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Systematic revision of the gastropod family Philinidae (Mollusca: Cephalaspidea) in the north-east Atlantic Ocean with emphasis on the Scandinavian Peninsula

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The taxonomy of the family Philinidae has been hampered by a lack of proper species descriptions combining morphological, anatomical, and phylogenetic data within a comparative framework. To date, most descriptive work has been based on shells alone and on few specimens. We here followed an integrative taxonomic approach to study the diversity of the family in the north-east Atlantic, with emphasis on the Scandinavian Peninsula, by combining shell and morpho-anatomical characters with molecular phylogenetic inference. Synonyms, ecology, and geographical distributions are given for each species and a dichotomous key for species identification is provided. Anatomical dissections, examination of shells, radulae, gizzard plates, male reproductive systems, and molecular phylogenetics based on the mitochondrial cytochrome *c* subunit I (COI) were used to discriminate amongst species and define diagnostic characters. Nineteen species of Philinidae were recognized, including two new to science (***Philine indistincta* sp. nov.** and ***Philine grandioculi* sp. nov.**). The presence of *Philine quadripartita* (and not *Philine aperta*) in the north-east Atlantic is confirmed. Species can be best differentiated by their external morphology, shells, and male reproductive system. The generic division of Philinidae into *Johania*, *Laona*, *Philine*, and *Praephiline* was not supported and all species have been ascribed to the genus *Philine*.

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ADDITIONAL KEYWORDS: integrative taxonomy – *Philine*.

INTRODUCTION

What is Philinidae? Morphology, biology, and phylogeny

Philinidae is a family of marine gastropods included in the order Cephalaspidea (Malaquias *et al*., 2009). The shell of philinid species is often internal and varies between 1 and 40 mm in length; it is weakly calcified, whitish transparent with a 'plate-like', ovate to elongate shape (Burn & Thompson, 1998). The wide aperture normally covers about two thirds of the shell. Shells can be smooth but often sculpture is present; pits can be separated forming a punctuate sculpture or be connected, resulting in chains. Sometimes the pits are fused, forming transverse grooves or a reticulate pattern of raised transverse and longitudinal lines.

The body colour is usually whitish, sometimes with coloured patches, dots, or stripes (Burn & Thompson, 1998; Rudman, 1998). The body is cylindrical or dorsally flattened and is larger than the shell. The cephalic shield comprises nearly half of the body length and is often longitudinally grooved (Rudman, 1972; Burn & Thompson, 1998; present study; Fig. 1). The eyes are rarely visible and the Hancock's organ is generally inconspicuous (Burn & Thompson, 1998), although it is prominent in some species [e.g. *Philine ventricosa* (J. G. Jeffreys, 1865); present study]. The foot is short and supplemented by a posterior pallial lobe and thick parapodial lobes, which are folded upwards to enclose the body (Rudman, 1972; Burn & Thompson, 1998; present study).

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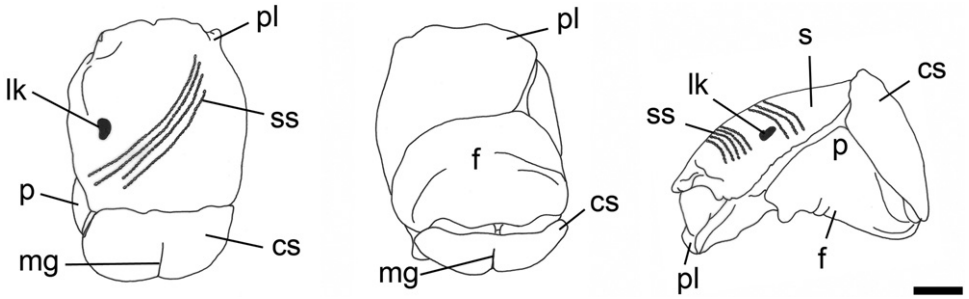

Figure 1. External morphology of *Philine*, left to right: dorsal, ventral, and right lateral view. Abbreviations: cs, cephalic shield; f, foot; lk, larval kidney; mg, median groove; p, parapodium, pl, pallial lobe; s, shell; ss, shell sculpture. Scale bar = 0.5 mm.

The philinid species have a monaulic reproductive system (Rudman, 1978; Hadfield & Switzer-Dunlap, 1984). The morphology of the penis can vary extensively (Rudman, 1972), from hammer-shaped and smooth in *Philine approximans* Dautzenberg & Fischer H., 1896, to cylindrical with cone-shaped warts in *Philine scabra* (Müller, 1784), cylindrical with narrow finger-like tips in *Philine azorica* Bouchet, 1975, to a plump cylinder with a flap and a spine at the top in *Philine monilifera* Bouchet, 1975 (Bouchet, 1975).

Philinids typically have a radula lacking a rachidian tooth but some species can have it reduced (e.g. *Philine gibba* (Strebel, 1908); Rudman, 1972). One inner lateral plus one to six outer lateral teeth are present. Jaws are absent (Rudman, 1978; Burn & Thompson, 1998; present study). The gizzard most often contains three chitinous or calcareous plates, which can be equal as in *P. scabra* or different in size and shape as in *Philine quadripartita* Ascanius, 1772. In some species like *Philine lima* (Brown, 1827), these plates are absent (present study).

The family Philinidae has a worldwide distribution, occurring across all latitudes. The species inhabit soft substrates of mud and sand from shallow waters down to the deep sea (e.g. 2525 m; Rudman, 1972; Lancaster, 1983; Høisæter, 2010). They can live epifaunally but mostly burrow within the first 15 cm of sediment (Burn & Thompson, 1998) using their cephalic shield as a shovel (Trueman & Brown, 1992).

Philinidae are mostly carnivorous, feeding on foraminifera, small gastropods and bivalves, echinoids, polychaetes, crustaceans, fish remains, and there are even records of cannibalism (Burn & Thompson, 1998). Items like naviculate diatoms and remains of zooplankton have also been found in the gut contents of these snails (Lancaster, 1983). *Philine denticulata* (J. Adams, 1800) from Denmark may be herbivorous, as more plant material than foraminifera has been found in their guts (Horikoshi, 1967). Seager (1982) listed brittle stars, fish, sea stars, polychaetes, and other gastropods as possible predators of philinids and Stimpson (1850) found specimens of *Philine formosa* Stimpson, 1850 in the gut content of fish.

Philinid species in cold water, such as *Philine quadripartita* [= *Philine aperta* (Linnaeus, 1767)] and *P. gibba*, can reach four and three years of age, respectively and spawn more than once during their lifetime, with a spawning period from July to August in *P. quadripartita* and during May (Antarctic winter) in *P. gibba* (Brown, 1934; Lancaster, 1983). The species *P. quadripartita* in Great Britain spawns during July to August and this is strongly correlated with water temperature (as *P. aperta*, Lancaster, 1983). *Philine denticulata* in Denmark spawns from May to August and has an annual life cycle with high mortality during autumn. The Antarctic species *P. gibba* spawns during May and June at the beginning of winter, induced by water temperature (Seager, 1979). In the latter species there are no free-swimming larvae because the animals stay within the protective egg capsules until metamorphosis about 120 days after spawning. It takes a further 90 days for the mantle to develop and enclose the shell. This species is thought to survive for two reproductive seasons (Seager, 1979, 1982).

In Philinidae the operculum is lost during metamorphosis of the veliger larvae and a black larval kidney is visible during the larval stages (Thorson, 1946) and sometimes in juveniles (present study; see Fig. 2A). Egg masses of philinids resemble gelatinous balloons connected to the substrate by a mucus thread (Horikoshi, 1967; Rudman, 1972; Seager, 1979; Hadfield & Switzer-Dunlap, 1984).

According to Rudman (1972, 1978), species of the family Philinidae evolved from primitive cylichnid snails, with increasing specialization of feeding mechanisms, such as loss of jaws, the rachidian tooth, and marginal teeth (in most species), and development in some species of calcareous gizzard plates with unequal shape and size (e.g. *P. aperta* and

P. quadripartita). This evolutionary scenario is only in part supported by molecular phylogenetic evidence (Bayesian and parsimony multilocus analyses; Malaquias *et al*., 2009), where Philinidae was retrieved as sister to Aglajidae, a family of predatory snails that have lost the gizzard, jaws, and largely the radula (Rudman, 1978). However, the relationship between the clade Philinidae–Aglajidae and Cylichnidae has remained unclear because the phylogenetic position of the latter was unstable in the various analyses. Moreover, the monophyly of Cylichnidae (with *Cylichna* and *Scaphander*) was not confirmed (Malaquias *et al*., 2009). The relationship between these two genera and their position in the Cephalaspidea tree-of-life are unanswered questions that have great implications for our understanding of the evolution of philinid snails.

Taxonomic history of Philinidae with emphasis on the Scandinavian species

The earliest Philinidae species described were in the genera *Bulla* Linnaeus, 1758, and *Lobaria* Müller, 1776; both names mostly used during the late 1700s (Linnaeus, 1767; Müller, 1784; Gmelin, 1791; Dillwyn, 1817). Lamarck (1801) created the genus *Bullaea*, which was used for about 50 years referring mostly to species now ascribed to *Philine* (e.g. *Philine catena*, *Philine pruinosa*, *Philine punctata*, and *Philine scabra*) (Clark, 1827; M. Sars, 1835; Philippi, 1836; MacGillivray, 1844; Philippi, 1844; Thorpe, 1844).

The family Philinidae in Scandinavia includes species that have been ascribed by recent authors to seven different genera: *Philine* Ascanius, 1772, *Laona* A. Adams, 1865, *Johania* Monterosato, 1884, *Philinorbis* Habe, 1950, *Rhinodiaphana* Lemche, 1967, *Retusophiline* Nordsieck, 1972, and *Praephiline* Chaban & Soldatenko, 2009 (Hansson, 1998; Chaban & Soldatenko, 2009; Høisæter, 2009). Ascanius (1772) described *Philine* (based on the species *P. quadripartita*) as animals having an oval and hyaline body, flat below and folded laterally upwards, with a shield-shaped shell. The genera names *Laona* (type species: *Laona zonata* A. Adams, 1865) and *Johania* [type species: *Johania retifera* (Forbes, 1844)] were introduced based on shell characters alone. *Laona* because of a decussate shell surface and a different shell shape (not specified by the author), and *Johania* because of a reticulate pumice-like layer covering the umbilicate external shell. No anatomical or morphological data were given to support the division. *Philinorbis* (type species: *Philinorbis teramachii* Habe, 1950) was introduced for a Japanese species. *Rhinodiaphana* was introduced [type species: *Rhinodiaphana ventricosa* (Jeffreys, 1867)] because of morphological and anatomical characters (shell, radula, and prostate). Nordsieck (1972), based on shell characters and the lobes of the cephalic shield, introduced the subgenus *Retusophiline* for *Philine lima*. *Praephiline* was introduced for *Philine finmarchica* M. Sars, 1859, based on differences between the gizzards and male reproductive systems of the latter species and *P. aperta*.

Thus, most authors have not recognized *Laona* and *Johania* as valid names (e.g. G. O. Sars, 1878; Friele, 1879; Kobelt, 1888; Friele & Grieg, 1901; Gordon, 1901; Gilman, 1909; Johnson, 1915; Dall, 1921; Thompson, 1988; Schiøtte, 1989; van der Linden, 1995; Høisæter, Sneli & Brattegard, 2001; Price, Gosliner & Valdés, 2011). Nevertheless, both names have been used and can even be found amongst recent literature (e.g. Hansson, 1998; García & Bertsch, 2009; Høisæter, 2009, 2010).

Pilsbry (1895), based on differences on the shell sculpture, in part supported the division of Philinidae into three genera, giving them the rank of sections. Lemche (1948), based also on shell sculpture, considered three 'groups' of Philinidae but did not attribute any taxonomic rank: *'(1) those without sculpture except slight lines of growth; (2) those with simple spiral striae on the shells; and (3) those showing some sort of catenoid sculpture.'* Lemche (1948) pointed out that a division into genera would warrant additional data on the anatomy and morphology of species to support a formal systematic arrangement.

Rudman (1972) found it unnecessary to separate *Philine* into several genera because no characters or phylogenetic hypotheses were known to support such division. Bouchet (1975) and van der Linden (1995) followed this view and considered *Philine* the only valid genus in the family.

Recent reviews of Scandinavian molluscs referred to eight to 13 species of Philinidae with total diversity amounting to 15 species (Table 1). In Scandinavia the Oslofjord (previously Christianiafjord) has received considerable attention since early times. Danielssen (1859) reported 16 species of cephalaspidean gastropods in seven genera for the area, including four species of *Philine*, and M. Sars (1870) compiled an inventory containing 16 cephalaspid species including six *Philine*, two of them [*Philine flexuosa* M. Sars, 1870 and *Philine vitrea* M. Sars, 1870 (as *Utriculopsis vitrea*)] new to science. M. Sars (1835) and Nordgaard (1913) studied the molluscs of the south-west coast of Norway (Vestlandet). The former author described the species *Philine granulosa* M. Sars, 1835 (as *Bullaea*), collected off Bergen, whereas the latter referred to the species *Philine quadripartita* (as *P. aperta*).

Tate (1880) differentiated between boreal and arctic species, listing four and six species of cephalaspids, respectively; *Philine quadrata* was included as boreal, *P. scabra* and *P. punctata* as arctic. G. O. Sars (1878)

Table 1. List of species of Philinidae cited for Scandinavia in selected key works

Species	Lemche (1948)	Thompson (1988)	Hansson (1998)	Høisæter *et al.* (2001)	Høisæter (2009)	Present study
Philine angulata Jeffreys, 1867	x	x	x	x	x	x
Philine catena (Montagu, 1803)	x	x	x	x	x	x
Philine confusa nom. nov.	As *Diaphana minuta*	–	As *Diaphana vitrea*	As *Utriculopsis vitrea*	As *Diaphana hiemalis*	x
Philine denticulata (Adams, 1800)	x	x	x	x	x	x
Philine finmarchica (M. Sars, 1859)	x	–	x	x	As *Laona*	x
***Philine indistincta* sp. nov.**	–	–	–	–	–	x
Philine infortunata Pilsbry, 1895	x	–	x	x	x	x
Philine lima (Brown, 1827)	x	–	x	x	x	x
***Philine grandioculi* sp. nov.**	–	–	–	–	–	x
Philine pruinosa (W. Clark, 1828)	x	x	x	Both *P. pruinosa* and *P. flexuosa*, not as synonym	As *Laona*, both *P. pruinosa* and *P. flexuosa*, not as synonym	x
Philine punctata (Adams, 1800)	x	x	x	x	x	x
Philine quadrata (Wood, 1839)	Both *P. quadrata* and *P. polaris*, not as synonym	x	x	x	x	x
Philine quadripartita Ascanius, 1772	As *Philine aperta*	As *P. aperta*	As *P. aperta*	As *P. aperta*	As *P. aperta*	x
Philine retifera (Forbes, 1844)	–	–	–	–	Only cf. as *Johania*	?x
Philine scabra (Müller, 1784)	x	x	x	x	x	x
Philine ventricosa (Jeffreys, 1867)	As *Philine ventrosa*	–	As *Rhinodiaphana*	As *Rhinodiaphana*	As *Rhinodiaphana*	x
Philine sp. 1	–	–	–	–	–	x
Philine sp. 2	–	–	–	–	–	x
Philine sp. 3	–	–	–	–	–	x

wrote a comprehensive summary of the molluscs of arctic Norway in which shells, morpho-anatomical details, ecology, and distribution of species were described in detail. This is still nowadays the chief work for the study of molluscs in the region. Twelve species of *Philine* were studied by the author, three of which were described as new to science, namely *Philine fragilis* G. O. Sars, 1878, *Philine cingulata* G. O. Sars, 1878, and *Philine velutinoides* G. O. Sars, 1878. The cephalaspids collected during the Norwegian North-Atlantic Expedition 1876–1878 were studied by Friele (1879, 1886) and Friele & Grieg (1901) with a total of 20 cephalaspids being mentioned, amongst them seven species of *Philine*. Knipowitsch (1902) wrote about the species found during the Russian expedition to Svalbard 1899–1900 where six cephalaspid species were found, including two species of *Philine*, one new to science (*Philine intermedia* Knipowitsch, 1902).

Müller (1776, 1784) created a list of species of animals for Denmark and Norway with very concise descriptions. The only cephalaspid gastropods included were *P. quadripartita* (as *Lobaria quadriloba* Müller, 1776) and *P. scabra* (as *Bulla*). A more extensive account of Scandinavian mollusc species was produced by Lovén (1847), referring to 18 species with short descriptions and distribution data (including a new species of *Philine*: *Philine scutulum* Lovén, 1847).

Lemche (1948) listed 63 species in 19 genera including 13 philinid species in his major revision of the North Atlantic Cephalaspidea. He stressed the fact that cephalaspideans encompass many species that are difficult to differentiate. As the variable shape of the shell has been the most commonly used character for discrimination between species, anatomical or morphological data have been largely ignored and in most cases soft parts are unknown. Despite his awareness, the author himself contributed little to change the *status quo* that has remained nearly unchanged until the present time.

More recently, Jensen & Knudsen (1995) referred to 17 species in seven genera of cephalaspids in Denmark, including seven *Philine* species. An annotated check-list of marine molluscs compiled by Høisæter (1986) contained 12 species of the genus *Philine* in Norwegian and surrounding waters. Høisæter, Brattegard & Sneli (1997) and Høisæter *et al*. (2001) listed, respectively, 29 and 30 species of cephalaspids in Norway, referring to a total of 13 *Philine* species, whereas Hansson (1998) mentioned the occurrence of 42 species of cephalaspids in 21 genera including 11 species of Philinidae for the whole of Scandinavia.

In an article on marine, benthic, shell-bearing gastropods along the Norwegian coast, Høisæter (2009) listed 35 species of cephalaspids in 17 genera including 13 *Philine* species. Here *Philine retifera* (as *Johania*) was cited for the first time for Norway but with uncertain taxonomic status. Later, the author recorded high abundances of *Philine finmarchica* M. Sars, 1859 (as *Laona*) along the Norwegian continental slope, making the family Philinidae the most abundant gastropod taxon in this ecological zone of the deep sea (Høisæter, 2010).

Recently, Price *et al*. (2011) demonstrated that the name *P. aperta*, a long-standing name for the largest and 'better known' eastern Atlantic species, refers in fact to an Indo-Pacific species, being the correct name for the European species *P. quadripartita* with the type locality in Norway (see Systematic results).

Aims

The study of the family Philinidae in Europe and particularly in Scandinavia is hampered by the lack of sound morphological, anatomical, and molecular data for most species. Shell characters have largely dominated the systematics of the group. This is a pervasive problem amongst shelled cephalaspids not only in Europe but also worldwide, leading to confusing taxonomy, enormous lists of available genera and species names, difficulties in establishing characters to separate between species and higher taxonomic categories, and ultimately in reconstructing phylogenetic relationships (discussed in Gosliner, 1991; Mikkelsen, 1996, 2002; Malaquias & Reid, 2008).

The aim of this work was to revise the systematics of the genera and species of the north-east Atlantic Philinidae, with emphasis on the Scandinavian Peninsula, by combining shell and morphoanatomical characters together with molecular phylogenetic inference. Synonyms, ecology, and geographical distributions are given for each species. A dichotomous key for species identification is provided.

MATERIAL AND METHODS

Sampling of taxa, synonymies, and geographical distributions

Specimens were obtained by fieldwork along the coast of Norway and from dry and wet collections housed at several European museums, namely the University Museum of Bergen, University of Bergen, Norway (ZMBN), Museum of Natural History and Archaeology, Norwegian University of Science and Technology, Trondheim, Norway (NTNU), Natural History Museum of Oslo, University of Oslo, Norway (ZMO), Swedish Museum of Natural History, Stockholm, Sweden (SMNH), Zoological Museum, University

of Copenhagen, Denmark (ZMUC), and Museum für Naturkunde, Berlin, Germany (ZMB). Type specimens were studied whenever they were possible to trace.

Fieldwork was undertaken along the coast of Norway from the Skagerrak Sea (between Norway and Denmark) and the Bergen area on the southwest coast. Samples were collected using a modified Rothlisberg & Pearcy epibenthic sampler (RP-sledge; Brattegard & Fosså, 1991). Sediment samples were transferred to trays with seawater and left untouched for a couple of hours. Specimens were sorted and separated to morphospecies under a dissecting microscope. They were fixed for DNA extraction by dumping them in absolute ethanol. For anatomical dissection, specimens were frozen in seawater overnight, defrosted, and preserved in absolute ethanol. This procedure keeps the body of the animal fully extended, easing the dissection and interpretation of anatomical characters.

The literature was extensively reviewed and we have attempted to ensure that all synonymies are given. Geographical distributions are based on examined material and reliable literature records.

Anatomical and scanning electron microscopy (SEM) work

Dorsal and ventral views of the whole specimen were taken with an automontage microscope camera (Leica M205 C). Shell (sh) height (H) was measured with a digital calliper. Shells were put in 10% bleach solution for up to 3 h and rinsed in distilled water to remove the tissue and periostracum and then photographed with an automontage system.

The cephalic shield was dorsally opened by axial incision. The digestive tract (from buccal mass to gizzard) and the male reproductive system were removed from the body cavity. The gizzard was cut longitudinally, the gizzard plates detached, cleaned in bleach for up to 30 min and drawn with a camera lucida in dorsal, ventral, and lateral views and photographed with an automontage system. A dorsal standard view of the male reproductive system was drawn.

The buccal mass was put in bleach for up to 1 h to disintegrate the tissue around the radula and rinsed in distilled water afterwards. Shells, gizzard plates, and radulae were mounted on SEM stubs with carbon sticky tabs and coated with gold-palladium after drying. SEM (Zeiss Supra 55VP) images were taken for the complete radula and details (as convenient), complete shell (dorsal and ventral views and close-ups of the surface and apex), and gizzard plates (dorsal and ventral views including close-ups of surface).

For *P. pruinosa* (Clark, 1827) and *Philine grandioculi* sp. nov., images of the radula were taken under a light microscope (LM) with an automontage camera (Leica DN6000B). Radulae were mounted on a slide with a cover slip using glycerine. SEM preparation was not possible because of the small size of radulae.

Molecular phylogenetic analyses

Pieces of the foot or mantle were cut off with tweezers. Whenever original fixation allowed, tissue was taken from the dissected specimens. In the case of very small specimens the shell was crushed and the whole animal used. Extraction methods were those of Williams, Reid & Littlewood (2003) and partial sequences of the mitochondrial gene cytochrome *c* oxidase subunit I (COI; *c.* 650 bp) were amplified according to the method described in Malaquias & Reid (2009). Successful PCRs were purified with Exo-Sap according to the protocol described in Carmona *et al*. (2011) and sequencing was conducted with BigDye terminator on an Automatic Sequencer 3730XL (Applied Biosystems).

The species *Scaphander lignarius* (GenBank DQ974663.1) was chosen as outgroup based on Malaquias *et al*. (2009) and Price *et al*. (2011). Sequences were assembled and edited with SEQUENCHER v. 4.10.1 (Gene Codes Corporation), aligned in Clustal_X (Thompson *et al*., 1997), and further optimized by eye in MacClade v. 4.06 (Maddison & Maddison, 2000). The best-fit evolutionary model [General Time Reversible model with invariant sites and gamma distribution (GTR + I + G)] (Table 2)

Table 2. Summary of data set with best-fit evolutionary model and estimated parameters

Parameter	COI
No. of specimens (ingroup)	27
No. of specimens (outgroup)	1
Included characters	709
No. of parsimony informative characters	245
Best-fit model	(GTR + I + G)
Frequency A	0.4119
Frequency C	0.1778
Frequency G	0.1519
Frequency T	0.2584
Gamma distribution shape parameter	0.5040
Proportion of invariable site	0.4574
Rate matrix [A–C]	6.7244
Rate matrix [A–G]	107.0636
Rate matrix [A–T]	8.5335
Rate matrix [C–G]	10.5560
Rate matrix [C–T]	57.5560
Rate matrix [G–T]	1.0000

COI, mitochondrial cytochrome *c* subunit I.

was determined in MODELTEST (v. 3.6) (Posada & Crandall, 1998) using the Akaike information criterion. MrBayes v. 3.1.2 (Ronquist, Huelsenbeck & Mark, 2005) was used for Bayesian inference analysis and to estimate node support (posterior probabilities) with three runs of 2 000 000 generations each. Convergence was checked in TRACER v. 1.5 (Rambaut & Drummond, 2003) and a burn-in of 10% (2000 trees) was decided. Parsimony analysis (using default settings), bootstrap support (500 replicates), uncorrected *p*-distances between all taxa, and level of saturation for first, second, and third codon positions (*p*-distances against transitions plus transversions) were calculated in PAUP* (Swofford, 2002).

Sequences were verified by both forward and reverse comparisons, and have been deposited in GenBank (JX944792–JX944813).

RESULTS

Systematic descriptions

Class Gastropoda Cuvier, 1795

Order Cephalaspidea Fischer, 1883

Family Philinidae Gray, 1827

Genus *Philine* Ascanius, 1772

Philine Ascanius, 1772: 331.

Lobaria O. F. Müller, 1776: 226; Gmelin, 1791: 3424.

Bullaea Lamarck, 1801: 63, in part; Clark, 1827: 337, 339; M. Sars, 1835: 73; Thorpe, 1844: 137, 138, 251; Wood, 1848: 180.

Johania Monterosato, 1884: 147; Høisæter, 1986: 16, Høisæter, 2009: 79.

Laona A. Adams, 1865: 324; Nordsieck, 1972: 21; Høisæter, 2009: 80; Høisæter, 2010.

Utriculopsis M. Sars, 1870: 177.

Hermania Monterosato, 1884: 147.

Ossiania Monterosato, 1884: 147.

Rhinodiaphana Lemche, 1967: 207–214; Høisæter, 2009: 78.

Retusophiline Nordsieck, 1972: 52 (as a subgenus).

Praephiline Chaban & Soldatenko, 2009: 205–211; Bouchet, 2011.

Diagnosis (based on north Atlantic species): Body flat, white or whitish translucent, sometimes small dots or patches of colour can be present; cephalic shield, parapodia, short foot, pallial lobe present; external seminal groove; in veligers and some adults larval kidney visible. Shell in almost all cases internal, thin, white to transparent, mostly flattened plate-like, but can be globose, aperture large, covering more than half of the shell; usually not umbilicated; if present, sculpture consisting of pits, fused pits, or reticulate ridges. Three gizzard plates often present, widest part in the mid-region, usually boat-shaped in lateral view; ventral surface sculptured dorsal surface sculptureless. Jaws absent; radula usually lacking central tooth; one usually denticulated inner lateral tooth, up to six smooth outer lateral teeth present (mostly two or fewer; can be absent). Male reproductive system simple with prostate and penial sheath, separate ejaculatory duct can be present, no accessory glands; penial papilla with variable shape.

Philine angulata J. G. Jeffreys, 1867 (Fig. 2A–F)

Philine angulata J. G. Jeffreys, 1867: 451; Pilsbry, 1895: 17, pl. 3, figs 41, 42; Kobelt, 1896: 155, pl. 19, figs 26, 27; Lemche, 1948: 67, fig. 75; van der Linden, 1994: 43, figs 8, 13, 14; Moreno & Templado, 1998, 1998: 44, fig. 2. (see Warén, 1980: 35, for location of type material).

?*Ossiania angulata* – Moore, 1937; Winkworth, 1932 (based on Lemche, 1948).

Philinorbis angulata – Nordsieck, 1972: 22.

Diagnosis: Shell internal, white, upper outer lip flattened and keeled, outer keel ending in wing-like protrusion, with sculpture of mostly fused pits arranged in transverse lines. Body creamy orange with small black dots. Rachidian tooth absent, one inner lateral, two outer lateral teeth. Gizzard with plates.

Type locality: Not specified (somewhere along the north coasts of the UK; see Remarks).

Material examined: Ålesund, Norway, one sh, ZMO D4347, H = 2.1 mm. Kjosen, Tromsø, Norway, one sh fragment, ZMO D33769, H = 2.3 mm. Gullmarn, Sweden, two specimens (spcs), ZMK unnumbered, H = 0.9, 1.2 mm. Gullmarn, Sweden, one spc, ZMK unnumbered, H = ?.

Shell (Fig. 2D–F): Maximum H = 2.3 mm. Thin; white; squarish-oval in shape, aperture wide with thin parietal callus, upper outer lip flattened and keeled, outer keel ending in wing-like protrusion, five rows of spiral striae between the keels, apex obtuse, not umbilicated; sculpture consisting of transverse lines of pits mostly, but not always connected to form chains or grooves.

Animal (Fig. 2A–C): Body with small black dots, mantle thin. Cephalic shield blunt, median groove absent.

Radula: Lemche (1948) gave the radular formula $16 \times 2.1.0.1.2$; shaped as in *P. punctata*.

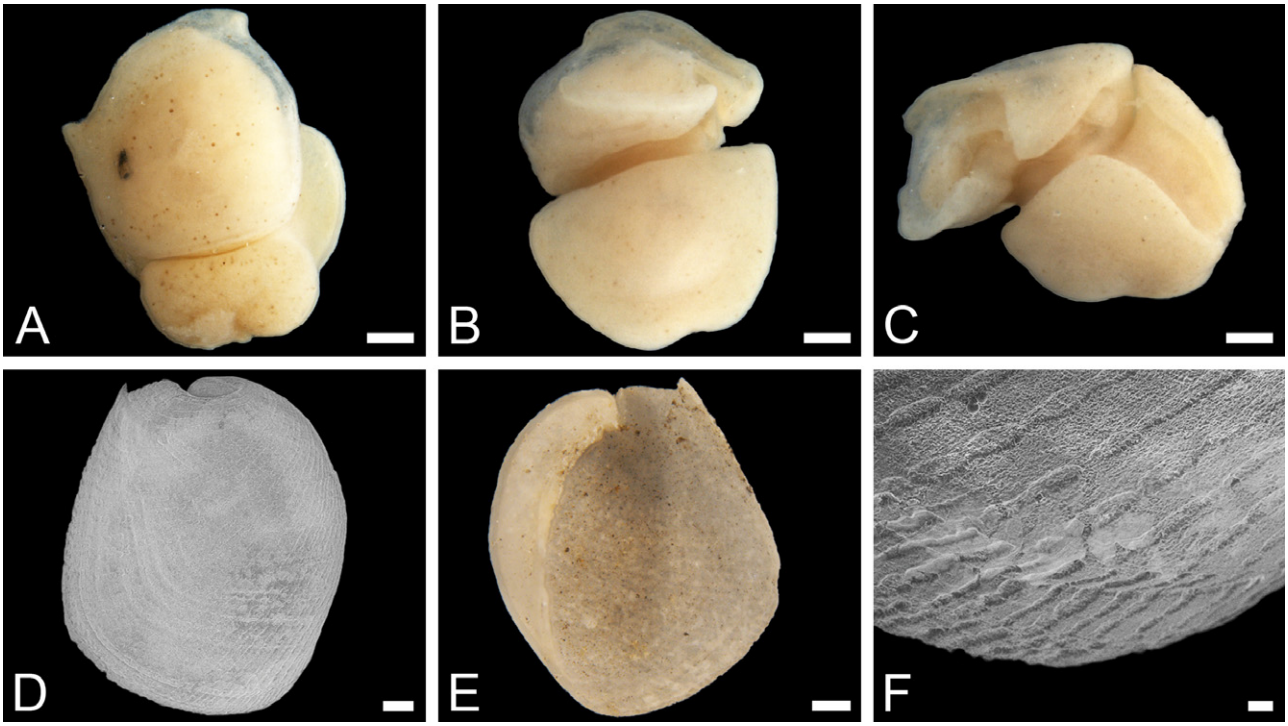

Figure 2. *Philine angulata*. A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (scanning electron micrograph, SEM). E, ventral view of shell (automontage picture). F, sculpture on dorsal surface of shell (SEM). Scale bars: A–C, E = 250 μm; D = 200 μm; F = 30 μm.

Gizzard: Lemche (1948) found the gizzard plates to be identical to those of *P. punctata*.

Male reproductive system: Unknown.

Ecology: Occurs at depths down to 160 m (Thompson, 1988) on sand, fine shell sand, and mud (Høisæter, 2009) as well as coarse sand and shell-gravel (Sneli *et al*., 2005). Moreno & Templado (1998) found it on coarse sand at 15 m depth.

Distribution: North-east coast of the USA, the Faeroes, Shetlands, British Isles, and Norway south of Tromsø (J. G. Jeffreys, 1867; Thompson, 1988; Høisæter *et al*., 2001; Sneli *et al*., 2005; present study). Also present in the Mediterranean Sea (Thompson, 1988), off Mauretania, and south of Lanzarote, Canary Islands (van der Linden, 1995).

Remarks: Amongst Scandinavian philinids *P. angulata* is the only species with a wing-like protrusion of the shell's outer lip making this species easily recognizable. Lemche (1948) found *P. angulata*, apart from some small shell differences, to be almost identical to *P. punctata*, and wondered whether they are really two species or if it could be a case of sexual dimorphism. However, this would not explain the putative differences because these snails are hermaphroditic. J. G. Jeffreys (1867) as well as Lemche (1948) described the sculpture of the shell as punctuate; however, specimens examined by van der Linden (1994), Moreno & Templado (1998), and the present study showed the pits to be fused in most parts of the shell, forming grooves. J. G. Jeffreys (1867) did not specify the type locality of the species but referred to specimens from Larne, Antrim (north-east Northern Ireland), Aberdeenshire (north-east Scotland), the Hebrides, and the Shetland Islands.

Philine catena (Montagu, 1803)

Bulla catena Montagu, 1803: 215, pl. 7, fig. 7; Dillwyn, 1817: 478; Brown, 1827: pl. 38, figs 33, 34; A. Adams, 1855: 601, pl. 125, fig. 163.

Bullaea catena – Clark, 1827: 337; MacGillivray, 1844: 187; Alder, 1848: 24.

Philine catena – J. G. Jeffreys, 1867: 449; G. O. Sars, 1878: 294, pl. 26, fig. 6, pl. XII, fig. 6; Pilsbry, 1895: 13, pl. 4, fig. 64, pl. 5, figs 23–25; Thompson, 1988: 58, fig. 20; Gaglini, 1991: 12; Malaquias, Martínez & Abreu, 2002: 71, fig. 3B.

? *Hermania catena* – Fisher, 1935, Moore, 1937 (based on Lemche, 1948).

Philine (Hermania) catena – Nordsieck, 1972: 19, pl. OIII, fig. 3.

Bullaea catenata – Thorpe, 1844: 138.
Philine catenata– Locard 1886: 82.
Bulla catina Brown, 1844: 57, pl. 19, figs 33, 34.
Bullaea angustata Philippi, 1836: 121, pl. 7, fig. 17a–d. Pilsbry, 1895: 13, 14. Lemche, 1948: 93.
Philine angustata – Locard, 1886: 82.
Bullaea sculpta Wood, 1848: 180, pl. 21, fig. 10.

Diagnosis: Shell internal, pellucid white with chain-like sculpture in transverse lines. Body cream or pale brown with small brown dots. Rachidian tooth absent, one rounded inner lateral tooth with denticulation along inner edge, one rounded outer lateral tooth. Gizzard contains three equal angular pointed gizzard plates. Feather duster-shaped prostate emerging from sack-like penial sheath.

Type locality: Bigberry Bay, south coast of Devon, England, UK.

Material examined: None.

Shell: Internal, thin; pellucid white; squarish-oval in shape, aperture wide, apex obtuse, slightly sunken, slightly umbilicated; sculpture consisting of transverse lines of pits connected by narrow grooves to form chains (Clark, 1827).

Animal: Body cream or pale brown with small brown dots on dorsal surface. Cephalic shield blunt, median groove absent (Thompson, 1988).

Radula: Radular formula *c.* 30 × 1.1.0.1.1 (Lemche, 1948). Rachidian tooth absent. Inner lateral teeth with broad base, curved and rounded tips, inner edge denticulate. Outer lateral teeth with narrow base, straight and rounded tip (G. O. Sars, 1878).

Gizzard: Contains three equal angular plates, which are sharply pointed at the ends (Clark, 1827).

Male reproductive system: A figure in Thompson (1976) shows a sack-like penial sheath with a prostate shaped like a feather duster.

Ecology: From pools at lowest low tide (Clark, 1827) and under boulders on beaches down to 2000 m (Thompson, 1988). Clark (1827) reported it from fine sand, MacGillivray (1844) found it on the beach and on sea anemones and sea squirts. Thompson (1988) mentioned that *P. catena* can be predated by flatfish.

Distribution: From Lofoten southwards along the entire coast of Norway (Høisæter *et al*., 2001), down to the British Isles, Mediterranean Sea, and Canaries (Nordsieck, 1972).

Remarks: Specimens of this species were not available for study. The species is, apart from the coloration, similar to *P. scabra* but the shell is broader and has a smooth margin, with conspicuously different sculpture consisting of elongated rather than rounded pits as in *P. scabra*. The radula has the same formula but differs greatly in the number of rows, with *P. scabra* having fewer than 20 and *P. catena* about 30 (Lemche, 1948). A groove on the cephalic shield was not mentioned in *P. catena*. Montagu (1803) listed *P. punctata* as synonym of *P. catena*, but the former species has a different shell sculpture and is here not considered a valid synonym of *P. catena*. It is not entirely clear whether the name *Bullaea* (= *Philine*) *angustata* was introduced by Bivona or Philippi. It seems that Philippi described this species based on material collected (and eventually informally named) by Bivona (see Philippi, 1836: 121; Pilsbry, 1895: 13; Lemche, 1948: 93).

PHILINE CONFUSA NOMEN NOVUM (FIG. 3A–F)

?*Philine laevissima* M. Sars, 1859: 85.
?*Bulla vitrea* – M. Sars, 1865: 197.
Utriculopsis vitrea M. Sars, 1870: 177, pl. 11, fig. 15 (neotype here selected ZMBN 88007).
?*Diaphana globosa* – G. O. Sars, 1878: 290, pl. 18, figs 3c, 4.

Diagnosis: Shell partly external, transparent, smooth. Body white, foot large, larval kidney not visible. Gizzard not surrounded by muscle fibres, contains no plates. Obvious separation between short, broad, prostate and tubular penial sheath. COI sequence: GenBank JX944804 (ZMBN 87081).

Type locality: Hauglandsosen, Norway.

Material examined: Hauglandsosen, Norway, two spcs (dissected and one sequenced), ZMBN 87081, H = 2.4, 2.6 mm. Hauglandsosen, Norway, one spc (examined), ZMBN 88007, H = 2.5 mm, neotype.

Etymology: The name comes from the very complex nomenclatural history of this species.

Shell (Fig. 3D, E): Maximum H = 2.6 mm. Partly external, thin; transparent; globose, aperture wide; smooth.

Animal (Fig. 3A–C): Body white. Cephalic shield tapering posteriorly, median groove absent. Foot large, reaching beyond the shell, undivided. Larval kidney not visible through shell.

Radula: Radular formula ?? × 3.1.?.1.3.

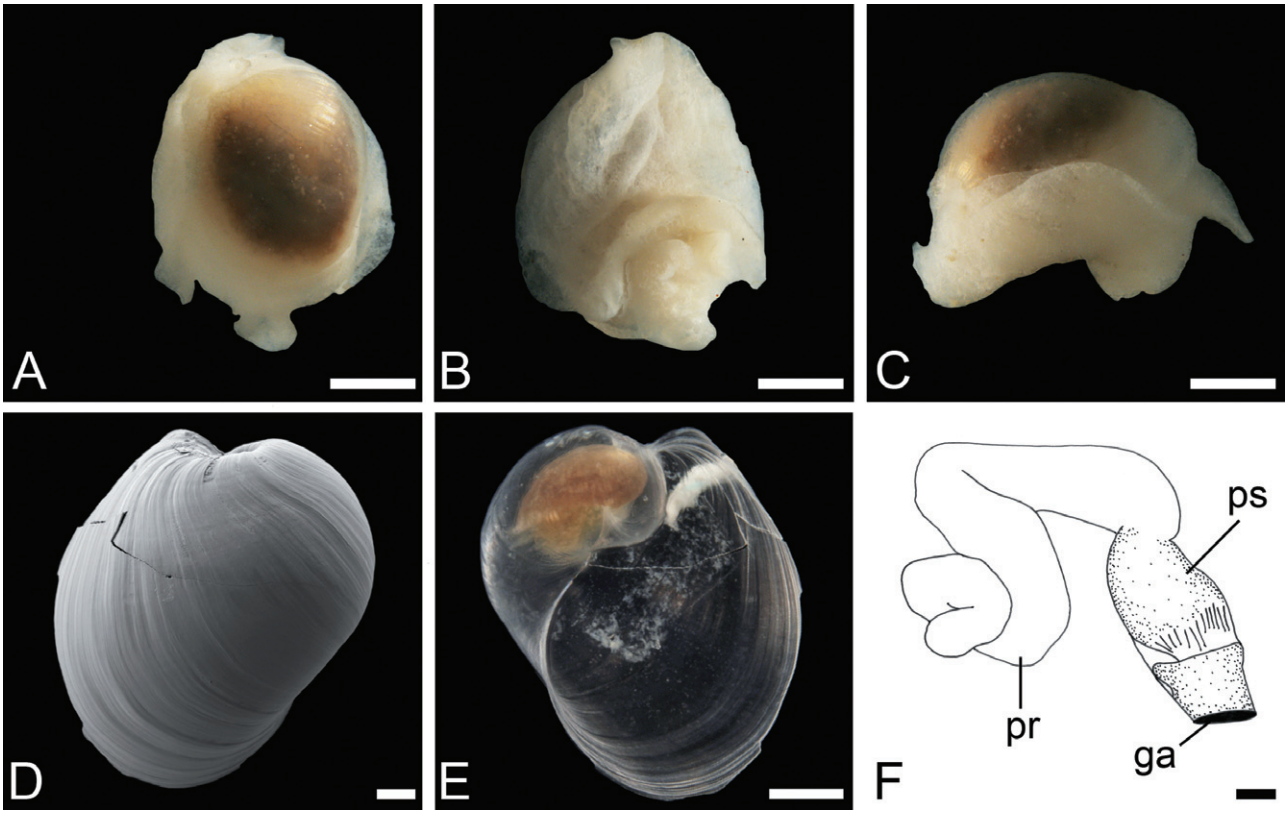

Figure 3. *Philine confusa*. A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (scanning electron micrograph). E, ventral view of shell (automontage picture). F, male reproductive system (drawing). Abbreviations: ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A–C, E = 0.5 mm; D = 200 μm; F = 100 μm.

Gizzard: Gizzard globose, not surrounded by muscle fibres, no plates.

Male reproductive system (Fig. 3F): Obvious separation between short, broad, prostate and tubular penial sheath.

Ecology: Between 55 and 219 m (M. Sars, 1870).

Distribution: Only known from Norway: Lofoten, the Oslofjord, and the Bergen area (M. Sars, 1865; present study).

Remarks: Extensive confusion surrounds the names *Philine vitrea*/*Philine infortunata* Pilsbry, 1895. M. Sars (1859) described vaguely the species *Philine laevissima* from a single shell without providing an illustration and no types are available. Later, M. Sars (1865) claimed to have found complete animals of this species in the Oslofjord and transferred it to the genus *Bulla*, renaming it *Bulla vitrea* because the name *Bulla laevissima* was already occupied by *B. laevissima* Bellardi, 1854 (Schiøtte, 1998). Five years later, M. Sars (1870) described *Utriculopsis vitrea* as a new genus and species, considering his *P. laevissima* to be a senior synonym.

Utriculopsis vitrea was described having an external and globose shell (M. Sars, 1870; 65–68, pl. 11, figs 15–18), which resembles more a shell of a *Diaphana* rather than a typical philinid shell. This apparently led G. O. Sars (1878) to consider that *U. vitrea* was described based on specimens from two different species. He ascribed the shells to *Diaphana globosa* (Lovén, 1846) (G. O. Sars, 1878: 290) and the animals to *U. vitrea*, which he reassigned to the genus *Philine* (G. O. Sars, 1878: 298). He considered a shell collected by himself at Lofoten in northern Norway to typify the shell of M. Sars's *P. vitrea* (G. O Sars, 1878: 298, pl. 26, fig. 8).

Pilsbry (1895) attributed authorship of *P. vitrea* to G. O. Sars and replaced the name with *P. infortunata* because the former was already occupied by *P. vitrea* Gould, 1859. Pilsbry (1895: 23) also referred to an undescribed species of Monterosato-labelled *P. vitrea* collected at 90 m deep in Palermo, Italy

(Mediterranean Sea). However, this latter species was never formally described by Monterosato.

The material here studied shows that the species *U. vitrea* as described by M. Sars (1870) exists and belongs in the genus *Philine*. Moreover, G. O. Sars's concept of *P. vitrea* (= *P. infortunata* Pilsbry, 1895) refers to a different and likely valid species (see Remarks of *P. infortunata*).

Therefore, we introduce the replacement name *Philine confusa* for *U. vitrea* M. Sars, 1870 and designate a neotype to promote taxonomic stability.

PHILINE DENTICULATA (J. ADAMS, 1800) (FIGS 4A–I, 5A–C)

Bulla denticulata J. Adams, 1800: 1, pl. 1, figs 3–5.

?*Voluta denticulata* – Laskey, 1811 (based on Lemche, 1948).

Philine denticulata – Horikoshi, 1967; Platts, 1985: 153; Thompson, 1988: 56, fig. 19c, d; Dantart, Frechilla, Ballesteros, 1990: 120, figs 2.8, 3.2; Høisæter *et al*., 2001: 254.

Philine sinuata – G. O. Sars, 1878: 298 pl. 26, fig. 9, pl. 12, fig. 9; Kobelt, 1896: 142, pl. 18, figs 14, 15.

Philinorbis sinuata – Nordsieck, 1972: 23, pl. OIII, fig. 14.

Philine nitida J. G. Jeffreys, 1867: 456, 457; Pilsbry, 1895: 18, pl. 4, figs 79–81; Kobelt, 1896: 157, pl. 19, figs 30, 31.

Diagnosis: Shell external, whitish to transparent, squarish-oval in shape, small spines at end of keels on upper outer lip, apex protruding, shell surface smooth. Body yellowish with brown dots, mantle forming a frill at the posterior end of the shell. Rachidian tooth absent, one rounded inner lateral tooth with denticulate inner edge, one rounded outer lateral tooth. Gizzard not surrounded by muscle fibres, without gizzard plates. Short, thick, flattened prostate emerging from tubular penial sheath.

Type locality: The Wash, England, UK.

Material examined: Silavågen, Norway, six spcs (dissected), ZMBN 82073, H = 1.0–1.5 mm, soft bottom, mud-like. Southport, England, UK, one sh, ZMBN 22169, H = 1.0 mm. Barmanfjorden, Norway, one spc (dissected), NTNU 65953, H = 1.0 mm.

Shell (Fig 4D–H): Maximum H = 1.5 mm. External, thin; whitish to transparent; squarish-oval in shape, aperture wide with thin transparent parietal callus, outer lip completely smooth, upper outer lip usually flattened with two small spines at the end of the keels, apex protruding, slightly umbilicated; shell surface smooth.

Animal (Fig. 4A–C): Body yellowish with small brown dots, mantle not covering the shell in most parts but forming a frill at the posterior end of shell. Cephalic shield tapering posteriorly, median groove absent. Larval kidney visible through shell. Salivary glands slightly longer than buccal mass.

Radula (Fig. 5A–C): Radular formula $12 \times 1.1.0.1.1$. Rachidian tooth absent. Inner lateral teeth with broad base, curved and rounded tips, inner edge denticulate. Outer lateral teeth with broad base, curved and rounded tip.

Gizzard: Gizzard globose, not surrounded by muscle fibres, no plates.

Male reproductive system (Fig. 4I): Short, thick, flattened prostate with longitudinal folds emerging from tubular penial sheath.

Ecology: The species is found on sand (J. Adams, 1800; Høisæter, 2009), shell-gravel, mud (Sneli *et al*., 2005), and on silty sand where it can occur at very high densities (Horikoshi, 1967). It inhabits shallow subtidal waters but was found once in the intertidal zone (Thompson, 1988). According to Horikoshi (1967), the species has an annual life cycle, spawning from May to August. The spawn consists of globular gelatinous masses with the eggs (Thorson, 1946, misidentified as *P. punctata*). The species might be herbivorous because it lacks gizzard plates and only two of 2555 animals examined had eaten foraminifera whereas large amounts of plant material was found in the snails (Horikoshi, 1967).

Distribution: Norway from Ullsfjord (69°35′N) southwards to Møre and Romsdal (62°10′N) (Høisæter, 2009). The Faeroe Islands (Sneli *et al*., 2005), Denmark, British Isles including Shetland, and the Mediterranean Sea (Horikoshi, 1967).

Remarks: J. G. Jeffreys (1867) concluded that the shell of this species is internal because one of his specimens had the mantle still attached to the spire of the animal's shell and the remaining parts were torn off. However, Horikoshi (1967) stated otherwise and during the present work it was confirmed that the shell is external. The keels of the shell can be very faint and rounded without small spines (Thompson, 1988; present study). *Philine sinuata* Stimpson, 1850 is often regarded as a synonym of *P. denticulata* (e.g. G. O. Sars, 1878) but, as J. G. Jeffreys (1867) pointed out, they are different species. This was confirmed by Franz & Clark (1969) who after studying US specimens from nearby the type locality (Boston harbour)

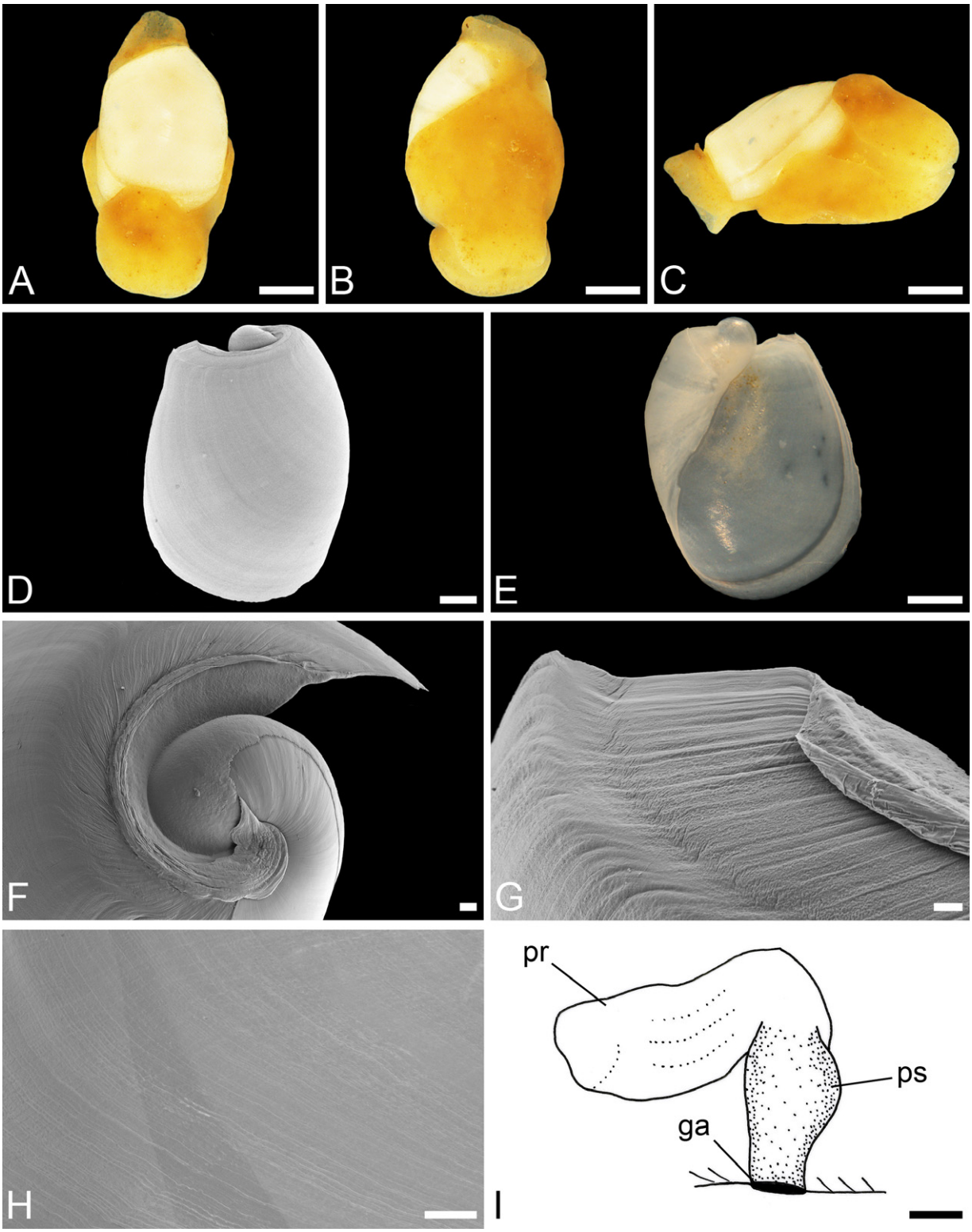

Figure 4. *Philine denticulata*. A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (scanning electron micrograph, SEM). E, ventral view of shell (automontage picture). F, apical view of shell (SEM). G, detail of keels (SEM). H, dorsal surface of shell (SEM). I, male reproductive system (drawing). Abbreviations: ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A–C = 0.5 mm; D = 200 μm; E = 250 μm; F = 20 μm; G = 10 μm; H = 30 μm; I = 100 μm.

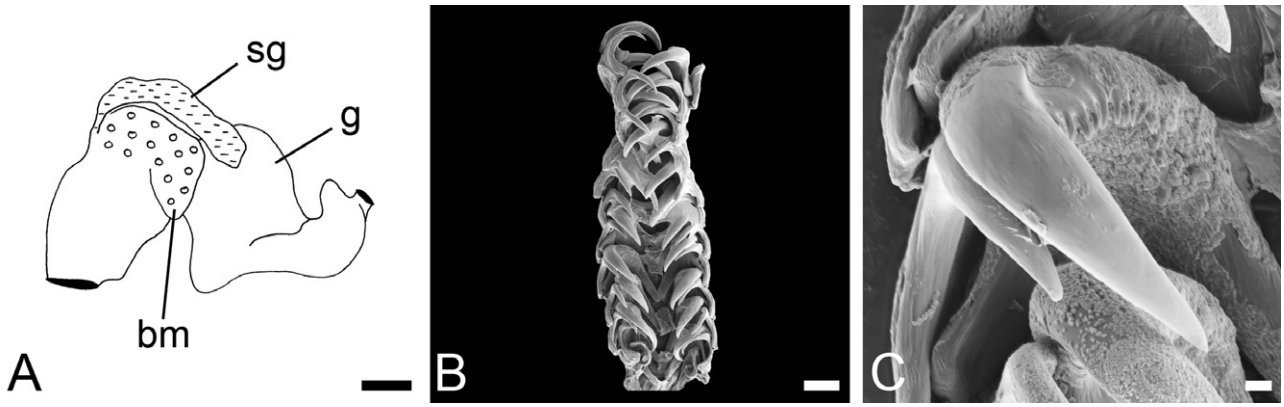

Figure 5. *Philine denticulata*. A, buccal mass (bm), salivary gland (sg), and gizzard (g). B, radula (scanning electron micrograph, SEM). C, detail of radula (SEM). Scale bars: A = 125 μm; B = 20 μm; C = 2 μm.

found *P. sinuata* to have an internal shell and a radula formula of 2.1.0.1.2.

Philine finmarchica M. Sars, 1859 (Figs 6A–I, 7A–H, 8A–H, 9A–D)

Philine finmarchica M. Sars, 1859: 49; G. O. Sars, 1878: 296, pl. 18, fig. 10, pl. 12, fig. 1; Pilsbry, 1895: 14, pl. 5, figs 17–19; Kobelt, 1896: 150, pl. 19, figs 13, 14; Friele & Grieg, 1901: 114; Lemche, 1948: 65, 96; Marcus & Marcus, 1969: 10, figs 13–16; Kantor & Sysoev, 2006: 256, pl. 127, figs A, B. (lectotype here selected: ZMO D1740).

Laona finmarchica – Nordsieck, 1972: 21, pl. OIII, fig. 9 (with question mark).

Praephiline finmarchica–Chaban & Soldatenko, 2009: 205–211, fig. 1c, e, f; fig. 2b, e. syn. nov.

Philine ossian-sarsi Friele, 1877: 9, fig. 19; Friele & Grieg, 1901: 114 (type seen: ZMBN 17193).

Philine ossiansarsi – Pilsbry, 1895: 14, frontispiece, figs 19–22; Nordsieck, 1972: 20, pl. OIII, fig. 7.

Philine cingulata G. O. Sars, 1878: 297, pl. 26, fig. 7, pl. 12, fig. 3; Pilsbry, 1895: 15, pl. 5, figs 4–6; Kobelt, 1896: 140, pl. 18, figs 10, 11 (type seen: ZMO D1743).

Laona (Ossiania) cingulata – Nordsieck, 1972: 21, pl. OIII, fig 11.

Philine fragilis G. O. Sars, 1878: 296, pl. 18, fig. 11, pl. 12, fig. 2; Pilsbry, 1895: 15, pl. 5, figs 20–22; Kobelt, 1896: 152, pl. 19, figs 19, 20; Friele & Grieg, 1901: 114; Odhner, 1915: 231. (type seen: ZMO D1738).

Laona fragilis – Nordsieck, 1972: 21, pl. OIII, fig. 10. syn. nov.

Philine ossiani Kobelt, 1896: 161. syn. nov.

Philine intermedia Knipowitsch, 1902: 54, pl. 19, figs 34, 35. syn. nov.

Diagnosis: Shell internal, white, with sculpture of fused pits arranged in transverse lines. Body completely white, larval kidney not visible. Rachidian tooth absent, one flattened inner lateral tooth with denticulation along inner edge. Gizzard surrounded by muscle fibres, contains three equal, spindle-shaped gizzard plates. Long, thin, convoluted, nodulose prostate emerging from sack-like penial sheath, which tapers towards genital aperture, separate ejaculatory duct. COI sequence: GenBank JX944799 (ZMBN 102288).

Type locality: Finnmark, Norway (likely to be Vadsø).

Material examined: 63°10′N, 04°49′E, off Ålesund, Norway, one spc (dissected), ZMBM 85971, H = 6.4 mm. 62°29.2′N, 01°44.5′E, off Ålesund, Norway, one spc (dissected), ZMBN 85973, H = 5.6 mm. 62°42.4′N, 01°11.2′E, off Ålesund, two spcs (dissected), ZMBN 85987, 4.8, 5.5 mm. 69°01.4′N, 08°24.6′W, south off Jan Mayen, one spc (dissected), ZMBN 85991, H = 8.8 mm. 69°58.1′N, 12°34.0′E, north off Lofoten, one spc (dissected), ZMBN 86000, H = 3.2 mm. Svalbard, Norway, one spc (dissected), ZMBN 8612, H = 8.0 mm. 71°42′N, 37°01′E, Barents Sea, two spcs (dissected), ZMBN 8613, H = 4.9, 8.6 mm. 72°27′N, 35°01′E, Barents Sea, two spcs (dissected), ZMBN 8622, H = 9.1, 9.5 mm. Skjerstadfjorden, Norway, four spcs (dissected), ZMBN 12570, H = 9.3–10.9 mm. Finnmark, Norway, nine spcs (dissected; one sequenced), ZMBN 102288, H = 5.6–6.8 mm. 62°56.9′N, 07°00.1′E, north of Faroe Islands, one spc (dissected), NTNU 62348, H = 4.5 mm. 62°56.9′N, 07°00.1′E, north of Faroe Islands, one spc (dissected), NTNU 62349, H = 6.2 mm. Vadsø, Norway, one sh, ZMO D1740, H = 7.0 mm. Tromsø and Vadsø, Norway, one spc, ZMO D15768, H = 7.1 mm. Tromsø, Norway, six spcs, ZMO D1739, H = 4.8–6.6 mm. Lofoten, Norway, one sh., ZMO D1743, H = 2.5 mm. Unknown locality, one sh, ZMO D1738, H = 10.9 mm. Norske Nordhavsexpedition (St. 18), one sh. ZMBN 17193, H = ? (shell damaged).

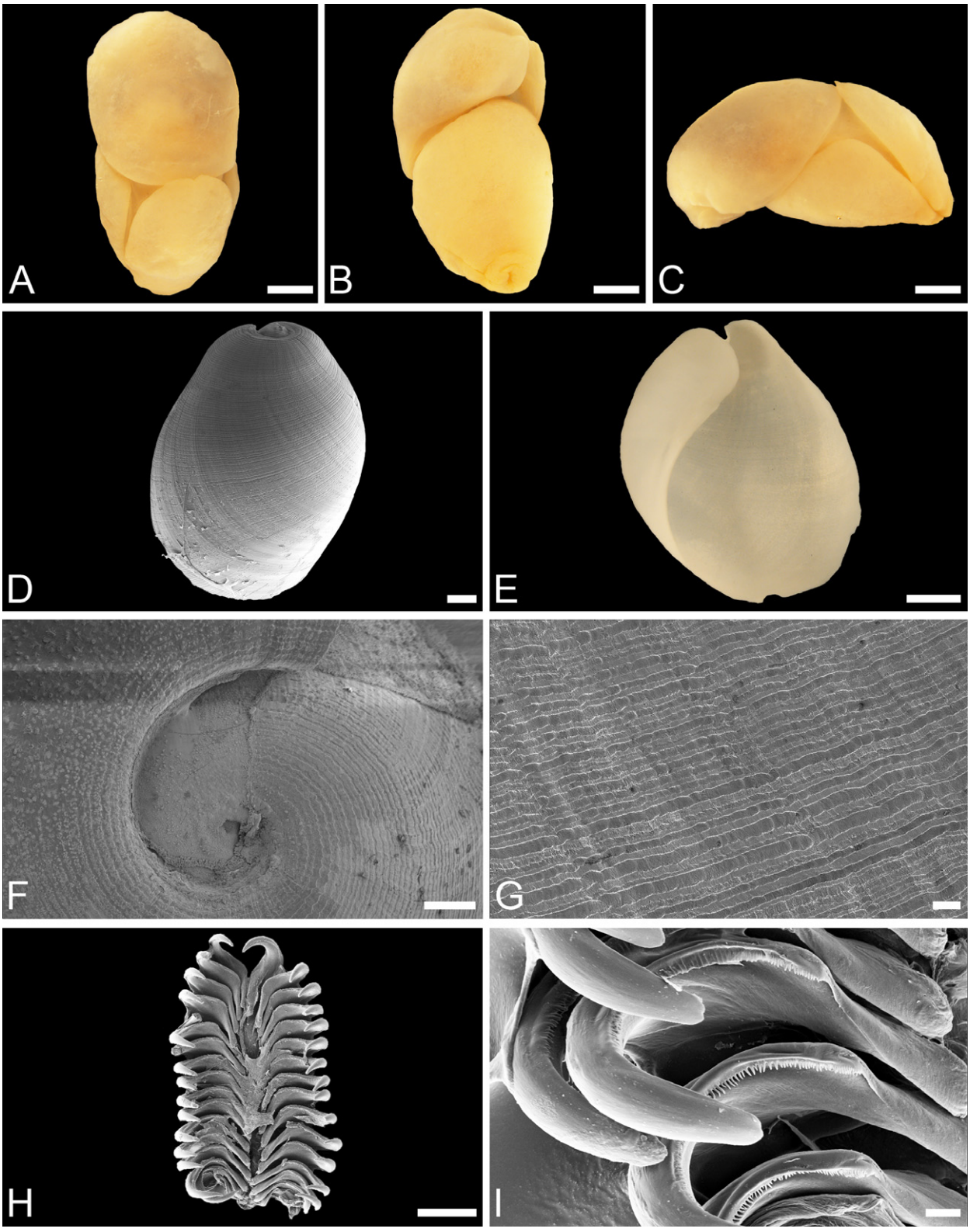

Figure 6. *Philine finmarchica*. A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (scanning electron micrograph, SEM). E, ventral view of shell (automontage picture). F, apex of shell (SEM). G, sculpture on dorsal surface of shell (SEM). H, radula (SEM). I, detail of radula (SEM). Scale bars: A–C = 250 μm; D = 0.5 mm; E = 1 mm; F, H = 200 μm; G = 50 μm; I = 20 μm.

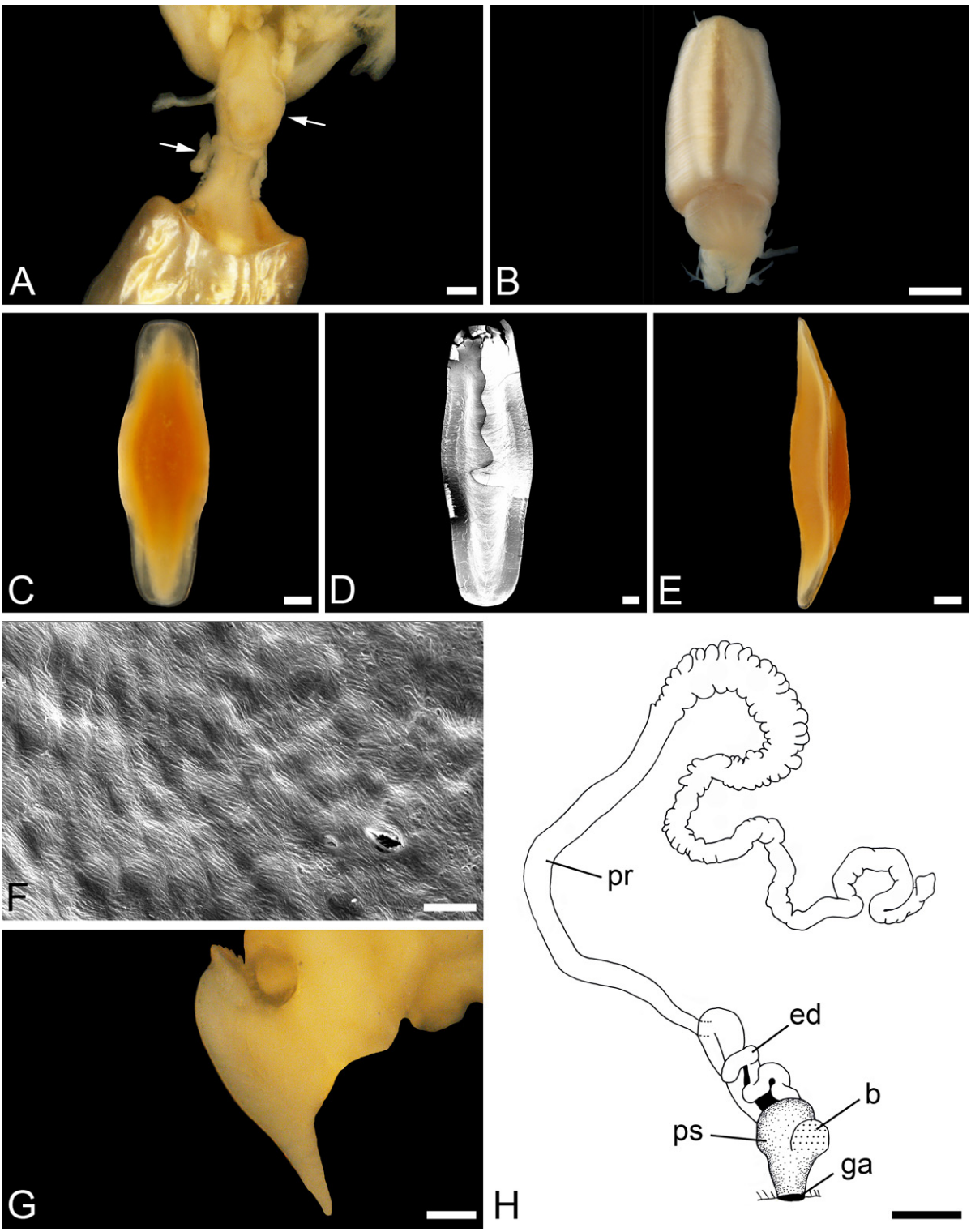

Figure 7. *Philine finmarchica*. A, buccal mass (right arrow) and salivary glands (left arrow). B, gizzard (automontage picture). C, dorsal view of gizzard plate (automontage picture). D, ventral view of gizzard plate (scanning electron micrograph, SEM). E, lateral view of gizzard plate (automontage picture). F, ventral surface of gizzard plate (SEM). G, penial papilla (automontage picture). H, male reproductive system (drawing). Abbreviations: b, bulb; ed, ejaculatory duct; ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A, C, E = 0.5 mm; B, H = 1 mm; D = 200 μm; F = 10 μm; G = 250 μm.

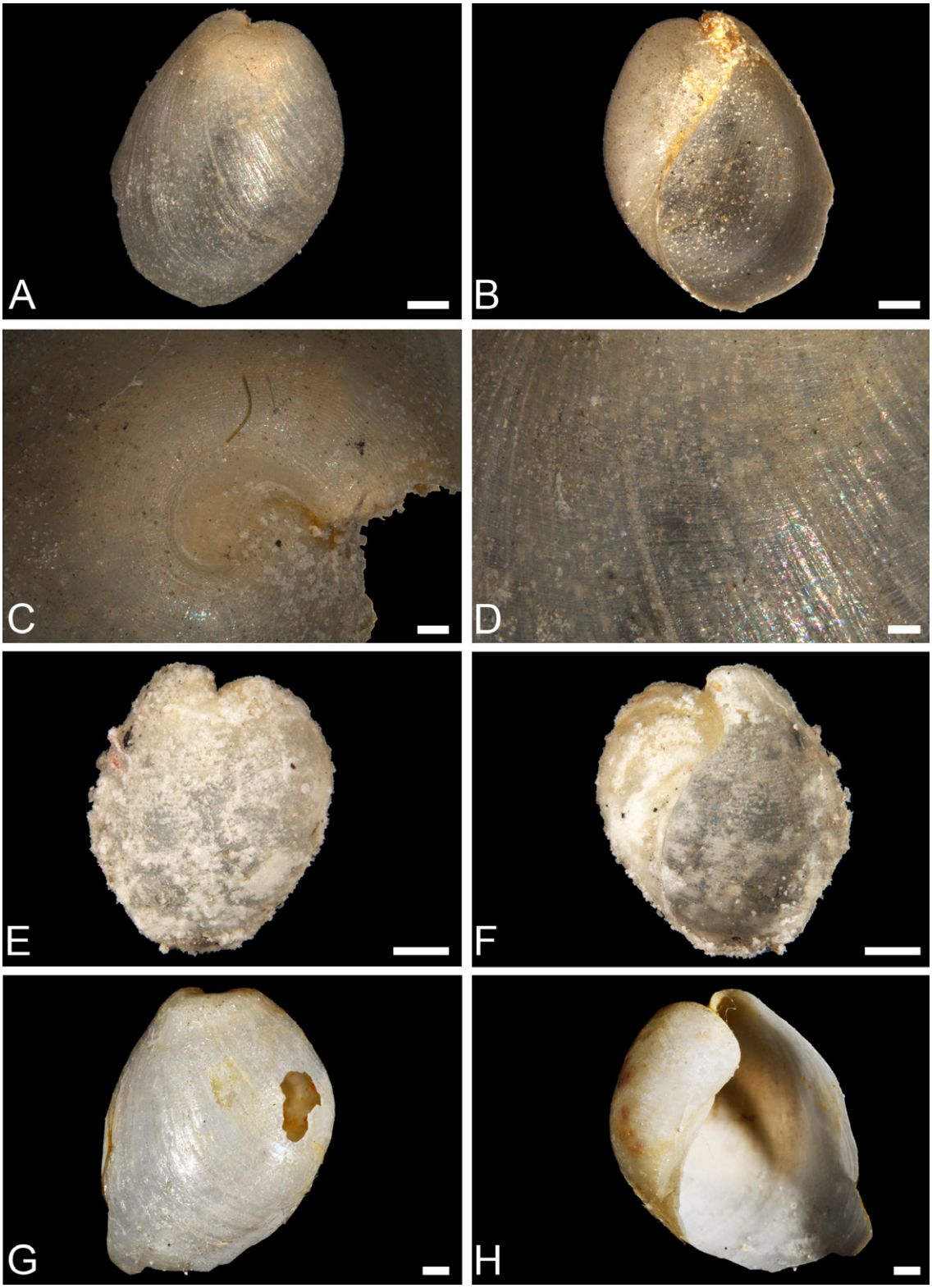

Figure 8. A–D, *Philine finmarchica*, lectotype, ZMO D1740. A, dorsal view of shell. B, ventral view of shell. C, apex of shell. D, sculpture on dorsal surface of shell. E, F, *Philine cingulata*, type specimen, ZMO D1743. E, dorsal view of shell. F, ventral view of shell. G, H, *Philine fragilis*, type specimen, ZMO D1738. G, dorsal view of shell. H, ventral view of shell. Scale bars: A, B, G, H = 1 mm; C, D = 250 μm; E, F = 0.5 mm.

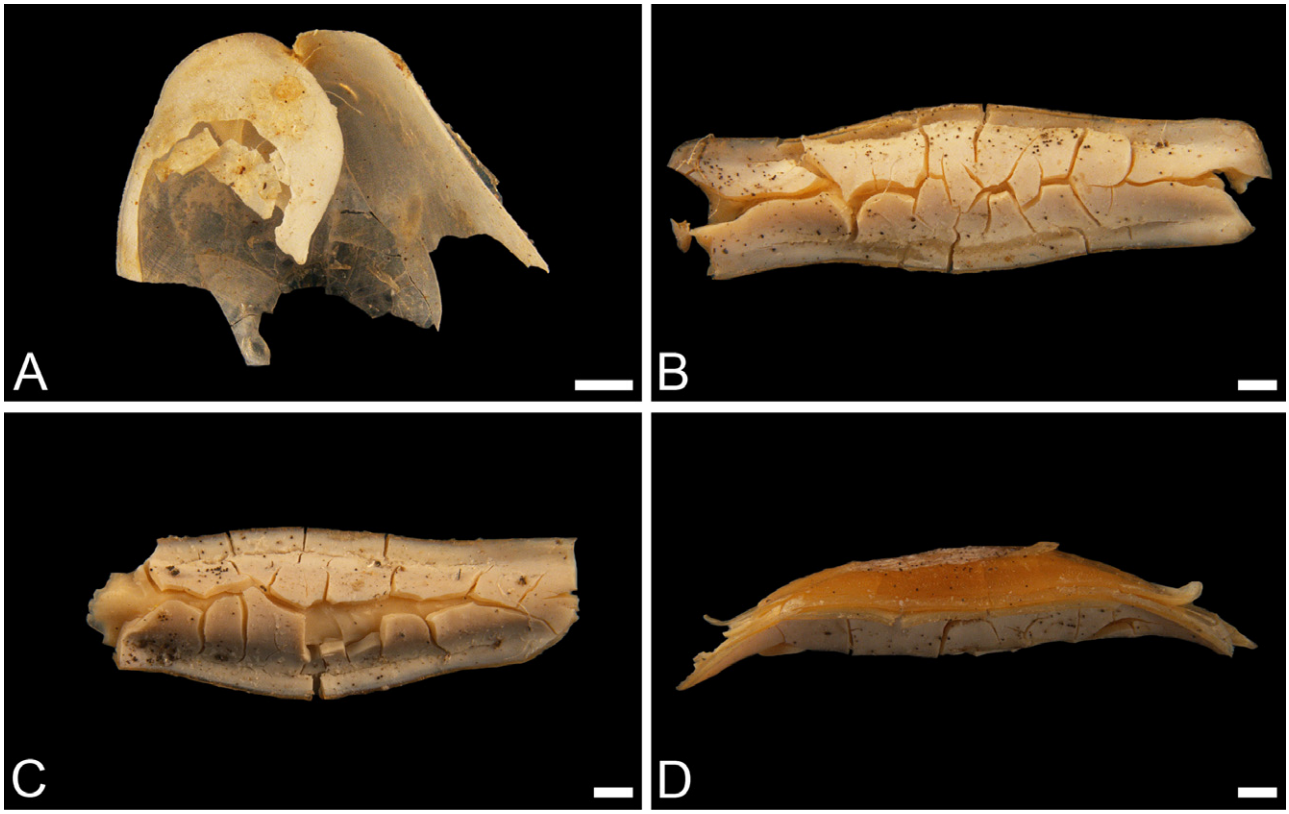

Figure 9. *Philine ossiansarsi*, type specimen, ZMBN 17193. A, ventral view of shell (automontage picture). B, C, ventral view of gizzard plate (automontage picture). D, lateral view of gizzard plate (automontage picture). Scale bars: A = 1 mm; B–D = 0.5 mm.

Shell (Fig. 6D–G): Maximum H = 10.9 mm. Internal, thick; white; squarish-oval in shape, aperture wide with thin white parietal callus, outer lip smooth, apex obtuse, slightly sunken, slightly umbilicated; sculpture not visible through mantle, consisting of transverse lines of pits fused to form grooves.

Animal (Fig. 6A–C): Body completely white, mantle thick. Cephalic shield indented, median groove absent. Larval kidney not visible through shell. Salivary glands shorter than buccal mass.

Radula (Figs 6H, I, 7A): Radular formula 15–16 × 1.0.1 Rachidian tooth absent. Inner lateral teeth with broad base, curved and rounded tips, inner edge denticulate.

Gizzard (Fig. 7B–F): Gizzard elongate cylindrical, surrounded by muscle fibres, contains three equal, spindle-shaped plates. Dorsal surface inside the gizzard of amber colour, ventral surface lighter, surrounded by transparent margin. Microsculpture on ventral surface only.

Male reproductive system (Fig. 7G, H): Obvious separation between long, thin, convoluted, nodulose prostate and sack-shaped penial sheath with bulb, tapering towards the genital aperture. Separate ejaculatory duct. Penial papilla hammer-shaped, upper part verrucose.

Ecology: In Norway this species was found to be dominant on the continental slope down to 1000 m, but still was found at 2304 m (Høisæter, 2010). It lives at temperatures around 0 °C (Odhner, 1915) and was found on mud (Knipowitsch, 1902). The gizzard of some specimens contained foraminifera (Odhner, 1915; present study).

Distribution: Amphiatlantic Arctic species occurring in North America north of Cape Cod, Greenland, Iceland, and over Svalbard and the Barents Sea to east Siberia. In Norway it is found north of Bodø and on the continental slope as far south as Ålesund (Platts, 1985; Kantor & Sysoev, 2006; Price *et al.*, 2011; present study).

Remarks: Pilsbry (1895) used the drawings of G. O. Sars (1878) but misnumbered the figures; *Philine finmarchica* in Pilsbry are illustrated in figs 17–19 (pl. 5) and not in figs 14–16 (p. 5) as claimed by the author, which depict *P. quadrata*. According to G. O. Sars (1878), *P. finmarchica* is of white colour, whereas *P. quadrata* (as *Philine polaris* Aurivillius, 1887) may have a yellowish colour. Live material was not accessed during the present work and this chromatic difference could not be checked. However, the latter two species have different shell shapes and sculptures and distinct anatomies (for comparison see systematic description of *P. quadrata*).

There is some confusion about the type specimens of *P. finmarchica* housed in the Zoological Museum of Oslo. Three different lots from different locations were categorized as type material (ZMO D140, ZMO D15768, and ZMO D1739). ZMO D1739 contains specimens from Tromsø, which is outside the type locality region – the county of Finnmark. ZMO D15768 contains specimens preserved in ethanol and an old label with *Philine finmarchica* nov spec and the locations Tromsø and Vadsø, the latter a city in the Finnmark county but this name seems to have been added later to the label. Therefore, there is some uncertainty as to whether these specimens could belong to the type series. The last lot of *P. finmarchica* (ZMO D1740) contains one shell from Vadsø. On the new label G.O. Sars is named as collector; the old label does not include this information. As the locality lies within the type locality Finnmark, a lectotype was selected from this lot. G. O. Sars (1878) referred to the occurrence of this species along the entire coast of Finnmark, being particularly abundant in Vadsø.

PHILINE INDISTINCTA SP. NOV.

(FIGS 10A–H, 11A–E, 12A–F)

Diagnosis: Shell internal, transparent with chain-like sculpture in transverse lines. Body white, larval kidney not visible. Rachidian tooth absent, one flattened inner lateral tooth with denticulation along inner edge, one rounded outer lateral tooth. Gizzard surrounded by muscle fibres, contains three equal, spindle-shaped gizzard plates. Thick prostate emerging from elongated sack-like penial sheath with large bulb. COI sequence: GenBank JX944798 (ZMBN 82108).

Type locality: Bergen, Norway.

Material examined: Bergen (Byfjorden), Norway, two spcs (dissected), ZMBN 11394, H = 4.2, 4.3 mm. Bergensfjordene, Norway, seven spcs (dissected), ZMBN 11396, H = 4.2–4.8 mm. Silavågen, Norway, one spc (dissected and sequenced), ZMBN 82108. 62°35.2′N, 06°26.5′E, Norway, one spc (dissected), ZMBN 82092, H = 5.7 mm. Florø, Norway, one sh, ZMBN 28427, H = 4.4 mm.

Holotype: Bergen, Norway, one spc (dissected), ZMBN 88020, H = 4.8 mm.

Etymology: The name stems from the fact that this species has an undistinguishable external morphology from its sister species *P. scabra*.

Shell (Fig. 10D–H): Maximum H = 5.7 mm. Internal, thin; transparent; elongated-oval cylindrical in shape, aperture wide with thin, whitish parietal callus, outer lip scalloped, apex obtuse, not umbilicated; sculpture visible through mantle, consisting of transverse lines of rounded or oval pits connected to form chains.

Animal (Fig. 10A–C): Body white, mantle thick. Cephalic shield indented, median groove present. Larval kidney not visible through shell. Salivary glands much longer than buccal mass.

Radula (Fig. 11A–C): Radular formula 14–18 × 1.1.0. 1.1. Rachidian tooth absent. Inner lateral teeth with broad base, curved and flattened tips, inner edge denticulate. Outer lateral teeth with broad base, straight to curved and rounded tip.

Gizzard (Fig. 12A–F): Gizzard elongate cylindrical, surrounded by muscle fibres, especially thick in the middle, contains three equal, spindle-shaped plates with two longitudinal slits on ventral surface. Dorsal surface inside the gizzard of amber colour, ventral surface more whitish, surrounded by transparent margin. Microsculpture on ventral surface, some specimens had accretion of crystals on the dorsal surface.

Male reproductive system (Fig. 11D, E): Obvious separation between long, thick, prostate and elongate sack-shaped penial sheath with thick wall and large empty bulb, tapering slightly towards the genital aperture. Prostate thinner towards the penial sheath. Penial papilla hook-shaped, upper part verrucose.

Ecology: Specimens were found between 18 and 20 m on mud-like soft bottom. Foraminiferans and one bivalve were found inside the gizzards.

Distribution: Norway from Silavågen (66°19.20′N), Ålesund, Florø, and Bergen.

Remarks: This species has an external morphology indistinguishable from *P. scabra.* Anatomically however, it has a different male copulatory system with a large bulb expansion on the penial sheath;

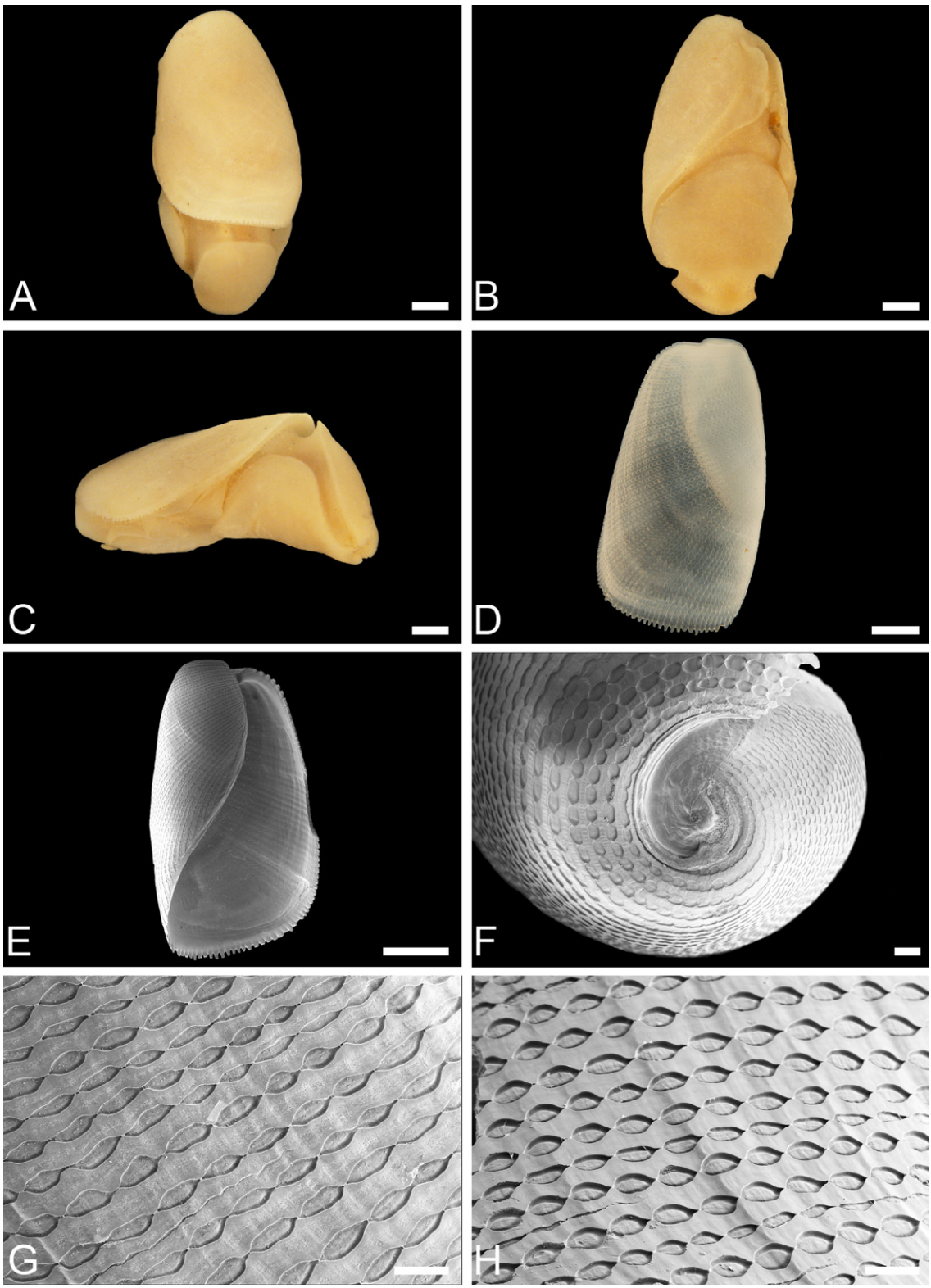

Figure 10. ***Philine indistincta*** **sp. nov.** A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (automontage picture). E, ventral view of shell (scanning electron micrograph, SEM). F, apex of shell, holotype (SEM). G, sculpture on dorsal surface of shell (SEM). H, sculpture on dorsal surface of shell (SEM). Scale bars: A–E = 1 mm; F–H = 100 μm.

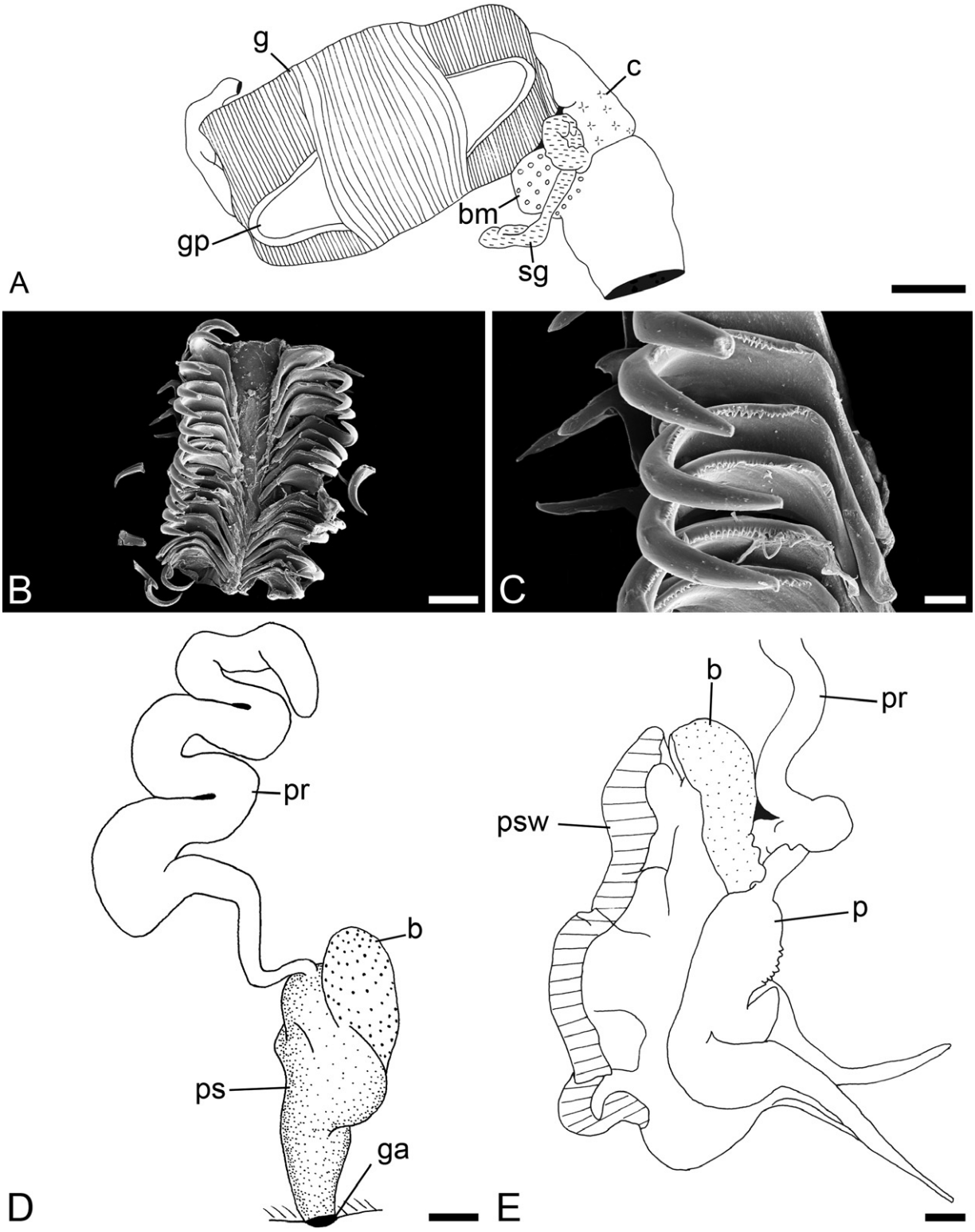

Figure 11. ***Philine indistincta*** **sp. nov.** A, gizzard with gizzard plate, crop, buccal mass, and salivary gland. B, radula (scanning electron micrograph, SEM). C, detail of radula (SEM). D, male reproductive system, holotype (drawing). E, detail of male reproductive system with penial sheath partly removed. Abbreviations: b, bulb; bm, buccal mass; c, crop; g, gizzard; ga, genital aperture; gp, gizzard plate; p, penial papilla; pr, prostate; ps, penial sheath; psw, penial sheath wall; sg, salivary gland. Scale bars: A = 0.5 mm; B = 100 μm; C = 20 μm; D = 250 μm; E = 125 μm.

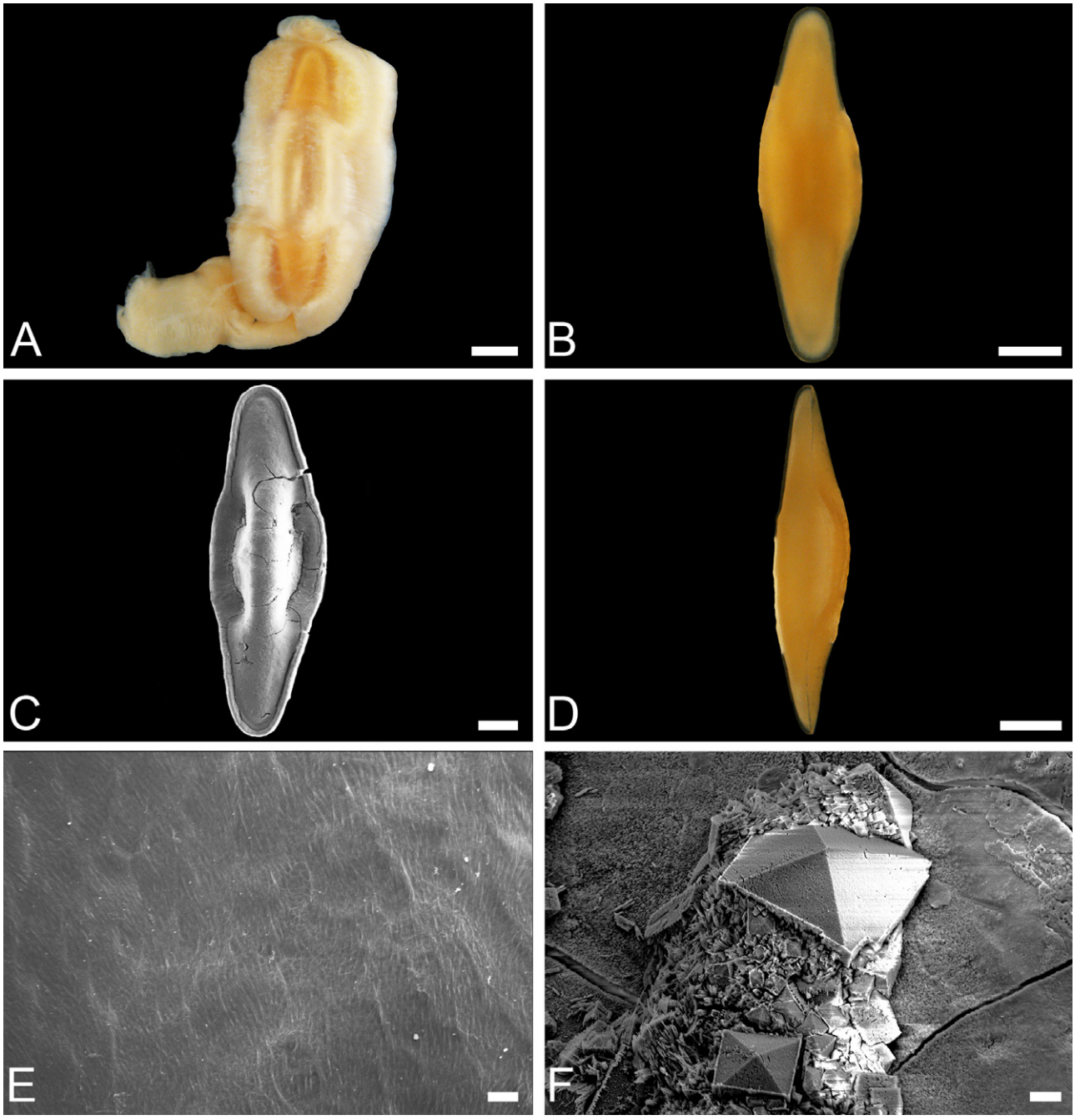

Figure 12. ***Philine indistincta*** **sp. nov.** A, gizzard (automontage picture). B, dorsal view of gizzard plate (automontage picture). C, ventral view of gizzard plate, holotype (scanning electron micrograph, SEM). D, lateral view of gizzard plate (automontage picture). E, ventral surface of gizzard plate, holotype (SEM). F, dorsal surface of gizzard plate with crystals (SEM). Scale bars: A, B, D = 0.5 mm; C = 200 μm; E, F = 5 μm.

presence of an elongate penial sheath (rounded in *P. scabra*); and a prostate duct shorter and wider than in *P. scabra*. Moreover, molecular phylogenetics analysis supported the separation between these two species, with a genetic distance for the COI gene of 7.6–8.2% (uncorrected *p*-distance) (Fig. 33).

PHILINE INFORTUNATA PILSBRY, 1895 (FIG. 13A–C)

Philine vitrea M. Sars, 1870: 177, pl. 11, fig. 15 (non Gould, animal only); G. O. Sars, 1878: 298, pl. 26, fig. 8.

Philine infortunata Pilsbry, 1895: 16, pl. 5, figs 12, 13 (lectotype here selected; ZMO D1737).

Figure 13. *Philine infortunata*, lectotype (= *Philine vitrea* G. O. Sars type ZMO D1737). Scale bars: A, B = 0.5 mm; C = 250 μm.

Diagnosis: Shell external, transparent, globose-oval in shape, apex sunken, smooth. Body transparent.

Type locality: Lofoten, Norway.

Material examined: Lofoten, Norway, one sh, ZMO D1737, H = 3.5 mm.

Shell (Fig. 13A–C): External, thin; transparent; globose-oval in shape, aperture wide, outer lip completely smooth, apex sunken; shell surface smooth, very faint growth lines (G. O. Sars, 1878).

Animal: Unknown.

Radula: Unknown.

Gizzard: Unknown.

Male reproductive system: Unknown.

Ecology: Unknown.

Distribution: Lofoten.

Remarks: A detailed discussion on the extensive confusion surrounding the names *P. vitrea*/*P. infortunata* can be found in the Remarks section for *P. confusa*. The shell housed at the Zoological Museum, Oslo (ZMO) labelled as the type of *P. vitrea* M. Sars (ZMO D1737) is the one used by G. O. Sars (1878) to describe and illustrate his concept of *P. vitrea* that Pilsbry (1895) later replaced with the name *P. infortunata* because the former was already occupied by *P. vitrea* Gould, 1859 from Hong Kong (see Remarks of *P. confusa*).

The shell studied and illustrated by G. O. Sars (1878: 298, pl. 26, fig. 8) and later reproduced by Pilsbry (1895: 16 pl. 5, figs. 12, 13) is similar to *P. quadripartita* (as *P. aperta*) but according to G. O. Sars (1878: 298) has a sufficiently different outline and spire to warrant taxonomic separation. Comparison of this shell (ZMO; D1737) with shells of *P. quadripartita* confirmed these differences. Moreover, the more plate-like shell of *P. quadripartita* is straighter in the upper part than the more globose and rounded shell of *P. infortunata*. *Philine quadripartita* lacks an umbilicus whereas *P. infortunata* is umbilicated.

Therefore, until further evidence is available we include this species as valid in the foregoing account and we select the shell used by G. O. Sars (1878: 298, pl. 26, fig. 8; ZMO, D1737) as lectotype of *P. infortunata*.

PHILINE LIMA (BROWN, 1827) (FIG. 14A–J)

Bulla lima Brown, 1827: pl. 38, figs 39, 40.
Utriculus lima Brown, 1844: 58, pl. 19, figs 39, 40.
Philine lima – G. O. Sars, 1878: 300, pl. 18, fig. 12 a-f, pl. 12, fig. 8; Kobelt, 1888: 283; Pilsbry, 1895: 20, pl. 5, figs 7–11; Kobelt 1896: 147, pl. 19, figs 5, 6; Drygalski, 1897: 187; Dautzenberg & Fischer, 1912: 40; Odhner, 1915: 232; Marcus & Marcus, 1969: 12, fig. 17; Høisæter, 2009: 81.
Philine (*Retusophiline*) *lima* – Nordsieck, 1972: 20, pl. 0III, fig. 5.
Retusophiline lima – Kantor & Sysoev, 2006: 257, pl. 128, fig. A.
Bullaea punctata Møller, 1842: 6.
Bulla lineolata Couthouy, 1839: 179, pl. III fig. 15.
Philine lineolata– Stimpson, 1851: 51.
Philine frigida Knipowitsch, 1896: 302. syn. nov.

Diagnosis: Shell internal, whitish to transparent, elongated-oval in shape, apex protruding, with chain-like sculpture in transverse lines. Body white. Rachidian tooth absent, one flattened inner lateral

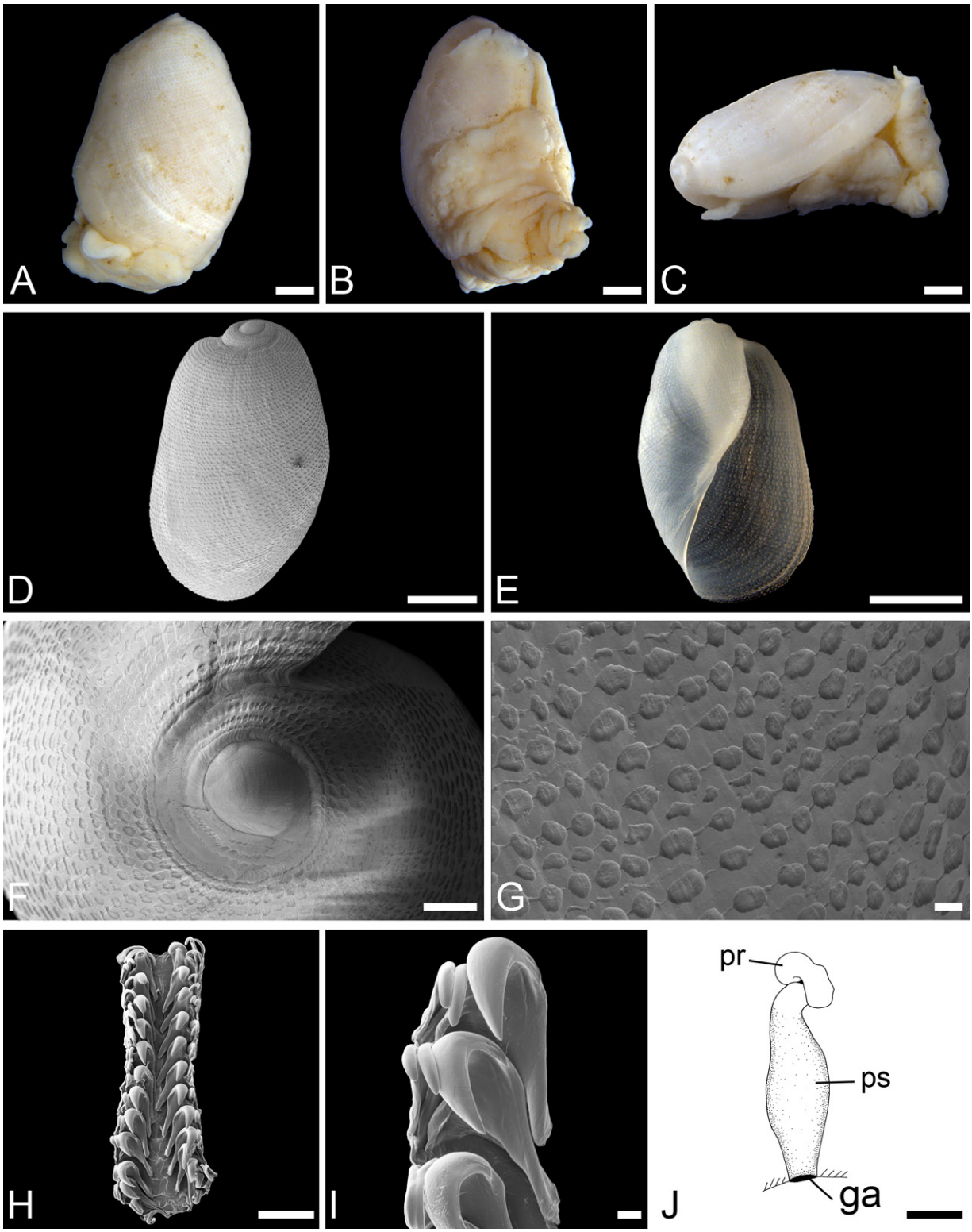

Figure 14. *Philine lima*. A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (scanning electron micrograph, SEM). E, ventral view of shell (automontage picture). F, apex of shell (SEM). G, sculpture on dorsal surface of shell (SEM). H, radula (SEM). I, detail of radula (SEM). J, male reproductive system (drawing). Abbreviations: ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A–E = 1 mm; F, H = 200 μm; G = 50 μm; I = 20 μm; J = 250 μm.

tooth with smooth inner edge, two rounded outer lateral teeth. Gizzard not surrounded by muscle fibres, without gizzard plates. Short, thick prostate emerging from tubular penial sheath.

Type locality: Greenock, west Scotland, UK.

Material examined: Hammerfest, Norway, one sh, ZMBN 22012, H = 2.9 mm. Tromsø, Norway, one sh, ZMBN 28763, H = 4.3 mm. Toppsund, Norway, one spc (dissected), ZMBN 82199, H = 6.3 mm. 62°30.5′N 01°51.1′E, off Ålesund, Norway, two spcs (examined), ZMBN 86185, H = 4.3, 4.7 mm. 62°36.2′N, 02°14.0′E, off Ålesund, Norway, two spcs (dissected), ZMBN 86186, H = 5.0 mm. Barents Sea, two spcs (dissected), ZMB 117523, H = 2.6, 7.0 mm.

Shell (Fig. 14D–G): Maximum H = 7.0 mm. Internal, thick; whitish to transparent; elongated-oval cylindrical in shape, aperture wide with thin whitish transparent parietal callus, outer lip slightly scalloped, apex protruding, slightly umbilicated; sculpture visible through mantle, consisting of transverse lines of pits connected by narrow grooves to form chains.

Animal (Fig. 14A–C): Body uniformly white, mantle thick. Cephalic shield lobed posteriorly, median groove present. Larval kidney not visible through shell.

Radula (Fig. 14H, I): Radular formula 13 × 2.1.0.1.2. Rachidian tooth absent. Inner lateral teeth with broad base, curved and flattened tips, inner edge smooth. Outer lateral teeth with broad base, curved and rounded tip.

Gizzard: Gizzard globose, not surrounded by muscle fibres, no plates.

Male reproductive system (Fig. 14J): Short, thick prostate emerging from tubular penial sheath.

Ecology: Occurs from 2 to 720 m on mud, mud with stones, gravel, shells, rotting plant debris, sand, and algae (Odhner, 1906–07; 1915).

Distribution: This species has a northern amphiatlantic distribution from Massachusetts over Greenland, Svalbard to Murman coast, White Sea, Kara Sea, Franz Joseph Land (Odhner, 1915). In Norway it is found northwards of the Lofoten (Høisæter *et al*., 2001) but on the continental slope as far south as Ålesund (Høisæter, 2009).

Remarks: Pilsbry (1895) quoted that Monterosato found this species in the Mediterranean Sea. However given the distribution reported by other authors this seems unlikely and might result from a misidentification. *Bullaea punctata*, *Philine lineolata*, and *Philine frigida* are considered synonyms of *P. lima* based on resemblance of the shell shape. Moreover, Knipowitsch (1896), whilst describing *P. frigida*, highlighted the possibility that the latter species could be the same as *P. lima*.

PHILINE GRANDIOCULI SP. NOV.

(FIGS 15A–F, 16A–D)

Diagnosis: Shell internal, transparent, smooth. Body white, larval kidney visible, large eyes. Rachidian tooth absent, one inner lateral tooth with coarse denticulation along inner edge, one rounded outer lateral tooth. Gizzard not surrounded by muscle fibres, contains no gizzard plates. Long and thin prostate with blind caecum, clearly separated from tubular penial sheath. COI sequence: GenBank JX944805 (ZMBN 88009).

Type locality: South-west off Lofoten, Norway (67°43′19.8120″N, 10°16′30.0900″E).

Material examined: South-west off Lofoten, 67°43′19.8120″N, 10°16′30.0900″E, one spc ZMBN 88010, H = 2.7 mm (holotype). South-west off Lofoten, 67°52′97″N, 11°19′16″E, Norway, one spc (dissected and sequenced), ZMBN 88009, H = 3.2 mm. West of Sørøya, Finnmark, 70°46′30″N, 20°13′94″E, Norway, one spc, ZMBN 88011, H = 1.31 mm.

Etymology: The species name stems from the presence of large, conspicuously visible eyes.

Shell (Fig. 16A–D): Maximum H = 3.2 mm. Internal, thin; transparent; elongate globose in shape, aperture wide with thin transparent parietal callus, outer lip completely entire, apex sunken, umbilicated; shell surface smooth.

Animal (Fig. 15A–D): Body white, posterior pallial lobe, mantle thin. Cephalic shield tapering posteriorly, median groove absent. Larval kidney visible through shell. Large eyes, brownish Hancock's organs.

Radula (Fig. 15E): Radular formula 14 × 1.1.0.1.1. Rachidian tooth absent. Inner lateral teeth with broad base, curved and rounded tips, inner edge coarsely denticulate. Outer lateral teeth with broad base, curved and rounded tip.

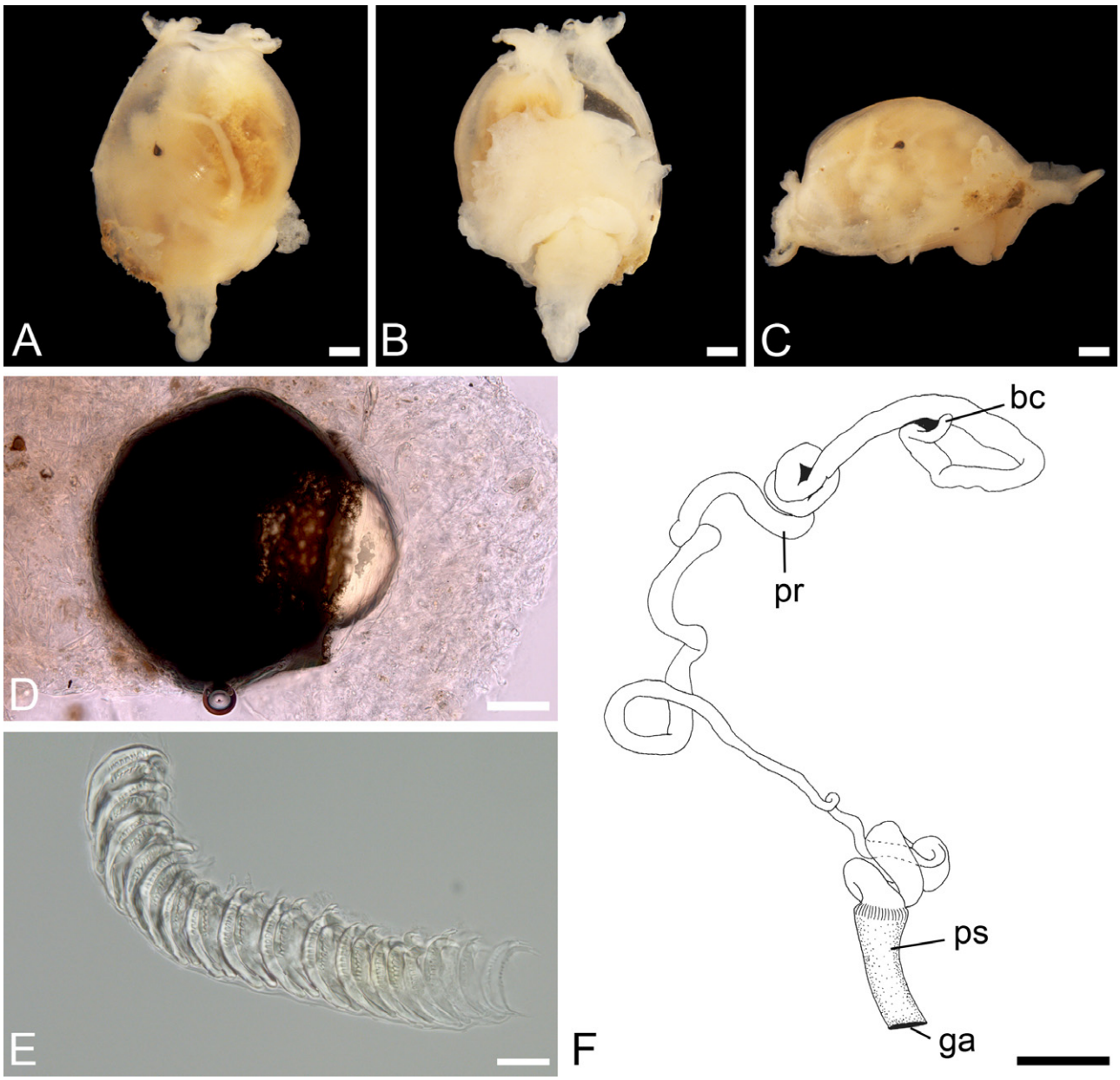

Figure 15. ***Philine grandioculi*** **sp. nov.** A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, eye (light microscopy, LM). E, radula (LM). F, male reproductive system (drawing). Abbreviations: bc, blind caecum; ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A–C = 0.5 mm; D = 50 μm; E = 25 μm; F = 250 μm.

Gizzard: Gizzard globose, not surrounded by muscle fibres, no plates.

Male reproductive system (Fig. 15F): Obvious separation between long, thin, convoluted prostate and tubular penial sheath, prostate thick and convoluted just after the penial sheath, becoming suddenly thin, blind caecum at end of prostate.

Ecology: Occurs from 212 to 219 m on sandy mud.

Distribution: South-west of Lofoten Islands and west of Sørøya, Finnmark.

Remarks: Additionally to *P. grandioculi* there are five other species with smooth shells (*P. confusa*, *P. denticulata*, *P. infortunata*, *P. ventricosa*, and *P. quadripartita*). The species *P. quadripartita* and *P. denticulata* have flattened plate-like shells, which are not umbilicated, whereas *P. grandioculi* and the other three species have more rounded, deeper umbili-

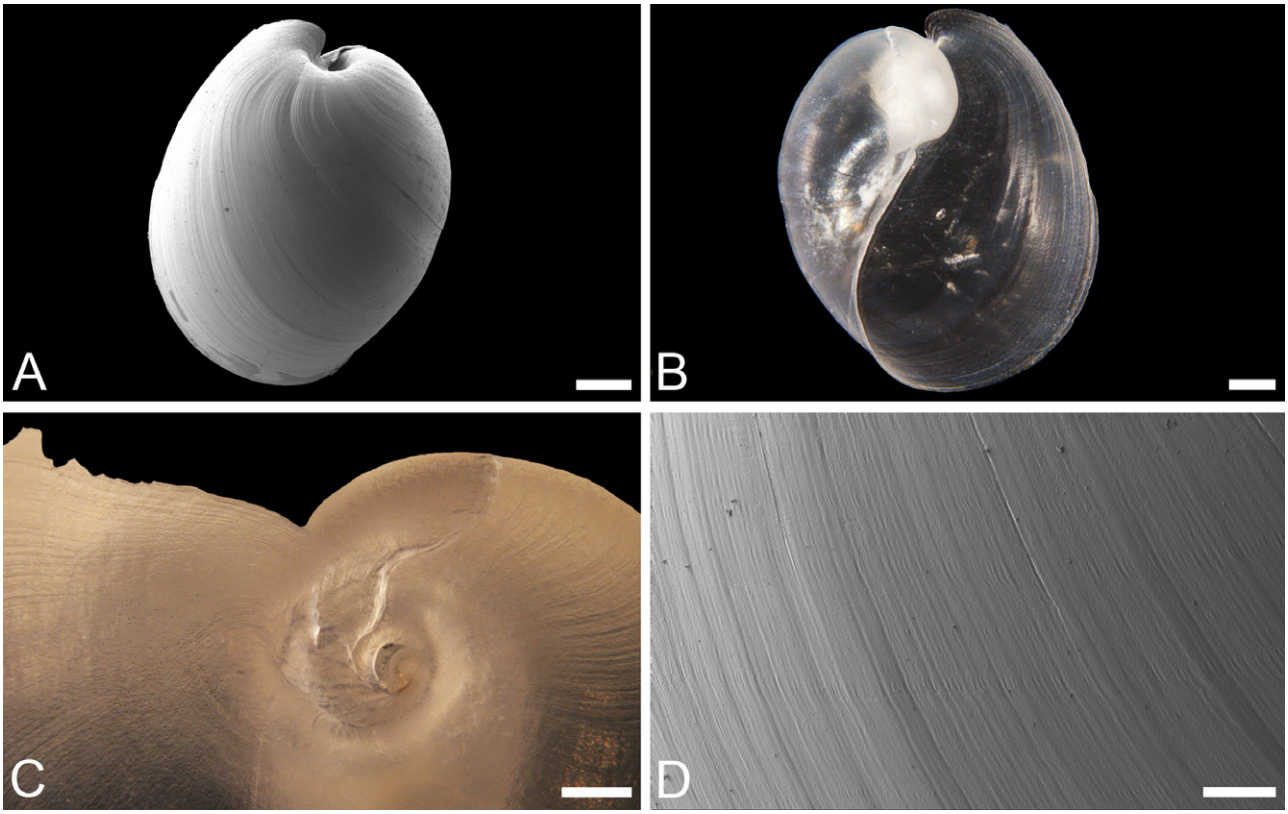

Figure 16. ***Philine grandioculi*** **sp. nov.** A, dorsal view of shell (scanning electron micrograph, SEM). B, ventral view of shell (automontage picture). C, apex of shell (automontage picture). D, dorsal surface of shell (SEM). Scale bars: A, B = 0.5 mm; C = 200 μm; D = 100 μm.

cated shells. Furthermore, *P. quadripartita* has distinct radula and gizzard plates (see *P. quadripartita* description). Shells of *P. ventricosa* have a nonsunken apex and have a more circular outline compared to *P. confusa*, *P. infortunata*, and *P. grandioculi*. In contrast to *P. confusa* the shell of *P. grandioculi* is more elongate with a straighter outline and an umbilical channel. Compared to *P. infortunata* its outline is straighter and the aperture is smaller because the whorls increase faster in size in *P. infortunata* than in *P. grandioculi*. The radular formula of *P. grandioculi* is different to *P. confusa* and *P. ventricosa*. Regarding the male reproductive system, *P. confusa* has a short, thick, nonconvoluted prostate, whereas *P. ventricosa* and *P. grandioculi* have long and twisted prostates. A striking character in *P. grandioculi* is the large eyes, which were not observed in specimens of the same size in the other species (for *P. infortunata* only shells were available).

PHILINE PRUINOSA (CLARK, 1827) (FIG. 17A–G)

Bullaea pruinosa Clark, 1827: 339; Thorpe, 1844: 137.

Philine pruinosa – Lovén, 1847: 141; Sowerby, 1859: pl. 20, fig. 25; J. G. Jeffreys, 1867: 454; G. O. Sars, 1878: 301, pl. 18, fig. 8 a, b, e, pl. 12, fig. 12; Pilsbry, 1895: 26, pl. 4, figs 73–76 (not 77 and 78); Odhner, 1906–07: 61, pl. 3, fig. 3; Lemche, 1948, 65, 66, 96, figs 73, 74; Platts, 1985: 153.

Laona pruinosa – A. Adams, 1865: 324; Nordsieck, 1972: 21, pl. OIII, fig. 8; Gaglini, 1991: 13; Høisæter, 2009: 80.

Philine flexuosa M. Sars, 1859: 85; M. Sars, 1870: 181; G. O. Sars, 1878: 363, pl. 12, fig. 13; Pilsbry, 1895: 21, pl. 4, figs 86–89, Odhner, 1906–07: 61.

Laona flexuosa – Nordsieck, 1972: 21; Høisæter, 2009: 80.

Philine granulosa M. Sars, 1869: 258 (non *Bullaea granulosa* M. Sars; according to G. O. Sars, 1878: 374 and Lemche, 1948).

Philine membranacea Monterosato, 1880: 78; Pilsbry, 1895: 22; Gaglini, 1991: 12.

Diagnosis: Shell internal, whitish transparent, sometimes brownish transverse band, oval in shape, apex obtuse, with reticulate sculpture of raised dots mostly

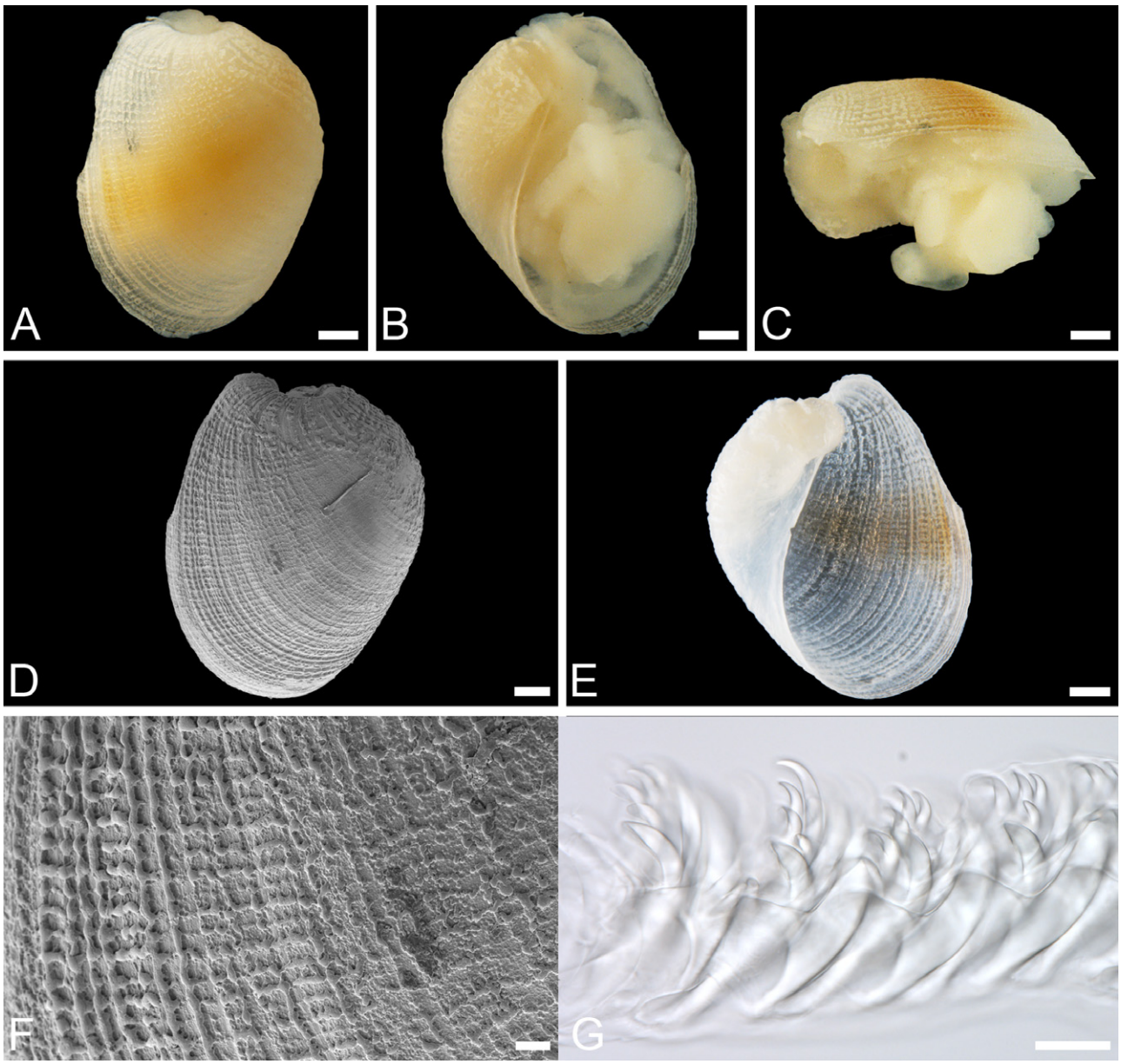

Figure 17. *Philine* cf. *pruinosa*. A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (scanning electron micrograph, SEM). E, ventral view of shell (automontage picture). F, sculpture on dorsal surface of shell (SEM). G, detail of radula (light microscope picture). Scale bars: A–C, E = 0.5 mm; D = 200 μm; F = 50 μm; G = 20 μm.

fused to form lines. Body white. Rachidian tooth absent, one inner lateral tooth, six outer lateral teeth. Gizzard not surrounded by muscle fibres, without gizzard plates. COI sequence: GenBank JX944808 (ZMBN 87076).

Type locality: Budleigh, Salterton, England, UK.

Material examined: Oslofjord, Norway, one sh, ZMBN 28704, H = 4.6 mm. Tjärnö, Sweden, one spc (dissected and sequenced), ZMBN 87076, H = 1.9 mm. Unknown locality, two sh, ZMO D1742, H = 3.5, 4.1 mm. Ålesund, Norway, two sh, ZMO D1741, H = 10.9, 12.1 mm.

Shell (Fig. 17D–F): Maximum H = 4.6 mm. Internal, thin; whitish transparent, sometimes brownish transverse band; oval in shape, aperture wide with thin whitish parietal callus, outer lip smooth, apex obtuse, slightly sunken, slightly umbilicated; sculpture con-

sisting of transverse and longitudinal lines of raised dots mostly fused to form chains in a reticulate pattern.

Animal (Fig. 17A–C): Body with white dots along margins, mantle posteriorly notched (Lovén, 1847). Larval kidney visible through shell.

Radula (Fig. 17G): Radular formula 6.1.0.1.6. Rachidian tooth absent. Inner lateral teeth with broad base, curved tips, inner edge smooth. Outer lateral teeth with broad base, curved tip (G. O. Sars, 1878).

Gizzard: Gizzard tubular sack, not surrounded by muscle fibres, no plates.

Male reproductive system: Unknown.

Ecology: Found down to 400 m (Thompson, 1988); on sandy mud (J. G. Jeffreys, 1867), sand with spongespicules and sand with shell-gravel (Sneli *et al*., 2005).

Distribution: In Norway from Lofoten southwards to the Swedish west coast (Høisæter, 2009), Tjärnö, Sweden (58°52′N). The Faeroes (Sneli *et al*., 2005), British Isles (Platts, 1985), Mediterranean Sea (Thompson, 1988).

Remarks: Lemche (1948) regarded *P. pruinosa* and *P. flexuosa* as synonyms because they share the same radular formula and the type material shows no differences. The radulae drawn by G. O. Sars (1878) show no differences either. Nordsieck (1972) regarded the species as distinct and thought that *Laona membranacea* Monterosato might be a Mediterranean form of *P. flexuosa*. WoRMS (Gofas, 2010) lists *Laona flexuosa* as valid and CLEMAM (http://www.somali.asso.fr/clemam/biotaxis.php) includes *P. membranacea* as a synonym of *P. flexuosa*. Høisæter (2009) did not discuss this taxonomic problem and considered *P. pruinosa* and *P. flexuosa* to be valid species. *Philine granulosa* M. Sars, 1869 was only mentioned and not described by M. Sars. G. O. Sars (1878: 374) considered this species a synonym of *P. pruinosa*.

Pilsbry (1895: pl. 4, figs 74–78) illustrated *P. pruinosa* using drawings from G. O. Sars (1878), but mixed up under the name *P. pruinosa* drawings belonging to two different species. Figures 74–76 represent shells of *P. pruinosa* (pl. 18, fig. 8a, b, e in G. O. Sars, 1878) and figs 77–78 the live animal of *P. ventricosa* (pl. 18, fig. 8c, d in G. O. Sars, 1878). As a result of this mislabelling, pictures of *P. ventricosa* often get associated with *P. pruinosa* (e.g. Rudman, 2007). The impact of the English text of Pilsbry's (1895) monographs compared with the Norwegian text by G. O. Sars (1878) was much broader and this led subsequent authors to perpetuate the mistakes repeatedly. The small size of the specimen studied during this work precluded proper mounting of the radula for SEM. Light microscopy observations revealed the presence of at least four outer lateral teeth on each side, which is more than in any other Atlantic species. Because of this and the shell characters the specimen is here identified provisionally as *P. pruinosa*.

Two lots of specimens of *P. flexuosa* are housed at the Zoological Museum of Oslo as type material (ZMO D1741, ZMO D1742). ZMO D1742 contains two shells and an old label '*Philine flexuosa* M Sars?'. The question mark on the label seems to indicate some uncertainty to whether these specimens belong to the material originally studied by M. Sars. Moreover there is no indication of a locality. The lot ZMO D1741 contains one shell collected at Ålesund, but the type locality is the Oslofjord. Both lots were studied by Lemche, who identified them as *P. pruinosa* (Ann-Helen Rønning, pers. comm.).

PHILINE PUNCTATA (J. ADAMS, 1800) (FIGS 18A–I, 19A–C)

Bulla punctata J. Adams, 1800: 2, pl. 1, figs 6–8.

Bullaea punctata – Clark, 1827: 339; Brown, T. 1844: 58; MacGillivray, 1844: 187; Thorpe, 1844: 137; Alder, J., 1848: 25. Forbes & Hanley, 1853a: pl. UU, fig. 5.

Philine punctata – Forbes & Hanley 1853a, pl. UU, fig. 5; Kobelt, 1896: 156, pl. 19, fig. 28; Thompson, 1988: 62; van der Linden, 1994: 46, figs 17, 18; Høisæter, 2009: 80.

?Bullaea punctulata – MacGillivray, 1844: 68 (misspelling).

Philine pusilla M. Sars, 1859: 85 (G. O. Sars, 1878: 375).

Diagnosis: Shell internal, whitish transparent with punctuate sculpture in transverse lines. Body yellowish with small brown dots, larval kidney visible. Rachidian tooth absent, one flattened inner lateral tooth with denticulation along inner edge, two rounded outer lateral teeth. Gizzard not surrounded by muscle fibres, contains two paired and one smaller unpaired kidney-bean shaped gizzard plates. No obvious separation between prostate and penial sheath.

Type locality: Tenby, Wales, UK.

Material examined: Raunefjorden, Norway, one spc (dissected), ZMBN 82075, H = 1.2 mm, shell sand.

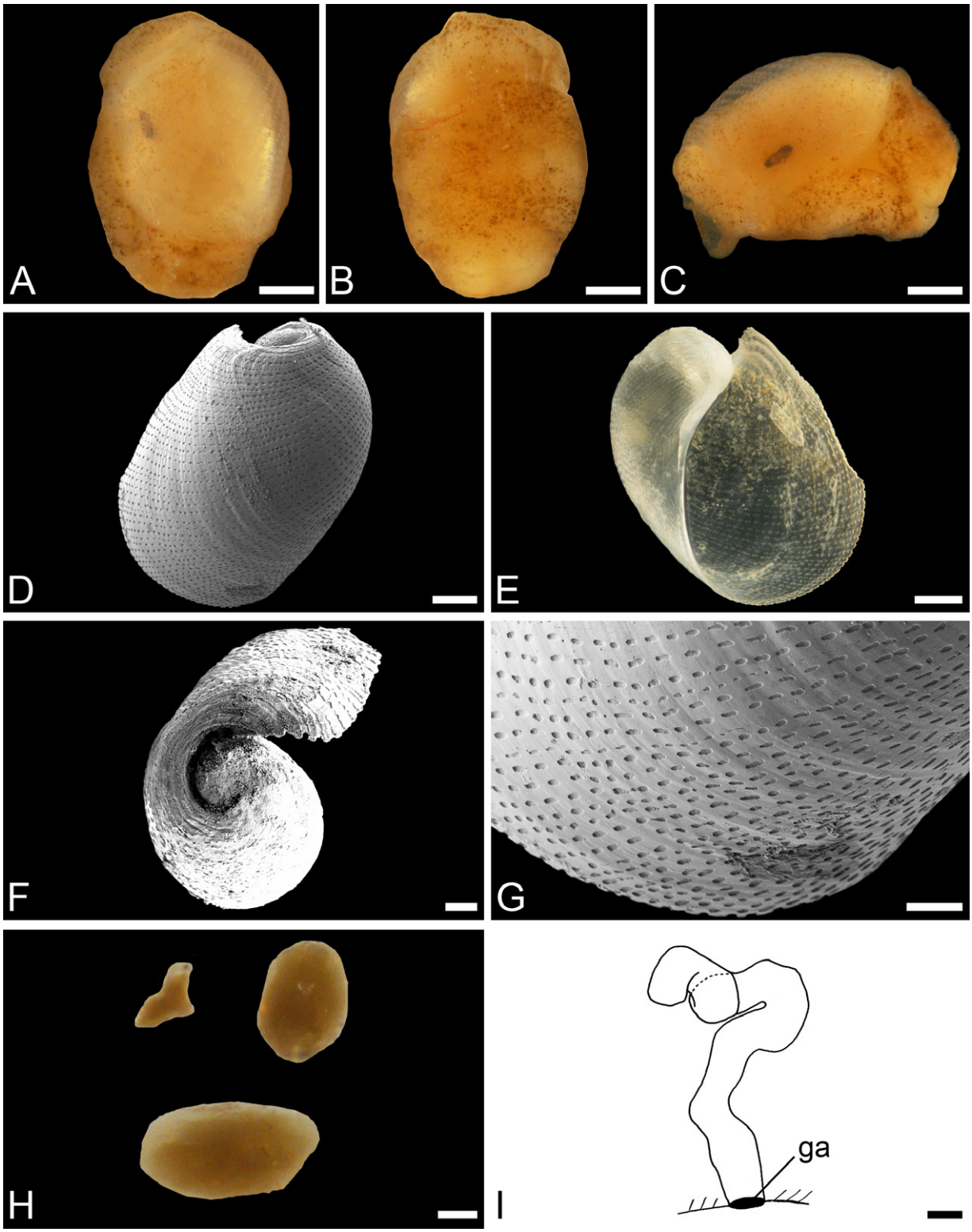

Figure 18. *Philine punctata*. A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (scanning electron micrograph, SEM). E, ventral view of shell (automontage picture). F, apex of shell (SEM). G, sculpture on dorsal surface of shell (SEM). H, lateral view of small unpaired gizzard plate and top view of large paired plates (automontage pictures). I, male reproductive system (drawing). Abbreviation: ga, genital aperture. Scale bars: A–C = 0.5 mm; D, E = 200 μm; F = 100 μm; G = 20 μm; H = 50 μm; I = 250 μm.

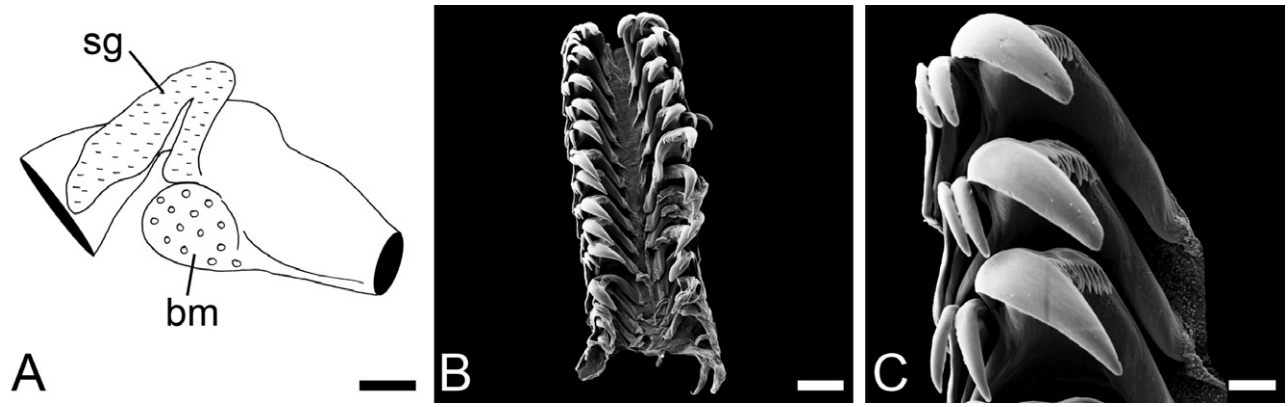

Figure 19. *Philine punctata*. A, buccal mass (bm) and salivary gland (sg). B, radula (scanning electron micrograph, SEM). C, detail of radula (SEM). Scale bars: A = 125 μm; B = 50 μm; C = 10 μm.

Stokken, Norway, one spc (dissected), ZMBN 82079, H = 1.5 mm. Haramsfjorden, Norway, three spcs (dissected), ZMBN 82080, H = 1.1–1.5 mm. Grasøyane, Norway, 1 D, ZMBN 82081, H = 2.8 mm. Nesna, Norway, two spcs (dissected), ZMBN 82083, H = 1.4, 1.5 mm. Vefsnfjorden, Norway, one spc (dissected), ZMBN 82084, H = 1.6 mm.

Shell (Fig. 18D–G): Maximum H = 2.8 mm. Internal, thin; whitish to transparent; squarish-oval in shape, aperture wide with thin whitish parietal callus, outer lip slightly scalloped, apex obtuse, slightly umbilicated; sculpture visible through mantle, consisting of transverse lines of pits not connected.

Animal (Fig. 18A–C): Preserved animal yellowish with small brown dots, mantle thin. Cephalic shield pointed, median groove absent. Larval kidney visible through shell. Salivary glands much longer than buccal mass.

Radula (Fig. 19A–C): Radular formula 16 × 2.1.0.1.2. Rachidian tooth absent. Inner lateral teeth with broad base, curved and flattened tips, inner edge denticulate. Outer lateral teeth with broad base, curved and rounded tip.

Gizzard (Fig. 18H): Gizzard globose, not surrounded by muscle fibres, contains two paired and one smaller unpaired kidney-bean shaped plates. Unpaired plate with tip on dorsal side. Plates uniformly brown.

Male reproductive system (Fig. 18I): Flat tube, no obvious separation between prostate and penial sheath.

Ecology: Occurs on soft bottom, sand, shell sand, rocks, slag, and gravel between 6 and 240 m depth. It can be found associated with red algae (present study).

Distribution: Present in Greenland, the Faeroes, Shetlands, Norway southwards from Norland county (66°16′N), the British Isles, Baltic Sea, and the Mediterranean (Thompson, 1988; Høisæter, 2009; Wiese, 2009; present study).

Remarks: Several authors (e.g. Thorpe, 1844; J. G. Jeffreys, 1867; Locard, 1886; Pilsbry, 1895) attributed this species to Clark (1827) but the latter author only re-assigned this J. Adams' species to the genus *Bullaea* (Clark, 1827: 339). Montagu (1803) regarded *P. punctata* (as *Bulla*) as a senior synonym of *P. catena* (as *Bulla*) described by himself, which has a chain-like sculpture of pits on the shell rather than separate pits as in *P. punctata*. As Clark (1827) pointed out, this synonymization cannot be valid not only because the species have a distinct shell sculpture but also because *P. punctata* lacks large and thick gizzard plates like those present in *P. catena*. The nomenclatural problems surrounding this species became even more acute after J. G. Jeffreys (1867) considered both *Bulla punctata* J. Adams, 1800, and *Bullaea punctata* Clark, 1827, valid and regarded the former species a synonym of *P. catena* (Montagu, 1803), a view followed, amongst others, by Pilsbry (1895). Forbes & Hanley (1853a) in their index (Xlii) considered the species to be in the genus *Philine* but in the caption of the figure (pl. UU, fig. 6), they did not change the genus name from *Bullaea* to *Philine*. *Philine pusilla* M. Sars, 1859 was described in one short sentence and later considered to be a synonym of *P. punctata* by G. O. Sars (1878). *Bullaea alata* Forbes, 1844 is listed as synonym of *P. punctata* on CLEMAM (http://www.somali.asso.fr/clemam/biotaxis.php) but this is doubtful because the former species was described as having a smooth shell margin, whereas *P. punctata* has a different shell shape with indentations along the shell margin (J. G. Jeffreys, 1867; present study Fig. 18F).

PHILINE QUADRATA (WOOD, 1839) (FIGS 20A–I, 21A–C)

Bulla quadrata Wood, S., 1839: 461, pl. vii, fig. 1.

Bullaea quadrata – Alder, 1848: 26. syn. nov.

Philine quadrata – Forbes & Hanley, 1853b: 541; M. Sars, 1859: 49; J. G. Jeffreys, 1867: 452; G. O. Sars, 1878: 299, pl. 18, fig. 9, pl. 12, fig. 7 Pilsbry, 1895: 19, pl. 5, figs 14–16, pl. 3, fig. 43; Grieg, 1913: 42; Marcus & Marcus, 1969: 12, figs 18, 19; Platts, 1985: 153; van der Linden, 1995: 75.

Ossiania quadrata – Monterosato, 1884: 147; Kantor & Sysoev, 2006: 256, pl. 127, fig. F.

Laona (Ossiania) quadrata – Nordsieck, 1972: 22, pl. OIII, fig. 12.

Philine scutulum Lovén, 1847: 141.

Philine formosa Stimpson, 1850: 334.

Philine polaris Aurivillius, 1887: 371, 380, pl. 12, figs 21, 22, pl. 13, fig. 18; Pilsbry, 1895: 22, pl. 3, figs 39, 40; Taylor, 1899: 241; Platts, 1985: 153.

Retusophiline polaris – Kantor & Sysoev, 2006: 257, pl. 128, fig. B.

Diagnosis: Shell internal, white, quadrate-oval in shape, apex obtuse, with chain-like sculpture in transverse lines. Body white. Rachidian tooth absent, one flattened inner lateral tooth with denticulate inner edge, two rounded outer lateral teeth. Gizzard not surrounded by muscle fibres, without gizzard plates. Short, thick, wrinkly prostate emerging from tubular penial sheath. COI sequences: GenBank JX944809 (ZMBN 89012.1), JX944810 (ZMBN 86184.2), JX944811 (ZMBN 88012.2), JX944812 (ZMBN 88013), JX944813 (ZMBN 86184.1).

Type locality: Corraline Crag, Sutton, England, UK.

Material examined: Eidfjorden, Norway, two spcs (dissected), ZMBN 61999, H = 3.6, 5.6 mm. Bergen, Norway, one spc (dissected), ZMBN 10744, H = 6.1 mm. Hjeltefjorden, Norway, one spc (dissected), ZMBN 10745, H = 4.6 mm. Husøy, Norway, one spc (dissected), ZMBN 13171, H = 5.5 mm. Eiterfjorden, Norway, one spc (dissected), ZMBN 82047, H = 4.1 mm. Breisunddjupet, Norway, one spc (dissected), ZMBN 82050, H = 3.2 mm. Ellingsøyfjorden, Norway, one spc (dissected), ZMBN 82051, H = 1.9 mm. 66°00′N, 12°55′E, Sundøy, Norway, four spcs (dissected), ZMBN 82060, H = 4.0–4.6 mm. 61°38.2′N, 16°27.7′W, between Iceland and the Faroe Islands, five spcs (dissected; two sequenced), ZMBN 86184, H = 2.2–2.6 mm. 62°31.5′N 01°26.6′E, off Ålesund, one spc (dissected), ZMBN 86187, H = 3.8 mm. 62°20.3′N, 01°24.7′E, off Ålesund, one spc (dissected), ZMBN 86189, H = 5.6 mm. 62°36.2′N, 02°14.0′E, off Ålesund, H = 6.2 mm. Barents Sea, four spcs (dissected), ZMB 117523, H = 3.8–7.1 mm. Unknown locality, two spcs (examined), NTNU 30382, H = 2.8, 3.6 mm. Strindfjorden, Norway, one spc (dissected), NTNU 30384, 3.4 mm. Unknown locality, one spc (dissected), NTNU 63678, 1.5 mm. West off Lofoten, 67°50′48.60″, 011°48′51.00″, two spcs (sequenced), ZMBN 88012, H = 3.8, 4.9 mm. West off Lofoten, 67°52′58.20″, 011°19′09.60″, one spc (sequenced), ZMBN 88013, H = 4.3 mm.

Shell (Fig. 20D–G): Maximum H = 7.1 mm. Internal, thick; white; quadrate-oval in shape, aperture wide with thick, white parietal callus, upper outer lip slightly scalloped, apex obtuse, slightly sunken, not umbilicated; sculpture visible through mantle, consisting of transverse lines of pits connected by narrow grooves to form chains.

Animal (Fig. 20A–C): Body uniformly white, mantle thick. Cephalic shield blunt posteriorly, median groove present. Larval kidney not visible through shell. Salivary glands slightly longer than buccal mass.

Radula (Fig. 21A–C): Radular formula $12 \times 2.1.0.1.2$. Rachidian tooth absent. Inner lateral teeth with broad base, curved and flattened tips, inner edge denticulate. Outer lateral teeth with broad base, curved and rounded tip.

Gizzard: Gizzard globose, not surrounded by muscle fibres, plates absent.

Male reproductive system (Fig. 20H, I): Short, thick, wrinkly prostate emerging from tubular penial sheath. Penial papilla cone-shaped.

Ecology: Occurs down to 2355 m on soft bottom, mud, clay, sand, coarse sand, shell sand, rocks, and gravel (present study). Two specimens contained foraminiferans in their guts.

Distribution: Amphiatlantic species occurring from New England, USA, eastwards to Greenland and Iceland, the Barents and White Seas. Found down the entire coast of Norway, the Faeroes, British Isles, southwards to the Mediterranean, Azores, Morocco, and St. Helena (Thompson, 1988; van der Linden, 1995; Høisæter *et al*., 2001; Sneli *et al*., 2005).

Remarks: Lemche (1948) reported that *Philine polaris* has a shell pattern more similar to that of *P. finmarchica* than to *P. quadrata*, which is incongruent with the original description of *P. polaris*. However, the sculpture varies in different parts of the shell and both sculpture types can be found on specimens of

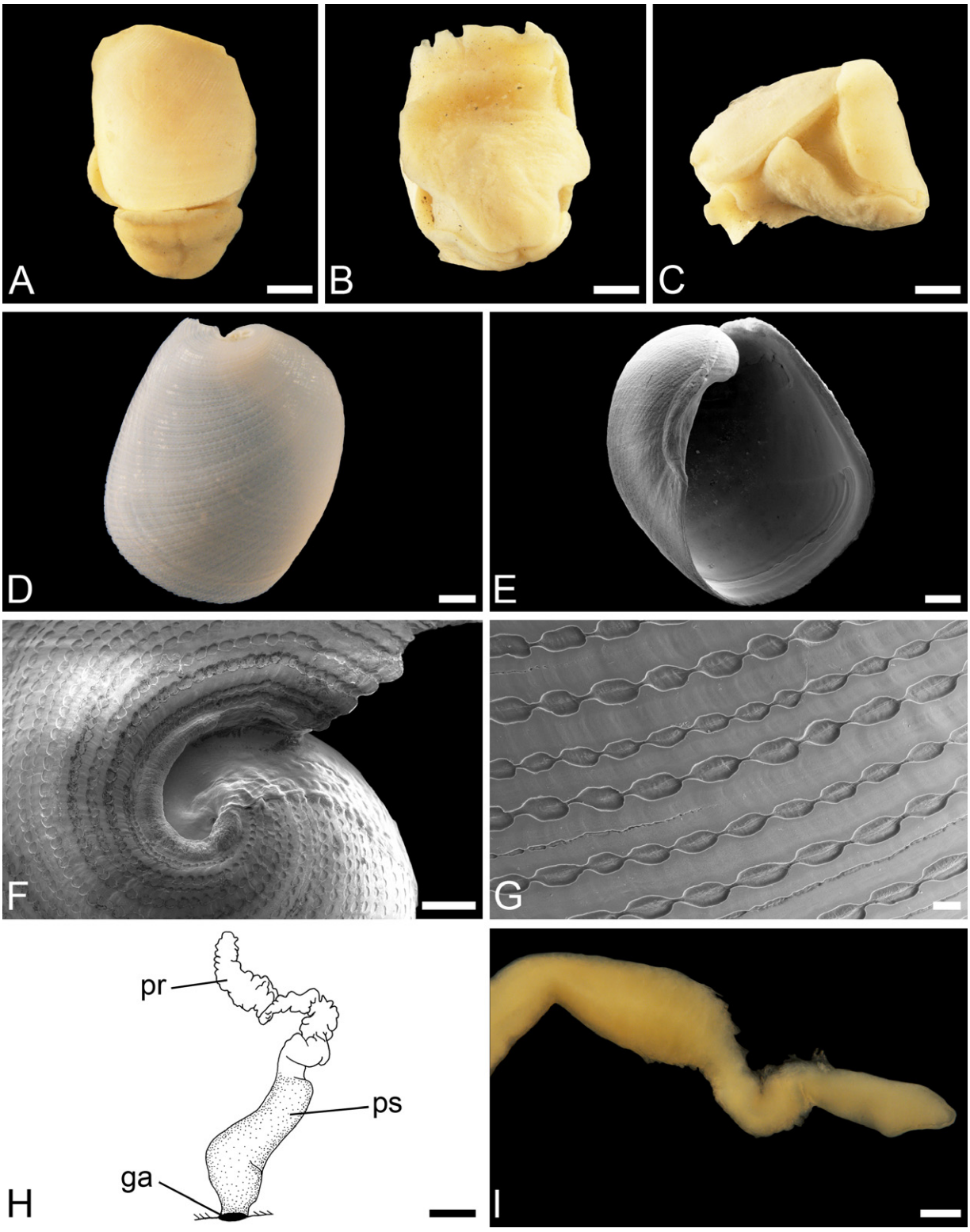

Figure 20. *Philine quadrata.* A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (automontage picture). E, ventral view of shell (scanning electron micrograph, SEM). F, apex of shell (SEM). G, sculpture on dorsal surface of shell (SEM). H, male reproductive system (drawing). I, male reproductive system, penial sheath partly removed to show penial papilla. Abbreviations: ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A–C = 1 mm; D, E, H = 0.5 mm; F = 200 μm; G = 50 μm; I = 250 μm.

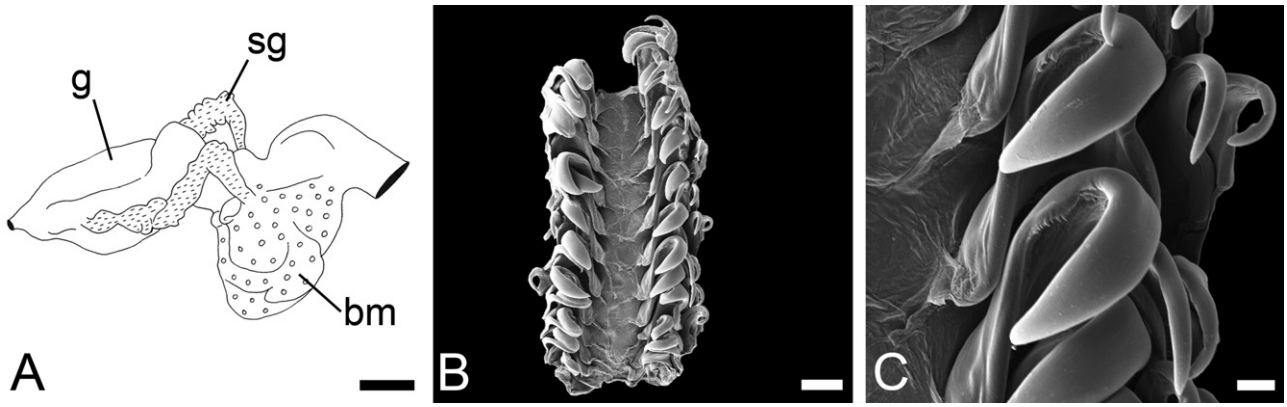

Figure 21. *Philine quadrata*. A, buccal mass (bm), salivary glands (sg), and gizzard (g). B, radula (scanning electron micrograph, SEM). C, detail of radula (SEM). Scale bars: A = 0.5 mm; B = 100 μm; C = 20 μm.

P. finmarchica and *P. quadrata* (present study). Nevertheless, the description of the radula of *P. polaris* by Aurivillius (1887) with two outer laterals and one inner lateral teeth does not match that of *P. finmarchica*, which only has one inner lateral tooth (G. O. Sars, 1878). We did not trace the type material of *P. polaris* but based on the similarities of the shell (shape and sculpture) and radula we consider *P. polaris* to be a synonym of *P. quadrata*. G. O. Sars (1878) mentioned a more or less yellowish colour of the animals in *P. polaris*, making it easy to differentiate between this species and *P. finmarchica* but we could not confirm this feature because only preserved specimens were studied. There is also some confusion between *P. quadrata* and *P. finmarchica* in Pilsbry (1895) because the author mistakenly depicted the former species in pl. 5, figs 14–16, and not figs 17–19 (as claimed), which refer to *P. finmarchica* as represented in G. O. Sars (1878). Høisæter (2009) did not refer to *P. polaris* but WoRMS (Rosenberg, 2011) lists it as a valid species.

Philine quadripartita Ascanius, 1772 (Figs 22A–F, 23A–E, 24A–F)

Philine quadripartita Ascanius, 1772: 329, pl. 10, figs A, B; Lovén, 1847: 141; Nordsieck, 1972: 20, pl. OIII, fig. 6, pl. OVI, fig. 27.

Bulla (Philine) quadripartita – A. Adams, 1855: 599, pl. 125, fig. 159.

Lobaria quadriloba Müller, 1776: 226; Gmelin, 1791: 3143.

Bulla bulla DaCosta 1778: 30, pl. II, fig. 3. syn. nov.

Bulla aperta – Bruguiere, 1789: 375; Gmelin, 1791: 3424; Montagu, 1803: 208; Dillwyn, 1817: 477.

Bullaea aperta – Thorpe, 1844: 137.

?*Bullaea planciana* Lamarck, 1801: 63 (based on Price *et al*., 2011).

Philine aperta – Sowerby, 1859: pl. 20, fig. 20; J. G. Jeffreys, 1867: 457, pl. 8, fig. 7; G. O. Sars, 1878: 298, pl. 11, fig. 15; Monterosato, 1884: 146; Pilsbry, 1895: 10, pl. 3, figs 47–56, pl. 9, figs 1–7; Brown, 1934: 179–210, figs 1–38; Lemche, 1948: 61, 90, fig. 66. Thompson, 1988: 54, fig. 18; van der Linden, 1995: 67; Moen & Svensen, 2004: 316; Høisæter, 2009: 80.

Philine apertissima deFolin, 1893: 147 (based on Price *et al*., 2011).

Philine milne-edwardsi Locard 1897: 34, pl. 1, figs 7–9.

Diagnosis: Shell internal, whitish transparent, smooth. Body whitish transparent, larval kidney not visible. Rachidian tooth absent, one rounded inner lateral tooth with denticulation along inner edge. Gizzard not surrounded by muscle fibres, contains two paired and one unpaired spindle-shaped gizzard plates with pores. Long, thin, convoluted, prostate emerging from sack-like penial sheath that tapers towards genital aperture, with blind caecum, separate ejaculatory duct.

Type locality: Arendal, Norway.

Material examined: Bergen, Norway, one spc (dissected), ZMBN 102289, H = 12.0 mm. Bergen, one spc (dissected), ZMBN 7753, H = 15.4 mm. Bergen, one spc (dissected), ZMBN 26473, H = 3.5 mm. Herdlefjorden, Norway, two spcs (dissected), ZMBN 10741, H = 4.4, 6.4 mm. Kvitsøy, Norway, one spc (dissected), ZMBN 11391, H = 11.8 mm. Jondal, Norway, five spcs (dissected), ZMBN 11393, H = 5.0–9.2 mm. Godøysund, Norway, six spcs (dissected), ZMBN 13172, H = 7.4–14.1 mm. Jondal, Norway, three spcs (dissected), ZMBN 15305, H = 7.2–8.4 mm. Abelvær, Norway, two spcs (dissected), ZMBN 40450, H = 14.4, 14.8 mm. Sørfjorden, Norway, two spcs (dissected),

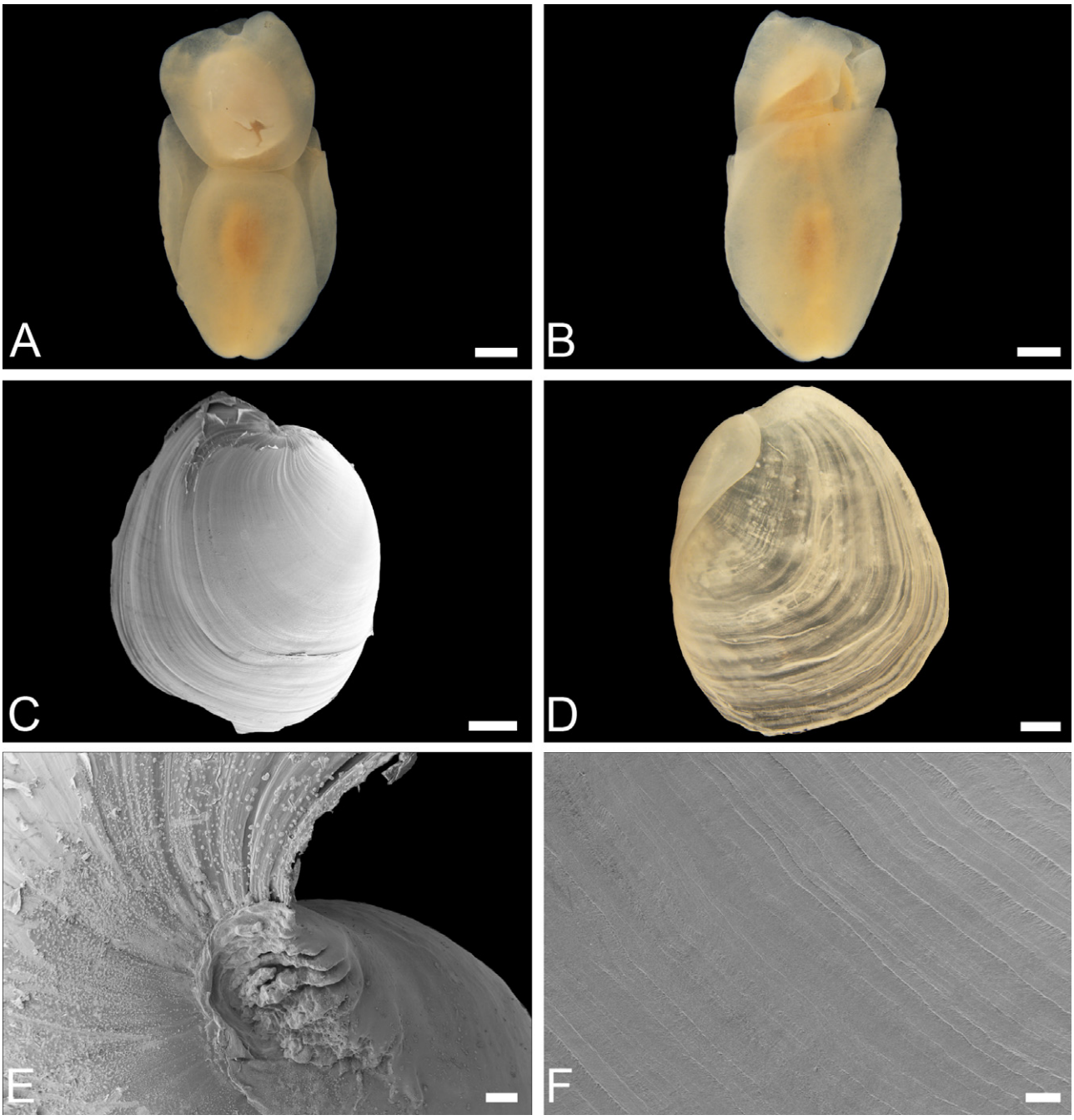

Figure 22. *Philine quadripartita.* A, dorsal view of complete animal. B, ventral view of complete animal. C, dorsal view of shell (scanning electron micrograph, SEM). D, ventral view of shell (automontage picture). E, apex of shell (SEM). F, dorsal surface of shell (SEM). Scale bars: A–D = 1 mm; E = 100 μm; F = 50 μm.

ZMBN 61989, H = 3.9, 4.2 mm. Langevåg, Norway, one spc (dissected), ZMBN 61992, H = 8.1 mm. Samlafjorden, two spcs (dissected), ZMBN 61993, H = 3.4 mm. Sicily, Italy, one spc (dissected), ZMBN 102290, H = 17.0 mm.

Shell (Fig. 22C–F): Maximum H = 17.0 mm. Internal; whitish transparent; oval in shape, aperture very wide, with parietal callus, outer lip smooth, apex obtuse, slightly sunken, with layers on ventral side, not umbilicated; smooth.

Animal (Fig. 22A, B): Body completely whitish transparent, mantle thick. Cephalic shield sometimes slightly indented, median groove present, posterior pallial lobe with dorsal notch. Larval kidney not

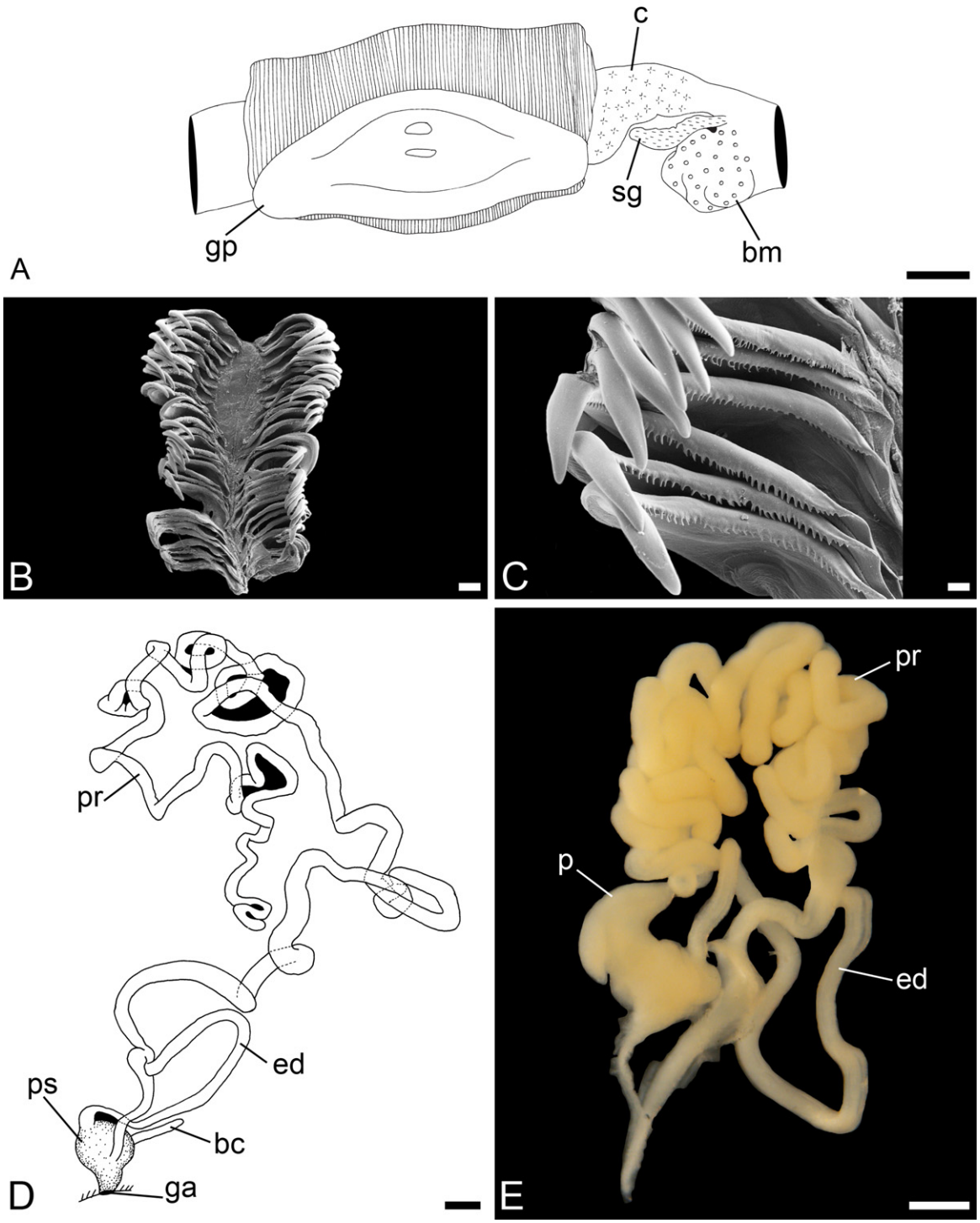

Figure 23. *Philine quadripartita.* A, gizzard with gizzard plates, crop, salivary glands, and buccal mass. B, radula (scanning electron micrograph, SEM). C, detail of radula (SEM). D, male reproductive system (drawing). E, male reproductive system, penial sheath removed. Abbreviations: bc, blind caecum; bm, buccal mass; c, crop; ed, ejaculatory duct; ga, genital aperture; gp, gizzard plates; p, penial papilla; pr, prostate; ps, penial sheath; sg, salivary glands. Scale bars: A, D = 0.5 mm; B = 100 μm; C = 20 μm; E = 250 μm.

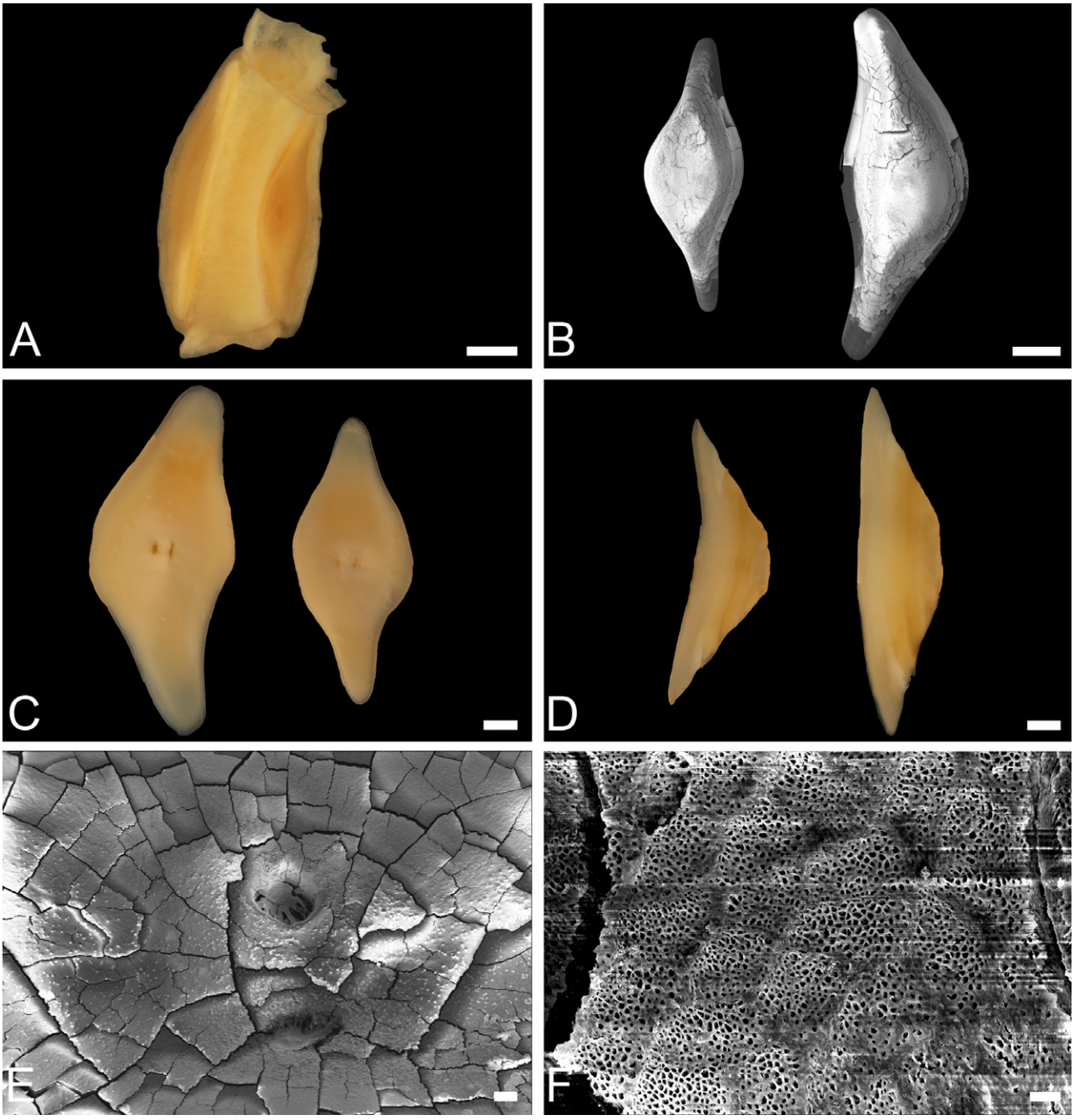

Figure 24. *Philine quadripartita*. A, gizzard (automontage picture). B, dorsal view of gizzard plates, paired plate on right (scanning electron micrograph, SEM). C, ventral view of gizzard plates, paired plate on right (automontage picture). D, lateral view of gizzard plates, paired plate on right (automontage picture). E, pores on ventral surface of paired gizzard plate (SEM). F, ventral surface of unpaired gizzard plate (SEM). Scale bars: A = 0.5 mm; B–D = 1 mm; E = 100 μm; F = 5 μm.

visible through shell. Salivary glands slightly longer than buccal mass.

Radula (Fig. 23B, C): Radular formula $28 \times 1.0.1$. Rachidian tooth absent. Inner lateral teeth with broad base, curved and rounded tips, inner edge denticulate.

Gizzard (Fig. 24A–F): Gizzard elongate cylindrical, not surrounded by muscle fibres, contains two curved paired and one smaller symmetrical unpaired spindle-shaped plates, two pores on ventral surface of all plates, in very young specimen all the way through. Dorsal surface inside the gizzard

brown-yellowish, ventral surface creamy. Microsculpture on ventral surface only.

Male reproductive system (Fig. 23D, E): Obvious separation between long, thin, convoluted prostate and sack-shaped penial sheath with blind caecum, tapering towards the genital aperture. Separate ejaculatory duct. Penial papilla hammer-shaped, upper part smooth, contained in blind caecum.

Ecology: Occurs down to 140 m (Nordsieck, 1972) on sand, brown algae, and mud (present study). Brown (1934) found that the veligers settle down in areas overgrown by eel grass and move to muddy substrate after two years. The diet consists of gastropods, bivalves, and polychaetes (Thompson, 1988), as well as foraminiferans and soft-bottom echinoderms (J. G. Jeffreys, 1867), which are taken alive or recently deceased (Jaeckel, 1952). *Philine quadripartita* is eaten by the brittle star *Ophiocomina nigra* (Abildgaard, in O.F. Müller, 1789) (Brown, 1934), some flatfish, and haddock, which they try to avoid by secreting sulphuric acid (Thompson, 1988).

Distribution: In Norway southwards of Fleinvær (67°10′N) along the entire coast (Høisæter, 2009). Faeroes, Shetland, British Isles, North Sea (Platts, 1985), Baltic Sea (Wiese, 2009), Mediterranean Sea, Black Sea, Cape Verde Islands (Nordsieck, 1972).

Remarks: This eastern Atlantic species has been chronically mistaken with *P. aperta*, an Indo-Pacific species (type locality: Indian Ocean coast of South Africa) (Price *et al*., 2011). This was clearly demonstrated in the recent review of the systematics of the *P. aperta* species-complex and closely related species performed by Price *et al*. (2011).

Philine quadripartita is the largest species of Philinidae inhabiting European waters. The number of radular rows seems to be variable. Price *et al*. (2011) reported 16–19, Lemche (1948) 18–25, and Thompson & Brown (1976) up to 36 rows. In the present study, a maximum of 28 rows was found. Compared to *P. aperta*, the species *P. quadripartita* has smaller, narrower gizzard plates with slightly different microsculpture. Further, the penial papilla is smaller but extends in a blind caecum beyond the penial sheath, which is not the case in *P. aperta*. Price *et al*. (2011) also found differences in the shape of the egg masses.

Some authors have included *Philine emarginata* J. Adams, 1800 as a synonym. However, the description is rather short and the shell figured looks quite different.

Philine retifera (Forbes, 1844)

Bulla retifer Forbes, 1844: 187.

Johania retifera – Monterosato, 1884: 147; Nordsieck, 1972: 19, pl. OIII, fig. 1; Høisæter, 2009: 79.

Philine retifera – Kobelt, 1888: 284; van der Linden, 1995: 75, figs 19, 24, 25.

Philine (*Johania*) *retifera* – Pilsbry, 1895: 27, pl. 4, figs 66–68.

Bulla vestita Philippi, 1844: 95, pl. 20, fig. 4.

Bulla (*Scaphander*) *vestita* – A. Adams, 1855: 574, pl. 121, fig. 48.

Scaphander vestita Sowerby, 1873: pl. *Scaphander* 1, fig. 2. syn. nov.

Philine trachyostraca Watson 1897: 236; Malaquias, 2004: 236, fig. 3C–E (lectotype examined, NMW.1955.158.02421).

Diagnosis: Shell external, with sculpture of raised longitudinal and transverse lines forming a white reticulate pattern on dark background. Body pale yellow.

Type locality: Aegean Sea (Serpho).

Material examined: Funchal Bay, Madeira Island, two sh examined, NMW.1955.158.02421 and NMW.1955.158.02467, H = 1.77, 3.0 mm.

Shell: External; elongate, squared-oval in shape, aperture wide with thick parietal callus, apex obtuse, slightly sunken, umbilicated; white sculpture consisting of raised longitudinal and transverse lines forming a reticulate pattern (Forbes, 1844; van der Linden, 1995; Malaquias, 2004).

Animal: Body pale yellow (Philippi, 1844).

Radula: Unknown.

Gizzard: Unknown.

Male reproductive system: Unknown.

Ecology: Down to 300 m depth on silt and clay (Høisæter, 2009) as well as on muddy sand with decaying dead algae (Mifsud, 2007).

Distribution: ?Norwegian Trench (60°31′N) and?Fensfjorden (Høisæter, 2009; as *Johania* cf. *retifera*). Mediterranean Sea (Monterosato, 1884), off Mauritania (van der Linden, 1995) and Madeira Island (Watson, 1897; Malaquias, 2004).

Remarks: Apart from two shells from Madeira Island (see Material examined), no additional specimens were available for study. Høisæter (2009) attributed, based on sculpture and shape of the shell, two specimens from the Norwegian Trench at 60°31′N to the

species *P.* cf. *retifera* (as *Johania*). However, *P. retifera* is a southern European/northern Africa species (Templado, 2011) and its occurrence in Scandinavia would imply a significant northwards expansion of its geographical range. Further material is necessary to confirm the occurrence of this species in the Scandinavian peninsula.

It is unclear whether Forbes (1844) or Philippi (1844) has priority as author because both publications are from the same year. However, Forbes' publication is a report from 1843 and was therefore probably published earlier than Philippi's work.

PHILINE SCABRA (MÜLLER, 1784) (FIGS 25A–H, 26A–C, 27A–G)

Bulla scabra Müller, 1784: 90; Bruguiere, 1789: 376.

Philine scabra – Malm, 1855: 45; G. O. Sars, 1878: 294, pl. 18, fig. 13, pl. 12, fig. 4; Pilsbry, 1895: 12, pl. 5, figs 1–3; Kobelt, 1896: 148, pl. 19, figs 7, 8; Friele & Grieg, 1901: 113; Lemche, 1948: 66, 67, 91, 92.

Hermania scabra – Monterosato, 1884: 147.

Philine (*Hermania*) *scabra* – Nordsieck, 1972: 19, pl. OIII, fig. 2.

Bulla pectinata Dillwyn, 1817: 481.

Bullaea pectinata – Alder, 1848: 25. syn. nov.

Bullaea granulosa M. Sars, 1835: 73, pl. 14, fig. 36.

Bullaea catenulifera MacGillivray, 1844: 187.

Bullaea catenulifera Thorpe, 1844: 251.

Philine loveni Malm, 1855: 45; G. O. Sars, 1878: 295, pl. 26, fig. 5, pl. 12, fig. 5; Pilsbry, 1895: 14, pl. 4, figs 83–85; Kobelt, 1896: 149, pl. 19, figs 9, 10; Friele & Grieg, 1901: 113.

Philine (*Hermania*) *loveni* – Nordsieck, 1972: 20, pl. OVII, fig. 4 (not pl. OVII, fig. 3).

Diagnosis: Shell internal, transparent with chain-like sculpture in transverse lines. Body white, larval kidney not visible. Rachidian tooth absent, one flattened inner lateral tooth with denticulation along inner edge, one rounded outer lateral tooth. Gizzard surrounded by muscle fibres, contains three equal, spindle-shaped gizzard plates. Long, thin prostate emerging from sack-like penial sheath that tapers towards genital aperture. COI sequences: GenBank JX944792 (ZMBN87087), JX944793 (ZMBN 87078.2), JX944794 (ZMBN 88014), JX944795 (ZMBN 87077), JX944796 (ZMBN 81821), JX944797 (ZMBN 87078.1).

Type locality: Not specified (Denmark and/or Norway).

Material examined: Herdlefjorden, Norway, one spc (dissected), ZMBN 10746, H = 5.1 mm. Hjeltefjorden, Norway, five spcs (dissected), ZMBN 10747, H = 4.3–10.4 mm. Bergensfjordene, Norway, one spc (dissected), ZMBN 11397, H = 5.8 mm. Husnesfjord, Norway, one spc (dissected), ZMBN 11398, H = 6.4 mm. Hauglandsosen, Norway, one spc (dissected and sequenced), ZMBN 81821, H = 6.0 mm. Sifjorden, Norway, one spc (dissected), ZMBN 82089, H = 2.1 mm. 62°35.2′N, 06°26.5′E, Brattvåg, one spc (dissected), ZMBN 82092, H = 4.9 mm. Kristiansund, Norway, two spcs (dissected), ZMBN 82102, H = 2.1, 3.2 mm. Gjerdesvika, Norway, two spcs (dissected), ZMBN 82106, H = 3.8, 4.3 mm. Bjørnafjorden, Norway, two spcs (dissected; one sequenced), ZMBN 87077, H = 5.2, 5.5 mm. Bjørnafjorden, Norway, two spcs (dissected and sequenced), ZMBN 87078, H = 3.1 mm. Tjärnö, Sweden, one spc (dissected), ZMBN 87079, H = 4.2 mm. Hauglandsosen, Norway, one spc (dissected and sequenced), ZMBN 87087, H = 3.4 mm. Strindfjorden, Norway, two spcs (dissected), NTNU 30383, H = 6.1, 7.0 mm. 67°50.81′N, 11°45.85′E, one spc (sequenced), ZMBN 88014, H = 2.8 mm.

Shell (Fig. 25E–H): Maximum H = 10.4 mm. Internal, thin; transparent; elongated-oval cylindrical in shape, aperture wide with thin, whitish parietal callus, outer lip scalloped, apex obtuse, not umbilicated; sculpture visible through mantle, consisting of transverse lines of pits connected to form chains.

Animal (Fig. 25A–D): Body white, mantle thick. Cephalic shield indented, median groove present. Larval kidney not visible through shell. Salivary glands slightly longer than buccal mass.

Radula (Fig. 26A–C): Radular formula 17–22 × 1.1. 0.1.1. Rachidian tooth absent. Inner lateral teeth with broad base, curved and flattened tips, inner edge denticulate. Outer lateral teeth with broad base, straight to curved and rounded tip.

Gizzard (Fig. 27A–E): Gizzard elongate cylindrical, surrounded by muscle fibres, especially thick in the middle, contains three equal, spindle-shaped plates with two longitudinal slits on ventral surface. Dorsal surface inside the gizzard of amber colour, ventral surface more whitish, surrounded by transparent margin. Microsculpture on ventral surface only.

Male reproductive system (Fig. 27F, G): Obvious separation between long, thin, convoluted prostate and elongate sack-shaped penial sheath tapering towards the genital aperture. Prostate thinner towards the penial sheath. Penial papilla cone-shaped, verrucose.

Ecology: Specimens found down to 900 m (Sneli *et al.*, 2005) on sand, sand mixed with shell-gravel, fine shell sand, coarse scree, and mud. Foraminiferans were occasionally found in the gizzard. The egg

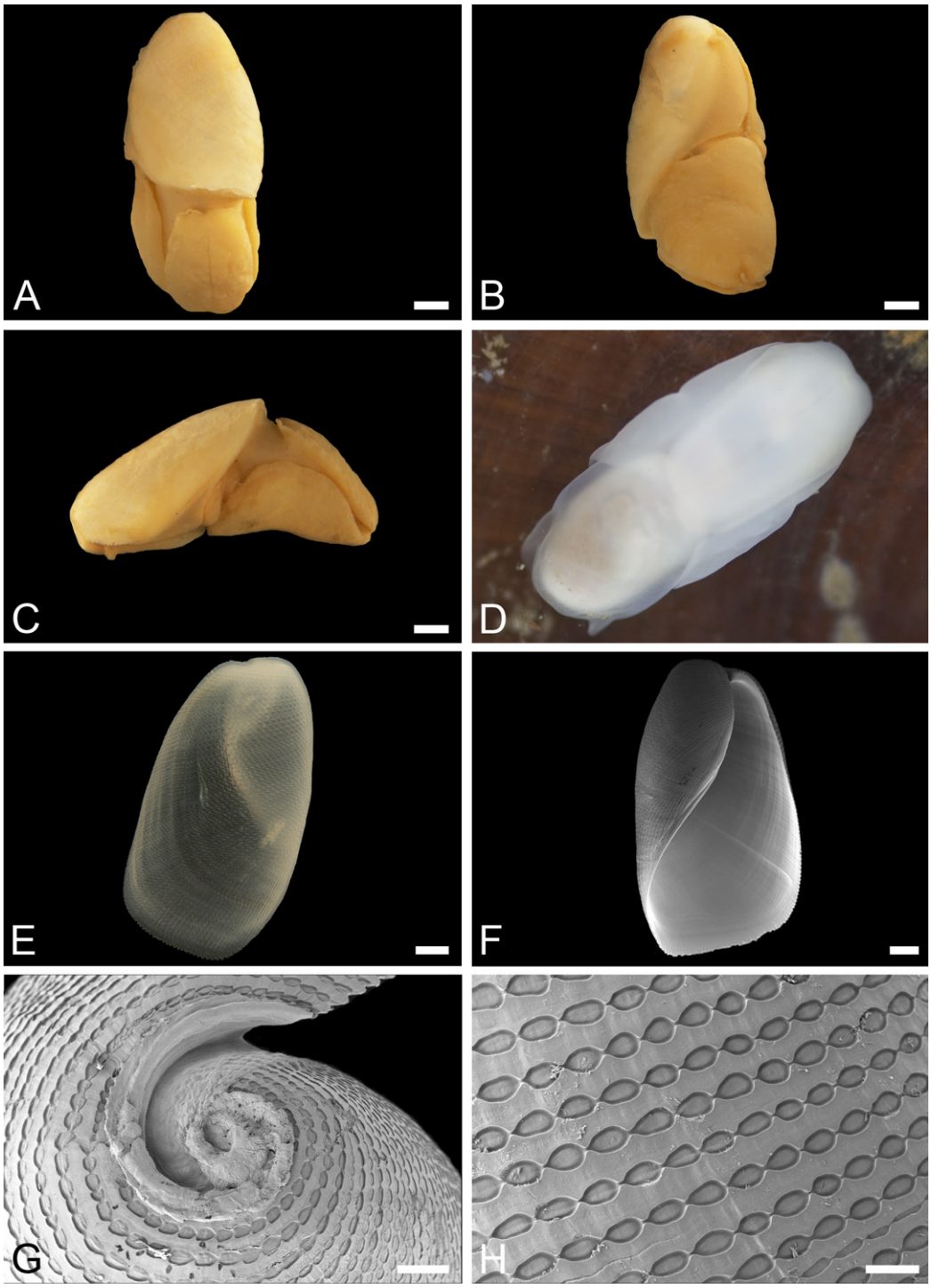

Figure 25. *Philine scabra*. A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, live animal (height = 3.1 mm). E, dorsal view of shell (automontage picture). F, ventral view of shell (scanning electron micrograph, SEM). G, apex of shell (SEM). H, sculpture on dorsal surface of shell (SEM). Scale bars: A–C = 1 mm; E, F = 0.5 mm; G = 200 μm; H = 100 μm.

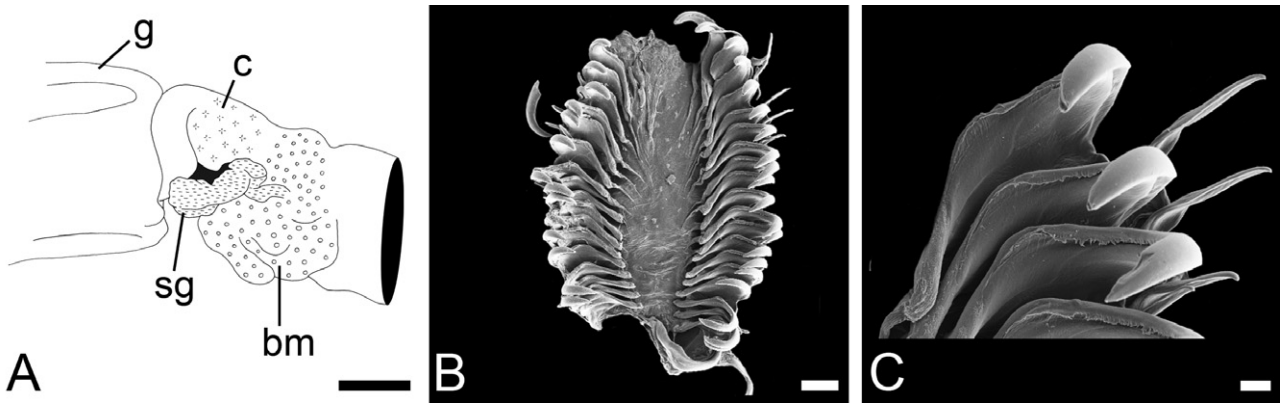

Figure 26. *Philine scabra*. A, buccal mass (bm), salivary gland (sg), crop (c), and gizzard (g). B, radula (scanning electron micrograph, SEM). C, detail of radula (SEM). Scale bars: A = 0.5 mm; B = 100 μm; C = 20 μm.

mass contains only 70 embryos, larvae lack pigments of the velum and statocysts (Thorson, 1946).

Distribution: Present in Greenland, Iceland, Norway south of Hammerfest, Sweden. From the British Isles to the Mediterranean Sea, Madeira, and West Africa (G. O. Sars, 1878; Thompson, 1988; Høisæter *et al*., 2001; present study).

Remarks: G. O. Sars (1878) described the main difference between *P. loveni* and *P. scabra* as the presence of a lobed cephalic shield in the latter, and like Pilsbry (1895) claimed that *P. scabra* has a scalloped shell margin, whereas in *P. loveni* the margin is smooth. In the specimen examined during this study a median groove on the cephalic shield was almost always present, but sometimes so shallow that was difficult to discriminate. Some specimens had a slightly indented cephalic shield, but never formed lobes. The presence of this indention could not be related to the shell being scalloped, as both types of shell margins were found on specimens with and without an indented cephalic shield. Because of this lack of distinction and the fact that the male reproductive system showed no differences, *P. loveni* is here considered a synonym of *P. scabra*. The drawing in Nordsieck (1972: pl. OVII, fig 3), taken from G. O. Sars (1878) to illustrate *Philine* (*Hermania*) *loveni*, is in fact *P. lima* in G. O. Sars (1878). *Bullaea granulosa* M. Sars, 1835 is, according to G. O. Sars (1878: 374), a synonym of *P. scabra* and a different species from *P. granulosa* M. Sars, 1869, which is a synonym of *P. pruinosa* (see Remarks for *P. pruinosa*).

Philine ventricosa (J. G. Jeffreys, 1865) (Figs 28A–H, 29A–G)

Amphisphyra globosa J. G. Jeffreys, 1858 (non Lovén): 47, pl. II, fig. 6.

Amphisphyra ventricosa J. G. Jeffreys, 1865: 332.

Rhinodiaphana ventricosa – Lemche, 1967; Høisæter, 1986: 5411; Høisæter, 2009: 78.

Utriculus ventrosus J. G. Jeffreys, 1867: 425.

Amphisphyra ventrosa – Kobelt, 1896: 66, pl. 11, figs 15, 16.

Philine velutinoides G. O. Sars, 1878: 302, pl. 26, fig. 10a–c, pl. 18, fig. 8 c, d, pl. 12, fig. 14 (type ZMO D1745); Pilsbry, 1895: 21, pl. 4, figs 77, 78 (as *P. pruinosa*), pl. 5, figs 26–28; Kobelt, 1896: 143, pl. 18 figs 16, 17. (type: ZMO D1745).

?*Philinorbis velutinoides* – Nordsieck, 1972: 23, pl. OIII, fig. 16., pl. OVII, fig. 4, pl. OVII, fig. 4.

Diagnosis: Shell internal, brownish transparent, smooth. Body white with opaque dots along the margins of cephalic shield, foot, parapodial lobes and posterior pallial lobes, larval kidney not visible. Rachidian tooth absent, one rounded inner lateral tooth with minute denticulation along inner edge, two rounded outer lateral teeth. Gizzard not surrounded by muscle fibres, no gizzard plates. Long and thin prostate clearly separated from tubular penial sheath. COI sequences: GenBank JX944800 (ZMBN 88008), JX944801 (ZMBN 81820), JX944802 (ZMBN 87080.2), JX944803 (ZMBN 87080.1).

Type locality: Isle of Skye, west Scotland, UK.

Material examined: Hauglandsosen, Norway, one spc (dissected), ZMBN 81820, H = 3.3 mm. Hauglandsosen, Norway, one spc (dissected), ZMBN 81821, H = 6.0 mm. Hauglandsosen, Norway, nine spcs (dissected; one sequenced), ZMBN 87080, H = 2.1–3.8 mm. Lofoten, Norway, one sh, ZMO D1745, H = 3.3 mm. West off Lofoten, 67°52′97″N, 11°19′16″E, Norway, 1 spc (sequenced), ZMBN 88008, H = 2.2 mm. Lofoten, Norway, one sh, ZMO D1745, H = 3.1 mm.

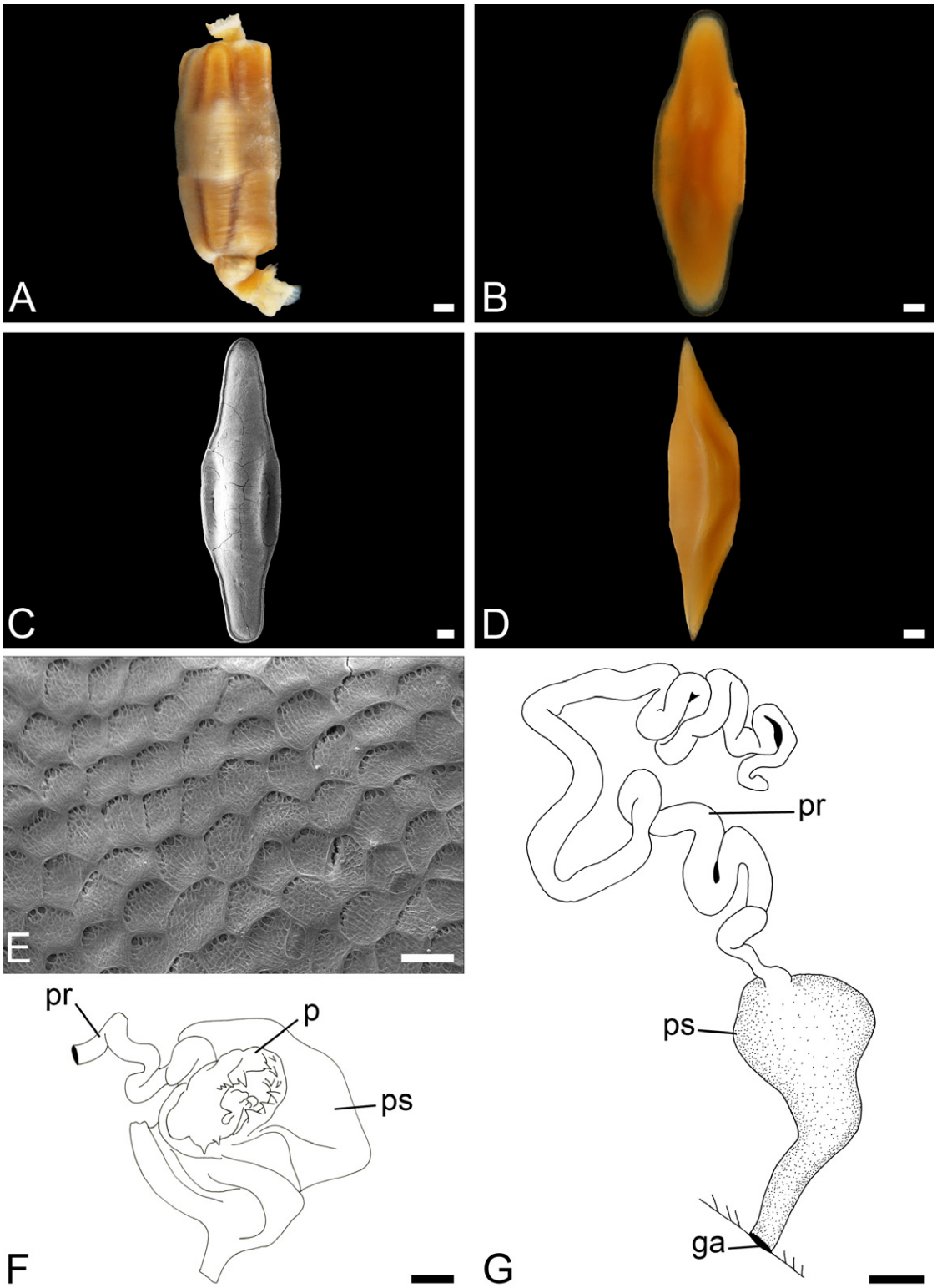

Figure 27. *Philine scabra*. A, gizzard (automontage picture). B, dorsal view of gizzard plate (automontage picture). C, ventral view of gizzard plate (scanning electron micrograph, SEM). D, lateral view of gizzard plate (automontage picture). E, ventral surface of gizzard plate (SEM). F, male reproductive system, penial sheath removed (drawing). G, male reproductive system. Abbreviations: ga, genital aperture; p, penial papilla; pr, prostate; ps, penial sheath. Scale bars: A, B, D = 125 μm; C, F = 200 μm; E = 10 μm; G = 0.5 mm.

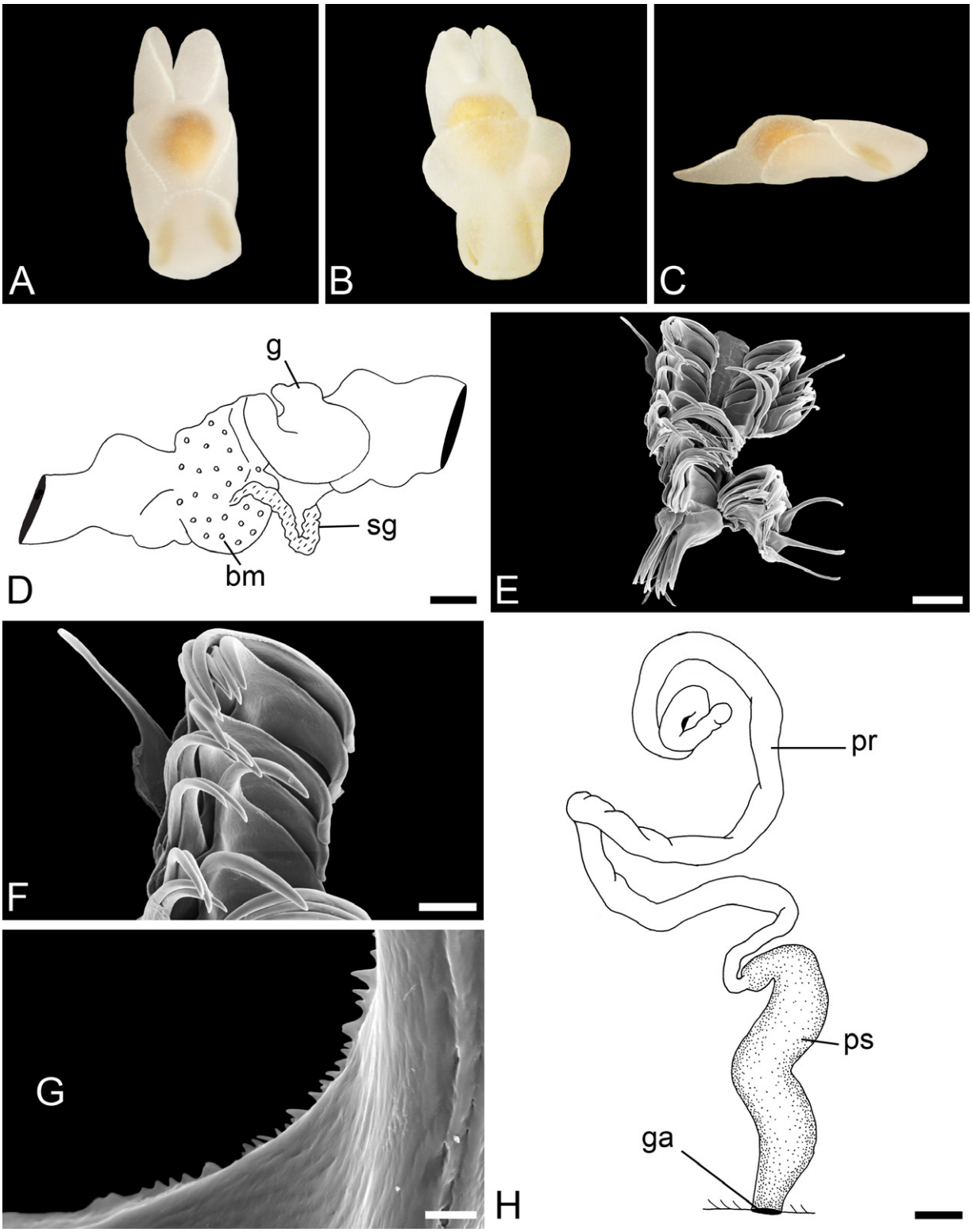

Figure 28. *Philine ventricosa*. A, dorsal view of live animal (~ 7 mm). B, ventral view of live animal. C, right lateral view of live animal. D, buccal mass, salivary gland, and gizzard. E, radula (scanning electron micrograph, SEM). F, detail of radula (SEM). G, detail of denticulation on lateral tooth (SEM). H, male reproductive system (drawing). Abbreviations: bm, buccal mass; g, gizzard; ga, genital aperture; pr, prostate; ps, penial sheath; sg, salivary gland. Scale bars: D = 200 μm; E = 50 μm; F = 20 μm; G = 2 μm; H = 250 μm.

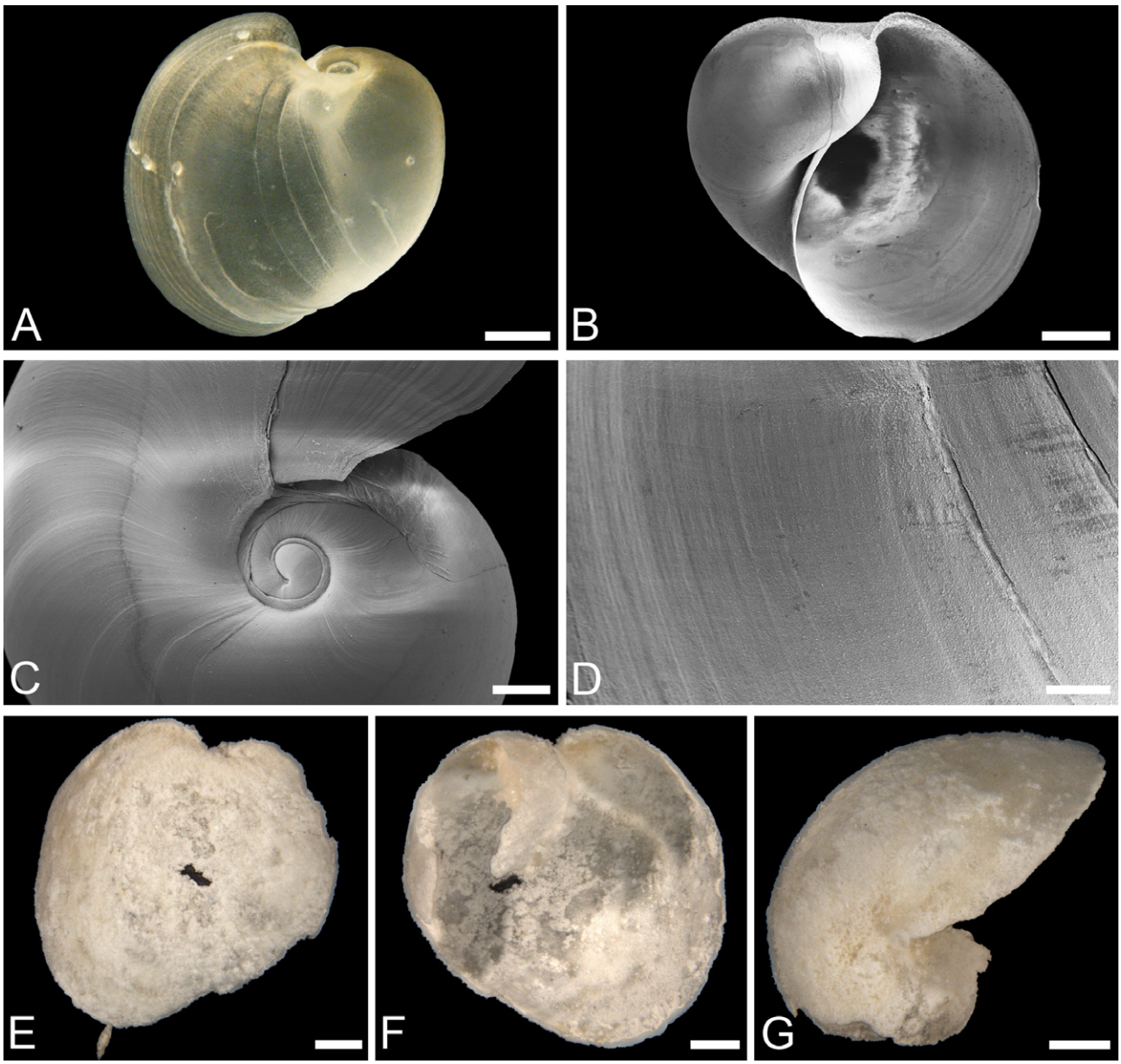

Figure 29. A–D, *Philine ventricosa*. A, dorsal view of shell (automontage picture). B, ventral view of shell (scanning electron micrograph, SEM). C, apex of shell (SEM). D, sculpture on dorsal surface of shell (SEM). E–G, *Philine velutinoides* type (ZMO D1745). E, dorsal view of shell. F, ventral view of shell. G, apex of shell. Scale bars: A, B, E–G = 0.5 mm; C = 200 μm; D = 100 μm.

Shell (Fig. 29A–D): Maximum H = 6.0 mm. Internal, thin; brownish transparent; globose in shape, aperture wide with thin transparent parietal callus, outer lip smooth, apex obtuse and sunken, umbilicated; shell surface smooth.

Animal (Fig. 28A–C): Body whitish transparent with opaque dots along margins of cephalic shield, foot, parapodial lobes, and bifurcated posterior pallial lobe, mantle thin. Cephalic shield tapering posteriorly, median groove absent. Larval kidney not visible through shell. Large brownish Hancock's organs. Salivary glands slightly longer than buccal mass.

Radula (Fig. 28D–G): Radular formula 15 × 2.1.0.1.2. Rachidian tooth absent. Inner lateral teeth with broad base, curved and rounded tips, inner edge minute denticulate. Outer lateral teeth with narrow base, curved but sometimes straight and rounded tip.

Gizzard: Gizzard globose, not surrounded by muscle fibres; plates absent.

Male reproductive system (Fig. 28H): Obvious separation between long, thin, convoluted prostate and tubular penial sheath.

Ecology: Occurs on soft bottom and mud between 80 and 220 m depth.

Distribution: In Norway known from Lofoten and Bergen area (60°25′N) (Høisæter *et al*., 2001; present study). Sneli *et al*. (2005) reported one doubtful specimen from the Faeroes. Also found around the British Isles (Kobelt, 1896).

Remarks: The single specimen found at the Isle of Skye (Scotland) was identified as *Amphisphyra globosa* by J. G. Jeffreys (1858). Later he considered it to be a new species and described it as *A. ventricosa*; however, he did not provide any further explanation (J. G. Jeffreys, 1865: 332). In 1867 he redescribed the same specimen, this time as *Utriculus ventrosus* (J. G. Jeffreys, 1867: 425), according to him because of shape and sculpture differences with *A. globosa*, apparently ignoring his previous 1865 description of *A. ventricosa*. G. O. Sars (1878: 302) described the new species *Philine velutinoides* and discussed the possible, synonym of the latter with Jeffreys' *U. ventrosus*. However, in what seems to presumably be a remark added at a later point, G. O. Sars stated in the Remarks section of his book that both species were the same (G. O. Sars, 1878).

Lemche (1967) transferred *U. ventrosus* to the new genus *Rhinodiaphana* within the family Diaphanidae based on presence of an external shell, lack of gizzard plates, and large tubular prostate, but he stated that he was unsure about the correct taxonomic placement of this species. The radula and male reproductive system depicted by Lemche (1967) look typically philinid and the absence of gizzard plates is also not uncommon in philinids. Lemche (1967) based his description on a single specimen, which seemed to be juvenile (specimen fully stretched = 3.5 mm); moreover he stated that 'the several genital glands seem rather small, indicating that the specimen was not quite ready to spawn'. The fact that the shell was external might either be because it was torn off or that the mantle had not yet grown over the shell. It has been observed in *P. gibba*, *P. scabra*, *P. punctata*, and *P. quadripartita* (as *P. aperta*) that after settling and losing the velum the mantle is not yet completely formed (Horikoshi, 1967; Seager, 1979). Nevertheless, the radula, male reproductive system, shell, and Hancock's organs of the larger specimens studied during the present work (all with shell completely enclosed by the mantle) resembled the illustrations depicted by Lemche (1967).

Some confusion about this species also stems from the fact that G. O. Sars (1878) seems to have misnumbered his drawings, listing the shells of *P. pruinosa* under the same number as the animal of his *P. velutinoides* (pl. 18, figs 8a, b, e: shells of *P. pruinosa*, figs 8c, d: animal of *P. velutinoides*) and the shell of *P. velutinoides* on a different plate (pl. 26, fig. 10a–c: shell of *P. velutinoides*). Pilsbry (1895) probably did not notice this when he used G. O. Sars' drawings and referred to the animal of *P. velutinoides* as *P. pruinosa*, trigging thereafter a mistake that has been perpetuated over time by nearly all authors (e.g. Rudman, 2007).

PHILINE SP. 1 (FIG. 30A–I)

Diagnosis: Shell internal, tapering posteriorly, transparent with chain-like sculpture in transverse lines. Body white, larval kidney visible. Rachidian tooth absent, one rounded inner lateral tooth with coarse denticulation along inner edge, two rounded outer lateral teeth. Gizzard not surrounded by muscle fibres, contains three equal, kidney-bean shaped gizzard plates. Prostate broad and coiled, penial sheath elongate sack-like.

Material examined: Bremsnesfjorden, 63°07′N, 07°41′E, Norway, one spc (dissected), ZMBN 82072, H = 2.4 mm.

Shell: Internal, thin; transparent; oval in shape, posteriorly tapering, aperture wide, apex obtuse; sculpture visible through mantle, consisting of transverse lines of pits connected to form chains.

Animal (Fig. 30A–C): Body completely white, mantle thin. Cephalic shield blunt, median groove absent. Larval kidney visible through shell.

Radula (Fig. 30D, E): Radular formula 13 × 2.1.0.1.2. Rachidian tooth absent. Inner lateral teeth with broad base, curved and rounded tips, inner edge coarsely denticulate. Outer lateral teeth with broad base, curved and rounded tip.

Gizzard (Fig. 30F–H): Gizzard globose, not surrounded by muscle fibres, contains three equal kidney-bean shaped plates with tip on dorsal side. Plates uniformly brown.

Male reproductive system (Fig. 30I): Obvious separation between broad, tubular coiled prostate emerging from elongate sack-shaped penial sheath. Prostate thinner towards the penial sheath.

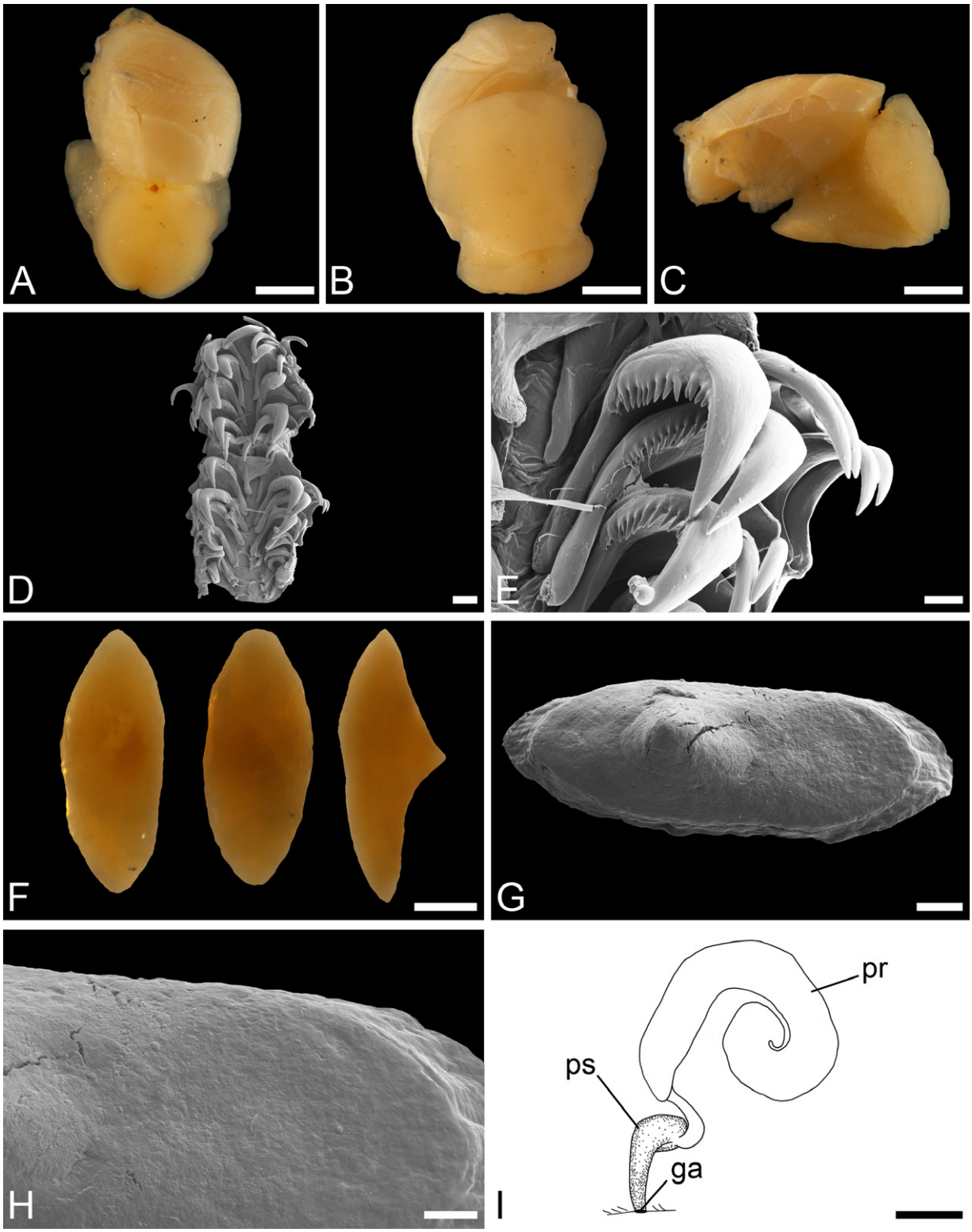

Figure 30. *Philine* sp. 1. A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, radula (scanning electron micrograph, SEM). E, detail of radula (SEM). F, left to right: dorsal, ventral, and lateral view of gizzard plate (automontage picture). G, dorsal view of gizzard plate (SEM). H, dorsal surface of gizzard plate (SEM). I, male reproductive system (drawing). Abbreviations: ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A–C = 0.5 mm, D = 30 μm, E = 10 μm, F = 50 μm, G = 20 μm, H = 5 μm, I = 250 μm.

Ecology: Between 180 and 200 m deep on rock, gravel, and sand ground bottom.

Distribution: Norway, Bremnesfjorden, 63°07′N, 07°41′E.

Remarks: The specimen could not be assigned to any described species. It resembles *P. punctata* because of shell shape, animal external morphology, and size. However, detailed study of its morphology and anatomy revealed significant differences. The animal lacks coloration along the body (dark dots), the shell has fused pits forming chains, the gizzard plates have equal sizes, and the male reproductive system is made up of a distinct penial area and a coiled prostate duct that narrows towards the penial area.

PHILINE SP. 2 (FIG. 31A–F)

Diagnosis: Shell may be internal, whitish transparent, elongate-oval in shape, apex obtuse, with reticulate sculpture. Body white. Gizzard not surrounded by muscle fibres, with gizzard plates. Obvious separation between flat, tubular prostate emerging from tubular penial sheath with two folds. COI sequences: GenBank JX 944806 (ZMBN 81806), JX 944807 (ZMBN 88015).

Material examined: Hauglandsosen, Norway, one spc (dissected and sequenced), ZMBN 81806, H = 2.2 mm. 67°53′37″N, 11°19′16″E, one spc, (sequenced), ZMBN 88015, H = 2.6 mm.

Shell (Fig. 31D, E): ?Internal, thin; transparent; elongate-oval in shape, aperture wide with thin, whitish parietal callus, outer lip smooth, apex obtuse, slightly sunken, umbilicated; sculpture consisting of transverse and longitudinal lines forming a reticulate pattern.

Animal (Fig. 31A–C): Body white, mantle seems to be torn off. Cephalic shield blunt, median groove absent. Larval kidney not visible through shell.

Radula: Unknown.

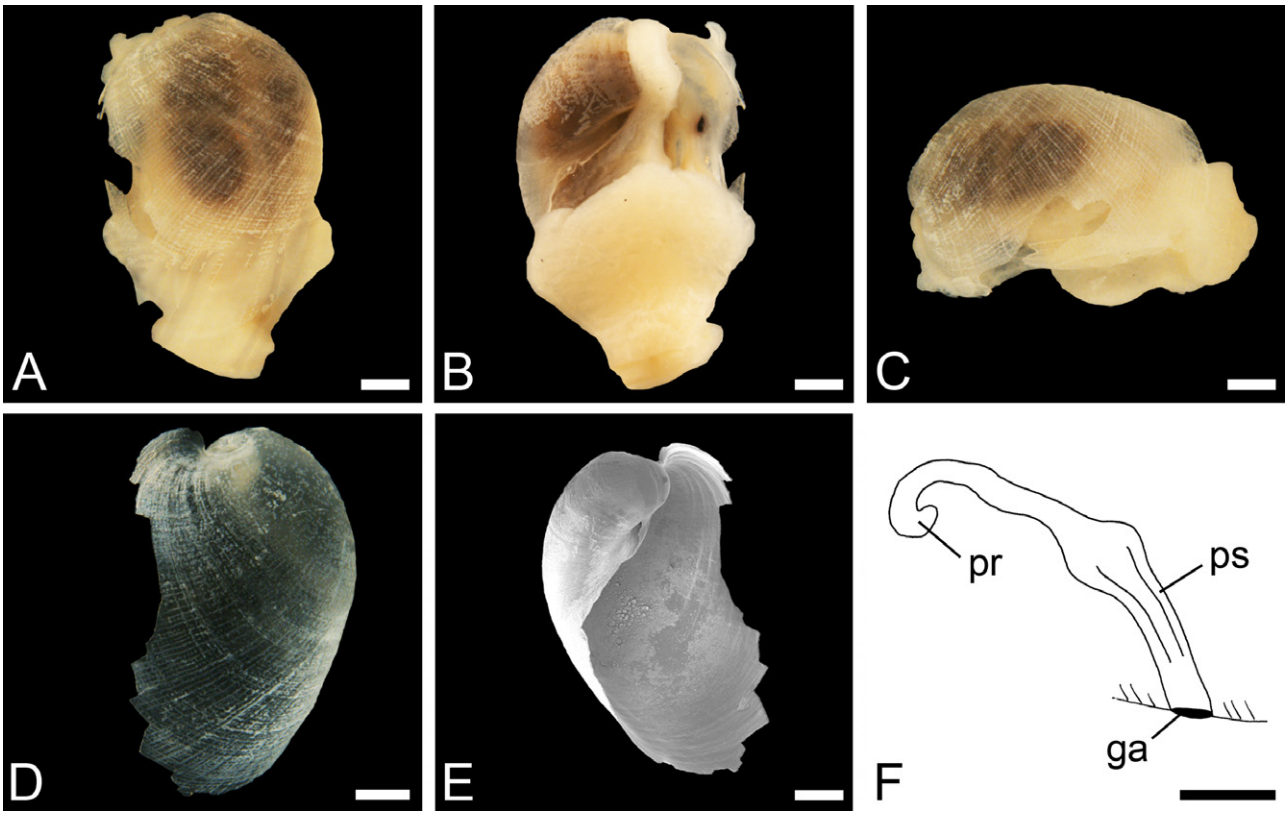

Figure 31. *Philine* sp. 2. A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (automontage picture). E, ventral view of shell (scanning electron micrograph). F, male reproductive system (drawing). Abbreviations: ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A–E = 300 μm; F = 250 μm.

Gizzard: Gizzard globose, not surrounded by muscle fibres, contains kidney-bean shaped, brown plates.

Male reproductive system (Fig. 31F): Obvious separation between flat, tubular prostate emerging from tubular penial sheath with two folds.

Ecology: Between 198 and 240 m deep on mud.

Distribution: Norway, Hauglandsosen, 60°25′N.

Remarks: This species resembles *P. pruinosa* but the shell pattern is not as coarse and lacks the brownish transverse band often present in the latter species. Moreover, molecular phylogenetics analysis showed them to be different, with an uncorrected *p*-distance of 11.6% for the COI gene (Fig. 33). The only other European species with a coarse shell sculpture is *P. retifera* but the latter has a reticulated shell sculpture, not present in the examined specimen and its presence in Scandinavia remains doubtful (see Remarks for *P. retifera*). Either *P. retifera* occurs as far north as Norway or this is a new species also with a coarse, sculptured shell. Further material is necessary to clarify the taxonomic identity of these specimens.

Philine sp. 3 (Fig. 32A–C)

Diagnosis: Shell external; transparent; cylindrical in shape with chain-like sculpture in transverse lines. Larval kidney visible.

Material examined: Faeroes, 63°02.7′N, 07°01.7′W, one spc, NTNU 63677, H = 3.3 mm.

Shell (Fig. 32A–C): External, thin; transparent; cylindrical, elongate-oval in shape, aperture wide with thin parietal callus; outer lip smooth, apex obtuse, slightly sunken, not umbilicated; sculpture consisting of transverse lines of pits connected to form chains.

Animal: Larval kidney visible through shell.

Radula: Unknown.

Gizzard: Unknown.

Male reproductive system: Unknown.

Ecology: Found at 1022 m depth.

Distribution: Faeroes.

Remarks: This species is different from typical philinid shells, resembling more a *Cylichna* in its elongate, tightly coiled cylindrical shell shape. However, the shell is not as thick as in *Cylichna*, with a larger aperture, and is sculptured with catenoid chains typical of philinids.

Phylogenetic analysis

The phylogeny included ten species (Fig. 33), which represents about 60% of the diversity of philinid gastropods recognized in Scandinavia (based on present account; see Tables 1, 3) and about 30% of the European diversity (based on CLEMAM, 2012, with modifications after results of present account). Concerning species recognition, both parsimony (not depicted) and Bayesian trees were nearly congruent. The only difference was the support achieved by the cluster of specimens of *P. scabra* that received maximum support in the parsimony analysis [bootstrap (BS) = 100%] but a low posterior probability (PP = 0.7) in the Bayesian analysis. Intraspecific genetic variability (uncorrected *p*-distance) ranged between 0 and 1%, whereas interspecific differences for sister

Figure 32. *Philine* sp. 3. A, dorsal view of shell. B, ventral view of shell. C, apex of shell. Scale bars: A, B = 0.5 mm; C = 100 μm.

KEY TO NORTH-EAST ATLANTIC SPECIES OF THE FAMILY PHILINIDAE*

1.	Cephalic shield lobed	*Philine lima*
–.	Cephalic shield without lobes	2
2.	Shell at least partly external	3
–.	Shell completely internal	6
3.	Shell smooth	4
–.	Shell sculptured	5
4.	Shell completely external, animal with dark dots	*Philine denticulata*
–.	Shell partly external, animal white	*Philine confusa*
5.	Shell with reticulate pumice-like sculpture	*Philine retifera*
–.	Shell with chain-like sculpture	*Philine* sp. 3
6.	Shell with reticulate sculpture	7
–.	Shell smooth or sculptured differently	8
7.	Gizzard plates present	*Philine* sp. 2
–.	Gizzard plates absent	*Philine pruinosa*
8.	Shell smooth	9
–.	Shell sculptured	11
9.	Animal without bifurcated pallial lobe	10
–.	Animal with bifurcated pallial lobe	*Philine ventricosa*
10.	Shell globose	*Philine grandioculi*
–.	Shell plate-like	*Philine quadripartita*
11.	Shell elongated, cylindrical	12
–.	Shell not elongated, plate-like	13
12.	Penial sheath with bulb, prostate short	*Philine indistincta*
–.	Penial sheath lacks bulb, prostate long and coiled	*Philine scabra*
13.	Shell keeled with wing-like protrusion	*Philine angulata*
–.	Shell without wing-like protrusion	14
14.	Gizzard plates present	15
–.	Gizzard plates absent	*Philine quadrata*
15.	Kidney-bean shaped plates	16
–.	Spindle-shaped plates	17
16.	Three equal plates	*Philine* sp. 1
–.	Two paired and one smaller unpaired plate	*Philine punctata*
17.	Shell sculpture consists of fused pits forming a groove	*Philine finmarchica*
–.	Shell sculpture consists of chain-like connected pits	*Philine catena*

*The species *Philine infortunata* is not included because it is only known from the shell.

species pairs ranged between 7.6 and 8.2% (*P. scabra*/*P. indistincta* sp. nov.), 10.6% (*P. pruinosa*/*Philine* sp. 2), and 19.7% (*P. finmarchica*/*P. quadripartita*).

DISCUSSION

A total of 19 species of *Philine* have been identified here, with two described as new to science (*P. indistincta* and *P. grandioculi*). The species *P. indistincta* has a shell and external morphology that are undistinguishable from its sister *P. scabra*. However, they have different anatomies, particularly the reproductive systems with distinct prostate and penis morphologies (see Figs 10–12, 25–27). Additionally, they differ genetically by 7.6–8.2% (uncorrected *p*-distance for COI gene; Fig. 33). Reciprocal monophyly between these species had maximum support in the parsimony analysis (BS = 100%) and was not contradicted in the Bayesian analysis (Fig. 33). The species *P. grandioculi* has a conspicuous and unique feature, the presence of large visible eyes (Fig. 15D).

Formal description of the three unidentified and putatively new species to science will require additional specimens for morphoanatomical comparison with other Atlantic philinids and for molecular phylogenetic analysis. Only one specimen was available for morphological characterization for each of these species.

Philine retifera has been referred only by Høisæter (2009) to Norway and with taxonomic uncertainty (as *Johania* cf. *retifera*). We decided to include the species in the present account but its occurrence in Scandinavia requires further confirmation.

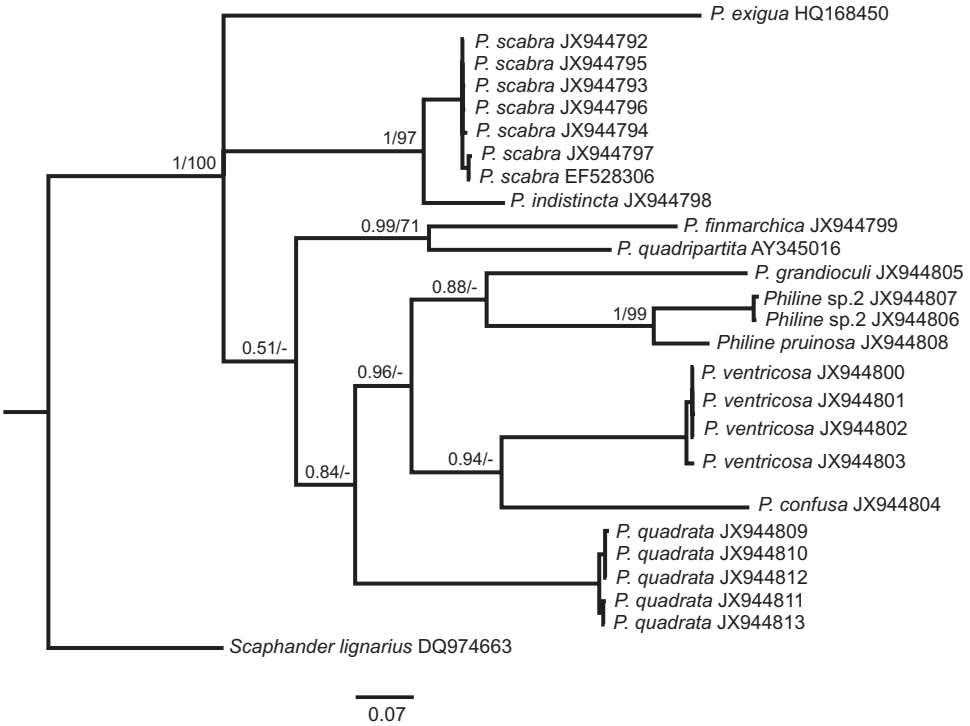

Figure 33. Phylogenetic hypothesis for *Philine* species based on Bayesian inference analysis of mitochondrial cytochrome *c* subunit I gene sequences. Numbers above branches represent posterior probabilities (on left side of dashed line) and parsimony bootstrap support (on right side of dashed line).

The division of the family Philinidae into the genera *Johania*, *Laona*, and *Philine* is based on shell characters alone. The genera *Retusophiline* was introduced for *P. lima* because of putative differences in the shell and cephalic shield (Nordsieck, 1972) and *Praephiline* was introduced for *P. finmarchica* because of anatomical differences (Chaban & Soldatenko, 2009; see Introduction). This classification has been used in part by some authors (e.g. Kantor & Sysoev, 2006; Høisæter, 2009, 2010) but questioned or ignored by the large majority (e.g. G. O. Sars, 1878; Lemche, 1948; Rudman, 1972; Bouchet, 1975; van der Linden, 1995). This generic division did not receive support either in the molecular phylogenetic analysis (Fig. 33) or during a preliminary cladistics analysis based on morphoanatomical characters (not depicted). Therefore we here assign all species to the nominal genus *Philine*. A proper testing of the generic classification of Philinidae would require a broader taxa set and a molecular phylogenetic framework based on several gene markers.

The external morphology of philinids (size, shape of cephalic shield, presence of visible eyes) and the shell (shape and sculpture) were found to be good diagnostic characters (see Key). Only the *P. scabra*/*P. indistincta* and *P. pruinosa*/*Philine* sp. 2 species pairs were not possible to separate based on these features. The male copulatory system is unique to each species and is therefore the most reliable systematic character.

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Table 3. List of specimens used in the phylogenetic analyses with voucher numbers and GenBank accession number

Taxon name	Voucher no.	GenBank accession nos	Locality
Philine pruinosa	ZMBN 87076	JX944808	Tjärnö, Sweden
Philine confusa	ZMBN 87081	JX944804	Hauglandsosen, Norway
Philine exigua	–	HQ168450	Solomon Islands, West Pacific
Philine finmarchica	ZMBN 102288	JX944799	Finnmark, Norway
Philine indistincta	ZMBN 82108.2	JX944798	Silavågen, Norway
Philine quadrata	ZMBN 86184.1	JX944813	South off Iceland
Philine quadrata	ZMBN 86184.2	JX944810	South off Iceland
Philine quadrata	ZMBN 88012.1	JX944809	Off Lofoten, Norway
Philine quadrata	ZMBN 88012.2	JX944811	Off Lofoten, Norway
Philine quadrata	ZMBN 88013	JX944812	Off Lofoten, Norway
Philine quadripartita (as *P. aperta*)	–	AY345016	Spain
Philine scabra	ZMBN 87077	JX944795	Bjørnafjord, Norway
Philine scabra	ZMBN 81821	JX944796	Hauglandsosen, Norway
Philine scabra	ZMBN 87087	JX944792	Hauglandsosen, Norway
Philine scabra	ZMBN 87078.1	JX944797	Bjørnafjord, Norway
Philine scabra	ZMBN 87078.2	JX944793	Bjørnafjord, Norway
Philine scabra	–	EF528306	Sweden
Philine scabra	ZMBN 88014	JX944794	Off Lofoten, Norway
Philine sp. 2	ZMBN 81806	JX944806	Hauglandsosen, Norway
Philine sp. 2	ZMBN 88015	JX944807	Off Lofoten, Norway
Philine grandioculi	ZMBN 88009	JX944805	Off Lofoten, Norway
Philine ventricosa	ZMBN 88008	JX944800	Off Lofoten, Norway
Philine ventricosa	ZMBN 87080.1	JX944803	Norway
Philine ventricosa	ZMBN 87080.2	JX944802	Norway
Philine ventricosa	ZMBN 81820	JX944801	Norway
Scaphander lignarius	–	DQ974663	Portugal

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