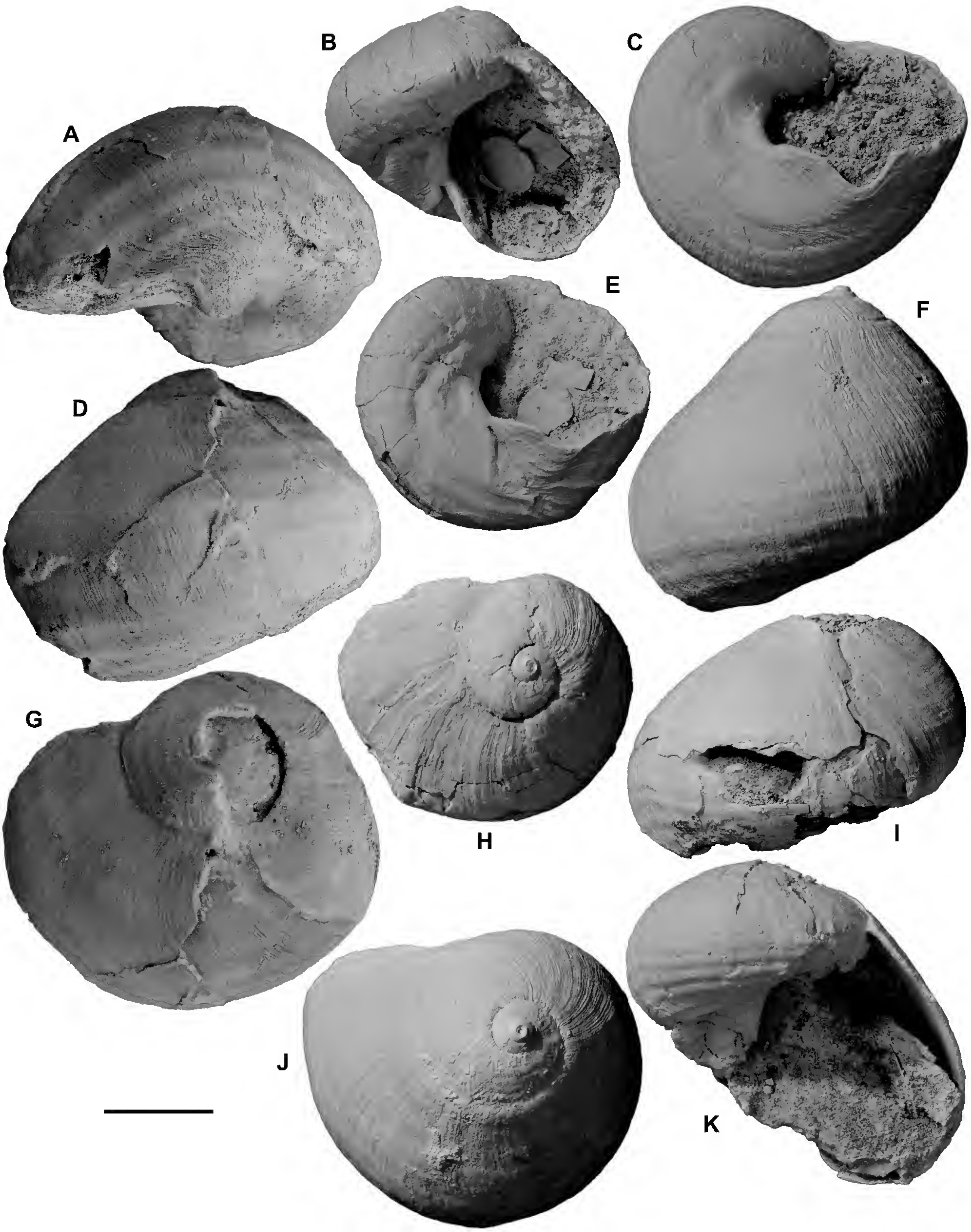

Figure 28. Specimens of *Janthina chavani* (Ludbrook). *(A, D, G)* holotype of *Kaneconcha knorri* Kaim, Tucholke & Warén, ZPAL Ga16/1, Institute of Paleobiology, Warsaw; *Knorr* dredge stn 180-2-26, 23°23'N 45°23'W, Kane Megamullion, mid-Atlantic ridge, 3293–2827 m, late Piacenzian (Institute of Paleobiology photos). *(B, E, H)* GNS TM4495, T22/f8506, Nukumaruan (Gelasian), road cut above Makohine Stream, 2 km S of Ohingaiti, Rangitikei Valley, New Zealand. *(C, F, J)* GNS WM14468, Roe Calcarenite, all data as for Figs 27A–H; basal, posterior and apical views of specimen in Fig. 27G. *(I, K)* GNS GS11225, incomplete specimen, Darkies Spur Fm, Nukumaruan (Gelasian), Darkies Spur Road, c. 30 km N of Napier, Hawke's Bay, New Zealand. Scale bar 10 mm.

1); lowest lens of Nukumaru Limestone, Waitotara "desert", coast W of Whanganui (GS4258, R22/f6488, grid ref. R22/581489; 1; Fleming, 1953b: 139); 0.1 m-thick sandy shell lens in massive mudstone, "undifferentiated Upper Okiwa Group" between Tuha Sand and Ohingaiti Sand (Fleming, 1953b: 133, 136), road cut on hillside 200 m E of Makohine Stream, 2 km S of Ohingaiti, Rangitikei Valley (T22/f8506, grid ref. T22/550356; GNS TM4495, 1, Figs 28B, E, H; D. Cowe collection, 1967, several); Tewkesbury Formation (late Nukumaruan), shellbed enclosing Vinegar Hill Tephra (MIS 61, 1.75 Ma; Pillans *et al*., 2005: 79, figs 5A, 11; Townsend *et al*., 2008: fig. 35), Brunswick Road, SE side Kai Iwi Valley, W of Whanganui (GS15348, R22/f6542A, grid ref. R22/773506; 1).

The only other material observed in world museums is the type material of *Hartungia dennanti chavani*, listed above.

Distribution. *Janthina chavani* is particularly abundant in the type area, in Roe Calcarenite (late Piacenzian) on the Roe Plain, southeastern Western Australia. It is also abundant at a few quarries in Bridgewater Limestone (late Piacenzian–Calabrian?) around Naracoorte, South Australia, and Tate's two paralectotypes of *Heligmope dennanti* from the upper part of Hallett Cove Sandstone near Hallett Cove in South Australia are also *J. chavani*. Ludbrook (1978) also recorded it from a few other localities in South Australia. Ludbrook (1983, 1984) also recorded *J. chavani* from Point Ellen Formation at Cape Jervis, Fleurieu Peninsula, mainland South Australia, and at Point Ellen, Vivonne, Kangaroo Island, South Australia. Ludbrook (1983: 45, figs 3h–j; Geological Survey of South Australia GSSA10025a–c, three illustrated) recorded 17 specimens from Point Ellen and four from Cape Jervis; further specimens have since been collected by T. A. Darragh at Point Ellen (listed above). Many fragments and a few complete specimens have also been seen from "lower" Ascot Formation in water wells in the Perth Basin, Western Australia (material in WAM). In New Zealand it is much less common and widespread than *J. typica*, and is recorded from only 13 localities in Mangapanian and Nukumaruan (late Piacenzian–early Calabrian) rocks in Hawke's Bay and Whanganui Basin. In Japan, a few specimens have been collected from near the Pacific coast of SE Honshu Island, and two were reported by Tomida *et al*. (2013) from Hioki, Miyazaki Prefecture, near the east coast of Kyushu. The single Atlantic record is from Kane Megamullion, on the mid-Atlantic ridge (Kaim *et al*., 2012), where specimens apparently were dredged from "normal" seabed, and not from a hydrothermal seep site as Kaim *et al*. (2012) thought. Late Pliocene–early Pleistocene rocks of suitable facies for the preservation of *Janthina* apparently are not exposed on the Atlantic islands where *J. typica* occurs, although the records from São Vicente, Madeira, and from Selvagem Grande Island require re-collection to be certain of their identities and are possibly *J. chavani*.

Dimensions. See Table 5.

Diagnosis. Teleoconch moderate-sized to very large for *Janthina* (up to H 48, D 40 mm), covered with fine, straight, closely spaced axial ridges; axial ridges tending to fade out over last whorl of large specimens; 8–11 spiral folds per whorl (9 or 10 on most specimens) but most specimens with spiral folds significantly less obvious than on *J. typica*; at least two spiral folds suppressed on upper sutural ramp. Outer lip sinus small, basal, as in *J. typica*, but slightly wider, narrowly V-shaped in some specimens. Teleoconch increasing in height with weak allometry; most juvenile specimens with low spires, most large specimens taller and narrower than all other large *Janthina* species, although much shorter and wider than *Recluzia* species.

Table 5. Dimensions of *Janthina chavani* (*dimensions from original publications; specimens with very weak spiral folds indicated within parentheses; *NSF*, number of spiral folds). Stage abbreviations: *Wm*, Mangapanian New Zealand Stage (late Piacenzian–early Gelasian, 3.0–2.4 Ma); *Wn*, Nukumaruan New Zealand Stage (Gelasian–early Calabrian, 2.4–1.63 Ma).

locality	height	diam.	NSF	H/D
Hartungia dennanti chavani holotype*	44	38	—	1.16
Kaneconcha knorri holotype*	32	34.5	—	0.93
Parajanthina japonica holotype*	31.2	37.3	11	0.84
Australian specimens, all from Roe Plain:				
88 km W of Eucla Motel (WAM)	33.1	29.6	9	1.12
88 km W of Eucla Motel	27.0	25.9	9	1.04
88 km W of Eucla Motel	36.0	29.3	9	1.23
88 km W of Eucla Motel	47.9	37.9	9	1.26
88 km W of Eucla Motel	44.0	37.4	(8)	1.18
88 km W of Eucla Motel	44.8	35.6	8	1.26
88 km W of Eucla Motel	40.8	35.4	8	1.15
88 km W of Eucla Motel	32.1	27.3	9	1.18
88 km W of Eucla Motel	29.2	25.7	10	1.14
88 km W of Eucla Motel	30.1	27.1	10	1.11
88 km W of Eucla Motel	38.3	33.0	9	1.16
88 km W of Eucla Motel	37.8	35.5	9	1.06
88 km W of Eucla Motel	36.4	31.5	9	1.16
88 km W of Eucla Motel	26.7	27.0	9	0.99
88 km W of Eucla Motel	33.0	29.6	11	1.11
88 km W of Eucla Motel	32.4	33.2	9	0.98
88 km W of Eucla Motel	38.1	38.1	(8)	1.0
88 km W of Eucla Motel	30.8	30.4	9	1.01
88 km W of Eucla Motel	24.6	23.6	11	1.04
88 km W of Eucla Motel	41.0	37.5	9	1.09
88 km W of Eucla Motel	40.7	39.1	9	1.04
126 km W of Eucla Motel (WAM)	44.8	37.8	(8)	1.19
126 km W of Eucla Motel	28.7	28.6	9	1.00
126 km W of Eucla Motel	29.4	26.6	9	1.11
126 km W of Eucla Motel	42.8	41.5	(10)	1.03
126 km W of Eucla Motel	30.5	28.0	9	1.09
84 km W of Eucla telegraph station (WAM)	40.3	32.4	8	1.24
84 km W of Eucla	35.8	34.9	9	1.03
84 km W of Eucla	37.3	33.5	9	1.11
84 km W of Eucla	35.2	31.5	9	1.12
84 km W of Eucla	29.6	28.6	8	1.03
74 km W of Eucla Motel (WAM)	24.3	26.8	9	0.91
74 km W of Eucla Motel	35.8	31.5	10	1.14
68 km W of Eucla Motel (WAM)	23.3	24.7	10	0.94
48 km W of Eucla Motel (WAM)	35.1	32.2	9	1.09
48 km W of Eucla Motel	21.6	22.2	9	0.97
48 km W of Eucla Motel	31.4	28.3	10	1.11
26 km W of Madura (WAM)	28.7	28.7	(9)	1.0
26 km W of Madura	26.8	28.5	9	0.94
26 km W of Madura	37.9	34.6	10	1.10
Hampton microwave tower (WAM)	22.8	23.7	10	0.96
640 m N of Hampton microwave (WAM)	25.7	28.3	9	0.91
NMV P322322, 88 km W of Eucla Motel	37.7	33.3	(9)	1.13
GNS WM14468, 16 km W of Madura	47.8	41.3	(6)	1.16
GNS WM14468, 16 km W of Madura	42.4	39.3	(8)	1.08
GNS WM14468, 16 km W of Madura	42.1	33.9	(7)	1.24
GNS WM14468, 16 km W of Madura	37.4	33.4	(10)	1.12
GNS WM14468, 16 km W of Madura	35.1	33.2	(10)	1.06
GNS WM14468, 16 km W of Madura	33.85	31.3	(11)	1.08
GNS WM14468, 16 km W of Madura	32.6	29.5	(9)	1.11
GNS WM14468, 16 km W of Madura	27.5	27.8	(5)	0.99
GNS WM14468, 16 km W of Madura	27.6	27.3	(8)	1.01
New Zealand specimens:				
T23/f6565, Te Ekaou Stream, OUGD, Wm	24.5	30.4	10	0.81
T22/f8506, above Makohine viaduct, Wn	23.9	28.0	(8)	0.85
T22/f8506, above Makohine Viaduct	20.6	26.5	9	0.78
T22/f8506, above Makohine Viaduct	23.8	25.7	9	0.93
GS4258, Nukumaru Limestone, Wn	27.0	27.4	(5)	0.99
OU8037, T23/f6563, Te Ekaou Stream, Wn	13.3	16.2	9	0.82
OU8125, T23/f6563, Te Ekaou Stream, Wn	20.5	25.3	9	0.81

Remarks. *Janthina chavani* resembles *J. typica* closely, but can be distinguished by three characters: (1) the spiral folds are weaker, particularly over the sutural ramp, than on *J. typica*. The two uppermost spiral cords, at least, are suppressed, so that the ramp is smooth (apart from the fine axial ridgelets) in almost all specimens. Many Roe Calcarenite specimens have very weak, almost uncountable spiral folds, and resemble *J. janthina* quite closely (Figs 27A–I, 28C, F, J). Spiral cords are not visible at all on spire whorls of most specimens, and only around the outer edges of the spire whorls of others. (2) The fine axial ridgelets tend to fade out after the spire whorls and, on many specimens, particularly the (slightly abraded?) Roe Calcarenite population, the axial ridgelets are very weak on or absent from the last whorl. (3) Teleoconch spire height exhibits a much greater range of variation than in any other *Janthina* species, tending to produce an allometrical change with growth from very low-spired juvenile specimens to tall-spired adults. Obviously, this third character is visible only in large collections, and it is doubtful whether it would have been recognized without observing the large number of beautifully preserved specimens from Roe Calcarenite in southeastern Western Australia. Once it became evident in Roe Calcarenite collections, the great shape variability of other populations in New Zealand, southern Australia and Japan became more comprehensible. Many specimens have an obviously convex (cyrtoconoid) spire outline, resulting from the change in shape during growth, but others have straight outlines. Still others have an unusually rapid whorl translation, so they accommodate the change in shape with a stepped spire, each succeeding whorl descending below the periphery of the preceding one.

Shape differences are shown in Fig. 29, a scatter diagram comparing height with width in *Janthina typica*, *J. chavani* and *J. krejcii* sp. nov. The field occupied by *J. typica* in Fig. 29 is aligned more nearly along the x = y diagonal axis than that of *J. chavani*. This demonstrates that on average, height is almost equal to diameter in *J. typica*, and there is little change in shape with growth, although most small specimens have shorter spires than large specimens; height increases regularly throughout growth. The field of *J. krejcii* sp. nov. lies well below but parallel to the x = y axis, confirming the very low, wide shape of this species. All specimens are wider than they are high, and again there is no obvious change of shape with growth, although only five specimens were complete enough to include in this diagram. However, the field occupied by *J. chavani* is aligned up a steeper axis than x = y. On average, small (juvenile) specimens are wider than they are high, large adults are markedly taller than they are wide, and there is a weak allometrical increase in height as the shell grows in *J. chavani*. Although the allometry is weak, 22 of the 50 plotted specimens of *J. chavani* (44%) are taller than all 29 specimens of *J. typica* plotted in Fig. 29, confirming the visual estimation of shape and size differences.

The sinus in the outer lip in *Janthina chavani* is basal, as in *J. typica*, but while in many specimens it is semicircular (Figs 28C, E), others have a wider, narrowly V-shaped sinus, and in still others it is intermediate in shape (Ludbrook, 1978: pl. 12, figs 3, 5–6, 10). Specimens of *J. chavani* reach 48 mm in height and 40 mm in diameter, with 8–11 spiral folds on the last whorl. Most specimens have 9 or 10 folds, as in *J. typica*. Presumably the allometrical increase in spire height in *J. chavani* produces a taller sutural ramp in adults that allows almost the same number of spiral folds to be present in both species, bordered above by an unfolded area in *J. chavani* that is absent from *J. typica*. The spiral folds of *J. chavani* also possibly are slightly narrower than those of *J. typica*, although any difference is not obvious. A high proportion of Roe Calcarenite specimens is conspicuously large, robust, thick-shelled, weakly sculptured and tall-spired for a fossil *Janthina* species, but this is presumably partly because of the large population available to select from. The weakly consolidated nature of the formation allows the excellent preservation and easy collection of fragile shells. Ludbrook (1978: pl. 12, figs 13–14) illustrated a specimen with all sculpture abraded off the earliest 1.5 teleoconch whorls, which are weakly inflated in this specimen, and labelled it as "showing smooth protoconch", but this is misidentified and does not resemble the very small, tall, pupiform, planktotrophic *Epitonium* protoconch of all living *Janthina* species. It is quite similar in appearance to the smooth apex of the holotype of *Eunaticina abyssalis* (Fig. 25G), although the outer layer is present and the smoothness results from surface abrasion rather than corrosion in this case. The protoconch of *J. chavani* has not been observed.

The younger Japanese specimens are referred to planktonic foraminiferal zones N21 and N22 and were identified by Japanese authors as *Janthina* (or *Hartungia*) *japonica*. They are relatively small and, consequently, have low spires (Tomida & Itoigawa, 1982: pl. 19, figs 1a–c, holotype of *Parajanthina japonica*; Tomida & Itoigawa, 1984: pl. 31, figs 1a–2b; 1989: pl. 23, figs 1a–2d; Noda *et al.*, 1995: figs 11.7a–d; Tomida & Kitao, 2002: figs 2.1a–2c; Tomida *et al.*, 2013: figs 3E–L). However, they agree with *J. chavani* in having weaker spiral sculpture than older specimens, they closely resemble most New Zealand specimens identified as *J. chavani*, and they overlap with the range of variation in spire height of New Zealand and southern Australian specimens. The apparent difference in spire height results from the scarcity of large adults in Japanese samples, and their abundance in Roe Calcarenite collections. Like New Zealand specimens, many Japanese ones also have been distorted and crushed to varying extents by compaction. In the writer's estimation, these youngest Japanese specimens fall within the range of variation of *J. chavani*.

The overall impression of the characters and range of variation of *Janthina chavani* is that this species is closely similar to *J. janthina* as well as to *J. typica*. It is feasible that it was the immediate ancestor of *J. janthina*. This closely similar appearance provides the main evidence that fossils allow for the evolutionary history of the entire group, and so must be given strong weight when evaluating the phylogeny of *Janthina*. The very weak spiral folds on some specimens of *J. chavani* from Roe Calcarenite are only slightly more obvious than the faint spiral folds and grooves on the base of some Recent specimens of *J. janthina*, and the most fundamental differences between them are the narrow basal sinus in the outer lip of *J. chavani* and its wider shape and more nearly central apex in *J. janthina*, the weakly trochiform shape of *J. janthina* compared with an evenly convex shape (although with a flattened sutural ramp) in *J. chavani*, and the presence of axial ridgelets over most of the spire whorls in *J. chavani*, whereas they are limited to the first c. 1–1.5 spire whorls in *J. janthina*. Weakening of the axial ridgelets and spiral folds and flattening of the sutural ramp in *J. chavani* compared with their state in *J. typica* are interpreted as

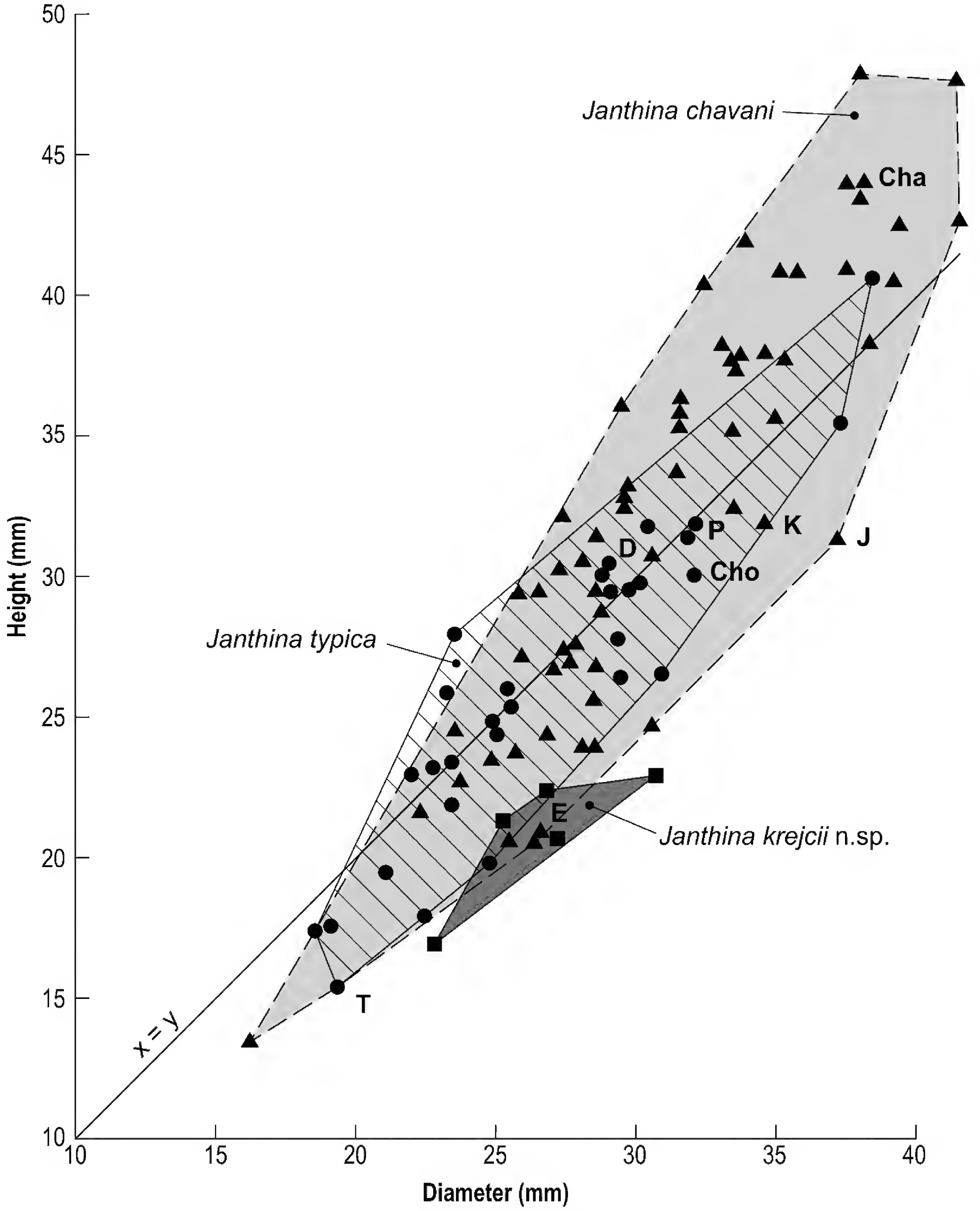

Figure 29. Scatter diagram comparing dimensions of the three extinct Plio-Pleistocene *Janthina* species. ▲ *Janthina chavani*; ● *Janthina typica*; ■ *Janthina krejcii*. Letters show positions of type specimens of synonyms: *Cha – Hartungia dennanti chavani* holotype; *Cho – Acrybia (Hartungia) chouberti* holotype; *D – Heligmope dennanti* lectotype; *E – Eunaticina abyssalis* holotype; *J – Parajanthina japonica* holotype; *K – Kaneconcha knorri* holotype; *P – Turbo postulatus* neotype; *T – Hartungia typica* neotype.

precursors to the more marked state of these characters in *J. janthina*. The much smaller sinus in the outer lip in *J. typica*, *J. krejcii* and *J. chavani* than in all living *Janthina* species seems to indicate that the function of the sinus has changed during the evolution of the genus. Wilson & Wilson (1956: 302) described the extrusion of capsules from between the gills and the bottom of the foot in *J. janthina*, so possibly the small early sinus aided this capsule extrusion, and the sinus only later came to be adapted to be used more continuously to accommodate the protruding head.

Time range. Late Piacenzian–early Calabrian; 3.0–c. 1.7 Ma (Mangapanian–Nukumaruan New Zealand Stages; latest Pliocene–early Pleistocene; Cooper, 2004: fig. 13.1, modified by inclusion of the Gelasian Stage in the Pleistocene); probably considerably younger (late Calabrian, 1.0 Ma, or even younger) in Bridgewater Limestone in SE South Australia. The equally meagre record in Japan and southern Australia confirms the mid-Piacenzian origination observed in New Zealand, but the upper limit is not constrained in any stratigraphical succession the writer is aware of.

Janthina globosa (Swainson, 1822)

Figs 2G–J, 30–31

Helix janthina Linnaeus.–Linnaeus, 1764: 670 (misidentification; see Laursen, 1953: 17, pl. 1, fig. 2).

Ianthina globosa Swainson, 1822: pl. 85, central fig. (Jan 1822); H. Adams & A. Adams, 1854: 87; Reeve, 1858: pl. 4, figs 18a–b; G. B. Sowerby II, 1882: 51, pl. 444, figs 16, 18; Tryon, 1887: 37, pl. 10, figs 11–14; Martens, 1904: 143; Iredale, 1910: 71; Oliver, 1915: 525; Morton, 1954: 167, fig. 1d (in part misidentified, = *J. pallida* Thompson).

Janthina prolongata Blainville, 1822: 155 (Aug 1822); Payraudeau, 1826: 121, pl. 6, fig. 1; Deshayes, 1843: 5; Küster, 1868: 6, pl. 1, fig. 6; Bennett, 1966: 41, pl. 9, fig. 1, pl. 10, fig. 1; Morton & Miller, 1968: 472; Keen, 1971: 442, fig. 689; Kilburn & Rippey, 1982: 79, fig. 38, pl. 11, fig. 17; Bosch *et al.*, 1995: 111, fig. 441; Okano & Wada, 2012: 58, fig. 2.

Ianthina nitens Menke, 1828: 84; Reeve, 1858: pl. 4, figs 16a–b; Benson, 1860: 409; G. B. Sowerby II, 1882: 51, pl. 444, fig. 21.

Ianthina elongata Blainville.–Maravigna, 1838: 63 (incorrect subsequent spelling of *I. prolongata*); Aradas & Benoit, 1874: 148.

Janthina rosea Anton, 1838: 50.

Janthina patula Philippi, 1844: 224, pl. 28, fig. 1.

Ianthina decollata Carpenter, 1857: 187; Reeve, 1858: pl. 4, figs 19a–b; Angas, 1867: 230; Keen, 1968: 410, pl. 59, figs 78a–c.

Ianthina iricolor Reeve, 1858: pl. 5, figs 23a–b; G. B. Sowerby II, 1882: 51, pl. 444, fig. 18.

Ianthina communis Lamarck.–Chenu, 1859: 118, figs 517–518 (misidentification).

Janthina (Janthina) nitens Menke.–Mörch, 1860: 280; Priolo, 1959: 183.

Janthina (Janthina) nitens var. *atlantica* Mörch, 1860: 280.

Janthina (Janthina) globosa Swainson.–Mörch, 1860: 280.

Janthina (Janthina) iricolor Reeve.–Mörch, 1860: 281.

Janthina (Janthina) decollata Carpenter.–Mörch, 1860: 281.

Janthina iricolor Reeve.–Mörch, 1860: 281; Hutton, 1880: 71; Yen, 1942: 219, pl. 20, fig. 123 (syntypes).

Janthina nitens Menke.–Küster, 1868: 7, pl. 1, figs 9–13; Monterosato, 1878: 95; Monterosato, 1884: 104; Bucquoy *et al.*, 1886: 434, text-fig. 6; Thiele, 1929: 225; Priolo, 1959: 183; Giannuzzi-Savelli *et al.*, 1999: 50, 51, figs 93a–b; Ardovini & Cossignani, 2004: 136.

Janthina decollata Carpenter.–Küster, 1868: 6, pl. 1, figs 7–8, pl. 2, fig. 12.

Janthina globosa Swainson.–Lischke, 1871: 169; Lischke, 1874: 53; Hutton, 1904: 80; Moss, 1908: 28; Suter, 1913: 300, pl. 44, fig. 14; Hedley, 1918: M61; Bucknill, 1924: 150, pl. 5, fig. 20; Powell, 1937: 74, pl. 10, fig. 29; Okutani, 1956: 43, text-figs 1–2; Cernohorsky, 1972: 198, pl. 56, fig. 9; Powell, 1976: 107, pl. 17, fig. 29; Kay, 1979: 158, fig. 55A, D; Powell, 1979: 254, pl. 48, fig. 22; Redfern, 2001: 76, pl. 36, fig. 316; Morley, 2004: 102; Robertson, 2007a: 5, fig. 2; Spencer *et al.*, 2009: 206; Raven & Bracegirdle, 2010: 27, bottom right fig.; Willan *et al.*, 2010: 386, text-fig.; Hernández *et al.*, 2011: 98, fig. 30 I; Janssen, 2012: 24, figs 5A–6B.

Janthina pallida var. *minor* Monterosato, 1878: 35.

Janthina nitens var. *minor* Monterosato, 1878: 35.

Janthina splendens Monterosato, 1884: 104 ("= *J. nitens*, var. *minor*" Monterosato).

Amethistina laeta Monterosato, 1884: 105 ("= *J. pallida*, var. *minor*" Monterosato).

Ianthina globosa var. decollata Carpenter.–Whitelegge, 1889: 262.

Janthina laeta (Monterosato).–Locard, 1898: 3, pl. 20, figs 31–34.

Janthina payraudeaui Locard in Locard & Caziot, 1901: 157 (refers to Payraudeau, 1826: 121, pl. 6, fig. 1).

Janthina sp.–Woodring, 1928: 405.

Violetta globosa (Swainson).–Iredale, 1929: 279; Allan, 1950: 95; Cotton, 1959: 376; Iredale & McMichael, 1962: 49; Kuroda *et al.*, 1971: 246, pl. 62, figs 11–12.

Janthina (Violetta) globosa Swainson.–Powell, 1946: 77, pl. 10, fig. 29; Powell, 1957: 98, pl. 10, fig. 29; Powell, 1962: 91, pl. 10, fig. 29; Kira, 1962: 30, pl. 14, fig. 24; Abbott, 1974: 113, col. pl. 3, fig. 1179.

Ianthina prolongata Blainville.–Laursen, 1953: 28, figs 30–35c.

Janthina cf. *pallida* Thompson.–Berry, 1958: 27.

Janthina communis Lamarck.–Pasteur-Humbert, 1962: 52, fig. 71 (misidentification as *J. janthina* Linnaeus).

Janthina exigua Lamarck.–Hodgkin *et al.*, 1966: 35, pl. 12, fig. 7 (misidentification).

Janthina pallida Thompson.–Wilson, 1993: 281, pl. 44, figs 38a–b (misidentification).

Janthina (Violeta) [sic] *globosa* (Swainson).–Rios, 1994: 101, pl. 33, fig. 414.

Janthina (Violetta) prolongata Blainville.–Okutani, 2000: 319, pl. 158, fig. 2.

Janthina (Janthina) prolongata Blainville.–Janssen, 2007a: 59, pl. 1, figs 5–6.

Janthina prolonga Blainville.–Severns, 2011: 198, upper fig (incorrect subsequent spelling of *J. prolongata* Blainville, 1822).

Type material. As with all living *Janthina* species other than *J. janthina*, Laursen (1953) did not discuss any type material of *J. globosa*, and provided no reasons for assigning particular names to particular species. Examination of the huge collections of *Janthina* specimens in world museums has demonstrated that Laursen (1953) recognized the five living species correctly, as was agreed by Robertson (2007a), although a little tentatively. As far as can be determined from the type material the writer has examined, Laursen also assigned the most appropriate names to the five species, but the more than 60 published names for living *Janthina* species must now be referred to type specimens that establish their identity unambiguously. The two specimens in UPSZTY illustrated by Laursen (1953: pl. 1, fig. 2) and referred to *Helix janthina* by Linnaeus (1764: 670) are *Janthina globosa* Swainson (UPSZTY756, marked with a letter "a", and UPSZTY2849, marked with a letter "b"; Erica Sjolin UPSZTY pers. comm. 26 Sep 2012). No type material of *J. globosa* Swainson is present in NHMUK (K. Way NHMUK pers. comm. 05 Feb 2013). It seemed possible that some is present in Swainson's material in the Manchester Museum. However, the catalogue of molluscan types in the Manchester Museum (McGhie, 2008) does not include any Swainson types. H. McGhie (Manchester Museum pers. comm. 27 Nov 2014) stated that he has been unable to recognize any Swainson types because Swainson's material has been incorporated in the general collection and there is no means of identifying it. It is concluded that none of Swainson's type specimens of Mollusca is recognisable in the Manchester Museum. No type material of *Janthina globosa* Blainville or of *J. prolongata* is present in MNHN, NHMUK, USNM or any other institutions the writer has consulted, and its location is unknown. *Janthina iricolor*, three syntypes NHMUK1976168, from "China", *ex* Cuming collection; two

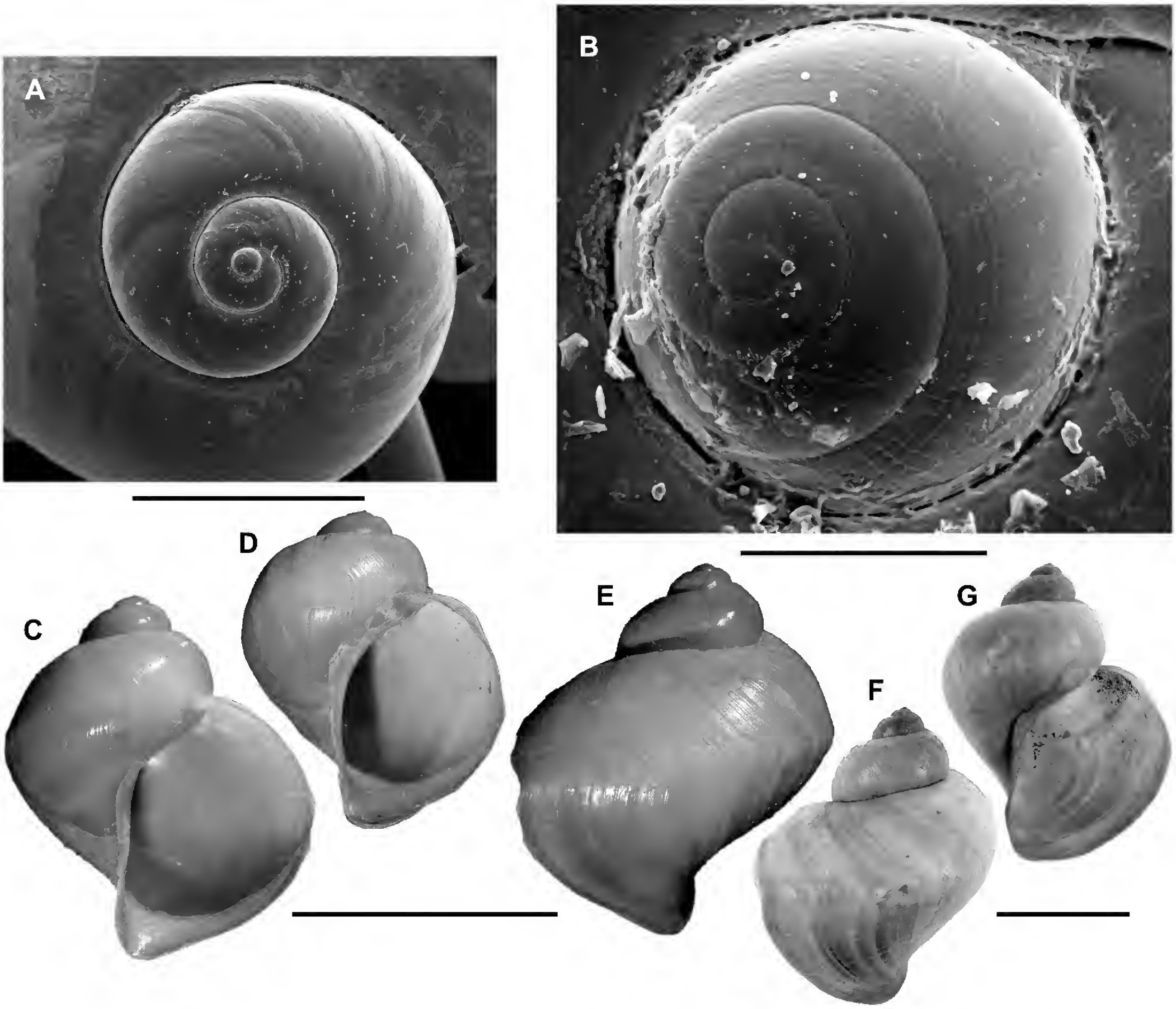

Figure 30. Specimens of *Janthina globosa* (Swainson). *(A–B)* GNS RM5222, Waipu Cove, Northland, New Zealand, SEM; apical views of shell (A) and protoconch (B), showing smooth teleoconch surface, and protoconch inclined only weakly. *(C–E)* Monterosato's type material, photos sent by M. Appolloni (MCZR) and M. Oliverio (University of Rome 1 "La Sapienza"); C, E, MCZR23423/1, lectotype designated here of *Janthina splendens* Monterosato; Alexandria, Egypt; D, MCZR23414/1, lectotype designated here of *Amethistina laeta* Monterosato; Algeria. *(F–G)* ZMB41985a, lectotype designated here of *Janthina patula* Philippi, 1844, from Naples, Italy; photos sent by C. Zorn (ZMB). Scale bars: A, 3 mm; B, 200 µm; C–G, 10 mm (longer bar applies to C–E, shorter bar to F–G).

of the syntypes were illustrated by Yen (1942: 219, pl. 20, fig. 123, 2 images). The larger of the syntypes illustrated by Yen (1942: pl. 20, fig. 123, right image), NHMUK1976168a, is here designated the neotype of both *Janthina globosa* Swainson, 1822 (Jan) and *Janthina prolongata* Blainville, 1822 (Aug).

Janthina nitens, no type material present in any museums the writer has consulted. Menke did not know the locality of his specimen. R. Janssen (SMF pers. comm. 18 Aug 2015) confirmed that no type material of *J. nitens* is present in the remnants of Menke's collection in SMF. Therefore, the neotype of *J. globosa* and *J. prolongata* designated above, NHMUK1976168a, is here also designated the neotype of *Janthina nitens* Menke, 1828. Dr K. Schniebs (Senckenberg Naturhistorische Sammlung Dresden, pers. comm. 23 Feb 2016) reported that all material of *Janthina* in Anton's collection was lost in or after the end of world war two, so no type material remains for *J. rosea*. Therefore, the neotype of *J. globosa*, *J. prolongata* and *J. nitens* designated above, NHMUK1976168a, is here also designated the neotype of *Janthina rosea* Anton, 1838. The remaining two syntypes of *Janthina patula* Philippi, ZMB41985 (photographs sent by C. Zorn, ZMB pers. comm. 30 Jan 2016; Figs 30F–G) are labelled "Neapel" (Naples). This name previously was assumed to be a synonym of *J. pallida*, but the deep sinus in the outer lip and the protruding, pointed anterior end of the columella demonstrate that the illustrated syntype is a tall, narrow specimen of *J. globosa* rather than of *J. pallida*. As the writer has seen only the illustrated photographs (Figs 30F–G), the illustrated syntype ZMB41985a is here designated the lectotype of *Janthina patula* Philippi, 1844, in case the remaining paralectotype is not conspecific.

Type material of Carpenter's (1857) *Janthina* species was not included in Carpenter's illustrations of the Mazatlan fauna (Brann, 1966: 14). However, that is not surprising because, as Keen (1968) pointed out, Carpenter illustrated only his smaller specimens, with camera lucida drawings. Keen (1968: 408, 410, pl. 59, figs 78a–80) illustrated the type material in NHMUK of all three names proposed by Carpenter and recorded three syntypes of *Ianthina decollata*, demonstrating that they are typical specimens of *J. globosa*. Type material of all three names, from Mazatlan, western Mexico, is still present in NHMUK: *I. decollata*, one syntype remaining, NHMUK1857.6.4.878 (K. Way NHMUK pers. comm. 05 Feb 2013).

The name *Janthina nitens* var. *atlantica* Mörch (1860: 280) was defined by a list of references, the first of which was "Janthina *communis* Q. et G., Ast[rolabe], t. 29, fig. 1–4", followed by a further six references (Mörch did not italicize *Janthina* in headings in this paper). The other references are to M. E. Gray (1842: pl. 48, fig. 1, and pl. 117a, figs 2b–c), Chenu (1859: 118, fig. 518), Woodward (1851: 148), Gray (1857: 52, fig. 30) and Cuvier (1808: pl. 1, figs 3–5). Most of these figures show *J. globosa*, and these and Mörch's reference to the Mediterranean locality cited by Fabius Columna show that the name is a synonym of *J. globosa*. The original material illustrated in the figures referred to by Mörch (1860: 280) all constitutes syntypes of *J. nitens* var. *atlantica*. Kathe Jensen (ZMUC pers. comm. 18 Aug 2015) stated that she was unable to find type material in ZMUC. Quoy & Gaimard's (1833: pl. 29, figs 1–4) illustration, supposedly of "*J. communis*", i.e., *J. janthina*, from "Océan Atlantique", shows a specimen with egg capsules attached beneath its float, and so is clearly not *J. janthina*, although the drawings are so crude that the species is not identifiable from this drawing. Also, the specimens illustrated by Quoy & Gaimard (1833: pl. 29) are not present in MNHN (P. Bouchet MNHN pers. comm. 5 Apr 2016). The location of any of the other specimens illustrated in the references cited by Mörch (1860: 280) also is unknown. Therefore, the neotype of *J. globosa*, *J. prolongata*, *J. nitens* and *J. rosea* designated above, NHMUK1976168a, is here also designated the neotype of *J. nitens* var. *atlantica*.

It has been assumed previously that Monterosato's (1878: 35) identification of *Janthina pallida* was correct. However, his type material is present in MCZR. Massimo Appolloni (MCZR) and Marco Oliverio (Department of Biology and Biotechnologies "Charles Darwin", University of Rome 1 "La Sapienza") sent the writer photographs of some of Monterosato's type material. The syntype examined of *Amethistina laeta* Monterosato, 1884 (= *J. pallida* var. *minor* Monterosato, 1878), MCZR23414/1, is a small specimen (H 11.8 mm), one of five specimens of *Janthina globosa* from Algiers, labelled "*Amethistina laeta* 1884 Monts [Monterosato] Alger (Joly)". Because of confusion about the application of this name, which (as with *J. splendens*) has usually been assumed to refer to *J. pallida*, the illustrated specimen (Fig. 30D), MCZR23414/1, is here designated the lectotype of *Amethistina laeta* Monterosato, 1884. *Janthina splendens* Monterosato, 14 syntypes in MCZR; six syntypes are from Algiers, labelled "*J. splendens* Monts Alger! (Joly)", two from Alexandria, Egypt, labelled "*J. splendens* Allesandria (Lothellerie)", two from "Is. di Lipari", and four labelled "Pal. coll. Di Blasi". The illustrated syntype (Fig. 30C, E) from Alexandria is a small specimen (H 13.7 mm) of *J. globosa*. Because of confusion about the application of this name, the illustrated specimen, MCZR23423/1, is here designated the lectotype of *Janthina splendens* Monterosato, 1884. *Janthina payraudeaui*, type material not in MNHN, location unknown; referring to Payraudeau's (1826: 121, pl. 6, fig. 1) illustration of a specimen *J. globosa* from Corsica. The neotype of *Janthina globosa* Swainson and *J. prolongata* Blainville designated above, NHMUK1976168a, is here also designated the neotype of *Janthina payraudeaui* Locard, 1901.

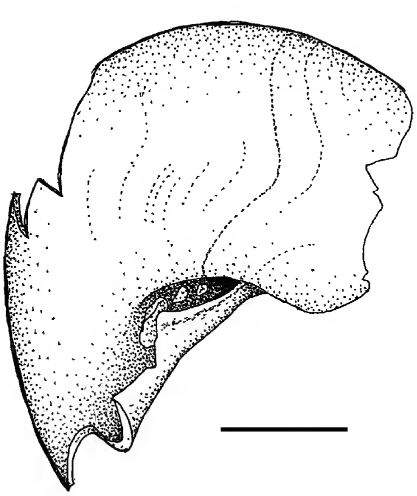

Figure 31. *Janthina globosa* (Swainson), Pliocene (Piacenzian–Gelasian), Bowden, Jamaica (USNM135575), specimen recorded by Woodring (1928: 405); basal fragment of last whorl showing sinus in growth lines (camera lucida drawing); greatest diameter 4.2 mm. Scale bar 1 mm.

Other material examined. Fossils: **Philippine Islands:** Janssen (2007a: 59, pl. 1, figs 5A–6B) recorded and illustrated two small specimens of *Janthina globosa*, one from each of his localities Anda1 and Anda2, near the village of Anda on Cabarruyan Island, Lingayen Gulf, Pangasinan province, west coast of Luzon, Philippine Islands. A combination of planktonic foraminiferans and pteropods at this locality demonstrated a Piacenzian (late Pliocene) age (Janssen, 2007a: 110). Helwerda *et al.* (2014: 101) pointed out that the age of the Anda localities might be as young as Gelasian, based on planktonic foraminifera, and is uncertain at present; they are accepted as Piacenzian–Gelasian in the present paper. The small specimen, a little over 9 mm high, from Anda1 (RGM517582; Janssen, 2007a: pl. 1, figs 5A–B) clearly reveals the lack of sculpture, near-spherical shape, anterior apertural prolongation, and moderately deep mid-outer lip sinus of *J. globosa*. Also, the specimen from Anda 2 (RGM517583; Janssen, 2007a: pl. 1, figs 6A–B) reveals an incomplete but well-preserved *Janthina* protoconch. This material is critically important, as it is the first confirmation of the late Piacenzian–Gelasian (late Pliocene–earliest Pleistocene) occurrence of a living *Janthina* species.

Jamaica: Woodring (1928: 405) identified a small specimen from the famously diverse Pliocene locality at Bowden, Jamaica, as "*Janthina* sp.", and suggested it might be related to *J. globosa*. The Bowden "shellbed" has been dated as early Piacenzian, calcareous nannofossil zone NN16 (Aubry, 1993); as Piacenzian, based on planktonic Foraminifera (Berggren, 1993); as "early late Piacenzian" (Janssen, 1998: 97) based on planktonic Foraminifera, confirmed by the occurrence of the "pteropod" *Cavolinia tridentata* (Niebuhr, 1775), which did not evolve until Piacenzian time (Janssen, 1998: 105); as late Pliocene [i.e., Piacenzian] (Kohl & Robinson, 1998); and as 2.8–1.6 Ma, spanning the Plio-Pleistocene boundary (at this date, intended for late Gelasian–early Calabrian, the boundary dated at 1.8 Ma; Cotton, 1999). A late Piacenzian age is accepted here, recognising the rather poorly constrained age of this "shellbed". The "shellbed" is highly heterogeneous and possibly formed as an olistostrome (B. M. Landau pers. comm. 2008), contains microfossils reworked from a range of ages (Kohl & Robinson, 1998) and certainly contains macrofossils from a wide range of environments. The lithostratigraphy was described in detail by Pickerill *et al.* (1998), who demonstrated several lenses of coarse-grained lithologies within the lower part of the formation. Kohl & Robinson (1998: 43) concluded from the Foraminifera that the Bowden Formation was deposited by sediment gravity flows: "… the present study supports the downslope transport interpretation of other investigators … a shallow-water (inner neritic) fauna containing molluscs, corals and benthic foraminifera was redeposited in an outer neritic environment". The writer has examined Woodring's specimen (USNM135575, from USGS locality 2580, collected by J. Henderson). It is stark white, incomplete (part of the base originally missing), very small (H 5.7, D 4.7 mm; Woodring, 1928: 405), and has now largely disintegrated into five main fragments and several smaller ones. It is very thin-shelled, with an obvious but low, rounded spire as in *Janthina globosa*, a narrow inner lip reflected over the very narrow umbilical chink, and an almost completely smooth, evenly and strongly inflated exterior representing an originally subspherical, naticiform shell. The largest basal fragment (maximum dimension 4.2 mm; Fig. 31) bears very faint growth lines revealing a moderately deep sinus in the centre of the outer lip, agreeing with that of Recent specimens of *J. globosa*. One growth line is almost complete, and many others are faintly visible parallel to the complete one, all visible only in strongly oblique light. The protoconch is missing. Because of its evenly subspherical shape, low but obvious, rounded spire, lack of sculpture other than faint growth lines, and the moderately deep sinus with its apex located in the centre of the outer lip, the Bowden specimen also is identified as a late Piacenzian fossil specimen of *J. globosa*.

Mediterranean: Janssen (2012: 24, figs 6A–7B, 45H) recorded *Janthina globosa* (six samples) and another possibly distinct taxon referred to "*Janthina janthina*?" (19 samples) from late Pleistocene–Holocene core tops collected throughout the eastern Mediterranean Sea. The protoconch illustrated (Janssen, 2012: fig. 45H) as that of *J. janthina* is shorter and inclined at a much greater angle to the teleoconch coiling axis than in *Janthina* species illustrated previously (Robertson, 1971: pl. 5, fig. 17) and although the juvenile teleoconch (Janssen, 2012: figs 7A–B) lacks axial ridgelets, it closely resembles those studied here. Also, Robertson (1971: 7) described the angle of the protoconch to the teleoconch coiling axis as varying between 10° and 50° in *J. janthina*, and those examined here (Figs 32A–D) lie at a high angle to the teleoconch, indicating that Janssen's (2012) identification is correct. Specimens assigned to *J. globosa* (Janssen, 2012: figs 6A–B) also are correctly identified.

Present–day samples from Australia and New Zealand: **Australia:** ***Northern Territory***: Port Essington (AMS). ***Western Australia***: Broome (NMV); False Bay (AMS). ***South Australia***: Encounter Bay (SAM). ***New South Wales:*** Ulladulla (AMS); Nelson Bay (AMS); Curl Curl Beach (C83054, AMS); Maroubra (SAM; C51088, AMS); Collaroy Beach (C79166, C77799, AMS); Long Reef (AMS); Palm Beach (AMS); La Perouse (AMS); Coogee (C56764, AMS); Middle Harbour, Port Jackson (NMV); Manly Beach (NMV); Terrigal (AMS); Port Kembla (AMS); South Ocean Beach, Bermagui (AMS); Putty Beach, Kilcare (AMS); Wollongong (C11239, AMS); Mallacoota (NMV); Ulladulla (C83053, AMS). ***Queensland***: Caloundra (AMS); Fairfax I., Bunker Group (C69053, AMS); Keppell Bay (NMV); Lady Elliott I. (C73001, AMS). ***Tasmania***: Tasmania (many, NMNZ M210990).

Lord Howe Island (NMV; C13799, AMS); Blimey Beach (AMS). **Norfolk Island:** C59408 (AMS); specimen observed, AGB, in Mrs M. Hoare colln, Norfolk. **Kermadec Islands:** Raoul I. (NMV; AWM; AMS; NMNZ M200951, 10; M22294, 70); Denham Bay, Raoul I. (GNS WM8273, 1; NMNZ M201609, 1); 1.8km NW of Napier I., Raoul I. (NMNZ M226575, 1).

New Zealand: Spirits Bay (NMNZ M03935, 1); Tapotupotu, SE of Cape Reinga (NMNZ M308661, 30); Waikuku Beach, S of North Cape (NMNZ M044726, 4); Matai Bay, Karikari Peninsula (GNS RM3760, 2); Cable Bay, Doubtless Bay (GNS RM4063, 1); outer Bay of Islands (NMNZ M308652, 3); Otahei Bay, Bay of Islands (NMNZ M087147, 3); Russell, Bay of Islands (AWM); Bream Head, Northland (AWM18130); Mangawai Heads, Northland (GNS RM333, 2; AWM17547); Waipu Cove, S of Whangarei (GNS RM4322, 3); Pakiri Beach, N of Leigh (GNS RM5320, 4); Whangateau, Leigh (AWM30150); Piha Beach, W Auckland (GNS RM5310, 1); Muriwai Beach, W Auckland (GNS M5321, 3); Auckland (S492, S780, Suter Colln, GNS); Takapuna Beach, Auckland (AWM18131); Orakei, Auckland (GNS Suter colln, S780, 1); Auckland harbour (GNS Suter colln, S492, 1); Kaitoke Beach, Great Barrier I. (NMNZ M087145, 1); W coast Awhitu Peninsula, SW of Waiuku, SW Auckland (NMNZ M087148, 3; M277738, 1; M277739, 2); Matakana I., Bay of Plenty (AWM33258; AWM42753, 53; NMNZ M111096, 2); Papamoa Beach, Bay of Plenty (NMNZ M120140, 100; M120141, 40); Waihau Bay, Whangaparaoa, near East Cape (NMNZ M15032, 1).

Distribution. *Janthina globosa* is among the least common living *Janthina* species around New Zealand. It is recorded only from the northeastern North Island warm-water region, as far south as Awhitu Peninsula, SW Auckland, on the west coast and the eastern Bay of Plenty on the east coast. Nevertheless, samples of some hundreds of specimens have been collected in this area from time to time. It is much more common around eastern, northern and western Australia, and is one of the most common species in the North Pacific. Savilov (1969: 402) noted that the distribution of *J. globosa* in the Pacific is very similar to that of *J. janthina*, and many large schools contained both species, although *J. globosa* was much the less common. It was collected at 81 of the 393 *Vityaz* stations with *Janthina*. "Exceptionally large concentrations were observed in … the north and south subtropical current systems, as well as in the eastern regions of the Trade Wind Current. They also occurred near the coast of California. Only single young individuals (1–3 mm) were observed in the western areas of the North Trade Wind Current and in the Trade Wind Countercurrent" (Savilov, 1969: 402). Berry (1958) reported that it is "of only occasional Californian occurrence". As noted above, Okano & Wada (2012) provided data on height and egg-capsule incidence for a collection of about 170 specimens cast ashore in September 2010 on the beaches of Iwami-cho, eastern Tottori Prefecture, Japan Sea coast of Honshu. Egg capsules were present in 41 of these specimens (24%); the largest shell was 40.35 mm high, and none with shells shorter than 27.4 mm had egg capsules attached to their floats. Suzuki & Shiga (2008) also recorded specimens rather surprisingly cast ashore in Hokkaido, the northernmost island of Japan.

Most importantly for the evolution of neustonic Epitoniidae, Piacenzian or possibly Gelasian fossil specimens of *Janthina globosa* are recorded here from two localities, in Jamaica and the Philippine Islands. Late Pleistocene–Holocene fossils are also reported widely in the Mediterranean Sea. This species has a much longer fossil record than any other living *Janthina* species, and is critical for demonstrating that a living *Janthina* species already had achieved a wide, presumably cosmopolitan distribution before *J. chavani* became extinct. This confirms that *J. globosa* and *J. janthina* had distinct origins.

Dimensions. See Table 6.

Table 6. Dimensions of *Janthina globosa*.

locality	height	diam.	H/D
Janthina iricolor syntype, neotype of *J. globosa*	31.3	31.8	0.98
Janthina iricolor syntype	38.2	36.6	1.04
Janthina iricolor syntype	33.6	32.4	1.04
GNS WM15254, Mauritius	37.7	31.2	1.21
GNS RM5321, Muriwai Beach, Auckland, NZ	27.6	25.4	1.09
GNS RM5321, Muriwai	26.5	23.9	1.11
GNS RM5321, Muriwai	21.5	19.9	1.08
NMNZ M201609, Raoul I., Kermadec Islands	23.2	20.7	1.12
NMNZ M200951, Raoul I., Kermadec Islands	27.1	22.5	1.20
NMNZ M308661, Tapotupotu, Cape Reinga, NZ	24.1	22.0	1.10
NMNZ M308661, Tapotupotu	24.3	20.6	1.18
NMNZ M277739, Irwins Gap, Waiuku, NZ	25.7	21.9	1.17
NMNZ M042102, Gove, NT, Australia	37.9	33.8	1.12
NMNZ M042102, Gove	38.5	33.5	1.15

Diagnosis. Moderately large (to c. 40 mm high), spire moderately tall, whorls strongly and evenly convex, suture deeply impressed; exterior lightly polished to glossy, without obvious sculpture. Sinus occupying entire height of outer lip, symmetrically V-shaped, deep but less so than in *J. exigua* and *J. umbilicata*; apex of sinus at centre of lip. Anterior end of columella drawn out anteriorly, forming a short, triangular projection. Most specimens uniform deep violet, slightly paler below suture than elsewhere; a few specimens paler. Lays ovate-triangular egg capsules on underside of float.

Remarks. The large size sets *Janthina globosa* apart from all living *Janthina* species other than *J. janthina*. Many shells reach 30 mm in height; Suter (1913: 300) recorded a New Zealand specimen with H 41, D 38 m, although it is not clear what this was based on, as a specimen this large is not present in his collection in GNS. As noted above, Okano & Wada (2012) also recorded Japanese specimens up to 40.35 mm high. Several large specimens examined (e.g., Gove, Northern Territory, Australia, NMNZ M042102, 2 specimens) have an unusually pale, matt, milky bluish-white shell, similar in tone to most specimens of *J. pallida*, but most specimens retain their deep violet, glossy shells until a large size. Its lack of sculpture, anterior prolongation of the columella, and polished, strongly and evenly convex whorls also make this species easily recognised. The sinus in the outer lip also is significantly deeper than that of *J. pallida*. The radular teeth of *J. globosa* (Laursen, 1953: fig. 33) are narrower and less strongly hooked than those of all other *Janthina* species. Priolo (1959: 183–184) provided a long list of references to usages of this name and its many synonyms in the literature on living Mediterranean molluscs.

Berry (1958) adopted the name *Janthina prolongata* for this species because he considered that "the recent … monograph by Laursen (1953) is … inconsistent in its application of the priority rule". Berry (1958) thought that Swainson's (1822: pl. 85) plate of *Janthina* was published in 1823, whereas he correctly dated Blainville's (1822) monograph. Therefore, Berry also adopted the name *J. globosa* Blainville, 1822 for the species identified here as *J. umbilicata*, as he thought *J. globosa* Blainville was the senior homonym of *J. globosa* Swainson. Berry's (1958) conclusions were followed by Keen (1971). However, Swainson's (1822: pl. 85) plate was published in January 1822, whereas Blainville's monograph was published in August 1822; these dates were confirmed by Rosenberg (2017).

A specimen of *Janthina globosa* collected alive after being cast ashore on a beach in northern New South Wales was photographed by Denis Riek [Brunswick Heads, NSW, pers. comm. 12 Nov 2015; illustrated on his web page (Riek, 2017); Fig. 5E] suspended from its float, with its head expanded but its snout rather contracted, revealing forked cephalic tentacles, and bearing pale pink egg capsules beneath the float. The external anatomy appears to be identical to that of *J. janthina*.

Time range. Late Piacenzian–Gelasian (at Bowden, Jamaica and Anda, Cabarruyan Island, Luzon, Philippines) to living, earliest record poorly constrained; recorded widely from late Pleistocene–Holocene core tops in the eastern Mediterranean.

Janthina janthina (Linnaeus, 1758)

Figs 1, 2A–F, 4A–E, 5A,D, 32–33

Helix janthina Linnaeus, 1758: 772; Linnaeus, 1767: 1246 (in part); Born, 1778: 392; Gmelin, 1791: 3645; Dillwyn, 1817: 938.

Janthina violacea Röding, 1798: 75; Mörch, 1853: 49; Hedley, 1918: M62; May, 1921: 63; May, 1923: pl. 29, fig. 5; Finlay, 1928: 246; Powell, 1937: 74, pl. 1, fig. 8; Powell, 1946: 77, pl. 1, fig. 8; Allan, 1950: 95, col. pl. 14, fig. 11, text-fig. 22.5; Powell, 1951: 27, fig. 123; Powell, 1957: 98, pl. 1, fig. 8; McMichael, 1960: 72, fig. 143; Powell, 1962: 90, pl. 1, fig. 8; Iredale & McMichael, 1962: 49; Grimmond, 1964: 24; Hodgkin, *et al.* 1966: 35, pl. 12, fig. 8.

Janthina fragilis Lamarck, 1801: 89; Roissy, 1805: 396, pl. 55, fig. 11; Lamarck, 1816, "Liste des objets": 12, pl. 456, figs 1a–b; Gray, 1827: 495; Lovén, 1847: 190, pl. 3, fig. (radula); Küster, 1868: 4, pl. 1, figs 3–4; Lischke, 1871: 168; Lischke, 1874: 52; Fischer, 1885: 774, fig. 541, pl. 10, fig. 27; Hutton, 1904: 80; Moss, 1908: 28, pl. 7, fig. 2; Pasteur-Humbert, 1962: 52, fig. 73.

Janthina penicephala Péron & Lesueur, 1807: pl. 27, fig. 1 (Mörch, 1860: 276), pl. 31 (Sherborn, 1929: 4831).

Janthina communis Lamarck, 1822: 206; Payraudeau, 1826: 120; Menke, 1843: 11; Deshayes, 1843: 4; Küster, 1868: 4, pl. 1, figs 1–2; Hutton, 1880: 71; Hutton, 1881: 164, pl. 7, fig. F (radula); Locard, 1898: 1; Suter, 1913: 299, pl. 44, fig. 11.

Ianthina fragilis Lamarck.–G. B. Sowerby I, 1822: 2nd *Ianthina* page, pl. 191, fig. 1; Reeve, 1842: 145, pl. 205, fig. 1 (repeat of Sowerby's 1822 fig.); Calder, 1849: 175; Reeve, 1858: pl. 2, figs 6a–b; Benson, 1860: 410; G. B. Sowerby II, 1882: 50, pl. 443, figs 1–4; Tryon, 1887: 36, pl. 10, figs 6–10; Whitelegge, 1889: 261.

Ianthina bicolor Menke, 1828: 84; Lesson, 1831: 365, pl. 8, fig. 2.

Janthina vulgaris Gray, 1847b: 148 (*nomen nudum*); Gray, 1850: 101 (error for *J. communis*).

Ianthina planispirata A. Adams & Reeve, 1850: 54, pl. 11, fig. 10; Benson, 1860: 410.

Ianthina communis Lamarck.–Forbes & Hanley, 1853, vol. 2: 549, pl. 69, figs 6–7; vol. 4: 260, pl. 133, fig. 1; H. Adams & A. Adams, 1854: 87; Reeve, 1858: pl. 1, figs 5a–b; Tenison Woods, 1878: 43; G. B. Sowerby II, 1882: 50, pl. 443, figs 7–8; Pritchard & Gatliff, 1900: 141; Tate & May, 1901: 407.

Ianthina britannica Forbes & Hanley, 1852, vol. 4: 260 (in synonymy); Reeve, 1858: pl. 3, figs 13a–b; G. B. Sowerby II, 1882: 50, pl. 443, figs 5–6, 14.

Ianthina violacea Röding.–H. Adams & A. Adams, 1854: 86–87, pl. 69, fig. 1; Angas, 1865: 190; Whitelegge, 1889: 261; Verco, 1908: 9; Oliver, 1915: 525; Cotton, 1932: 537; Cotton & Godfrey, 1932: 36, pl. 1, fig. 1; Verco, 1935: pl. 11, fig. 4; Cotton & Godfrey, 1938: 16; Macpherson & Chapple, 1951: 124; Kershaw, 1955: 312; Cotton, 1959: 376.

Ianthina planospirata A. Adams & Reeve.–H. Adams & A. Adams, 1854: 87; Reeve, 1858: pl. 2, figs 9a–b; G. B. Sowerby II, 1882: 50, pl. 443, figs 9–13 (incorrect subsequent spelling of *J. planispirata* A. Adams & Reeve, 1850).

Ianthina striulata Carpenter, 1857: 185; Keen, 1968: 408, pl. 59, fig. 79.

Ianthina striulata var. contorta Carpenter, 1857: 186; Keen, 1968: 408, pl. 59, fig. 80.

Ianthina affinis Reeve, 1858: pl. 1, figs 2a–b; Martens, 1904: 142.

Ianthina africana Reeve, 1858: pl. 2, figs 8a–b.
Ianthina balteata Reeve, 1858: pl. 3, figs 11a–b; Lischke, 1871: 168; Lischke, 1874: 53; Hedley, 1900: 141; Pritchard & Gatliff, 1900: 141; Martens, 1904: 142; Macpherson & Chapple, 1951: 124; Cotton, 1959: 376.
Ianthina caeruleata Reeve, 1858: pl. 2, figs 7a–b; Benson, 1860: 412; Whitelegge, 1889: 261.
Ianthina casta Reeve, 1858: pl. 1, figs 4a–b.
Ianthina depressa Reeve, 1858: pl. 3, figs 14a–b.
Ianthina fibula Reeve, 1858: pl. 4, figs 17a–b.
Ianthina grandis Reeve, 1858: pl. 1, figs 3a–b.
Ianthina involuta Reeve, 1858: pl. 3, figs 12a–b.
Ianthina roseola Reeve, 1858: pl. 1, figs 1a–b.
Ianthina smithiae Reeve, 1858: pl. 3, figs 15a–b; Benson, 1860: 410; Macpherson & Chapple, 1951: 124.
Ianthina trochoidea Reeve, 1858: pl. 2, figs 10a–b; G. B. Sowerby II, 1882: 50, pl. 444, fig. 15.
Janthina (Iodes) balteata Reeve.–Mörch, 1860: 274.
Janthina (Iodes) smithiae Reeve.–Mörch, 1860: 274.
Janthina (Iodes) planispirata A. Adams & Reeve.–Mörch, 1860: 274.
Janthina (Iodes) costae Mörch, 1860: 274.
Janthina (Iodes) caeruleata Reeve.–Mörch, 1860: 275.
Janthina (Iodes) depressa Reeve.–Mörch, 1860: 275.
Janthina (Iodes) casta Reeve.–Mörch, 1860: 275.
Janthina (Iodes) britannica Forbes & Hanley.–Mörch, 1860: 276.
Janthina (Iodes) paenicephala Péron.–Mörch, 1860: 276 (incorrect subsequent spelling of *J. penicephala* Péron & Lesueur).
Janthina (Achates) fibula Reeve.–Mörch, 1860: 277.
Janthina (Achates) violacea Röding.–Mörch, 1860: 277.
Janthina (Achates) carpenteri Mörch, 1860: 277.
Janthina (Achates) orbignyi Mörch, 1860: 277.
Janthina (Achates) fragilis Lamarck.–Mörch, 1860: 278.
Janthina (Achates) roseola Reeve.–Mörch, 1860: 278.
Janthina (Achates) trochoidea Reeve.–Mörch, 1860: 278.
Janthina (Achates) affinis Reeve.–Mörch, 1860: 278.
Janthina (Achates) africana Reeve.–Mörch, 1860: 279.
Janthina (Achates) grandis Reeve.–Mörch, 1860: 279.
Janthina (Achates) involuta Reeve.–Mörch, 1860: 279.
Janthina ianthina (Linnaeus).–Angas, 1867: 230.
Ianthina rotundata Leach.–Jeffreys, 1867: 186, frontispiece, pl. 3, fig. 1; Watson, 1886: 134.
Janthina balteata Reeve.–Küster, 1868: 9, pl. 2, fig. 4; Martens, 1904: 142; Suter, 1913: 298, pl. 44, fig. 10; Bucknill, 1924: 49, pl. 5, figs 18–18a; Okutani, 1956: 43, text-figs 3–10; Kira, 1962: 30, pl. 14, fig. 23.
Janthina planispirata A. Adams & Reeve.–Küster, 1868: 8, pl. 2, fig. 3; Iredale & McMichael, 1962: 49.
Janthina depressa Reeve.–Küster, 1868: 8, pl. 2, fig. 9.
Janthina casta Reeve.–Küster, 1868: 8, pl. 2, fig. 8.
Janthina fibula Reeve.–Küster, 1868: 9, pl. 2, fig. 5.
Janthina trochoidea Reeve.–Küster, 1868: 8, pl. 2, figs 1–2; Cossmann, 1925: 157, pl. 6, figs 1–2.
Janthina africana Reeve.–Küster, 1868: 8, pl. 2, figs 10–11.
Ianthina ianthina Linnaeus.–Hutton, 1873a: 6; Iredale, 1910: 71; Hedley, 1916: 192; Morton, 1954: 166, figs 1a–c; Cotton, 1959: 376; Salvat & Rives, 1975: 273, fig. 77.
Janthina bicolor Menke.–Monterosato, 1878: 95; Thiele, 1892: 590, pl. 23, fig. 2.
Janthina bicolor var. *conica* Monterosato, 1878: 95.
Janthina bicolor var. *major* Monterosato, 1878: 95.
Janthina bicolor var. *minor* Monterosato, 1878: 95.
Janthina rotundata Leach.–Monterosato, 1878: 95.
Jodes bicolor (Menke).–Monterosato, 1884: 105.
Ianthina fragilis var. *planispirata* A. Adams & Reeve.–Tryon, 1887: 36, pl. 9, figs 94–98.
Ianthina fragilis var. *britannica* (Leach) Jeffreys.–Tryon, 1887: 37, pl. 9, figs 100.1–5, pl. 10, figs 6–9.
Janthina smithiae Reeve.–Melvill & Standen, 1901: 172.
Janthina auriculata Martens, 1904: 142, pl. 4, fig. 15.
Janthina costae Mörch.–Martens, 1904: 142.
Janthina fragilis var. *planispirata* A. Adams & Reeve.–Hutton, 1904: 80.
Ianthina janthina Linnaeus.–Laursen, 1953: 15, figs 14–18, pl. 1, fig. 1; Macpherson & Gabriel, 1962: 118, fig. 145.
Janthina violaceae [sic] Röding.–Macpherson, 1958: 33, fig. 29.5.
Janthina janthina Linnaeus.–Berry, 1958: 27; Kira, 1962: 30, pl. 14, fig. 22; Bennett, 1966: 40, pl. 8, figs 1–3; Morton & Miller, 1968: 472, fig. 175.4; Keen, 1971: 442, fig. 688; Kuroda *et al*., 1971: 245, pl. 62, figs 9–10; Cernohorsky, 1972: 197, pl. 3, fig. 8; Abbott, 1974: 113, col. pl. 3, fig. 1178; Powell, 1976: 107, pl. 1, fig. 8; Kay, 1979: 158, fig. 55B; Powell, 1979: 254, pl. 48, fig. 20; Rehder, 1980: 53; Fretter & Graham, 1982: 392, fig. 279; Kilburn & Rippey, 1982: 79, fig. 39, pl. 11, fig. 18; Wells & Bryce, 1986: 60, fig. 152; Wilson, 1993: 281, pl. 44, figs 36a–b; Rios, 1994: 101, pl. 33, fig. 413; Bosch *et al*., 1995: 111, fig. 440; Giannuzzi-Savelli *et al*., 1999: 50, 51, fig. 92; Smith, 1998: 813, figs 15.151A, D–F; Okutani, 2000: 319, pl. 158, fig. 1; Redfern, 2001: 75, pl. 36, fig. 314A; Ardovini & Cossignani, 2004: 136; Morley, 2004: 102, back cover; Robertson, 2007a: 5, fig. 3; Beu & Marshall, 2008: 285; Poppe, 2008: 722, pl. 306, figs 4a–b; Spencer *et al*., 2009: 206; Raven & Bracegirdle, 2010: 28, top right fig.; Willan *et al*., 2010: 386, text-fig.; Luque, 2011: 209, text-fig.; Grove, 2011: 40, pl. 18, fig. 10; Severns, 2011: 198, pl. 82, fig. 2; Hernández *et al*., 2011: 98, figs 30E–H; Janssen, 2012: 24, figs 7A–B.
Janthina (Jodes) bicolor Menke.–Priolo, 1959: 185.
Janthina violacia [sic] Röding.–Penniket & Moon, 1970: 24, pl. 9, fig. 3.
Janthina (Janthina) janthina Linnaeus.–Higo *et al*., 1999: 173.

Type material. Laursen (1953: pl. 1, fig. 1) illustrated the four syntypes of *Helix janthina* in Linnaeus's collection held by the Linnean Society of London. Linnaeus's collection is stored in the Linnean Society's rooms in Burlington House, London, and is not registered. Laursen discussed the identity of these and the two specimens in UPSZTY that formerly belonged to Queen Louisa Ulrika (Laursen, 1953: 17, pl. 1, fig. 2). He recognized that the specimens in London are *Janthina janthina* whereas those in Uppsala are *J. globosa*. In the text Laursen (1953: 17) briefly discussed the identity of Linnaeus's specimens, noting that "Specimen no. 7 in fig. 15 is identical with the type represented in plate 1, fig. 1, middle". However, this seems to mean "type" in the sense of "a syntype" or "a type of specimen" in general, rather than "the type specimen", as Laursen (1953: 17) provided the following caption to fig. 15: "*Ianthina janthina* (Linné). Variations in the shape of the shell from the type specimen, no. 3, towards the trochoid forms (2–1) and the flattened forms (4–12), respectively. Linné's original material further includes nos. 7 and 12". It is clear from this that the specimens shown in Laursen's (1953: figs 1.3, 1.7 and 1.12; Fig. 33) are three of Linnaeus's four syntypes held by the Linnean Society of London. This mention in the caption possibly qualifies as a valid designation of the specimen in Laursen's (1953: fig. 15.3) illustration as the lectotype of *Helix janthina* Linnaeus, 1758 under ICZN Article 74.5, as *(a)* it is clear from the discussion on this page and in the caption to Laursen (1953: pl. 1) that Laursen was aware that Linnaeus's syntypes included two species, *(b)* the statement was published before 2000, *(c)* Laursen used the term "the type", and *(d)* the statement referred to an individual specimen. It seems likely that this is a separate specimen from the one mentioned by Laursen (1953: pl. 1, fig. 1, "middle"), which is significantly larger; apparently it is the specimen shown by Laursen (1953: pl. 15.7). However, no formal lectotype designation is included in Laursen's text, and it is unclear whether the statement in the figure caption was intended as a lectotype designation. Because of doubts about the validity of Laursen's (1953: 17, caption) lectotype designation, the syntype of *Janthina janthina* in Linnaeus's collection housed by the Linnean Society of London and illustrated by Laursen (1953: fig. 15.3; Fig. 33.3) is here designated the lectotype of *Helix janthina* Linnaeus, 1758. The two paralectotypes in UPSZTY referred to *Helix janthina* by Linnaeus (1764: 670) are listed above under *J. globosa.* The lectotype of *Helix janthina* is here also designated the neotype of *Janthina violacea* Röding, 1798, in order to refer this name unambiguously to *J. janthina*, rather than supplanting a later name. Laursen (1953) did not provide dimensions of the syntypes (which the writer has not seen), but judging from the original scale on Fig. 33 it is c. 25 mm in diameter. Linnaeus (1758: 772) stated its distribution as "Habitat in Europa, Asia, Africa; in M. Mediterraneo frequentior; etiam pelagica"; this wide distribution allows almost any type locality.

Janthina communis, three syntypes examined, formerly NHMG1094/79, now catalogued as NHMG-INVE41376, without locality. These are also the syntypes of *J. fragilis*, which was simply renamed *J. communis* by Lamarck; Lamarck (1822: 206) listed "*Janthina fragilis*. Encyclop. Pl. 456. F.1.a.b" (the proposal of *J. fragilis*) in the synonymy of *J. communis*. All three specimens are conspecific. The locality was stated by Lamarck (1822: 206) as "l'Océan Atlantique et la Méditerranée". However, Y. Finet (NHMG pers. comm. 27 Sep 2012) pointed out that, as with *J. exigua*, Rosalie de Lamarck's annotation on Lamarck's copy of *Animaux sans vertèbres* states that there was only one specimen in Lamarck's collection, so two of these specimens evidently are not original syntypes. The drawings in Lamarck (1816: pl. 456, fig. 1) are not accurate enough to distinguish specimens, so it is not possible to determine which syntype is the original. *Janthina penicephala*, from near the Cape of Good Hope (Mörch, 1860: 16), no type material in MNHN, location of type material not known. The lectotype of *Helix janthina* designated above in Linnaeus's collection housed by the Linnean Society of London is here also designated the neotype of *Janthina penicephala* Péron & Lesueur, 1807, in order to refer this name unambiguously to *J. janthina*, rather than supplanting a later name. *Janthina affinis*, 3 syntypes NHMUK1972018, without locality, *ex* Cuming collection. *Janthina africana*, 3 syntypes NHMUK1976163, from "Zanzibar", *ex* Cuming collection. *Janthina balteata*, 3 syntypes NHMUK1976164, from "Cape of Good Hope", *ex* Cuming collection. *Janthina casta*, 3 syntypes NHMUK1972020, without locality, *ex* Cuming collection. *Janthina caeruleata*, 3 syntypes NHMUK1976162, without locality, *ex* Cuming collection. *Janthina depressa*, 2 syntypes NHMUK1976166, without locality, *ex* Cuming collection. *Janthina fibula*, 3 syntypes NHMUK1976169, without locality, *ex* Cuming collection. *Janthina grandis*, 3 syntypes NHMUK1972019, without locality, *ex* Cuming collection. *Janthina involuta*, 3 syntypes NHMUK1976165, without locality, *ex* Cuming collection; these are unusual, distorted specimens of *J. janthina*. Mörch (1860: 279) stated that he had found the distorted condition in other species, and attributed it to "implantations d'Anatifes", i.e., *Lepas* specimens attached to the *Janthina* shell. *Janthina planispirata*, 3 syntypes NHMUK1951.3.14.1–3, from "Atlantic Ocean", *ex* Cuming collection. *Janthina roseola*, 3 syntypes NHMUK1973003, from "Nicobar", *ex* Cuming collection, 3 normal, faintly pinkish-mauve specimens of *J. janthina*. *Janthina smithiae*, 3 syntypes NHMUK1976167, from Glamorganshire, UK, *ex* Cuming collection. *J. trochoidea*, 2 syntypes NHMUK20130060, without locality, from the V.W. MacAndrew collection, purchased from G. B. Sowerby (K. Way, NHMUK, pers. comm. 19 Feb 2013), and so probably ultimately from the Cuming collection; 3 possible syntypes also in NMV, purchased from H. Cuming. No specimens considered to be original material of *Iodes angularis* Leach or *Janthina britannica* of Leach or Jeffreys are present in NHMUK (K. Way, NHMUK, pers. comm. 05 Feb 2013).

As noted above under *Janthina globosa*, Keen (1968: 408, 410, pl. 59, figs 78a–80) recorded and illustrated the type material of all three of Carpenter's (1857) *Janthina* names in NHMUK, recording 37 syntypes of *I. striulata* on Carpenter's tablets 868–876 (nine tablets) and two syntypes (only one then still preserved) of *I. striulata* var. *contorta* on tablet 877. All illustrated specimens are clearly *J. janthina*, as concluded by Keen (1968), although the illustrated syntype of *I. striulata* var. *contorta* is an unusual specimen with a folded columella. Type material of all three names is still present in NHMUK; *I. striulata*, 9 syntypes NHMUK1857.6.4.868–876; *I. striulata* var. *contorta*, 1 syntype NHMUK1857.6.4.877 (K. Way, NHMUK, pers. comm. 05 Feb 2013). All are from Mazatlan, Mexico.

The writer is not aware of the location of type material of *Janthina bicolor*, stated to be from Jamaica; R. Janssen (SMF pers. comm. 18 Aug 2015) confirmed that there is no type material of *J. bicolor* in the remnants of Menke's collection in SMF. However, *J. bicolor* is an earlier name than either *J. pallida* Thompson, 1840 or *J. umbilicata* Orbigny, 1841, so it is desirable to clarify its application with a neotype to avoid it supplanting later names. The lectotype of *Helix janthina* Linnaeus, 1758 and neotype of *Janthina violacea* Röding, 1798 designated above, the syntype of *Helix janthina* in Linnaeus's collection housed by the Linnean Society of London and illustrated by Laursen (1953: fig. 15.3), is here designated the neotype of *Janthina bicolor* Menke, 1828.

Janthina costae (Mörch, 1860: 274) was identified by a long list of published references, the first two pre-Linnean, followed by "Janthina *bicolor* O. Costa. Cat. syst. (1829), p. CVI, nº 27" (Mörch did not italicize generic names in this paper) and a further 14 references; Mörch apparently thought this was a species distinct from *J. bicolor*, i.e., *J. janthina*. He provided the locality "Méditerranée (Costa)". Kathe Jensen (ZMUC pers. comm. 18 Aug 2015) stated that there are three specimens in ZMUC identified as "possible syntypes" of *J. costae*, ZMUC GAS-719, with an early label reading "*Janthina costae* Mörch I. Canar [Canary Islands] McAndrew 1865 ii 8" (presumably collected by the naturalist Robert McAndrew). This is the only known possible type material. If the date is a collection date, it is unlikely that these are syntypes, but McAndrew likely collected them during his only visit to the Canary Islands in 1852 (MacAndrew, 2008: 72), Mörch saw them in McAndrew's collection, McAndrew sent

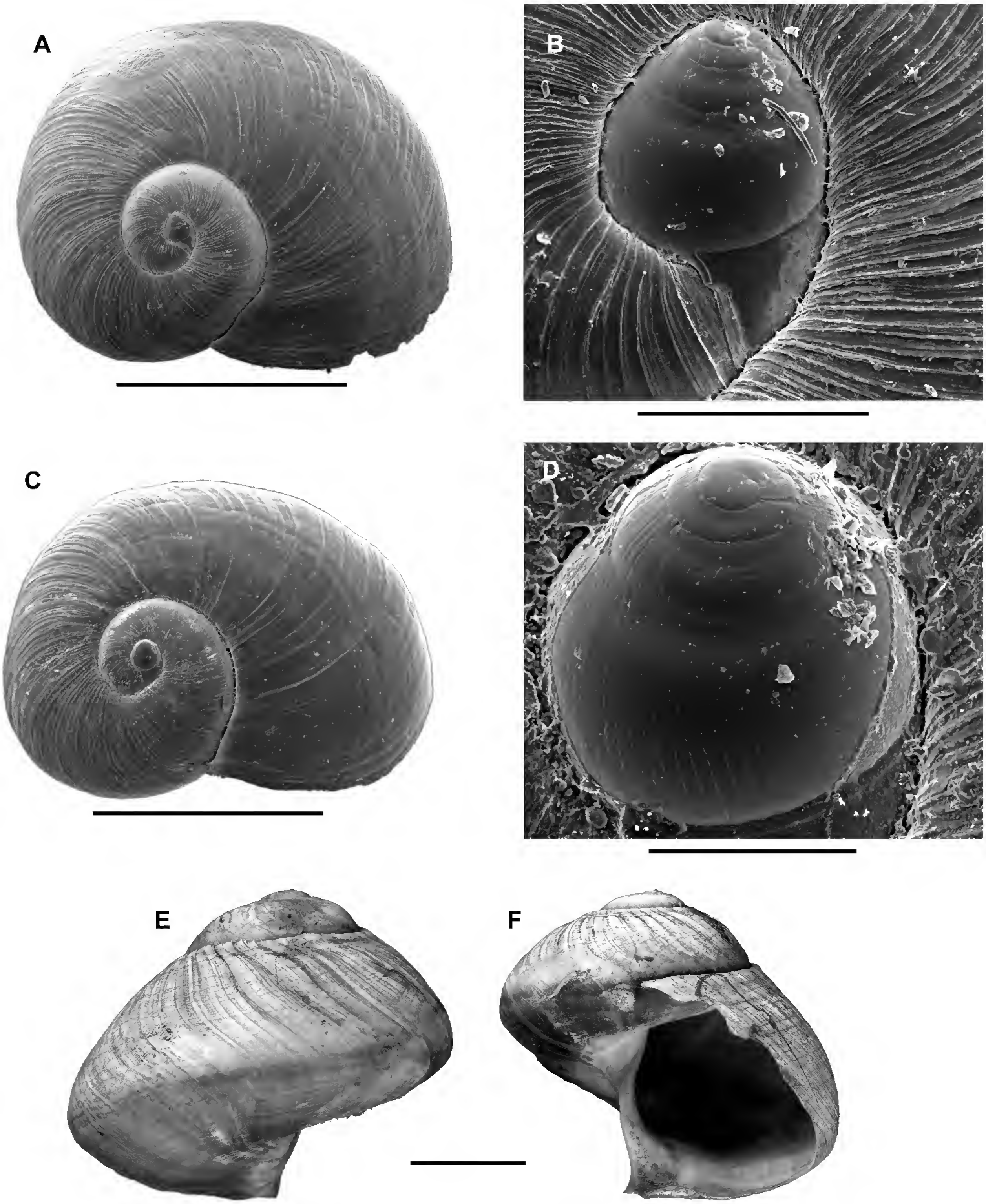

Figure 32. Specimens of *Janthina janthina* (Linnaeus). *(A–D)* GNS RM5844, Waikanae Beach, west Wellington, New Zealand; SEM, 2 specimens; apical views showing steeply inclined protoconch, slightly irregular teleoconch coiling, weak irregular spiral sculpture, and prominent axial riblets on early teleoconch whorls; B, protoconch of A enlarged; D, apex of protoconch of C enlarged. *(E–F)* NHMUK1854.12.4.399a, lectotype designated here of *Janthina orbignyi* Mörch, "Atlantic Ocean"; largest of seven syntypes in d'Orbigny's South American collection, illustrated by d'Orbigny (1841: 413, pl. 61, figs. 8–10); NHMUK photos sent by A. Salvador. Scale bars: A, C, 4 mm; B, 500 µm; D, 300 µm; E–F, 10 mm.

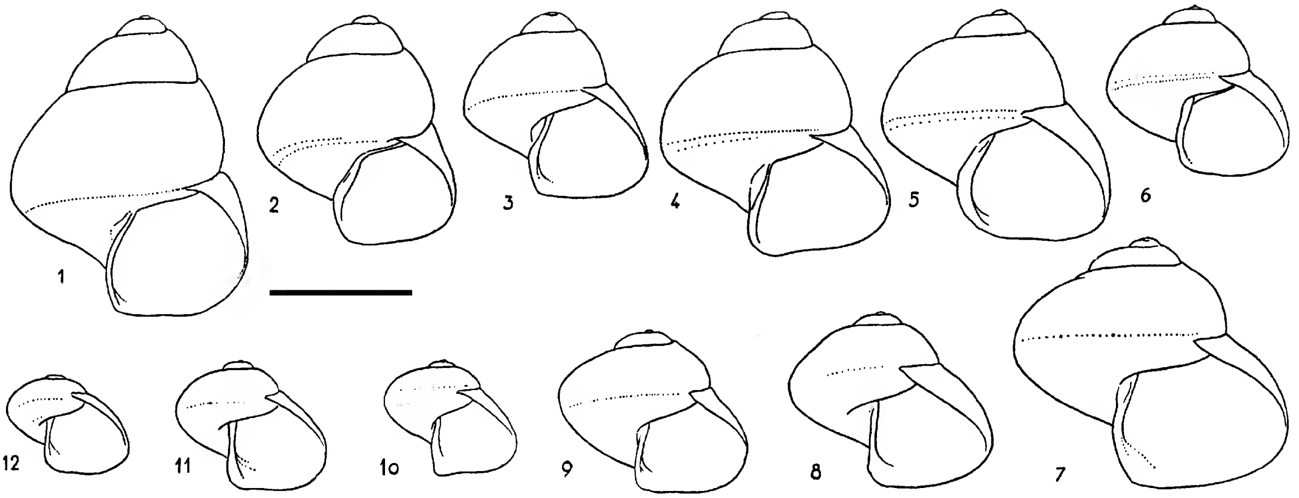

Figure 33. *Janthina janthina* (Linnaeus), range of variation in shell shape; copy at published size of Laursen (1953: fig. 15); numbers on figure as published by Laursen. Fig. 33.3, lectotype designated here of *Helix janthina* Linnaeus, 1758; Figs 33.7, 33.12, paralectotypes of *Helix janthina*; all three in collection of Linnean Society of London. Original scale bar included = 20 mm (i.e., figures reduced slightly).

them to Mörch, and they were received on 8 Feb 1865. They are assumed to be authentic syntypes. *Janthina carpenteri* (Mörch, 1860: 277) was proposed for "Janthina *striulata* Carp. Reig., p. 185.—*fragilis* Reeve, fig. 6. Var. *contorta* Carpenter, Cat. p. 186", i.e., *J. janthina*; no reason was given for renaming it. Kathe Jensen (ZMUC pers. comm. 21 Aug 2015) stated that there are at least three syntypes of *J. carpenteri* with animal tissue in one phial in the wet collection, ZMUC GAS-1501, from the Pacific Ocean off Valparaiso, Chile, collected on 23–26 Mar 1847 by Reinhardt during the first *Galathea* Expedition.

Janthina orbignyi (Mörch, 1860: 277) was proposed for "Janthina *fragilis* D'Orb. Amér., t. 61, fig. 8", i.e., again *J. janthina*. Kathe Jensen (ZMUC pers. comm. 18 Aug 2015) stated that she was unable to find any type material in ZMUC. This is not surprising, as the specimens of *J. janthina* illustrated under the name *J. fragilis* by d'Orbigny constitute the syntypes of *J. orbignyi*, and are in d'Orbigny's collection of South American Mollusca in NHMUK. Seven syntypes are present, NHMUK1854.12.4.399–400, bearing the locality "Atlantic Ocean", and labelled "illustrated in d'Orbigny, 1840. Voy. Amer. Meridian. Moll., 5: 413, pl. 61, figs. 8–10". Photographs of the four largest specimens were sent by Andreia Salvador (NHMUK pers. comm. 16 Feb 2016), demonstrating that all are specimens of *J. janthina*. The largest specimen (Figs 32E–F), NHMUK1854.12.4.399a, is here designated the lectotype of *Janthina orbignyi*. *Ianthina auriculata* holotype ZMB60008 (C. Zorn, ZMB pers. comm. 8 Sep 2015); from the Indian Ocean, *Valdivia* Station 258, near East Africa, 2°58'N 46°50'E, "ein Stück", i.e., it is the holotype. The illustration (Martens, 1904: 142, pl. 4, fig. 15) shows a typical trochiform specimen of *J. janthina* (not seen).

Laursen (1953: 16) listed "*Ianthina fragilis* var. *spiraelata* Mörch, 1860" in the synonymy of *Janthina janthina*. However, Mörch (1860: 278) listed "*Ianthina fragilis* … var. *spira elata*", i.e., a variety with an elevated spire, and did not intend to propose a new name.

Other material examined. Holocene fossils: trench excavated through uplifted Holocene terraces, Table Cape, Mahia Peninsula, central E North Island, New Zealand; from north-south transect, terrace 2 (1850±50 years old), basal sediment 117 m inland from high-tide line and 5.5 m above mean sea-level (GS15077, Y19/f062, grid ref. Y19/422212; 1, blue juvenile with low spire and diagnostic axial ridgelets; Beu, 2016: fig. 5P).

Present-day samples from Australia and New Zealand: **Australia:** ***Western Australia*:** Sunday I., Derby (WAM); Broome (NMV); Abrolhos Islands (SAM); Esperance (NMV); Cape Naturaliste (N2069, N2070, WAM); Leighton Beach (WAM 249-250); Cheyne Beach (WAM 2998); Cottesloe (C69307, AMS); Fremantle (N4021, WAM; NMV; AMS); Point Peron, Fremantle (WAM 367-40); Rottnest I. (NMV; WAM.909/10-31); Yalingup (N2072, N2073, N2459, N2461, WAM); Windy Harbour, Cape D'Entrecasteaux (WAM 213-65); Salmon Holes Beach, King George Sound (C69333, AMS); Albany (C56995, AMS; NMNZ M259093, 2). ***South Australia*:** Sleaford Bay (SAM). ***Victoria*:** Phillip I. (NMV); Gabo I. (NMV); Mallacoota (NMV). ***New South Wales*:** Narooma (NMV); Woody Head, Iluka (C70070, AMS); Minnie Waters (C70011, AMS); Port Stephens (NMV, AMS); Port Danger (C5332, AMS); Flat Rock, Richmond River (C50827, AMS); beach E of Bergalia, Moruya (AMS); Budgewai Beach (C70041, AMS); Nambuca Heads (NMV); Norah Head (C73966, AMS); Maroubra (C51089, C83051, AMS); Merimbula (NMV); Broulee, Bateman's Bay (NMV; C75537, AMS); Wooli (NMV, AMS); Manly Beach (NMV, AMS); Long Reef, Collaroy (C69101, C73827, AMS); Collaroy Beach (C79167, C 77764, AMS); Curl Curl Beach, Sydney (C50583, AMS); Bondi Beach (AMS); Harbord (AMS); Coogee, Sydney (NMV); Cronulla (AMS); Botany Bay (C83050, AMS); Broken Bay (NMV); Putty Beach, Kilcare (AMS); Newcastle (NMV); Wreck Bay, Sussex Inlet (AMS); Bombo, near Kiama (AMS); Port Kembla (AMS); Shellharbour (NMV); Ulladulla (AMS); Twofold Bay (C64284, AMS). ***Queensland*:** Darnley I., Torres Strait (C51507, AMS); Two Isles (WAM); NE Herald Cay, Coral Sea (C69064, AMS); West Cay, Diamond Islets (C69165, AMS); North Keppell I. (NMV); Frederick Reef (C68587, AMS); Tawnum Beach (AMS); Caloundra (NMV; C12497, AMS); Lady Elliott I. (WAM; C72669, C72994, C69177, AMS); Heron I. (NMV); Keppell Bay (C320, AMS); Point Lookout, Stradbroke I. (WAM 159-59; AMS); outer beach, Stradbroke I. (NMV; C13059, AMS); Moreton Bay (NMV). ***Tasmania*:** Beach End (C11220, AMS); Falmouth (M210983, NMNZ); Frederick Henry Bay (AMS); Clarke I. (NMV).

Lord Howe Island: (WAM; C13803, C29233, C80906, AMS; NMNZ M213985, 14); Anson Bay (NMNZ M212602, 6); Middleton Reef (NMNZ M171237, 1). **Norfolk Island:** (C59407, C31040, AMS; observed, AGB, collection of Mrs M. Hoare, Norfolk); Emily Bay (WM11213, GNS); Cemetery Bay (NMNZ M212604, 5). **Kermadec Islands:** Raoul Island (NMV; AWM; C36652, AMS; GNS WM15297, 73; NMNZ M202861, 60; M202870, 5; M214376, 70).

New Zealand: NW of Three Kings Islands (NMNZ M020819, 1); W Norfolk Ridge, W of Cape Reinga (NMNZ M171032, 2; M172330, 5); Te Werahi Beach, Cape Maria van Diemen (NMNZ M277691, 2); Tapotupotu, E of Cape Reinga (GNS RM4697, 1; RM6154, 12); Spirits Bay (NMNZ M277687, 2; M277689, 3); Tom Bowling Bay (NMNZ M011904, 2); Te Paki, Ninety Mile Beach (NMNZ M277686, 3); N end of Ninety Mile Beach (NMNZ M277690, 12; GNS RM4636, 5); The Bluff, Ninety Mile Beach (GNS RM4058, 3; NMNZ M277693, 4); Paua, Parengarenga Harbour (NMNZ M277692, 1); Tokerau Beach, Doubtless Bay (NMNZ M277688, 1); Cavalli Islands, Whangaroa (NMNZ M308660, 1); Takou Bay (GNS RM4442, 2; NMNZ M277685, 2); Russell, Bay of Islands (NMNZ M087141, 2); Whangarei Heads (NMNZ M02758, 3; AWM18331; AWM30529); Te Henga, W Auckland (M216304, NMNZ); Waitakere West, W Auckland (AWM18160); Piha Beach, W Auckland (NMNZ M090620, 5; GNS RM5309, 24); Bethells Beach, W Auckland (NMNZ M016304, 30; M087139, 40); Muriwai Beach, W Auckland (GNS RM330, 10; NMNZ M02757, 70; M011903, 4; M087144, 100; M160082, 8; AWM18330; AWM29270); Whatipu, Manukau Harbour, W Auckland (NMNZ M087142, 1); Pataua, Auckland (GNS RM5313, 1); W coast Awhitu Peninsula, SW of Waiuku, W Auckland (NMNZ M087143, 50; M277679, 1; M277680, 1; M277681, 7; M277682, 3; M 277684, 1; M277697, 6; M277698, 6; GNS RM5315, 2); Kaitoke Beach, Great Barrier I. (NMNZ M090518, 2); Tairua, Coromandel (NMNZ M090519, 7); Thames (AWM18329); Matakana Island, Bay of Plenty (AWM18328; AWM33270); Papamoa Beach, Bay of Plenty (NMNZ M120139, 150); Boulder Bay, Motuhora (Whale) Island, Bay of Plenty (NMNZ M040063, 18); Ohope Beach, Whakatane (NMNZ M040064, 50); Opotiki (AWM18327); beach E side Waitaki River, 5 km W of Opotiki (GNS RM5561, 1); platform E of Te Araroa, East Cape (GNS RM4900, 1); Aotea Harbour, W coast North Island (GNS RM4057, 8); S of Karioi mouth, W coast North Island (GNS RM4062, 11); beach S of Raglan (GNS RM4062, 1); Wainui Beach, Gisborne (NMNZ M308659, 6); Nukumaru Beach, Whanganui (GNS RM5625, 166); Foxton Beach (GNS RM5319, 2); Waitarere Beach, Levin (GNS RM2967, 45; NMNZ M014282, 8); Otaki Beach, W Wellington (NMNZ M102500, 2); Te Horo Beach, W Wellington (GNS RM5314, 8); Waikanae Beach, W Wellington (NMNZ M01128, 13; M018827, 25; M160083, 200; M303126, 3; M308073, 5; GNS RM5844, 80; RM5893, 120); Kapiti Island, W Wellington (NMNZ M02756, 30); Paraparaumu Beach, W Wellington (NMNZ M284746, 40); beach S of Opau Stream, W Wellington (GNS RM6716, 4); Swamp Bay, Greville Harbour, D'Urville Island (GNS RM4060, 1); Ocean Beach, Farewell Spit (NMNZ M023155, 5); Carters Beach, Westport (GNS RM5316, 3; RM5317, 5); Cape Foulwind, Westland (GNS RM4059, 1); Punakaiki Beach, Westland (NMNZ M131404, 1); Wakapatu Beach, N of Nugget Pt, Otago (NMNZ M111368, 3); Mason Bay, Stewart Island (GNS RM6717, 1; NMNZ M219479, 20); Chatham Islands (NMNZ M05151, 5; AWM16429); beach NW coast of Mangere I., Chatham Islands (GNS RM6012, 1).

Distribution. *Janthina janthina* is much the most common *Janthina* species in beach strandings in most parts of the world, although towards the southern limit of the Pacific range of *Janthina* in southern New Zealand (from Wellington west coast beaches southwards) small specimens of *J. exigua* are more common than *J. janthina*. It occurs throughout the world tropical to cool-temperate ocean, although Berry (1958) noted that it is "extremely rare" in California. Judged by specimens cast ashore, specimens of *J. janthina* are smaller around southern than northern New Zealand, and those collected on more oceanic islands (e.g., Lord Howe Island and the Kermadec Islands) are larger than any cast ashore in New Zealand, indicating that it reaches a larger size both in warmer water and in a more strictly oceanic environment than elsewhere. Savilov (1969: 399) reported specimens captured at 215 of the 393 *Vityaz* stations where *Janthina* was collected in the Pacific, with a winter northern boundary at about 40°N, where the sea surface temperature falls to 10°C. It was also observed near the North Island of New Zealand. "Very large concentrations of young *I. janthina*, up to 5 mm long, were noted during the *Vityaz* cruise in … the N subtropical circulation, including the Kuroshio [Current], and in the eastern areas of the North Trade Wind Current … It was almost absent in the Trade Wind Countercurrent area. However, this species reappeared in large numbers in the South Trade Wind Current, especially in its eastern part" (Savilov, 1969: 399).

One Holocene fossil is recorded above from New Zealand. Jung (1975: 119, figs 51–53) also recorded "*Janthina* sp. 1", probably based on larval shells of *J. janthina*, in late Pleistocene–Holocene core-tops from DSDP Site 147, drilled in the Cariaco Basin, Venezuela. His "*Janthina* sp. 2" (Jung, 1975: figs 54–55) is taller and more narrowly conical and probably represents a benthic *Epitonium* species. Janssen (2007b: 150, pl. 14, figs 3–4) also recorded Holocene fossils of "*Janthina* sp." from core-tops collected in the Red Sea. The larval shell illustrated shows no characters to distinguish it from the most common living species, *J. janthina*, although several other *Janthina* species are recorded as living in the Red Sea (Janssen, 2007b). As noted under *J. globosa*, Janssen (2012) also recorded late Pleistocene–Holocene fossils of *J. janthina* from 19 core-tops in the Mediterranean Sea.

Dimensions. See Table 7.

Diagnosis. Largest *Janthina* species, diameter reaching almost 50 mm; spire very low (mainly in small specimens) to moderately tall; height highly variable, but without consistent allometry; last whorl weakly angled at periphery, sutural ramp and base only weakly inflated, producing weakly trochiform teleoconch shape. Sculpture of many fine, close, irregular spiral threads, and a few low spiral folds on base of some specimens; most specimens with obvious, fine, closely spaced axial ridgelets on first 1–1.5 teleoconch whorls. Sinus occupying entire height of outer lip, wide, shallow, V-shaped, deeper in lower part of lip than higher up, apex in centre of lip; i.e., dorsal limb of lip curving forwards from sinus apex more strongly than ventral limb. Most specimens counter-

Table 7. Dimensions of *Janthina janthina*.

locality	height	diam.	H/D
Janthina affinis figured syntype	22.6	24.2	0.93
J. africana figured syntype	37.1	39.2	0.95
J. balteata figured syntype	15.6	19.9	0.78
J. casta figured syntype	31.9	42.1	0.76
J. caeruleata figured syntype	22.3	27.4	0.81
J. depressa figured syntype	26.1	35.0	0.75
J. fibula figured syntype	17.0	19.0	0.89
J. grandis figured syntype	43.9	45.7	0.96
J. involuta least distorted syntype	20.1	20.9	0.96
J. planispirata figured syntype	24.1	27.4	0.88
J. roseola unfigured syntype	22.0	23.2	0.95
J. smithiae figured syntype	13.6	17.3	0.79
Lord Howe Island, AMS (Bennett 1966: 41)	39.5	46.5	0.85
GNS RM4442, Takou Bay, Northland, NZ	34.3	38.4	0.89
GNS RM4442, Takou Bay	32.5	31.9	1.02
GNS WM15297, Raoul I., Kermadec Islands	32.7	35.9	0.91
GNS WM15297, Raoul I.	31.9	32.8	0.97
GNS RM7635, Ohope Beach, Whakatane, NZ	14.3	18.7	0.76
GNS WM15986, S. Lourenço Beach, Santa Maria I.	13.1	17.5	0.75
NMNZ M277685, Takou Bay, Northland, NZ	33.4	36.9	0.91
NMNZ M277685, Takou Bau	31.4	36.7	0.86
NMNZ M277686, Ninety Mile Beach, Northland, NZ	36.0	37.9	0.95
NMNZ M277698, Spirits Bay, Northland, NZ	34.8	38.0	0.92
NMNZ M277698, Spirits Bay	33.2	35.0	0.95
NMNZ M277691, Te Werahi Beach, Northland, NZ	34.0	37.7	0.90
NMNZ M052955, Lantana, Florida, USA	32.3	36.6	0.88
NMNZ M010983, Falmouth, Tasmania, Australia	32.0	35.9	0.89
NMNZ M010983, Falmouth	29.8	31.0	0.96
NMNZ M052953, Stradbroke I., Qld, Australia	31.6	35.8	0.88
NMNZ M052953, Stradbroke I.	31.6	34.6	0.91
NMNZ M052953, Stradbroke I.	29.0	34.0	0.85

shaded, darker violet on ventral surface and paler on dorsal surface, some with pale zone around centre of base; highly variable in all characters. Broods eggs in oviduct, releasing rapidly bursting packets of veligers.

Remarks. The huge number of specimens of *Janthina janthina* in collections all over the world exhibits a wide range of variation in both shape and colour. Failure to recognize this as the variation of a single species led to the recognition of many nominal species by early authors, particularly Reeve (1858). Laursen (1953: fig. 15) provided a useful figure of specimen outlines (Fig. 33) revealing the completely intergrading variation in shape, particularly in spire height, anterior columellar shape and the degree of angulation at the periphery of the last whorl, demonstrating that all these forms are part of the variation of one species. In collections the writer has examined, specimens resembling Laursen's (1953: fig. 15) numbers 5–9 are the most common shape, and juvenile specimens all resemble Laursen's numbers 10–12; extremely tall-spired forms such as Laursen's numbers 1–2 are rare. Wilson and Wilson (1956) & Wilson (1958) also compared the dimensions of a large number of stranded southern British specimens graphically, again demonstrating their intergradation. Specimens from near the southern limit of its range in New Zealand bear obvious, fine, close, axial ridgelets similar to those of *Janthina exigua* on the initial 1–1.5 teleoconch whorls, whereas the rest of the teleoconch surface is essentially smooth, with weak growth lines and many weak, irregular spiral threads. Laursen (1953: 18) described this sculpture as "The first 1½ whorls may have sharp, regular striae, which pass into a fainter, irregular striation", it was illustrated by Robertson (1971: pl. 5, fig. 17; 2007a: 8, upper left fig.), and this axial sculpture occurs on most specimens throughout its range. The remainder of the surface in *J. janthina* is not as smooth and polished as in *J. globosa* and *J. pallida*. Spiral coiling is rather irregular. A small proportion of adult shells also bears low spiral folds and grooves below the shoulder angulation, producing sculpture not unlike the more prominent and much more consistently present spiral folds of *J. typica* and *J. chavani*, although the folds are much fewer and weaker in *J. janthina* (Figs 2A, D, 4A, 5A). The radular teeth of *J. janthina* (Laursen 1953: figs 16–18) are moderately long and moderately strongly hooked, much longer than those of *J. pallida*, but similar to those of *J. exigua* and *J. umbilicata*. They vary significantly in length within one radula.

Priolo (1959: 185–186) provided a list of numerous usages in the literature on Mediterranean molluscs of the name *Janthina bicolor*, which he evidently considered to apply to a species distinct from *J. janthina*.

Time range. Holocene fossils and living only.

Janthina exigua Lamarck, 1816

Figs 2M, O, 34A–C, E–F

Janthina exigua Lamarck, 1816, "Liste des objets": 12, pl. 456, figs 2a–b; Eschscholtz, 1825: column 737; Gray, 1827: 495; Deshayes, 1843: 5; Gray, 1843: 241; Benson, 1860: 40; Küster, 1868: 7, pl. 2, figs 6–7; Monterosato, 1878: 95; Hutton, 1882: 128, pl. 14, fig. G (radula); Hutton, 1904: 80; Moss 1908: 28, pl. 7, fig. 1; Suter, 1913: 299, pl. 44, fig. 12; Oliver, 1915: 525; Bucknill, 1924: 50, pl. 19, fig. 4; Finlay, 1928: 246; Powell, 1937: 74, pl. 10, fig. 30; Mermod, 1953: 201, figs 200.1–2; Pasteur-Humbert, 1962: 52, fig. 72; Bennett, 1966: 41, pl. 9, fig. 2; Morton & Miller, 1968: 472, fig. 175.5; Cernohorsky, 1972: 198, pl. 56, fig. 10; Powell, 1976: 107, pl. 17, fig. 30: Kay, 1979: 158, fig. 55C; Powell, 1979: 254, pl. 48, fig. 21; Fretter & Graham, 1982: 394, fig. 281; Kilburn & Rippey, 1982: 79, pl. 11, fig. 19; Wells & Bryce, 1986: 60, fig. 153; Wilson, 1993: 281, pl. 44, figs 37a–b; Giannuzzi-Savelli *et al.*, 1999: 52, 53, figs 94a–d, 95a–b; Smith, 1998: 813, figs 15.151C, G; Morley, 2004: 102; Robertson, 2007a: 5, fig. 1; Beu & Marshall, 2008: 285; Poppe, 2008: 722, pl. 306, fig. 1; Spencer *et al.*, 2009: 206; Raven & Bracegirdle, 2010: 27, text-fig.; Willan *et al.*, 2010: 385, text-fig.; Grove, 2011: 40, pl. 18, fig. 9; Severns, 2011: 198, pl. 82, fig. 1; Hernández *et al.*, 2011: 97, figs 30A–D.

Ianthina exigua.–G. B. Sowerby I, 1822: 2nd *Ianthina* page, pl. 191, figs 2–3; Bronn, 1826: 328; d'Orbigny, 1841: 414; Reeve, 1842: 145, pl. 205, figs 2–3 (repeat of Sowerby's 1822 figs); d'Orbigny, 1846: 84; Forbes & Hanley, 1853, vol. 2: 555, pl. 69, figs 8–9; H. Adams & A. Adams, 1854: 87; Reeve, 1858: pl. 5, figs 21a–b; Chenu, 1859: 118, fig. 519; Benson, 1860: 408; Angas, 1865: 190; Angas, 1867: 231; Hutton, 1873a: 6; Martens, 1873: 39; Tenison Woods, 1878: 43; Hutton, 1880: 71; G. B. Sowerby II, 1882: 51, pl. 444, figs 23–24; Watson, 1886: 134; Tryon, 1887: 37, pl. 10, figs 17–22; Whitelegge, 1889: 262; Locard, 1898: 4; Pritchard & Gatliff, 1900: 140; Tate & May, 1901: 407; Martens, 1904: 143; Verco, 1908: 9; Iredale, 1910: 71; Macpherson & Chapple, 1951: 124; Laursen, 1953: 22, figs 22–24; Macpherson, 1958: 33, pl. 29, fig. 4; Macpherson & Gabriel, 1962: 119, fig. 146.

Janthina incisa Philippi, 1849: 149; H. Adams & A. Adams, 1854: 87; Tryon, 1887: 38.

Ianthina nana J. E. Gray, 1850: 9, 101 (caption to M. E. Gray, 1842: pl. 48, figs 3–4).

Ianthina incisa Philippi.–H. Adams & A. Adams, 1854: 87.

Ianthina bifida "Nuttall in Jay" Reeve, 1858: pl. 5, figs 25a–b.

Janthina capreolata Montrouzier, 1860: 114, pl. 11, fig. 4; Hedley, 1918: M61; May, 1921: 63; May, 1923: pl. 19, fig. 4; Fischer-Piette, 1950: 18; Allan, 1950: 95, text-fig. 22.4.

Janthina (Janthina) nana Gray.–Mörch, 1860: 281.

Janthina (Iodina) exigua Lamarck.–Mörch, 1860: 282; Powell, 1946: 77, pl. 10, fig. 30; Powell, 1957: 98, pl. 10, fig. 30; Powell, 1962: 91, pl. 10, fig. 30.

Janthina (Iodina) capreolata Montrouzier.–Mörch, 1860: 283.

Janthina (Iodina) bifida Nuttall.–Mörch, 1860: 283.

Ianthina vinsoni Deshayes, 1863: 94, pl. 11, figs 9–11.

Jodina exigua (Lamarck).–Monterosato, 1884: 106.

Janthina courcellei Mabille & Rochebrune in Rochebrune & Mabille, 1889: 45, pl. 6, figs 3a–b [*courcelli* in text, *courcellei* in caption; the latter adopted by Rosenberg (Malacolog 4.1.1)]; Forcelli, 2000: 82, original illus. copied; Petit, 2010: 48.

Janthina (Jodina) exigua Lamarck.–Thiele, 1929: 225, fig. 228; Abbott, 1974: 113, col. pl. 3, fig. 1181; Rios, 1994: 102, pl. 33, fig. 416.

Ianthina capreolata Montrouzier.–Cotton, 1932: 537; Cotton & Godfrey, 1932: 36; Cotton & Godfrey, 1938: 16; Kershaw, 1955: 312; Cotton, 1959: 376.

Iodina capreolata (Montrouzier).–Iredale & McMichael, 1962: 49.

Janthina (Violetta) exigua Lamarck.–Higo *et al.*, 1999: 173.

Type material. *Janthina exigua*, 3 syntypes MHNG1094/80 examined, now catalogued as MHNG-INVE51377, without locality; all are conspecific and agree with Laursen's (1953) and all later interpretations of *J. exigua*. However, as with *J. communis*, Rosalie de Lamarck's annotation on Lamarck's copy of *Animaux sans vertèbres* states that there is only one specimen in Lamarck's collection, so at least two and conceivably all three of these specimens are not original syntypes, although it is not possible to determine which is (Y. Finet, MHNG pers. comm. 27 Sep 2012). Two of the syntypes were illustrated by Mermod (1953: 201, figs 200.1–2), who described their angulated axial ridges commarginal with the mid-whorl sinus, and commented on the difficulty of matching any of them with the poor drawings in Lamarck (1816: pl. 456, figs 2a–b). The writer is not aware of the location of any type material of *Janthina incisa*, from Senegal; possibly in Philippi's collection in Museo Nacional de Historia Natural, Santiago, not available for consultation, so a new type is not designated here.

The term "aucta" in G. B. Sowerby I's (1822: second *Ianthina* p., pl. 191, fig. 3) caption to his second illustrated specimen of *Janthina exigua* does not constitute the proposal of a species-group name, but indicates that the illustration is enlarged. In an identical case, Petit (2009: 192, taxa note 27) stated that "The position taken here is that "*aucta*" is a descriptive term (= enlarged) and not an available name". The drawings in Reeve (1841–1842, vol. 2: pl. 205) are republications of the illustrations in G. B. Sowerby I (1822: pl. 191), and the term "aucta" appears in Reeve (1841–1842: pl. 205) also, at the bottom edge of the plate.

Janthina nana J. E. Gray (1850: 9, 101; caption to M. E. Gray 1842: pl. 48, figs 3–4) refers to an illustration by "Quoy, Voy. Astrol. t. 29, f. 5, 6", which shows a crudely drawn specimen of *J. exigua* from the Atlantic Ocean. Quoy & Gaimard (1833: caption to pl. 29) identified this specimen with the vernacular name "Janthine naine", as pointed out by Mörch (1860: 281; as "nain", sic), so Gray merely Latinized Quoy & Gaimard's species name. Lamarck (1922: 206) earlier provided *J. exigua* with the vernacular name "Janthine naine", so Quoy & Gaimard were repeating Lamarck's vernacular name. The specimen of *J. exigua* illustrated by Quoy & Gaimard (1833, pl. 29, figs 5–6) is the holotype of *J. nana*. However, this specimen is not recognisable in MNHN (P. Bouchet, MNHN, pers. comm. 5 Apr 2016), so the largest syntype of *J. exigua* in MHNG-INVE51377 is here designated the neotype of *Janthina nana* Gray, 1850. Petit (2012: 76) apparently was not aware of the publication of the name *Janthina nana* by Gray (1850: 101) and attributed the name to Couffon & Surrault (1909: 57), where it is a *nomen nudum*.

Janthina capreolata, two lots of two specimens each in MNHN formerly were considered syntypes (Fischer-Piette 1950: 18), but as Montrouzier (1860: 114) stated that the types were in "ma collection Musée de Bordeaux, 4 ex.", the MNHN specimens are not syntypes; 3 remaining syntypes MHNB2004.TY.160.0; photographs of MHNB syntypes sent 21 Sep 2012 (pers. comm. L. Charles, MHNB, and V. Héros, MNHN); from Art Island, New Caledonia. *Janthina vinsoni*, no type material in either MNHN or Université Lyon-1, where most of Deshayes's collection is stored (V. Héros, MNHN, pers. comm. 21 Sep 2012; E. Robert, Université Lyon-1, pers. comm. 02 Oct 2012), location unknown; from Réunion. *Janthina courcellei*, empty box in typothèque, MNHN, labeled "type perdu", apparently long lost; from Orange Bay, Tierra del Fuego. The largest syntype of *Janthina exigua*, MHNG-INVE51377, designated above as the neotype of *J. nana*, is here also designated the neotype of both *Janthina vinsoni* Deshayes, 1863 and *Janthina courcellei* Mabille & Rochbrune, 1889, in order to identify these names permanently with the present species.

Other material examined. Present-day samples from Australia and New Zealand: **Australia: *Western Australia*:** Cable Beach, Broome (NMV); Duke of Orleans Bay (AMS); Bunbury (AMS); Leighton (WAM); Point Peron, Fremantle (WAM.699/70-38, WAM.366/40, WAM.589/91-38); City Beach, Perth (AMS); Esperance (SAM, NMV); King George Sound (SAM); Albany (SAM); Rottnest I. (SAM); 300 fms, 120 mi W of Eucla (SAM); Ellensbrook Beach (SAM). ***South Australia*:** Coorong (SAM); Grange (SAM); Edithburgh (SAM); 165, 240 & 550 m, off Cape Jaffa (SAM); 190 m, 56 km SW of Neptune I. (SAM); ***Victoria*:** Portland (NMV); Mordialloc (NMV); Mallacoota (NMV, AMS); Warnambool (NMV); Curdie's Inlet (NMV); ***New South Wales*:** Newcastle (SAM); Cronulla (NMV); Port Stephens (NMV); Bondi, Sydney (NMV); Curl Curl Beach, Sydney (AMS); Collaroy Beach, Sydney (AMS); C83049, Botany Bay (AMS); Terrigal (AMS); C67422, Maroubra Beach (AMS); Stockton Beach, Port Stephens (AMS); C40693, South Ocean Beach, Bermagui (AMS); C11240, Wollongong (AMS); ***Tasmania*:** Tasmania (WAM, NMV, NMNZ); C12904, Flinders I. (AMS); ***Queensland*:** Point Lookout, Stradbroke I. (AMS).

Lord Howe Island: C59571 (AMS); **Norfolk Island:** C59409 (AMS); **Kermadec Islands:** Raoul I. (NMV; C36654, AMS; NMNZ M202863, 12; M272663, many).

New Zealand: NW of Three Kings Islands (NMNZ M109274, 2; M308654, 8); Middlesex Bank, NW of Three Kings Islands (NMNZ M112779, 1); 37–39 km SW of Great King, Three Kings Islands (NMNZ M094277, 1; M308655, 5; M308656, 1); W Norfolk Ridge, W of Cape Reinga (NMNZ M171012, 1; M171907, 3; M172329, 17); Cape Maria van Diemen (AWM30649); Spirits Bay (NMNZ M020279, 3); Ahipara Beach (GNS Suter colln, S2388, 7); Bayleys Beach, Dargaville (NMNZ M299995, 100); Cavalli Islands, Whangaroa (NMNZ M308653, 1); Maro Tiri I., Hen and Chickens Islands (GNS RM2672, 2); Bream Head, Whangarei (AWM18335); Leigh, N Auckland (NMNZ M087156, 20); Anawhata Beach, W Auckland (GNS RM5864, 60; RM6014, 5); Bethells Beach, W Auckland (NMNZ M016291, 12; M087157, 500; M308658, 40); Piha Beach, W Auckland (GNS RM5311, 100; NMNZ M087158, 300); Muriwai Beach, W Auckland (GNS RM332, 20; AWM18136; NMNZ M02762, 50; M087159, 1000; M145116, 100); Whatipu, Manukau Harbour, W Auckland (NMNZ M087155, 20); Mokohinau Islands (GNS Suter colln, S1658, 7); Kaitoke Beach, Great Barrier I. (NMNZ M087153, 5); W coast Awhitu Peninsula, SW of Waiuku, W Auckland (NMNZ M277699, 5; M277701, many; M277703, many; M277705, 1; M277707, 1; M277709, many; M277740, 3; M277741, 4); Matakana I., Bay of Plenty (AWM42757); Papamoa Beach, Bay of Plenty (NMNZ M120141, 4); Boulder Bay, Motuhora I., Whakatane (NMNZ M 033166, 20); Opotiki, Bay of Plenty (GNS RM331, 4); Te Kaha, Bay of Plenty (NMNZ M040065, 6); E of Te Araroa, East Cape (GNS RM4899, 3); Wainui Beach, Gisborne (NMNZ M308657, 4); Waimarama, Hawke's Bay (GNS RM334, 11); Nukumaru Beach, Whanganui (GNS RM5626, 100); Whanganui (GNS RM4053, 1); Otaki Beach, W Wellington (AWM18344); Waitarere Beach, Levin (GNS RM2967, 42; NMNZ M011127, 11); Waikanae Beach, W Wellington (NMNZ M01154, 15; M018897, 50; M160084, 100; M303125, 40; M308027, 400; GNS RM5852, 2360; RM5845, 300; RM5894, 100); Pukerua Bay, W Wellington (NMNZ M02760, 30); Porirua Harbour mouth (GNS RM4041, 1); Titahi Bay, W Wellington (NMNZ M02759, 20; M06945, 50); Lyall Bay, Wellington (NMNZ M087154, 7); Ocean Beach, Farewell Spit (NMNZ M023154, 9); Carters Beach, Westport (GNS RM5318, 20); Mason Bay, Stewart I. (AWM; NMNZ M019480, 15; M020278, 3); Chatham Islands (AWM16405; NMNZ M03853, 2; M05090, 3; GNS Suter colln, S2387, 8); Kaingaroa Beach, Chatham Islands (NMNZ M110413, 8); Te Whakaru, Chatham Islands (NMNZ M013073, 2); beach NW coast of Mangere I., Chatham Islands (GNS RM6013, 42).

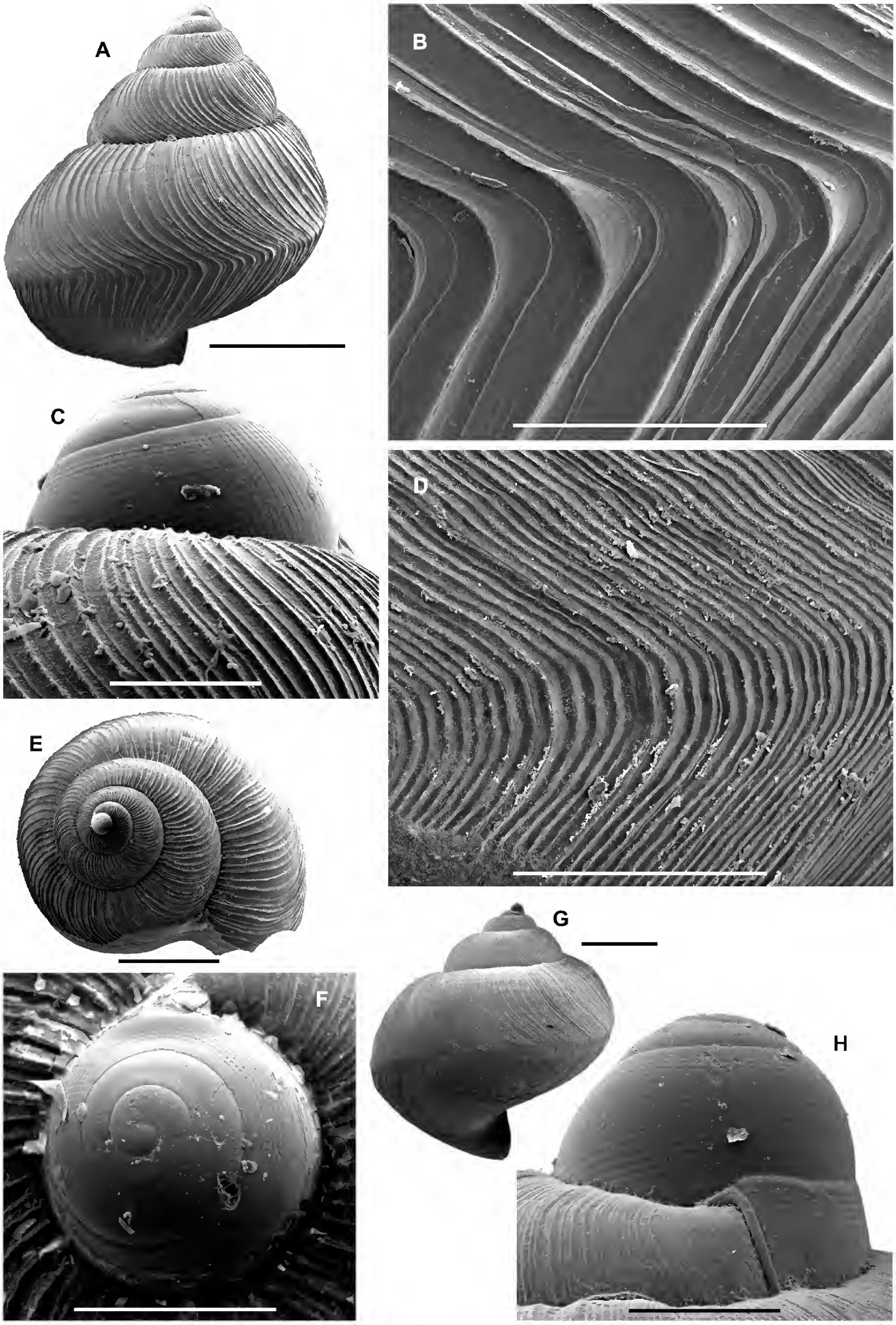

Figure 34. Specimens of *Janthina exigua* Lamarck and *Janthina umbilicata* d'Orbigny; SEM. *(A–C, E–F) Janthina exigua*, 2 specimens, GNS RM5852, Waikanae Beach, west Wellington, New Zealand; A, whole shell; B, sculpture on last whorl at apex of outer lip sinus; C, lateral view of protoconch; E, F, apical views of whole shell and protoconch. *(D, G–H) Janthina umbilicata*, GNS RM5312, Piha Beach, west Auckland, New Zealand; D, sculpture on last whorl at apex of outer lip sinus, to same scale as Fig. 34B; G–H, lateral views of whole shell and protoconch. Scale bars: A, E, G, 2 mm; B, D, 500 µm; C, H, 200 µm; F, 300 µm.

Distribution. The writer is not aware of fossils of *Janthina exigua*. *Janthina exigua* is probably the most widely recorded of all living *Janthina* species. However, its distribution provides some surprises. It is the most common *Janthina* species in most beach strandings around New Zealand and southern Australia, whereas it is one of the least common species in the North Pacific, although it is among species recorded from Japan (as far north as Boso Peninsula, Honshu; Higo *et al*. 1999: 173). There seem to be few records from northern Australia, including Queensland. Savilov (1969: 398–403) described the distribution of *Janthina* species at 393 stations where *Janthina* was sampled by RV *Vityaz* in the Pacific. *J. exigua* was collected at only four of these 393 stations, all near the North Island of New Zealand. However, Savilov also noted that Laursen (1953) recorded *J. exigua* from further north in the South Pacific, to 10°S, from New Caledonia east to Tahiti, in the southern Indian Ocean, and near Hawaii, and that Fowler (1948, 1949) and Wilson & Wilson (1956) recorded *J. exigua* from the southern coasts of Britain. In contrast to all these observations, Benson (1860: 406) noted that "*I. exigua* was the most widely distributed species met with" during a voyage from England to Calcutta in the *Malcolm*, correctly pointing out that *I. capreolata* Montrouzier is not separable. He first observed specimens two days before reaching Madeira (Benson, 1860: 405), and then observed specimens almost throughout the voyage. Benson's careful distinctions between subtle forms, his comments on the synonymy of Reeve's and other species names, and his references to publications by Coates (1825), Reeve (1858) and Mörch (1860) show that his observations are very reliable. *Janthina exigua* occurs throughout the world tropical and temperate ocean, as far south as Orange Bay, Tierra del Fuego (type locality of *J. courcellei*) and Mason Bay, Stewart Island, southern New Zealand (listed above), but most reporters have described it as less common than other species in the northern Pacific and Indian Oceans.

Dimensions. See Table 8.

Diagnosis. Small, few specimens over 20 mm high; spire tallest of all *Janthina* species, but height variable; whorls evenly and strongly convex, suture deeply impressed; sculpture of prominent, thin, closely spaced, commarginal axial ridgelets over entire teleoconch, c. 0.2–0.5 mm apart at periphery of large specimens, angulated in conformity with sinus. Sinus occupying entire height of outer lip, deep, sharply V-shaped, apex in centre of lip. Most specimens deep, intense violet, some paler, very few with pinkish tinge. Lays ovate-triangular egg capsules on underside of float.

Table 8. Dimensions of *Janthina exigua*.

locality	height	diam.	H/D
GNS RM5311, Piha Beach, W Auckland, NZ	19.5	16.7	1.17
GNS RM5311, Pih a Beach	18.3	16.1	1.14
GNS RM5311, Piha Beach	16.7	15.7	1.06
GNS RM5626, Nukumaru Beach, Whanganui, NZ	16.9	14.9	1.13
GNS RM5626, Nukumaru Beach	16.0	13.6	1.18
GNS RM5626, Nukumaru Beach	15.9	13.9	1.14
GNS RM5626, Nukumaru Beach	16.2	14.3	1.13
GNS RM5626, Nukumaru Beach	17.2	14.1	1.22
NMNZ M277699, Karioitahi Beach, Waiuku, NZ	20.7	17.6	1.18
NMNZ M277699, Karioitahi Beach	20.8	18.8	1.11
NMNZ M277699, Karioitahi Beach	20.3	17.8	1.14
NMNZ M277699, Karioitahi Beach	19.7	18.3	1.08
NMNZ M277699, Karioitahi Beach	22.0	17.2	1.28
NMNZ M214377, Raoul I, Kermadec Is.	18.1	15.1	1.20

Remarks. The small, deep violet species *Janthina exigua* is the most coarsely sculptured of living *Janthina* species, the only one with obvious, coarse axial ridges up to c. 0.5 mm apart over the entire exterior of large shells, resembling the axial sculpture of *J. typica*, *J. chavani* and *J. krejcii* sp. nov. and of a finely sculptured *Epitonium* species. Measurement of the spacing of the axial ridges on SEM images (Fig. 34B) showed that on this small specimen of *J. exigua* the ridges are c. 120–200 µm apart at the periphery, whereas on the specimen of *J. umbilicata* examined by SEM (Fig. 34D) the ridges are only c. 30–40 µm apart at the periphery. The axial lamellae of *J. exigua* also are considerably higher and more prominent than those of *J. umbilicata*. The apex of the outer lip sinus is at the periphery, i.e., in the centre of teleoconch whorls, and leaves a clear trace of the sinus apex around the centre of all whorls of tall-spired specimens. The consistently deep coloration is also a species character, the colour varying from deep reddish violet to (much more commonly) deep bluish violet, with a narrow paler zone beneath the suture in a few specimens. The radular teeth (Laursen, 1953: fig. 24) are similar to those of *J. umbilicata*, but have shorter bases, and some are less strongly hooked than those of *J. umbilicata*. The float (e.g., Laursen, 1953: fig. 1; Bennett, 1966: pl. 9, fig. 2) is proportionally the longest and narrowest of all *Janthina* species, although a specimen photographed alive in northern New South Wales by Denis Riek (Brunswick Heads, NSW; Fig. 5C) demonstrates that the float of *J. umbilicata* is indistinguishable from that of *J. exigua*. The distinctiveness of *J. exigua* is attested by the remarkably few synonyms it has received in this vastly over-named genus.

Time range. No fossil record; living only.

Janthina pallida Thompson, 1840

Figs 2K–L, 5B

Janthina pallida Thompson, 1840: 96, pl. 2, fig. 2 (under "*J. nitens*?", name attributed to Harvey; tentatively a new species).

Janthina pallida Harvey.–Thorpe, 1844: 152; Küster, 1868: 5, pl. 1, fig. 5; Monterosato, 1878: 95; Locard, 1898: 2; Dall, 1908: 318.

Ianthina striolata A. Adams & Reeve, 1850: 54, pl. 11, fig. 9; H. Adams & A. Adams, 1854: 87; Reeve, 1858: pl. 5, figs 24a–b; Hedley, 1900: 141; Pritchard & Gatliff, 1900: 141; Macpherson & Chapple, 1951: 124; Cotton, 1959: 376.

Ianthina pallida Harvey.–Forbes & Hanley, 1853: 553, pl. 69, figs 10–11; H. Adams & A. Adams, 1854: 87; Reeve, 1858: pl. 4, figs 20a–b; Benson, 1860: 412; G. B. Sowerby II, 1882: 51, pl. 444, figs 19–20.

Janthina (Amethistina) pallida Harway [sic].–Mörch, 1860: 281.

Janthina (Amethistina) striolata Adams & Reeve.–Mörch, 1860: 282.

Amethistina pallida (Harvey).–Monterosato, 1884: 105.

Janthina pallida (Harvey Mss) Thompson.–Bucquoy *et al*., 1886: 435, text-fig. 7.

Ianthina globosa var. *pallida* Harvey.–Tryon, 1887: 37, pl. 10, figs 15–16.

Janthina (Amethistina) pallida Harvey.–Thiele, 1929, p. 225; Priolo, 1959: 186.

Ianthina pallida Thompson.–Laursen, 1953: 31, figs 36–39; Macpherson & Gabriel, 1962: 119.

Ianthina globosa Swainson.–Morton, 1954: 167 (in part *J. pallida*, misidentified as *J. globosa*).

Janthina pallida (Harvey) Thompson.–Pasteur-Humbert, 1962: 53, fig. 75.

Janthina pallida Thompson.–Bennett, 1966: 47, pl. 10, figs 2–3; Fretter & Graham, 1982: 393, fig. 280; Kilburn & Rippey, 1982: 79; Wells & Bryce, 1986: 60, fig. 154; Giannuzzi-Savelli *et al.*, 1999: 54–57, figs 96a–101; Redfern, 2001: 76, pl. 36, fig. 317; Ardovini & Cossignani, 2004: 28, 136; Robertson, 2007a: 5, fig. 4; Luque, 2011: 209, text-fig.; Hernández *et al.*, 2011: 98, figs 30J–K.

Violetta pallida (Thompson).–Kuroda *et al.*, 1971: 246, pl. 62, fig. 15.

Janthina (Violetta) pallida Thompson.–Abbott, 1974: 113, col. pl. 3, fig. 1180; Higo *et al.*, 1999: 174.

Janthina (Violeta) [sic] *pallida* Thompson.–Rios 1994: 102, pl. 33, fig. 415.

Janthina (Amethistina) pallida Thompson.–Okutani, 2000: 319, pl. 158, fig. 3.

Janthina pallida Harvey in Thompson.–Poppe, 2008: 722, pl. 306, fig. 3.

Janthina exigua Lamarck.–Severns 2011: 198, lower fig (misidentification).

Type material. *Janthina pallida*, no type material in NHMUK, location of any type material not known; from Milton Malbay, County Clare, Ireland. Thorpe (1844: 152) also stated the locality as "Clare". *Janthina striolata*, three syntypes NHMUK1951.3.14.4–6, from "Pacific Ocean", *ex* Cuming collection. It would be preferable to use a specimen that has been included in a molecular study as the neotype for *J. pallida*, as for all other species, but this species has not been studied by this means. A. Adams & Reeve's (1850: 54, pl. 11, fig. 9) and Reeve's (1858: pl. 4, figs 20a–b) illustrated syntype of *J. striolata*, NHMUK1951.3.14.4, is here designated the neotype of *Janthina pallida* Thompson, 1840. The three syntypes of *Janthina striolata* are unusual specimens with weak, irregularly spaced, insignificant spiral threads around the last whorl, but are otherwise typical of *J. pallida*. Because of the cosmopolitan distribution of this as well as all other *Janthina* species and the very wide locality stated for *J. striolata*, the type locality of these names is not considered to be an important consideration for a neotype designation, and the designation of this neotype is necessary for the stabilization of the name *Janthina pallida*.

Other material examined. Present-day samples from Australia and New Zealand: **Australia:** ***Northern Territory***: Cape Wessel (WAM); E side Cape Wessel I., Arnhem Land (AMS C77883); Port Darwin (AMS C13905). ***Western Australia***: Cable Beach, Broome (NMV); City Beach, Perth (AMS); False Bay (AMS); King George Sound (many, SAMA); Cheyne Beach (WAM); Peaceful Bay, Bow Bridge (WAM); Bunbury (AMS); Windy Harbour, Cape D'Entrecasteaux (GNS WM15256, 1). ***South Australia***: Port Lincoln (WAM); ***Victoria***: Portland (SAMA; NMV); Mordialloc (NMV). ***Queensland***: Torres Strait (AMS).

Distribution. The writer is not aware of fossils of *Janthina pallida*. Laursen (1953: 33) recorded *Janthina pallida* from "the three oceans, but north of the equator … where the temperature does not drop below 15°C". This peculiar distribution, in which inter-ocean connections would not be possible, is proved incorrect by Benson's (1860) much earlier records of *J. pallida* collected from the *Malcolm* near Tristan da Cunha in the South Atlantic (30°S 18°W–33°S 10°W) and NE of St Paul and Amsterdam Islands, as well as midway between Natal and Western Australia (33°S 81°E–30°S 83°E) in the southern Indian Ocean. Bennett (1966: 47, pl. 10, figs 2–3) illustrated specimens collected alive in the North Pacific (31°06'N 130°06'W; and "in North Pacific waters") during a cruise c. 500 km west of California, 31°N 125–140°W. Australian beach records of *J. pallida* also disprove Laursen's statement. Although *J. pallida* has never been recorded from much of the coastline of Australia by Hedley, Iredale or other major Australian authors, museum collections show that it occurs sporadically around the southern, western and northern coasts (clockwise, from western Victoria to Torres Strait). It is relatively common in southern Western Australia, and specimens have been seen from South Africa (Table 9)—a pattern suggesting transport from the Atlantic via South Africa in the Antarctic Circumpolar Current. Kilburn & Rippey (1982: 79) also recorded specimens from South Africa. However, the writer is not aware of records from New Zealand, eastern Australia, or Norfolk Island, Lord Howe Island and the Kermadec Islands. It is one of the more northward-ranging species in the Atlantic, occurring in southern Britain, and seems to have a somewhat sporadic occurrence throughout the world tropical and warm-temperate ocean. Savilov (1969: 402) also noted that the *Vityaz* observed *J. pallida* only in the North Pacific. Samples were obtained at only 12 stations in the northern subtropical circulation, mainly in areas contiguous with the Kuroshio Current. However, it is evidently common in the Mediterranean (Figs 4A, 5B); 280 specimens were reported by Palazzi (1979) cast ashore on beaches in Sicily.

Dimensions. See Table 9.

Diagnosis. Moderate-sized (H to c. 30 mm), spire moderately tall, whorls strongly and evenly convex, suture deeply impressed; surface lightly polished, without obvious sculpture other than fine spiral threads on a few specimens. Sinus occupying entire height of outer lip, most shallowly V-shaped of all living *Janthina* species; apex in centre of lip. Anterior end of aperture evenly semicircular; many specimens with widely flared outer lip; central columella curved forwards (abaperturally). Almost uniform very pale violet, slightly paler dorsally; palest of all *Janthina* species. Lays ovate-triangular egg capsules on underside of float.

Remarks. Thompson (1840: 96, pl. 2, fig. 2) published the name *Janthina pallida* in the synonymy of "*J. nitens*?", and stated that the name *J. pallida* had been suggested verbally by his friend Harvey, who collected the specimens. Thompson (1840: 96) stated that it was most similar to *Ianthina nitens* Menke, as described and illustrated by Philippi in "Enumeration molluscorum Siciliae" (i.e., *Janthina globosa*), but differs in the columella being curved, instead of being straight, so that the anterior end of the aperture is rounded, and " … the colour … is very different". Thompson's (1840: pl. 2, fig. 2) drawing is an excellent one of *J. pallida* of all later authors, emphasising the evenly subcircular aperture. Many authors before 1961, beginning with Thorpe (1844: 152), have treated *J. pallida* as the valid name for this species. Therefore, the name *J. pallida* is conserved under ICZN Article 11.6.1. Following Article 11.6.1 the name should be attributed to Thompson

Table 9. Dimensions of *Janthina pallida*.

locality	height	diam.	H/D
Janthina striolata syntype, neotype of *J. pallida*	22.6	21.1	1.07
Janthina striolata syntype, NHMUK1951.3.14.5	24.0	22.2	1.08
GNS WM15256, Windy Harbour, S Western Australia	16.5	14.5	1.14
GNS WM19277, Muizenberg, False Bay, South Africa	18.6	16.2	1.15

(1840: 96), "its first publication as a synonym". The name has been attributed correctly by many later authors. Many others have attributed it to Harvey, but the name definitely was made available by Thompson (1840) according to Article 11.6.1. The name *J. pallida* was attributed to Harvey in 13 references listed by Priolo (1959: 186–187); only two of those Priolo cited attributed it to Thompson. Thorpe (1844: 152) provided a slightly muddled attribution of the name to "Thompson's Annals of Nat. Hist. 5. p. 96. t. 2. f. 2.", and was followed by Dall (1908: 318). Dall (1908) provided a publication date of 1817, even though Forbes & Hanley (1853: 553) provided the correct reference, despite attributing the name to Harvey. The name *Janthina pallida* was not published in 1817 (Sherborn, 1922–1933) and the page and figure numbers cited by both Thorpe and Dall are the same as for Thompson (1840), so their references were in error. Several other authors have published muddled references to this name, not having seen Thompson's (1840) paper.

Janthina pallida consistently is smaller than the largest specimens of *J. globosa*, but is otherwise very similar in most characters. The illustration by Ardovini & Cossignani (2004: 136) shows an unusually tall, narrow specimen. The obvious difference from *J. globosa* is that it lacks the small, angular, anterior extension of the columellar margin of the aperture of *J. globosa*, and instead the anterior end of the aperture is evenly and regularly curved in *J. pallida*. The outer lip sinus also is very shallow, considerably shallower than in all other living *Janthina* species. A unique character is that the central area of the columella is quite strongly convex, curving towards the anterior (abaperturally). Many specimens also have the outer lip quite broadly flared, or reflexed, a further unique character. Most specimens are also a much paler violet colour than all other *Janthina* species, fading almost to white on the sutural ramp of some specimens. Some specimens also have a weak spiral ridge or groove formed as the trace of the apex of the sinus in the outer lip, showing as a low spiral ridge on spire whorls of about 20% of specimens (as in Laursen, 1953: fig. 36), but this is an individual character. The radular teeth (Laursen, 1953: fig. 39) are much the shortest and most strongly hooked of all *Janthina* species. *Janthina pallida* also has a narrower distribution than most other *Janthina* species, and is one of the least common species throughout most of its range, particularly in the Southwest Pacific, although it is common in the Mediterranean and in southern Western Australia. Palazzi (1979) recorded 280 specimens collected on the beaches of Terrasini, Sicily. Priolo (1959: 186–187) also listed 21 references in the literature on Mediterranean molluscs mentioning *J. pallida*, including under other species names. Dimitris Poursanidis sent the writer photographs of living specimens collected at Arina Beach, Heraklion, Crete, revealing that the eggs are bright pink (Figs 4A, 5B), much deeper in colour than the other consistently pale pink *Janthina* eggs observed. These photographs also reveal that this is the one species of *Janthina* that does not seem to rest its head or snout in the (correspondingly very shallow) sinus in the outer lip. The specimens photographed by Dimitris Poursanidis did not expand out of their shells sufficiently to confirm their external anatomical characters fully, but do not appear to be distinguishable from other *Janthina* species anatomically.

Time range. No fossil record; living only.

Janthina umbilicata d'Orbigny, 1841

Figs 2N, Q, 34D, G–H

Janthina globosa Blainville, 1822: 155 (Aug 1822; junior homonym of *J. globosa* Swainson, Jan 1822); Berry, 1958: 27; Keen, 1971: 442, fig. 687.

Janthina umbilicata d'Orbigny, 1841: 414, pl. 20, figs 22–23; Hedley, 1918: M62; Bennett, 1966: 43; Bosch *et al.*, 1995: 111; Redfern, 2001: 75, pl. 36, figs 315A–B; Robertson, 2007a: 5, fig. 5; Spencer *et al.*, 2009: 206.

Ianthina umbilicata d'Orbigny.–Reeve, 1858: pl. 5, figs 22a–b; Benson, 1860: 411; G. B. Sowerby II, 1882: 52, pl. 444, fig. 22; Martens, 1904: 143; Iredale, 1910: 71, 74; Oliver, 1915: 525; Laursen, 1953: 26, figs 26–28.

Janthina (Iodina) umbilicata D'Orbigny.–Mörch, 1860: 283; Rehder, 1980: 53, pl. 7, fig. 7; Okutani, 2000: 319, pl. 158, fig. 4.

Ianthina (Iodina) megastoma A. Adams, 1861: 403; Tryon, 1887: 38.

Janthina nitida A. Adams, 1869: 620, footnote; Tryon, 1887: 38.

Iodina nitida (A. Adams).–Iredale, 1929: 279; Iredale & McMichael, 1962: 49.

Janthina laeta Monterosato.–Pasteur-Humbert, 1962: 52, fig. 74 (misidentification as *Amethistina laeta* Monterosato, 1884, = *J. globosa*).

Iodina umbilicata d'Orbigny.–Habe, 1964: 48, pl. 14, fig. 8; Kuroda *et al.*, 1971: 247, pl. 62, figs 13–14.

Janthina (Violetta) umbilicata d'Orbigny.–Higo *et al.*, 1999: 174.

Janthina exigua Lamarck.–Luque, 2011: 209, text-fig. (misidentification).

Type material. *Janthina umbilicata*, four syntypes NHMUK1854.12.4.403 (K. Way, NHMUK, pers. comm. 05 Feb 2013), from the "Atlantic Ocean"; recorded as present in the British Museum by Gray (1855: 36) and Reeve (1858: caption to pl. 5, figs 22a–b). *Janthina globosa* Blainville, location of any type material unknown. Because of confusion between the names *Janthina globosa* Swainson and *J. globosa* Blainville over many years, it is highly desirable to identify the name *J. globosa* Blainville unambiguously with the present species. The specimen illustrated as *J. umbilicata* by Reeve (1858: pl. 5, figs 22a–b), one of the syntypes of *J. umbilicata* in NHMUK1854.12.4.403, is here designated the neotype of *Janthina globosa* Blainville, 1822. *I. megastoma*, from the Indian Ocean, no type material known; the specimen illustrated as *J. umbilicata* by Reeve (1858: pl. 5, figs 22a–b), one of the syntypes of *J. umbilicata* in NHMUK1854.12.4.403, is here also designated the neotype of *Janthina megastoma* A. Adams, 1861.

No material in NHMUK is identified as *Janthina nitida*, but a board, NHMUK1870.1.3.7, has nine specimens attached of *J. umbilicata* remaining wholly or partially intact out of an original 21 specimens. It is labelled "*J. balteata* Reeve/ N. Atlantic/ Mrs Knocker" and as *Janthina nitida* was described within a paper by Captain Knocker, this presumably includes the original syntypes described by A. Adams (K. Way, NHMUK, pers. comm. 05 Feb 2013). Knocker (1869: 616–619) presented a long table of specimens collected at numerous stations across the Pacific and Atlantic Oceans, recording *J. nitida* from 13 stations but, of course, it is now impossible to tell which specimens were collected at which stations. Knocker's records are valuable, as he also records "*Ianthina* –?", "*I. fragilis*", "*I. exigua*", "*I.* –? Light mauve colour, globular" (i.e., presumably *J. pallida*) and "*I. bicolor*".

Other material examined. Present-day samples from Australia and New Zealand: **Australia**: ***Tasmania***: (NMNZ M202862). ***New South Wales***: Bermagui (AMS C40691, C40693); Port Stephens (NMV; AMS C91949); Putty Beach, Kilcare (AMS); Long Reef, Collaroy (AMS); Manly Beach, Sydney (AMS C32373, C56810); Cronulla (NMV); Botany Bay (AMS C83048). ***Queensland***: Green I. (AMS C9856); Rocky Isle (AMS); Caloundra (AMS); Point Lookout, Stradbroke I. (AMS).

Kermadec Islands: Raoul I., Kermadec Is (NMNZ M00991, M202862, many).

New Zealand: 13 km N of Great King I., Three Kings Islands (NMNZ M146405, 1); Cape Maria van Diemen (M277743, 1); South Cavalli Seamount (M281315, 1); Ocean Beach, Whangarei Heads (M150840, 6); Waipu Cove, Northland (GNS RM4781, 2); Uretiti Beach, Bream Bay (M277742, 1); Piha Beach, W Auckland (GNS RM5312, 8); SW of Waiuku, W coast Awhitu Peninsula, W Auckland (NMNZ M277700, 2; M277702, 4; M277704, many; M277706, 7; M277708, 3); Karioitahi Beach, W coast Awhitu Peninsula (M277710, 2); Papamoa Beach, Tauranga (M147404, 3); Boulder Bay, Motuhora I., Bay of Plenty (M042552, 1); Nukumaru Beach, W of Whanganui (GNS RM5627, 6).

Distribution. The writer is not aware of fossils of *Janthina umbilicata*. The 18 lots observed from the New Zealand region are listed above. *Janthina umbilicata* has not been recorded from New Zealand previously, other than in the list by Spencer *et al*. (2009: 206). The few records the writer is aware of from Australia are also listed above. There seem to be no records from the Northern Territory, Western Australia, South Australia or Victoria, and *J. umbilicata* and *J. pallida* seem to be largely mutually exclusive around Australia. The two species *Janthina exigua* and *J. umbilicata* seem to have closely similar distributions, *J. umbilicata* consistently being the less common, at least in the southern part of their range. Around New Zealand, small numbers of specimens occur in most large strandings of *J. exigua*, from Raoul Island, Kermadec Islands (where *J. umbilicata* is common) and from the Three Kings Islands to as far south as Whanganui, but the writer has seen no specimens of *J. umbilicata* from further south. Spencer (1982) reported that "seven *J. umbilicata* were found on Waitangi, Chatham Is.", but although this is quite feasible, the writer has not seen specimens from the Chatham Islands. Few specimens have been observed south of the northeastern North Island warm-water region, extending from North Cape to East Cape. Because relatively few earlier authors have distinguished it from *J. exigua*, the range of *J. umbilicata* is poorly known, but it seems likely to occur with *J. exigua* throughout the world tropical and temperate ocean, although not extending quite as far into the southern temperate zone as *J. exigua* does. In contrast to its uncommonness around Australia and New Zealand, Savilov (1969: 398–399) reported that *J. umbilicata* was the most widespread and abundant Pacific *Janthina* species, collected at 333 of the 393 *Vityaz* stations where *Janthina* was collected. At many stations very large numbers were collected, up to 1000 specimens per 20 minutes of sampling. The largest specimens were 14 mm high. "Exceptionally large concentrations of mature individuals and young up to 4–5 mm long were observed in the central regions of … the N and S subtropical circulation in the California Current belt and in the eastern regions of the trade wind currents. Their quantity, notably that of mature animals, decreased considerably in the trade wind countercurrent area" (Savilov, 1969: 399).

Table 10. Dimensions of *Janthina umbilicata*.

locality	height	diam.	H/D
GNS RM5627, Nukumaru Beach, Whanganui, NZ	14.8	13.4	1.10
GNS RM5627, Nukumaru Beach	13.7	11.8	1.16
GNS RM5627, Nukumaru Beach	12.6	11.4	1.11
GNS RM5627, Nukumaru Beach	10.8	9.5	1.14
NMNZ M277708, Karioitahi Beach, Waiuku, NZ	20.5	19.0	1.08
NMNZ M277708, Karioitahi Beach	20.0	18.9	1.06
NMNZ M277708, Karioitahi Beach	20.0	18.6	1.08
NMNZ M277704, Karioitahi Beach, Waiuku, NZ	19.2	17.2	1.12
NMNZ M277704, Karioitahi Beach	16.7	14.7	1.14
NMNZ M277704, Karioitahi Beach	16.5	14.4	1.15

Dimensions. See Table 10.

Diagnosis. Small, few specimens over 20 mm high; spire moderately tall, whorls evenly and strongly convex, suture deeply impressed; sinus occupying entire height of outer lip, deep, sharply V-shaped, with apex in centre of lip. Sculpture weak, of very fine, low, closely spaced, silky-looking, commarginal axial ridgelets over entire teleoconch surface, angulated in conformity with sinus; c. 30–40 µm apart at periphery. Most specimens deep, intense violet; a few paler, particularly large ones. Closely resembling *J. exigua* in all characters other than its much finer, lower axial sculpture and most specimens being slightly shorter. Lays ovate-triangular egg capsules on underside of float.

Remarks. *Janthina umbilicata* closely resembles *J. exigua*, and the two have been confused in several Australian and New Zealand collections. Besides a slightly shorter spire in most specimens of *J. umbilicata*, the main difference is that the axial sculpture is much lower, finer and more closely spaced in *J. umbilicata* than in *J. exigua*, producing a finely striate, silky-looking surface. As noted under *J. exigua*, measurement of the spacing of the axial ridges on SEM images showed that on the specimen of *J. umbilicata* (Fig. 34D) the ridges are only c. 30–40 µm apart at the periphery, whereas on the small specimen of *J. exigua* examined (Fig. 34B) the ridges are c. 120–200 µm apart at the periphery. The colour also is rather consistently deep bluish violet; a few paler specimens occur, particularly the largest ones seen, but less commonly than in samples of *J. exigua*. Few specimens show more than a very slight umbilical chink, as the inner lip is expanded slightly to cover the umbilicus in most adult specimens of this as in all other *Janthina* species, and the epithet "umbilicata" is no more appropriate for this species than for any other. The radular teeth (Laursen, 1953: fig. 28) are similar to those of *J. exigua*, although slightly shorter, and are moderately long and strongly hooked for a *Janthina* species. Rather strangely, this species was not mentioned, even in synonymy lists, by Küster (1868). Iredale (1910: 74) described *J. umbilicata* as "It has the form of *exigua*, Lam., but, being destitute of the rough sculpture of that shell, has a shiny appearance …", and pointed out that d'Orbigny (1841: 414) distinguished this species carefully from *J. exigua*. Living specimens from northern New South Wales illustrated in colour on his web page by Riek (2017; Fig. 5C) have a long, narrow float identical to that of *J. exigua*. The attached egg capsules are pale pink, as in *J. globosa*.

Time range. No fossil record; living only.

Recluzia Petit de la Saussaye, 1853

Recluzia Petit de la Saussaye, 1853: 117. Type species (by subsequent designation, Cossmann, 1925: 159): *Recluzia jehennei* Petit de la Saussaye, 1853 (= *Janthina lutea* Bennett, 1840); Recent, cosmopolitan.

Remarks. Iredale & McMichael (1962: 49) stated that the type species of *Recluzia* was selected originally by Petit de la Saussaye (1853), but Petit de la Saussaye named two species of *Recluzia* without designating a type species. A type species was not designated by most subsequent authors, and the earliest designation the writer is aware of is by Cossmann (1925: 159). However, this is of little consequence, as the two species included by Petit de la Saussaye are rendered absolute synonyms here.

The teleoconch of *Recluzia* is markedly to greatly taller and narrower than that of the tallest *Janthina* species, with a smooth, pale brownish-yellow shell (i.e., natural calcite colour), lightly polished in some specimens, and bears an obvious, slightly darker, thin, smooth periostracum that does not occur (or at least, is not obvious) on *Janthina* species. It also has evenly and strongly convex whorls, a deeply impressed suture, a straight, simple, acline outer lip without a sinus, and no obvious sculpture. The radulae of *Janthina* and *Recluzia* are indistinguishable. The protoconch (Churchill *et al*., 2011b: figs 1D–E; Figs 37A–G) also is closely similar to that of *Janthina* and all other planktotrophic Epitoniinae, pupiform, with a weakly impressed suture and sculpture of fine, low, closely spaced axial ridges on protoconch 2, although that of *Recluzia lutea* (Bennett, 1840) has one fewer whorls in protoconch 2 than those of *Janthina* species (2.2 whorls in *R. lutea*, 3.2 whorls in *Janthina* species). *Recluzia* differs from *Janthina* also by having simple rather than forked cephalic tentacles, no epipodia or purple gland, stylets in the inner salivary glands that are lacking in *Janthina*, adult statocysts that are lacking in *Janthina*, and small juvenile post-larval specimens riding on the adult's shell or float, rather than forming a float of their own as in *Janthina* (Table 1). *Recluzia lutea* was also said by Abbott (1968: 92) to have yellow egg capsules and brownish mucus bubbles, in contrast to the white to slightly purplish, pink or pale blue egg capsules and transparent colourless to faintly bluish mucus bubbles of all *Janthina* species. This is confirmed by Tony Healy's and Denis Riek's photographs of living specimens (Figs 6–7); the egg capsules of *Recluzia* species are a similar colour to the shell, whereas the head and foot are a paler, brighter yellow than the shell, and the float bubbles have a brown tinge. The float bubbles also have a much more irregular appearance than those of *Janthina* species.

Putative fossil record

The one sample of fossils the writer is aware of that has been identified as a species of *Recluzia* is in NMB, labelled as "?*Recluzia rollandiana* Petit". It is from NMB locality 17516, Cantaure Formation, lower shellbed, 300 m south of Casa Cantaure, 10 km west of Pueblo Nuevo, near San José, central Paraguaná Peninsula, northern Venezuela (Burdigalian, late early Miocene; six small shells, largest 6.5 mm high). The fauna from this locality was monographed by Jung (1965). However, the "?*Recluzia*" material is from a much larger and more diverse collection than Jung's, gathered subsequently during many visits by Win and Jack Gibson-Smith, and recently monographed by Landau *et al.* (2016). The teleoconch of these specimens indeed closely resembles that of *Recluzia lutea* in thinness and shape, its lack of sculpture other than faint growth lines, its inner lip being narrowly reflected over a very narrow umbilicus, and its straight, acline outer lip. However, the protoconch is present on two of the smallest shells (Figs 36A, C) and is significantly larger, taller, of c. 3.5 whorls, and with a more stepped outline than the pupiform one of 2.2 whorls in *Recluzia lutea* (Churchill *et al*., 2011b: figs 1D–E; Figs 37A–G). The *Recluzia* protoconch has almost flush sutures. It also has an almost smooth surface with weak sculpture of narrow, shallow, closely spaced axial grooves, but fainter spiral sculpture than that of *Janthina* species. The protoconch of the Casa Cantaure fossil has an even smoother surface with still weaker axial sculpture than that of *Recluzia* species and no spiral sculpture discernible at all, and has a much more deeply impressed suture than the protoconch of *Recluzia*, forming a narrow subsutural platform. These specimens evidently belong in Epitoniidae, and probably represent a benthic species of Epitoniinae with lecithotrophic development. They tentatively were referred to "*Alexania* aff. *floridana* Pilsbry, 1945" by Landau *et al*. (2016: 102, pl. 87, figs 1–2). Comparison with the protoconch of present-day specimens of *Alexania natalensis* would help identify these specimens.

Names proposed in *Recluzia*

As the species of *Recluzia* have not been revised previously, all names are listed here that the writer is aware of that have been referred to *Recluzia*, with comments on their status where necessary. Names are listed in chronological order of their proposal. The status of the 13 names that remain classified in *Recluzia* is clarified in the following sections.

1 *Helix johnii* Holten (1802: 76) (Jousseaume, 1872: 205; Winckworth, 1943: 148); refers to Chemnitz (1795: figs 2076–2077), i.e., the earliest reference making the non-binominal name *Helix johnii* Chemnitz available; probably northern Indian Ocean, locality unknown. Neotype designated below.

2 *Janthina lutea* Bennett (1840: 63, 298); taken at sea, 2°53'S 170°55'E, SW of the Phoenix Islands, Kiribati, central western Pacific Ocean. Discussed in detail below, with neotype designation.

3 *Janthina turrita* "von dem Busch" Philippi (1849: 15); no illustration, no locality, no types found; its dimensions lie in the centre of variation of *Recluzia* specimens (Fig. 35, point identified by "T"), and it is assigned to the synonymy of the more common species, *R. lutea*. A neotype is designated below.

4 *Recluzia jehennei* Petit de la Saussaye (1853: 118, pl. 5, fig. 3); Arabian Gulf. Remaining syntype illustrated (Figs 36F–G).

5 *Recluzia rollandiana* Petit de la Saussaye (1853: 119, pl. 5, fig. 12); "environs de Mazatlan" ["later identified as actually from New Caledonia" (Keen 1971: 903)]. Neotype designated below.

6 *Recluzia aperta* Jeffreys (1859: 114, pl. 3, figs 22a–c) = *Torellia vestita* Lovén ms Jeffreys (1867: 244, pl. 4, fig. 1); Britain; not *Recluzia* (*Torellia*, Family Capulidae).

7 *Recluzia bensoni* A. Adams (1861: 402); off Formosa; a small, narrow, juvenile *Recluzia* specimen. Holotype in NHMUK.

8 *Recluzia hargravesi* Cox (1870: 172, pl. 16, fig. 8); Port Stephens, New South Wales; extremely large as well as unusually tall and narrow. Holotype in NHMUK.

9 *Recluzia montrouzieri* Souverbie (1871: 334; 1872: 57, pl. 1, fig. 8); Art I., New Caledonia. Syntypes in MHNB.

10 *Lymnaea*? *palmeri* Dall (1871: 135; 1925: 25, pl. 17, fig. 8); delta of the Taqui River, head of the Gulf of California; holotype (in USNM) illustrated by Abbott & Dance (1982: 70, bottom right fig.) and here (Figs 36E, H).

11 *Recluzia globosa* E. A. Smith (1876: 551, pl. 30, fig. 8); Tarawa, Gilbert Islands. Holotype in NHMUK. Probably a juvenile specimen of *R. lutea*, but as it is unusually short and wide, also possibly an *Alexania* species, a benthic epitoniid. However, the dimensions (Table 12) fall within those of other small specimens of *R. lutea*, which are much shorter and wider than adults.

12 *Recluzia erythraea* Jickeli (1882: 367); Dahlak I., Red Sea; illustrated by Thiele (1928: fig. 6). Thiele gave no source for his figure, but it is assumed to be of the holotype; tall and narrow, resembling the holotype of *R. hargravesi* Cox, 1870 in proportions. Holotype in ZMB.

13 *Recluzia rollandiana* var. β *annamitica* Wattebled (1886: 67, pl. 3, figs 4a–b); Hué, Vietnam; "a considerable number of shells of this species was found thrown up on the beach of Thuan-an, at the end of a cyclone". Syntypes in MNHN, one illustrated here (Fig. 36K–L).

14 *Recluzia* sp.: Murdoch & Suter (1906: 301, pl. 27, figs 55–56) illustrated a specimen dredged in 200 m off Great Barrier Island, NE New Zealand, identified as "*Recluzia* sp." Charles Hedley suggested verbally to Murdoch and Suter that it was either a larval shell or a new genus related to *Janthina*. It is small (H 3.83, D 3.29 mm), trochiform, with almost flat sides, a narrowly rounded periphery and a blunt, narrowly rounded apex with no distinguishable protoconch, and is essentially smooth. Its colour was described as "yellowish-horn, white underneath the epidermis" (Murdoch & Suter, 1906: 302). The specimen, in Suter's collection in GNS (S3045) is a larval shell, probably of *Cabestana spengleri* (Perry, 1811) (Ranellidae).

15 *Recluzia effusa* [*ex* Martens ms] Thiele (1928: 78, footnote, fig. 2), has a diagnosis and apparently was not published elsewhere; from "chinesischen See". No dimensions or illustrations of the shell were provided. Thiele (1928: 78, footnote) stated that the shell is not well preserved; he published a section through the foregut and radula of the presumed type, so it is evidently preserved in ethanol, with the shell corroded. The name must be attributed to Thiele (1928); assumed to be a synonym of *R. lutea*. Holotype in ZMB.

16 *Recluzia insignis* Pilsbry & Lowe (1932: 80, pl. 9, fig. 3); from Montijo Bay, western Panama; pale brown, but with prominent cancellate sculpture, not a *Recluzia* species; tentatively identified as a synonym of the type species of *Alora*, *A. gouldii* (A. Adams, 1857) by Keen (1969; 1971: 436, fig. 669). However, the spire of the holotype is markedly taller and narrower and the sculpture is considerably more prominent than those of illustrated specimens of *A. gouldii* (Weil *et al.*, 1999: 145, fig. 439); possibly a distinct species of *Alora* or a similar genus; benthic Epitoniidae.

Dimensions and species of *Recluzia*

The only character that varies to any obvious extent in *Recluzia* is the spire height, a combined measure of the diameter and translation rate of the whorls. To try and understand this variation, some of the specimens available in AMS, GNS and NMNZ were measured (Tables 12, 13) and their height (H), diameter (D) and spire height (SH) compared in bivariate plots (Figs 35A–B). Initially this resulted in distinguishing two groups of shells, separated by spire height. If these are to be recognized as separate species, the earliest names for them are *R. lutea* for the more common, shorter, wider species and *R. johnii* for the much less common, taller, narrower one. As Bennett (1840) observed a large raft of specimens, he is very much more likely to have collected the more common, shorter *Recluzia* species than the rare, taller and narrower species.

The addition of a greater number of specimens made it seem more likely that the two groups intergrade in shape. A large lot in NMNZ (M155930, Great Exhibition Bay, Northland, New Zealand, Mar 1998; 59 specimens, of which 43 measured, Table 13) shows that (1) larger shells tend to have taller spires than smaller ones; i.e., height increases with growth; (2) many of the larger shells have a short, wide, shallow flare at the anterior end of the aperture, making their dimensions slightly taller and narrower than shells without the flare, although the whorls are actually no narrower than in specimens without the flare (e.g., see the illustration of *Recluzia lutea* by Habe & Tokioka, 1953: 57, fig. 12, identified as *R. montrouzieri*); and so (3) specimens identified as *R. lutea* largely intergrade in overall shape with specimens identified as *R. johnii*, although the spire outline of *R. johnii* is taller and straighter than in *R. lutea*. The majority of specimens in Fig. 35A assigned to *R. lutea* are included in the same field as specimens assigned to *R. johnii*, and the distinction between the two fields is slight. Comparisons of the height (H), width (diameter, D) and spire height (SH) of a number of specimens (Tables 12, 13) of the two species are summarized in Table 11. The overall shape is confirmed as similar, the means for H/D being 1.44 for *R. lutea* and 1.56 for *R. johnii*. Contrary to the conclusion about overall shape, the quite strongly distinct means of D/SH (1.51 for *R. lutea*, 1.20 for *R. johnii*) and the accompanying plot comparing diameter with spire height (Fig. 35B) show a clear distinction between the shorter-spired species *R. lutea* and the taller-spired species *R. johnii*. These fields overlap little (although the height of the spire was available for only nine of the 14 specimens of *R. johnii*). On average, diameter is 1.5 times spire height in *R. lutea*, whereas diameter is only slightly greater than spire height (1.2) in *R. johnii*. As seemed likely from visual estimation, *R. johnii* is considered here to be a rare, second *Recluzia* species with a taller, narrower and

Table 11. Summary of dimensions of *Recluzia johnii* and *R. lutea* (*mean*, arithmetic mean; *SD*, standard deviation).

species	H/D				D/SH			
	range	n	mean	SD	range	n	mean	SD
Recluzia johnii	1.40–1.69	14	1.56	0.119	0.93–1.36	9	1.20	0.185
Recluzia lutea	1.10–1.73	73	1.44	0.102	1.21–1.95	66	1.51	0.148

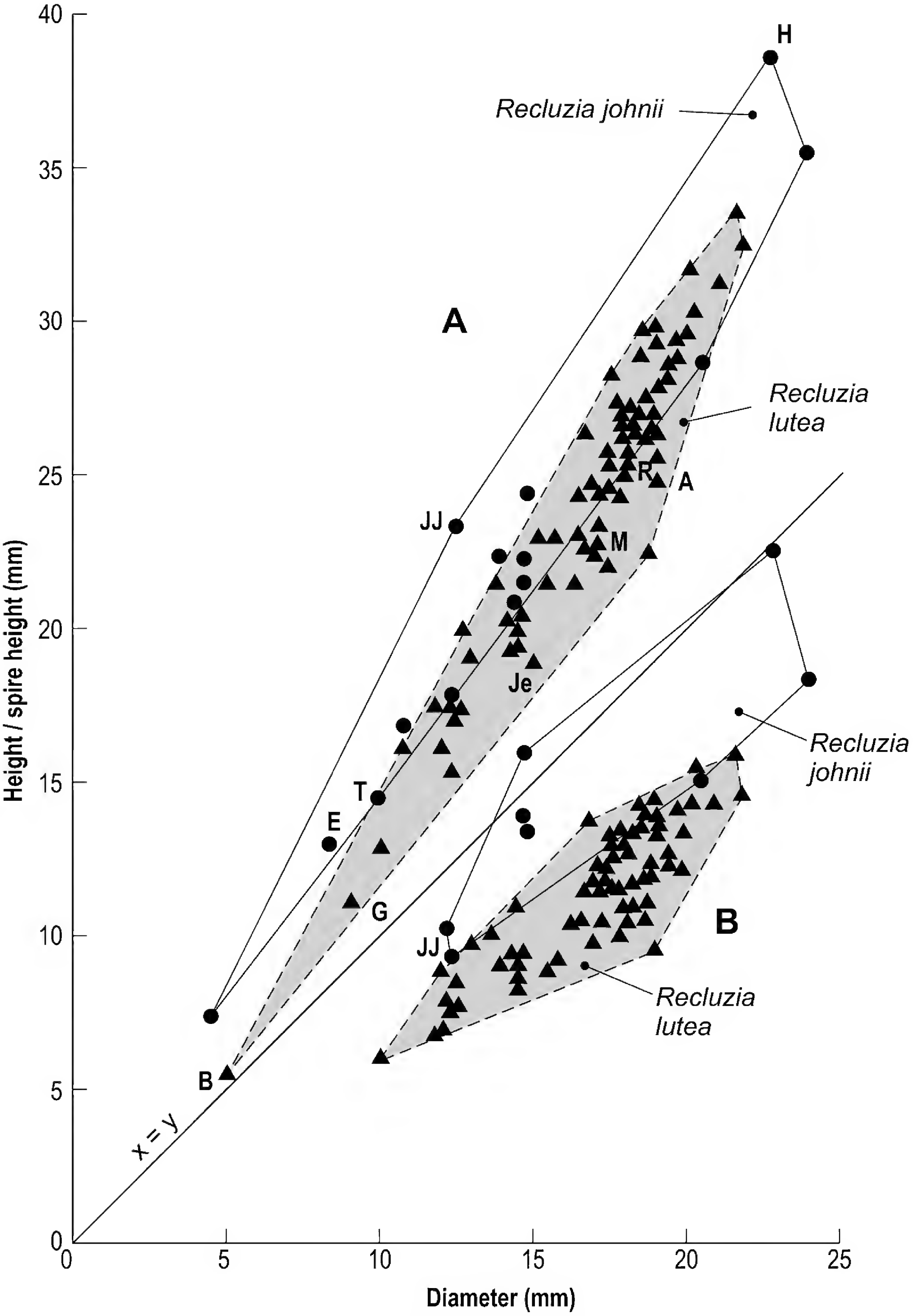

Figure 35. Scatter diagram comparing dimensions of *Recluzia* species. *(A)* diameter compared with height; *(B)* diameter compared with spire height. ▲ *Recluzia lutea* (Table 13); ● *Recluzia johnii* (Table 12, including Jousseaume's specimen of *Recluzia johnii*, MNHN). Letters show positions of type specimens of synonyms: *A — Recluzia annamitica* syntype; *B — Recluzia bensoni* holotype; *E — Recluzia erythraea* holotype; *G — Recluzia globosa* holotype; *H — Recluzia hargravesi* holotype (neotype of *Recluzia johnii*); *Je — Recluzia jehennei* syntype (neotype of *Janthina lutea*); *JJ — Recluzia johnii*, Jousseaume's specimen; *M — Recluzia montrouzieri* syntype; *R — Recluzia rollandiana* syntype (from Petit de la Saussaye, 1853); *T — Janthina turrita* syntype.

more straight-sided spire and narrower teleoconch whorls than *R. lutea*. Concomitant with the taller spire and narrower whorls, large specimens of *R. johnii* also have at least one more teleoconch whorl than *R. lutea* (6–7 compared with 4.5–5.5). Neotypes are provided here for some names to identify them unambiguously with one or the other species. Comparison of molecular sequences of *Recluzia* specimens obviously is desirable to confirm that two species exist.

Recluzia johnii (Holten, 1802)

Figs 2P, R, 36B, D, I–J

Helix johnii Holten, 1802: 76 (refers to Chemnitz, 1795: 284, pl. 210, fig. 2076).
Recluzia hargravesi Cox, 1870: 172, pl. 16, fig. 8; Angas, 1877: 190; Tryon, 1887: 38, pl. 10, fig. 23; Brazier, 1894: 536; Hedley, 1907: 481; Iredale, 1910: 71; Iredale, 1929: 279; Iredale & McMichael, 1962: 49.
Recluzia johnii (Chemnitz).–Jousseaume, 1872: 205; Tryon, 1887: 38, pl. 10, fig. 24; Hedley, 1910: 358; Winckworth, 1943: 148.
Recluzia erythraea Jickeli, 1882: 367; Tryon, 1887: 39; Thiele, 1928: 83, fig. 6.

Type material. Holten (1802) provided a list of binominal names from Martini & Chemnitz's (1769–1795) famous but non-binominal iconography in a catalogue prepared for the sale of Chemnitz's collection (Winckworth, 1943). Part of the collection was purchased for Peter the Great and is now in the Zoological Institute, Russian Academy of Sciences, St Petersburg (Martynov, 2002). Chemnitz's illustrated shell is not in ZMUC (J. Knudsen ZMUC pers. comm. 07 Feb 1978; AGB personal obs.). The possibility that Chemnitz's (1795: 284, pl. 210, figs 1076–1077) illustrated specimen of *Helix johnii* remains in Chemnitz's collection in the Zoological Institute, St Petersburg, was investigated at the writer's request by B. Sirenko (pers. comm. 07 Sep 2012); the illustrated specimen is not present. Chemnitz's drawing shows a cream and pale grey shell with a tall spire, closely similar in shape and general appearance to the holotype of *Recluzia hargravesi* (Figs 36I–J), although with a still slightly taller spire, a shallower suture, and one more teleoconch whorl. Jousseaume (1872: 203–206) discussed the identity of the specimen, translated Chemnitz's description and discussion into French, referred the specimen to *Recluzia*, and redescribed it carefully. Chemnitz received his specimen from "M. John, a missionary … living in Tranquebar, whom I must thank for many conchological riches. Whether it inhabits Coromandel, Ceylon, the Nicobar Islands or other parts of the East Indies, and whether it is a land, freshwater or marine shell he gave not the slightest information" (translation from Jousseaume, 1872: 204). The strongly and evenly inflated whorl shape, essentially smooth surface, circular aperture, faint spiral colour band at the continuation of the suture around the last whorl, and narrowly reflected inner lip agree with characters of *Recluzia johnii* of the present report. It seems feasible that this is the earliest name for a species of *Recluzia*, despite some early authors referring it to terrestrial gastropod groups such as *Pupa* Draparnaud, 1801 (i.e., *Pupilla* Fleming, 1828, Pupillidae; not *Pupa* Röding, 1798, Acteonidae) or *Cochlogena* Férussac, 1821, Helicidae. Férussac (1821: 57) cited the name as *Helix* (*Cochlogena*) *johnii* Chemnitz, but added "Habit. Les grandes Indes. Espèce incertain pour le genre", whereas Gray (1825: 412) simply listed it as *Pupa johnii* without comment. Smith (1910: 203) also doubted that this name referred to a *Recluzia* species because of its description by Chemnitz (1795) as "subkeeled", but this appears to refer only to the colour band around the last whorl in Chemnitz's (1795: pl. 210, fig. 2076–2077) drawings; the drawings show no obvious sculpture. Similar narrow, irregular colour bands or faint spiral grooves are present on many specimens of *Recluzia* (e.g., Habe & Tokioka, 1953: fig. 12). Jousseaume's note seems to have been inspired by a specimen in his collection, in MNHN (Figs 36B, D). The name has not been applied to any other mollusc during the last century, to the writer's knowledge, and Jousseaume (1872) and Winckworth (1943: 148) are followed in accepting it as the earliest name for a species of *Recluzia*.

Recluzia hargravesi, holotype NHMUK197432, stated to be from Miall River, Port Stephens, New South Wales, Australia, but corrected by the collector, W. Glover (cited by Brazier, 1894: 536) to the beach inside the North Head of Port Stephens. It is necessary to remove the name *Helix johnii* from uncertain status and associate it unambiguously with this species rather than *R. lutea*. The name *H. johnii* originally was not provided with a type locality. The holotype of *Recluzia hargravesi*, NHMUK197432 (Figs 36I–J) is here designated the neotype of *Helix johnii* Holten, 1802. Therefore, the type locality of *Helix johnii* becomes Port Stephens, New South Wales. Thiele (1928: fig. 6) illustrated the presumed holotype of *Recluzia erythraea*, ZMB/Moll-112603 (E. Strong, USNM, pers. comm. 20 Sep 2012; not seen), from Dahlak Island, Red Sea, showing that this name also refers to a tall, narrow specimen of *Recluzia johnii*.

Other material examined. **Australia**: ***New South Wales***: Collaroy Beach, Sydney (AMS); Maroubra Beach, Sydney (AMS); Middle Harbour, Port Jackson (NMV); Port Stephens (two lots, AMS); Port Macquarie (NMV). ***Queensland***: Green I. (AMS C9824); Palm Islands (AMS C9823); 31–37 m, Masthead I. (AMS C19351a); trawled, 150–200 m, Swain Reefs (GNS WM17360, 1); King's Beach, Caloundra (NMV); Wreck I., off Yeppoon (AMS); Fairfax I., Bunker Group (AMS C69053).

The only other specimens observed in world museums are the holotype of *Recluzia hargravesi*, listed above, and Jousseaume's specimen in MNHN. A specimen in MNHN labelled "Rade de Batavia", i.e., Jakarta, Indonesia (E. Strong, USNM, photograph sent pers. comm. 20 Sep 20012) has a tall, narrow spire and possibly belongs in *R. johnii*, but is too incomplete for certain identification.

Distribution. The tall-spired species *Recluzia johnii* is much rarer than *R. lutea*. In this study, almost all specimens observed are from Queensland and northern New South Wales, eastern Australia; none have been observed from New Zealand. Living specimens have also been collected on northern New South Wales beaches by Riek (2017; Fig. 7). However, the type specimens of the synonyms demonstrate that *R. johnii* also occurs in the northern Indian Ocean and the Red Sea. It probably occurs throughout the tropical Indo-West Pacific province. The writer is not aware of records from the Atlantic Ocean or the eastern Pacific, but this probably results merely from its rarity.

Dimensions. See Table 12.

Diagnosis. Moderately large (H to 39, D to 24 mm), larger than *Janthina* species other than *J. janthina* and *J. globosa*; taller and narrower than all other neustonic Epitoniidae including *Recluzia lutea*; mean height: diameter 1.56, mean diameter: spire height 1.20. Teleoconch of 6–7 whorls; whorls strongly and evenly inflated, of almost circular cross-section, narrower than in *R. lutea*; suture deeply impressed; without obvious sculpture. Aperture almost circular, almost all specimens without anterior spout-like expansion. Lays smooth, narrow, cylindrical to weakly club-shaped, yellow egg capsules on underside of float, as in *R. lutea*.

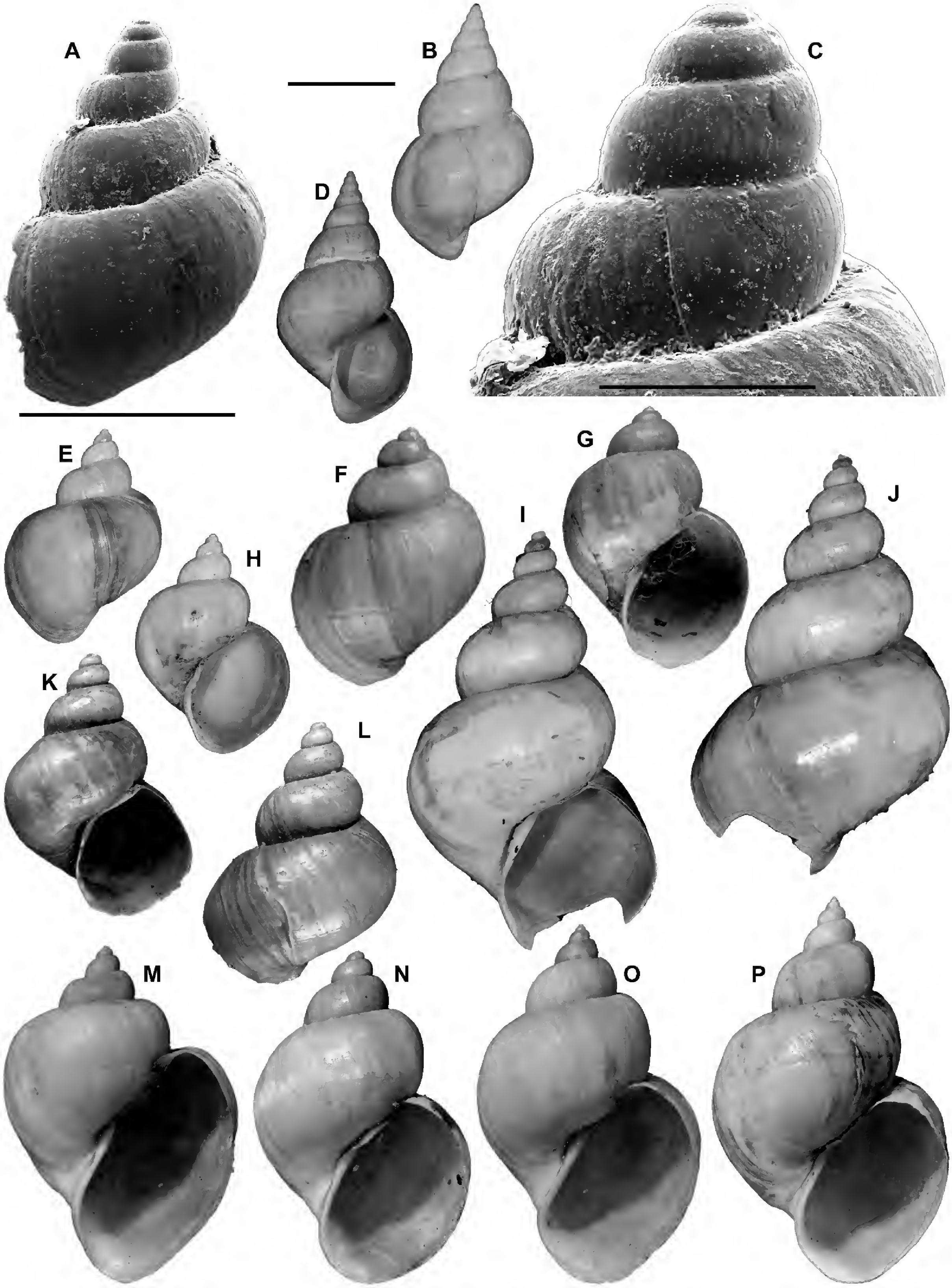

Figure 36. Putative fossil *Recluzia*, and specimens of *Recluzia johnii* (Holten) and *Recluzia lutea* (Bennett). *(A, C)* unidentified Epitoniidae formerly identified as *Recluzia* sp., NMB locality 17516, Casa Cantaure, Paraguana Peninsula, Venezuela; Cantaure Fm, Burdigalian (late early Miocene); SEM. *(B, D)* MNHN, Jousseaume collection, unlocalized specimen referred to *Recluzia johnii* (photos by E. Strong). *(E, H) Recluzia lutea*, USNM56411, holotype of *Lymnaea palmeri* Dall, Taqui River delta, head of Gulf of Mexico, eastern Pacific (photos by E. Strong). *(F–G) Recluzia lutea,* MNHN IM.25667, syntype of *Recluzia jehennei* Petit de la Saussaye and neotype designated here of *Recluzia lutea* Bennett, of *Janthina turrita* Philippi and of *Recluzia rollandiana* Petit de la Saussaye; Gulf of Arabia (MNHN photos). *(I–J) Recluzia johnii,* NHMUK197432, holotype of *Recluzia hargravesi* Cox and neotype designated here of *Helix johnii* Holten; Port Stephens, New South Wales, Australia (photos by E. Strong). *(K–L) Recluzia lutea,* MNHN IM.25668, one of two syntypes of *Recluzia annamitica* Wattebled; Thuan-an, Hué, Vietnam (MNHN photos). *(M–P) Recluzia lutea*, range of shape of large specimens in one collection; Great Exhibition Bay, northern North Island, New Zealand, Mar 1998; in collection of P. Poortman (Auckland) (specimen in Fig. 2S–T is from the same sample). Scale bars: A, 1 mm; C, 300 µm; uppermost bar, 10 mm, applies to all other figures.

Table 12. Dimensions of *Recluzia johnii* (*dimensions from original publications). *H,* height; *D,* diameter; *SH,* spiral height.

species/locality	H	D	SH	H/D	D/SH
R. hargravesi holotype, neotype of *R. johnii*	38.8	22.9	22.7	1.69	1.00
R. erythraea, from Jickeli*	13.0	8.5	—	1.53	—
R. turrita, from Philippi*	14.5	10.0	—	1.45	—
R. johnii, Jousseaume's specimen, MNHN	23.3	12.6	9.3	1.85	1.35
R. hargravesi, AMS, Queensland	16.9	10.9	—	1.55	—
R. hargravesi, AMS, Queensland	22.7	14.8	—	1.53	—
R. hargravesi, AMS, Queensland	22.5	13.9	—	1.62	—
R. hargravesi, AMS, Queensland	7.5	4.5	—	1.67	—
AMS C94285, Queensland	22.2	14.8	14.0	1.50	1.06
AMS C94286, Queensland	24.5	14.8	16.0	1.66	0.93
AMS C94287, Queensland	17.9	12.2	10.3	1.47	1.18
AMS C94287, Queensland	20.7	14.7	13.5	1.41	1.09
NMNZ M242099, Pearl Bay, Queensland	35.7	24.04	18.3	1.49	1.31
GNS WM17360, Swain Reefs, Queensland	28.8	20.5	15.1	1.40	1.36

Remarks. *Recluzia johnii* is so rare that little can be stated about it. It is concluded here that it is a second species of *Recluzia* with a taller, narrower spire with straighter outlines than in *R. lutea*, produced by its greater translation rate and slightly more numerous whorls of narrower cross-section. Most specimens have faint, irregular sculpture of weak spiral and axial grooves and ridges, varying individually, as in *R. lutea*. The teleoconch also tends to be a slightly warmer shade of yellow-brown than in *R. lutea*. Further material is required before the status and distribution of *R. johnii* is certain.

Riek (2017) published on his web page several excellent photographs of specimens collected alive on northern New South Wales beaches, showing two specimens of *Recluzia hargravesi* (i.e., *R. johnii*) feeding on the floating anemone *Actinecta* sp. The *Recluzia* specimens have extremely long, narrow, undivided cephalic tentacles, apparently much more extended than those in the photographs of *R. lutea*. However, the bright yellow animal, cylindrical egg capsules, and other characters are identical to those of *R. lutea*. It is notable that the floats of all specimens on this web page are as irregularly arranged as those of *R. lutea* in all other photographs observed, and it appears that the float of *Recluzia* species is less regular than and formed slightly differently from that of *Janthina*. Denis Riek (Brunswick Heads, NSW, pers. comm. 11 Nov 2015) confirmed that the cephalic tentacles of all *Recluzia* specimens he has seen are undivided; the double appearance in some of his photographs is due to reflection on the undersurface of the water in the aquarium. He also stated that the photographed specimens ate the *Actinecta* anemones voraciously; they had consumed one anemone before he reached home and they could be transferred to his aquarium. Thereafter he was able to photograph them consuming the remaining anemone.

An unlocalized specimen from Jousseaume's collection in MNHN (Figs 36B, D; point identified by "JJ" in Fig. 35; photographs provided by E. Strong, USNM, pers. comm. 20 Sep 2012) is similar in spire height to Chemnitz's (1795: 284, pl. 210, fig. 2076) drawing of the lost holotype of *Recluzia johnii*. It is unusually narrow, and has a still narrower appearance than other *Recluzia* specimens because its suture is markedly shallower and the spire outline consequently less strongly stepped than in any other *Recluzia* specimen the writer has examined (H 23.3, D 12.6, SH 9.3 mm; H/D = 1.85, D/SH = 1.35; i.e., intermediate between the means of *R. lutea* and *R. johnii*; dimensions included in Table 12 and in calculations of dimensions and means for *R. johnii*, including in Table 11). The anterior end of the aperture is flared narrowly. It is an unusually pale yellowish grey, similar to the colour of Chemnitz's (1795: 284, pl. 210, fig. 2076) drawing, and paler than all other specimens of *R. johnii* and *R. lutea* observed by the writer. It also has seven teleoconch whorls, indicating that the whorls are still narrower than those of other specimens assigned to *R. johnii*. This specimen presumably inspired Jousseaume's (1872) note on this species. It possibly represents a third living species of *Recluzia*. However, as only one specimen has been observed it must be assumed to be part of the variation of *R. johnii* until more specimens allow it to be evaluated more fully. The available material suggests that there are two species of *Recluzia*.

Recluzia lutea (Bennett, 1840)

Figs 2S–T, 36E–H, K–P, 37

Janthina lutea Bennett, 1840: 298 (refers to description by Bennett, 1840: 63).

Janthina turrita "von dem Busch" Philippi, 1849: 15; H. Adams & A. Adams, 1854: 87; Mörch, 1860: 284; Tryon, 1887: 39.

Recluzia jehennei Petit de la Saussaye, 1853: 118, pl. 5, fig. 3; H. Adams & A. Adams, 1854: 87; Mörch, 1860: 283; Küster, 1868: 11, pl. 1, fig. 15; Tryon, 1887: 39, pl. 10, fig. 28; Smith, 1910: 202; Fisher-Piette, 1950: 14; Bosch *et al*., 1995: 111, fig. 443.

Recluzia rollandiana Petit de la Saussaye, 1853: 119, pl. 5, fig. 2; H. Adams & A. Adams, 1854: 87, pl. 69, fig. 2; Chenu, 1859: 119, fig. 520; Mörch, 1860: 284; Küster, 1868: 12, pl. 1, fig. 14; Tryon, 1887: 38, pl. 10, figs 25–27; Abbott, 1963: 151; Habe, 1964: 48, pl. 14, fig. 7; Habe & Kosuge, 1966: 102, pl. 40, fig. 10; Bennett, 1966: 43, pl. 11, fig. 1; Abbott, 1968: 92, fig. 4; Cernohorsky, 1972: 198, pl. 56, fig. 11; Abbott, 1974: 113, fig. 1182; Powell, 1976: 107; Powell, 1979: 254, pl. 48, fig. 23; Colman, 1986: 3, text-fig.; Rios, 1994: 102, pl. 33, fig. 417; Spencer & Willan, 1996: 24; Smith, 1998: 813, fig. 15.151B; Spencer *et al*., 2009: 206; Raven & Bracegirdle, 2010: 28, text-fig.

Ianthina lutea Bennett.–Benson, 1860: 413.

Recluzia bensoni A. Adams, 1861: 402; Yen, 1942: 219, pl. 19, fig. 122; Tryon, 1887: 39.

Recluzia montrouzieri Souverbie, 1871: 334; Souverbie, 1872: 20: 57, pl. 1, fig. 8; Habe & Tokioka, 1953: 57, fig. 12.

Lymnaea? *palmeri* Dall, 1871: 135.

Recluzia globosa E. A. Smith, 1876: 551, pl. 30, fig. 8; Tryon, 1887: 39, pl. 10, fig. 29.

Recluzia rollandiana var. β *annamitica* Wattebled, 1886: 67, pl. 3, figs 4a–b; Tryon, 1887: 38, pl. 10, fig. 26.

Recluzia lutea (Bennett).–Oliver, 1915: 525; Hedley, 1918: M62; Powell, 1924: 285; Powell, 1937: 74; Powell, 1946: 77; Powell, 1957: 98; Powell, 1962: 91; Rehder, 1980: 53, pl. 7, fig. 6; Boone, 1984: 8; Higo *et al*., 1999: 174; Okutani, 2000: 319, pl. 158, fig. 5; Poppe, 2008: 722, pl. 306, fig. 2.

Recluzia palmeri (Dall).–Dall, 1925: 25, pl. 17, fig. 8; Keen, 1971: 443, fig. 690; Abbott, 1974: 114; Abbott & Dance, 1982: 70, bottom right fig.; Poorman, 1980: 183.

Recluzia effusa "Martens" Thiele, 1928: 78, footnote, fig. 2 (shell not illustrated).

Recluzia hargravesi Cox.–Allan, 1950: 95, text-fig. 22.6;

Wilson, 1993: 281, pl. 44, figs 35A–B (misidentification as *R. johnii* Holten, 1802).

Recluzia rollandiana bensoni A. Adams.–Kuroda *et al.*, 1971: 245, pl. 62, fig. 16.

Recluzia cf. *jehennei* Petit.–Churchill *et al.*, 2011a: 802, fig. 1 (upper); Churchill *et al.*, 2011b: 441, figs 1A–F.

Type material. No type material of *Janthina lutea* is present in any museums the writer has consulted, and there is nothing in Bennett's (1840) work to indicate that he retained any specimens. Bennett's (1840: 63) description stated merely that this is an elongate, yellow species of *Janthina* with narrower whorls than *J. janthina*; a neotype therefore is required to associate this name unambiguously with the present *Recluzia* species. The type locality is 2°53'S 174°55'E (Bennett, 1840: 62), a short distance southwest of the Phoenix Islands, Kiribati, central western Pacific Ocean. However, as *Recluzia lutea* is pelagic and almost cosmopolitan, occurring in all world tropical and temperate seas, selection of a neotype from near the original type locality seems unimportant in this case, particularly as almost no material from the central Pacific has been observed by the writer.

The writer also has been unable to trace any type material of *Janthina turrita*. Little that is diagnostic is available for this species, but the name "turrita" suggests that it applies to a *Recluzia* species rather than to *Janthina*, and the dimensions (H 14.5, D 10 mm) rule out a position in *Janthina*. The name was not illustrated and has been referred to again only by Tryon (1887: 39), who listed it among inadequately known species. The original description stated that the shell is fusiform, turreted, dark, smooth, with well-rounded whorls, deep sutures, and a short spire. The outer lip is straight and recedes strongly. The upper whorl surface is blue, and the base is pale reddish shading to rust red. The locality is unknown. Apart from the mysteries of the receding (incomplete?) lip and the colour, there seems to be little else this could refer to other than a *Recluzia* species. The late Dr Rudolf Kilias informed the writer that Dr Gerhard von dem Busch was a physician in Bremen. Enquiry at Übersee Museum Bremen revealed that von dem Busch's collection is indeed located there. *Janthina turrita* is listed in von dem Busch's manuscript catalogue with the locality "Adelaide". However, the specimen is not present (T. Kruckow, Übersee Museum Bremen pers. comm. 05 Mar 1975), presumably because it was sent to Philippi. The writer has also been informed by N. Bahamonde (Museo Nacional de Historia Natural, Santiago, pers. comm. 25 Mar 1975) that no material identified as *Janthina turrita* is present there in Philippi's collection. C. Zorn (ZMB pers. comm. 30 Jan 2016) has also informed the writer that no material bearing this name is present in ZMB. Therefore, this name also requires a neotype.

Recluzia jehennei, one figured syntype MNHN25667 (Figs 36F, G), listed by Fisher-Piette (1950: 14) as the holotype; "this shell was found in the open ocean, in the Gulf of Arabia, by Commandant Jehenne" (translation from Petit de la Saussaye, 1853: 119). *Recluzia rollandiana*, no type material present in MNHN. The description by Petit de la Saussaye (1853: 120) indicated that the specimen remained "belonging to M Rolland de Roquan", and so presumably is long lost; from "environs de Mazatlan" ("later identified as actually from New Caledonia"; Keen 1971: 903). The remaining syntype of *Recluzia jehennei*, MNHN25667 (Figs 36F, G) is here designated the neotype of *Janthina lutea* Bennett, 1840, the neotype of *Janthina turrita* Philippi, 1849 and the neotype of *Recluzia rollandiana* Petit de la Saussaye, 1853, to refer these names unambiguously to the present species rather than to *R. johnii*.

Recluzia bensoni, holotype NHMUK1878.1.28.394, labelled "China Sea, R. Benson", a small, narrow, juvenile specimen of *Recluzia lutea*, illustrated by Yen (1942: 219, pl. 20, fig. 122). Yen's illustration suggests that *R. bensoni* is possibly part of the variation of *R. johnii*, but the dimensions plot at the base of the field of *R. lutea* in Fig. 34. *Recluzia montrouzieri*, one specimen in MNHN presented by the author was formerly considered to be a syntype but, as with *Janthina capreolata*, the type material was stated by Souverbie (1871) to be in MHNB, and the MNHN specimen is not a type; two syntypes MHNB2004.TY.163, from Art Island, New Caledonia; photograph of syntypes sent by Laurent Charles, MHNB and Virginie Héros, MNHN (pers. comm. 21 Sep 2012).

Lymnaea palmeri, holotype USNM56411 (Dall, 1925: 25, pl. 17, fig. 8), from the delta of the Taqui River, near Guaymas, Mexico, head of the Gulf of California. Abbott & Dance (1982: 70, bottom right fig.) illustrated the holotype of *Lymnaea palmeri* clearly. This specimen agrees in shape with that of the taller specimens of *Recluzia lutea*, but its original stated dimensions placed it within the field of *R. johnii* in Fig. 34. The photographs (Figs 36E, H) sent by E. Strong (USNM pers. comm. 20 Sep 2012) show that the stated dimensions (Keen, 1971: 443) were probably inaccurate, but they have been retained in Table 13 and Fig. 35. The overall appearance is accepted here as confirming that *R. palmeri* is a synonym of *R. lutea*.

Recluzia globosa, holotype NHMUK1876.1.10.119, labelled "Tarawa, Gilbert Group, received from John Brazier Esq. per Mr Henry Adams", another small, very short specimen. All small specimens of *R. lutea* are very short compared with adults, and the dimensions of the holotype fall within the range of variation of *R. lutea* (Fig. 35). *Recluzia rollandiana* var. *annamitica*, two syntypes MNHN25668 (one in Figs 36K–L), from beach at Thuan-an, near Hué, Vietnam. *Recluzia effusa* holotype ZMB/Moll-13704 (E. Strong, USNM, pers. comm. 20 Sep 2012), not seen; from "chinesischen See". The status of this name is not clear, as the shell is poorly preserved, but it is assumed here to be a further synonym of the more common *Recluzia* species.

Other material examined. Present-day specimens from Australia and New Zealand: **Australia**: ***New South Wales***: Dingo Beach, Cape Gloucester (AMS); Catherine Hill Bay (AMS C11333); Port Macquarie (NMV); Collaroy Beach, Sydney (AMS); Cronulla, S of Sydney (AMS C75719). ***Queensland***: Michaelmas Cay, off Cairns (AMS C53537); King's Beach, Caloundra (NMV, AMS); Lady Elliott I. (AMS C69170). ***Tasmania***: Black Rocks, Richmond River (AMS C76081).

Kermadec Islands: Raoul I. (SAMA; AMS C36656; GNS WM5654, 1; NMNZ M202865, 5; M202866, 1; M200986, 3; M202867, 1; M214384, 20).

New Zealand: Twilight Beach, Cape Reinga (NMNZ M100807, 2); N end of Ninety Mile Beach (NMNZ M117600, 6; M117826, 7); S of Scott Pt., Ninety Mile Beach (NMNZ M117256, 20); S of the Bluff, Ninety Mile Beach (NMNZ M277745, 3); Great Exhibition Bay, Mar 1998 (GNS RM6748, 4; NMNZ M155930, 59; P. Poortman colln., 20); Rarawa, Great Exhibition Bay (NMNZ M081519, 1); Taupiri Bay, N of Whangarei (NMNZ M081518, 26); Laings Beach, Mangawai, Hauraki Gulf (AWM); Mangawai Heads (NMNZ M277744, 1); Tryphena, Great Barrier Island (Powell 1924: 285; in AWM); Whangamata, Bay of Plenty (AWM).

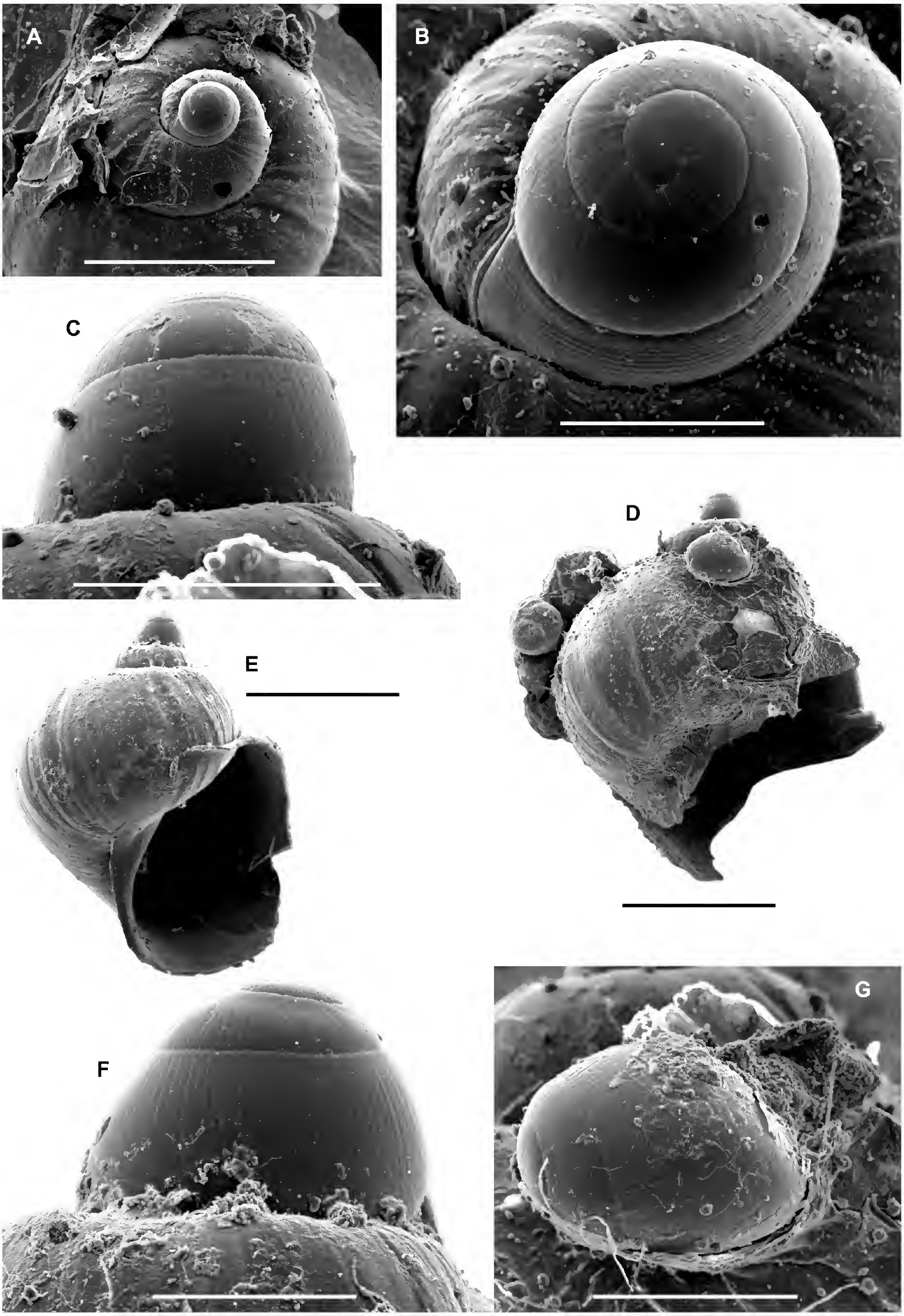

Figure 37. *Recluzia lutea* (Bennett), NMNZ M081518, small specimens and larval shells; beach, Taupiri Bay, Northland, New Zealand; SEM. *(A–B)* apical views of shell and protoconch. *(C–D, G)* apertural view of incomplete specimen with 10 larval shells attached to dried float material; C, lateral view of protoconch of large specimen; D, whole shell; G, larval shell attached by dried float material to large specimen below its protoconch. *(E–F)* third specimen, lateral views of shell and protoconch. Scale bars: A, D, E, 1 mm; B, F, 200 µm; C, G, 300 µm.

Distribution. *Recluzia lutea* occurs uncommonly throughout the world tropical and temperate ocean, but its limits are very poorly known. Large rafts of specimens are cast ashore in some locations, but much less frequently than for all *Janthina* species. In New Zealand, *R. lutea* is recorded only from the northeastern North Island warm-water region, in eastern Northland and the Bay of Plenty, as far southeast as Waihau Bay, easternmost Bay of Plenty. Much the largest lots have been seen from Great Exhibition Bay and Ninety Mile Beach in the northernmost North Island, where specimens are sometimes cast ashore in large numbers after unusually persistent onshore winds. Thompson (1991) gave a popular account of wash-ups of "about three hundred" specimens during Easter 1991 at Cape Maria van Diemen and Great Exhibition Bay, northernmost North Island. Large numbers of specimens also are cast shore from time to time all around eastern, northern and Western Australia. Specimens are also recorded from throughout the Indo-West Pacific province as far north as central Japan, in the Red Sea, and rarely in the eastern Pacific and the Atlantic Ocean.

Dimensions. See Table 13.

Diagnosis. Moderate-sized (H to 36, D to 22 mm), larger than *Janthina exigua* and *J. umbilicata* but smaller than all other *Janthina* species and *Recluzia johnii*; taller and narrower than all *Janthina* species, but shorter and wider than *R. johnii*; mean height: diameter 1.44, mean diameter: spire height 1.51. Teleoconch of 4.5–5.5 whorls; whorls strongly and evenly inflated, of almost circular cross-section, wider than in *R. johnii*; suture deeply impressed; without obvious sculpture. Aperture slightly flared anteriorly in many large specimens. Lays smooth, narrow, cylindrical to weakly club-shaped, yellow egg capsules on underside of float.

Remarks. *Recluzia lutea* is superficially smooth and lightly polished when the periostracum is removed, but most specimens are found with the thin, pale brown, matt periostracum still at least partly adhering. *Recluzia lutea* has strongly and evenly inflated whorls and a much more deeply impressed suture than in any *Janthina* species. Weak axial and spiral grooves and ridges occur on many specimens, varying individually. The outer lip is vertical and straight, i.e., with no sinus in the lip, and the inner lip is narrowly but variably reflected over the narrow umbilicus.

Bennett's (1840) description of *Janthina lutea* is quite adequate to make this name available, although which species he had is not determinable from the description. Bennett (1840: 298) stated "In the course of the narrative I have had occasion to mention a yellow and very rare species of this genus [*Janthina*]: and for which I would propose the name *Janthina lutea*". This is a reference to his earlier description (Bennett, 1840: 63): "One species of this family, which I obtained here, was new to me: and is certainly very rare: its shell was yellow: rather smaller and more elongated than *J. communis* [i.e., *J. janthina*]; and the whirl more prominent and spiral. The contained animal was also of a yellow colour: but in the form of the float and other respects, it closely resembled the ordinary blue shelled species". The neotype designated here establishes that this name applies to the shorter *Recluzia* species identified here as *Recluzia lutea*. Bennett (1834) earlier described a specimen of *Janthina* captured at sea at 0°14'S 20°07'W, NW of Ascension Island, central Atlantic Ocean, but did not mention the "yellow species".

Petit de la Saussaye (1853: 118–119, pl. 5, figs 2–3) named two short-spired species of *Recluzia*, distinguishing the two by *R. rollandiana* having more inflated whorls, a more deeply impressed suture, and more pronounced spiral striae than *R. jehennei*. However, his illustrated shells are both well within the range of variation of *R. lutea*. A. Adams (1861) provided no dimensions or illustration of *Recluzia bensoni*, but the holotype was illustrated by Yen (1942: pl. 19, fig. 122). The illustration and examination of the holotype (NHMUK1878.1.28.394) demonstrate that this is a very small, narrow specimen of *R. lutea*. Souverbie's (1872: pl. 1, fig. 8) illustration of a syntype and examination of the syntypes of *R. montrouzieri* demonstrate that this also is indistinguishable from the holotype of *R. rollandiana*, and falls within the variation of *R. lutea*. Wattebled's (1886: pl. 3, fig. 4) illustration of a syntype and examination of the syntypes of *Recluzia rollandiana* var. *annamitica* show that this also is closely similar to the type material of *R. rollandiana* and *R. jehennei*, and again is part of the variation of *R. lutea*. Four specimens (Figs 36M–P) from the same sample from Great Exhibition Bay, Northland, New Zealand, are illustrated to show the range of variation of *R. lutea*, although they do not include the most extreme specimens observed. The specimen in Fig. 2S–T is from the same sample.

A collection of specimens of *Recluzia lutea* cast ashore on the beach at Taupiri Bay, Northland, New Zealand (NMNZ M081518, collected by A. Allo, 24 Mar 1982; 12 moderate-sized to large shells plus 14 small juveniles) consists of specimens ranging in height from 29.4 mm to larval shells. Some of these were studied by SEM (Figs 37A–G). All specimens less than c. 13 mm high are short and wide and closely resemble *Alexania natalensis* and the holotype of *R. globosa* in all characters. Several have dried floats attached, each now forming a thin, dark brown, rigid, irregular mass. Several larval shells were incorporated in the float material of some of the moderate-sized specimens (some now separated). One small shell has 10 larval shells attached to the exterior of its teleoconch by dried float material (Figs 37C–D, G). These confirm statements by Colman (1986) and Churchill *et al*. (2011a) that juveniles of *R. lutea*, including recently metamorphosed larval shells, live attached to the floats of adults. Also, a photograph of a living specimen of *R. lutea* published on a web page (Churchill *et al*., 2011b: figs 1A–B; Riek, 2017; Fig. 6C) clearly shows a relatively large juvenile specimen of *R. lutea* on the float of an adult female, lying between the float and the foot. The protoconch in the specimens studied by SEM, although very similar to that of *Janthina* species, with very similar sculpture and an identical protoconch 1, is shorter and has a protoconch 2 of only 2.2 whorls, rather than 3.2 whorls in the *Janthina* species available for study. However, the significance of this apparent distinction is uncertain, in view of the lack of knowledge of the number of protoconch whorls in *J. pallida*.

Table 13. Dimensions of *Recluzia lutea* (*dimensions from original publications). *H,* height; *D,* diameter; *SH,* spire height.

species/locality	height	diameter	spire height	H/D	D/SH
Recluzia jehennei, from Petit de la Saussaye*	19	15	—	1.27	—
Recluzia rollandiana, from Petit de la Saussaye*	25	18	—	1.39	—
Recluzia globosa holotype	11.15	9.0	—	1.24	—
Recluzia montrouzieri, from Souverbie*	23	17	—	1.35	—
Recluzia bensoni, holotype	5.5	5.0	—	1.10	—
Recluzia annamitica, from Wattebled*	25	19	—	1.32	—
Recluzia palmeri holotype* (Keen, 1971: 443)	22.5+	13.0	—	1.73	—
Recluzia annamitica syntype, MNHN	22.6	17.8	10.0	1.23	1.78
Recluzia annamitica syntype, MNHN	22.1	17.3	10.6	1.28	1.63
Recluzia montrouzieri, MNHN	26.6	18.9	9.7	1.41	1.95
USNM721600, Cook Is.	17.2	12.5	7.7	1.38	1.62
USNM711796, Raroia, Tuamotu Islands	17.4	12.4	8.3	1.40	1.49
NMNZ M214384, Raoul I., Kermadec Islands	24.5	17.9	11.4	1.39	1.57
NMNZ M214384, Raoul I.	26.7	18.8	12.6	1.42	1.49
NMNZ M214384, Raoul I.	27.0	18.4	13.2	1.47	1.39
NMNZ M214384, Raoul I.	19.5	14.5	9.2	1.34	1.58
NMNZ M214384, Raoul I.	19.4	14.3	9.4	1.36	1.52
NMNZ M214384, Raoul I.	20.2	14.5	9.5	1.39	1.53
NMNZ M214384, Raoul I.	19.2	13.0	9.7	1.48	1.34
NMNZ M214384, Raoul I.	15.6	12.2	7.9	1.28	1.54
NMNZ M214384, Raoul I.	13.1	10.0	6.1	1.31	1.64
GNS WM5654, Raoul I., Kermadec Islands	24.7	17.2	11.6	1.44	1.48
NMNZ M155930, Great Exhibition Bay, NZ (n = 43)	33.7	21.7	16.1	1.55	1.35
NMNZ M155930, Great Exhibition Bay	30.4	20.2	15.5	1.50	1.30
NMNZ M155930, Great Exhibition Bay	31.7	20.1	14.6	1.58	1.38
NMNZ M155930, Great Exhibition Bay	29.6	19.7	14.4	1.50	1.37
NMNZ M155930, Great Exhibition Bay	29.9	18.5	14.1	1.62	1.31
NMNZ M155930, Great Exhibition Bay	30.0	18.9	14.2	1.59	1.33
NMNZ M155930, Great Exhibition Bay	24.1	16.7	11.3	1.44	1.48
NMNZ M155930, Great Exhibition Bay	29.1	19.9	13.5	1.46	1.47
NMNZ M155930, Great Exhibition Bay	28.8	19.6	12.3	1.47	1.59
NMNZ M155930, Great Exhibition Bay	27.8	19.1	13.3	1.46	1.44
NMNZ M155930, Great Exhibition Bay	26.3	18.8	11.8	1.40	1.59
NMNZ M155930, Great Exhibition Bay	27.3	19.3	12.7	1.41	1.52
NMNZ M155930, Great Exhibition Bay	27.4	17.7	13.0	1.55	1.36
NMNZ M155930, Great Exhibition Bay	27.0	18.6	13.4	1.45	1.39
NMNZ M155930, Great Exhibition Bay	26.4	18.4	11.9	1.43	1.55
NMNZ M155930, Great Exhibition Bay	27.2	17.8	12.9	1.53	1.39
NMNZ M155930, Great Exhibition Bay	27.2	17.6	13.0	1.55	1.35
NMNZ M155930, Great Exhibition Bay	25.6	18.1	13.4	1.41	1.35
NMNZ M155930, Great Exhibition Bay	28.7	18.3	14.2	1.57	1.29
NMNZ M155930, Great Exhibition Bay	27.2	18.0	10.6	1.51	1.70
NMNZ M155930, Great Exhibition Bay	25.3	17.5	12.5	1.45	1.40
NMNZ M155930, Great Exhibition Bay	25.9	18.1	10.9	1.43	1.66
NMNZ M155930, Great Exhibition Bay	26.6	16.8	13.9	1.58	1.21
NMNZ M155930, Great Exhibition Bay	23.1	16.5	10.5	1.40	1.57
NMNZ M155930, Great Exhibition Bay	25.3	17.5	11.5	1.45	1.52
NMNZ M155930, Great Exhibition Bay	23.8	17.1	10.7	1.39	1.60
NMNZ M155930, Great Exhibition Bay	22.8	16.9	9.8	1.35	1.72
NMNZ M155930, Great Exhibition Bay	21.5	15.4	8.9	1.40	1.73
NMNZ M155930, Great Exhibition Bay	21.5	16.2	10.4	1.33	1.56
NMNZ M155930, Great Exhibition Bay	23.0	15.8	9.3	1.46	1.70
NMNZ M155930, Great Exhibition Bay	23.1	14.3	11.0	1.62	1.30
NMNZ M155930, Great Exhibition Bay	20.2	14.6	8.9	1.38	1.64
NMNZ M155930, Great Exhibition Bay	21.4	13.9	9.9	1.54	1.40
NMNZ M155930, Great Exhibition Bay	20.7	14.5	8.6	1.43	1.69
NMNZ M155930, Great Exhibition Bay	19.9	13.7	10.1	1.45	1.36
NMNZ M155930, Great Exhibition Bay	17.3	12.2	7.8	1.42	1.56
NMNZ M155930, Great Exhibition Bay	17.3	12.0	8.9	1.44	1.35
NMNZ M155930, Great Exhibition Bay	16.0	12.1	6.9	1.32	1.75
NMNZ M155930, Great Exhibition Bay	16.2	10.9	6.9	1.49	1.58
NMNZ M155930, Great Exhibition Bay	28.3	17.5	13.3	1.62	1.32
NMNZ M155930, Great Exhibition Bay	26.7	18.2	12.9	1.47	1.41
NMNZ M155930, Great Exhibition Bay	24.3	17.1	11.9	1.42	1.44
NMNZ M155930, Great Exhibition Bay	24.9	17.3	12.4	1.44	1.40
NMNZ M155930, Great Exhibition Bay	24.7	16.9	11.4	1.46	1.48
GNS RM6748, Great Exhibition Bay, NZ	26.3	17.8	11.6	1.48	1.53
GNS RM6748, Great Exhibition Bay	28.8	19.1	14.1	1.51	1.35
GNS RM6748, Great Exhibition Bay	29.5	19.8	12.1	1.49	1.64
GNS RM6748, Great Exhibition Bay	28.6	19.1	13.3	1.50	1.44
R. rollandiana, colln. Cloue, MNHN	25.3	18.7	10.7	1.35	1.75
R. rollandiana, Madagascar, MNHN	26.3	18.0	11.0	1.46	1.64
R. rollandiana, Madagascar, MNHN	27.5	18.7	11.2	1.47	1.67

Conclusions

1. Janthinidae is a synonym of Epitoniidae; demonstrated also from molecular sequences by Churchill *et al*. (2011a) and Takano & Kano (2014).
2. *Janthina* evolved late in Miocene time from a benthic epitoniid resembling *Alora*, whereas *Recluzia* evolved independently during Holocene time from a benthic epitoniid resembling *Alexania* and *Surrepifungium*; i.e., adaptation to a neustonic life evolved twice in Epitoniidae.
3. Time ranges of fossil species of *Janthina* provide a Pliocene biostratigraphical zonation based on relatively large (20–40 mm) cosmopolitan gastropods, although fossils are probably too rare other than in New Zealand, southern Australia, Japan and possibly the Atlantic islands to be of practical use. The main event of utility for biostratigraphy is the abrupt (apparently punctuational) extinction of *J. typica* and origination of *J. chavani* at 3.0 Ma, in mid-Piacenzian time. Time ranges are:
    - *Janthina typica*: Messinian–early Piacenzian, c. 7–3.0 Ma;
    - *Janthina chavani*: late Piacenzian–Calabrian, 3.0–c. 1.6 Ma; probably younger (to 1 Ma or younger?) in Bridgewater Limestone in SE South Australia;
    - *Janthina krejcii* sp. nov.: Zanclean, c. 4.8–4.3 Ma, constrained by the stratigraphy of Santa Maria Island;
    - *Janthina globosa*: late Piacenzian or Gelasian (c. 3–2 Ma?) to Holocene;
    - All other *Janthina* and *Recluzia* species (*J. exigua*, *J. janthina*, *J. pallida*, *J. umbilicata*, *Recluzia johnii*, *R. lutea*): Holocene only.
4. These time ranges suggest a phylogeny in which the earliest neustonic epitoniid, *Janthina typica*, evolved during Messinian time from a benthic epitoniid. *Janthina typica* became extinct and *J. chavani* originated in mid-Piacenzian time, at 3.0 Ma, and *J. janthina* originated from *J. chavani* during late Calabrian time, or later. *Janthina krejcii* sp. nov. originated from *J. typica* during Zanclean time, and gave rise to two minor clades during late Piacenzian time: *Janthina globosa* (fossils recorded from late Piacenzian or Gelasian) and its daughter species *J. pallida*, and *J. exigua* and its daughter species *J. umbilicata.*
5. The suggested phylogeny and taxonomy should be evaluated by comparing molecular sequences of several (preferably all) living *Janthina* species, *Recluzia johnii*, *R. lutea*, *Alexania natalensis*, *Surrepifungium* and/or *Epidendrium* species, *Alora* species, and as many other species of benthic Epitoniidae as possible.

Appendix. Type designations—a summary of types, museum registrations, and pagination in the present work.

type status	museum	registration numbers	page	taxon
holotype	SMF	SMF10135a	173	*Janthina krejcii* sp. nov.
paratype	SMF	SMF10135b	173	*Janthina krejcii* sp. nov.
paratype	SMF	SMF10135c	173	*Janthina krejcii* sp. nov.
paratypes	GNS	WM18973 (10 specimens)	173	*Janthina krejcii* sp. nov.
neotype	NHMUK	NHMUK1976168a	182	*Janthina globosa* (Swainson, 1822)
neotype	NHMUK	NHMUK1976168a	182	*Janthina prolongata* Blainville, 1822
neotype	NHMUK	NHMUK1976168a	182	*Janthina nitens* Menke, 1828
neotype	NHMUK	NHMUK1976168a	182	*Janthina rosea* Anton, 1838
neotype	NHMUK	NHMUK1976168a	183	*Janthina nitens* var. *atlantica* Mörch, 1860
neotype	NHMUK	NHMUK1976168a	183	*Janthina payraudeaui* Locard, 1901
neotype	MIGM	MIGM1312	165	*Hartungia typica* Bronn, 1861
neotype	MIGM	MIGM1312	165	*Janthina hartungi* Mayer, 1864
neotype	AUGD	AUGD G5721	168	*Turbo postulatus* Bartrum, 1919
neotype	Lin.Soc.Lond.	lectotype of *Helix janthina*	187	*Janthina violacea* Röding, 1798
neotype	Lin.Soc.Lond.	lectotype of *Helix janthina*	187	*Janthina penicephala* Péron & Lesueur, 1807
neotype	Lin.Soc.Lond.	lectotype of *Helix janthina*	187	*Janthina bicolor* Menke, 1828
neotype	MHNG	MHNG-INVE51377	192	*Janthina nana* Gray, 1850
neotype	MHNG	MHNG-INVE51377	192	*Janthina vinsoni* Deshayes, 1863
neotype	MHNG	MHNG-INVE51377	192	*Janthina courcellei* Mabille & Rochbrune, 1889
neotype	NHMUK	NHMUK1951.3.14.4	195	*Janthina pallida* Thompson, 1840
neotype	NHMUK	NHMUK1854.12.4.403	196	*Janthina globosa* Blainville, 1822
neotype	NHMUK	NHMUK1854.12.4.403	196	*Janthina megastoma* A. Adams, 1861
neotype	NHMUK	NHMUK197432	201	*Helix johnii* Holten, 1802
neotype	MNHN	MNHN25667	204	*Janthina lutea* Bennett, 1840
neotype	MNHN	MNHN25667	204	*Janthina turrita* Philippi, 1849
neotype	MNHN	MNHN25667	204	*Recluzia rollandiana* Petit de la Saussaye, 1853
lectotype	SAMA	SAMA T1494A	168	*Heligmope dennanti* Tate, 1893
lectotype	ZMB	ZMB41985a	182	*Janthina patula* Philippi, 1844
lectotype	MCZR	MCZR23414/1	183	*Amethistina laeta* Monterosato, 1884
lectotype	MCZR	MCZR23423/1	183	*Janthina splendens* Monterosato, 1884
lectotype*	Lin.Soc.Lond.	not registered	187	*Helix janthina* Linnaeus, 1758
lectotype	NHMUK	NHMUK1854.12.4.399a	189	*Janthina orbignyi* (Mörch, 1860: 277)

* Specimen illustrated by Laursen (1953: fig. 15.3); see also Fig. 33.3 (p. 189).

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