

Xylodiscula planata sp. nov., a “lower” heterobranch gastropod from Norwegian waters

Tore Høisæter & Per J. Johannessen

SARSIA

Høisæter T, Johannessen PJ. 2001. *Xylodiscula planata* sp. nov., a “lower” heterobranch gastropod from Norwegian waters. *Sarsia* 86:325-332.



A small gastropod, closely related to a couple of species known from moderately deep water in the Mediterranean, is described as a new species based on nine specimens. The snails were found in four grab samples, one on a sandy-rocky bottom in outer Sognefjorden, two on silty-sandy bottom in outer Hardangerfjorden, both from 34 m, and finally one from 54 m depth outside Sotra, W of Bergen. This is the first record of a member of the heterobranch family Xylodisculidae from Norwegian waters. The specimens were all found in the immediate vicinity of salmon farms, and a preference by the species for the reducing environment of decaying, surplus fish feed is suggested.

Tore Høisæter (corresponding author) & Per Johannessen, University of Bergen, Department of Fisheries and Marine Biology, PO Box 7800, N-5020 Bergen, Norway. *Present address: Section of Applied Environmental Research, Bergen High-Technology Centre, N-5020 Bergen, Norway. E-mail: tore.hoisater@ifm.uib.no*

Keywords: Heterobranchia; Xylodisculidae; western coast of Norway; fauna associated with surplus fish feed.

INTRODUCTION

Two specimens of a small, unusual gastropod were found during routine monitoring of the environmental conditions of a salmon farm in the outer parts of Sognefjorden, western Norway. Subsequently, seven further specimens have turned up in grab samples from two other fish farms. The gastropod looks superficially like *Skeneopsis planorbis* (Fabricius, 1780), but several shell characters suggest that it is unrelated to that species. None of the other species listed in the checklist of Høisæter (1986), could be mistaken for the specimens found. Since the publication of the check-list, Warén (1989, 1991, 1992) has described a number of small, globular or low-spined gastropods from the Norwegian fauna. Most of these are from waters deeper than 200 m, from the shelf outside western and north-western Norway, while the present material was found on rather shallow, sandy-rocky bottoms in the outer parts of fjords. None of the species described by Warén from Norwegian waters are at all like our specimens. However, our specimens more or less fit the description of a “skeneimorph” gastropod from moderately deep water in the Mediterranean, described by Warén (1992) and assigned by him to the genus *Xylodiscula* Marshall, 1988. Study of the radula supports the conclusion that our specimens belong to this genus, although sufficiently distinct from any described species to warrant its description as a new species.

MATERIAL AND METHODS

The material has been collected during routine monitoring of the environmental impact of salmon farms. Over the last 20 years, more than 100 fish farms have been monitored in this way, almost all by the same group of biologists, and with the same methodology, sampling of several sites on the bottom close to the fish enclosures, with a 0.2 m² van Veen grab.

The new species have been found close to three such fish farms: In Rysjedalsvika, municipality of Hyllestad, on the northern shore of the outer parts of Sognefjorden, 61°06.9'N, 05°16.4'E. (locality A); near the northern tip of Fjelbergøy, south of Halsnøy in Klosterfjorden, 59°45.5'N, 05°41.0'E (locality B); and in Skorposen, close to Algrøy west of Sotra, 60°19.9'N, 04°56.7'E (locality C) (see Table 1, and map Fig. 1).

Locality A is a little bay where a salmon farm has been active at intervals since 1987. Altogether fifteen 0.2 m² van Veen grab samples were taken at five different localities within the bay in May 1993 and March 1995. The only grab sample in which the new species was found, was one of two taken in 1995 at a site just outside a floating platform used for cleaning the fish enclosure nets, at 34 m, on sandy bottom (Table 1).

Locality B is just outside the northernmost point of Fjelbergøy. Three replicate grab samples at each of three different localities at varying distances from a fish farm, were taken on four occasions in 1997. The new species

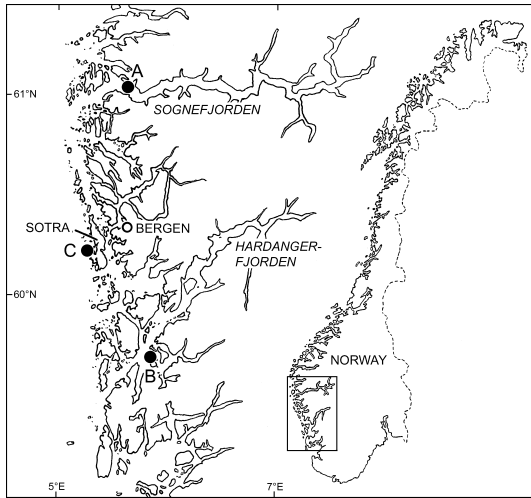


Fig. 1. Map of the part of the Norwegian coast where the new species has been found.

was collected only at the sampling locality closest to the fish farm, c. 20 m outside the nets. At this locality, the species was recovered in one of the replicates at each of two dates, two specimens in March (B_1), and three in April (B_2). The sediment (Table 1) smelled of decaying fish feed, and remnants of feed were found in the grab samples.

Locality C is in Skorposen, west of Sotra, in the outer coastal zone outside Bergen. The locality is partly sheltered from the North Sea by a little island. Like the other two localities this one is also in close proximity to a salmon farm, 15 m outside the nearest fish enclosure, in relatively coarse sediment at 54 m depth. This locality was sampled at five occasions, from March to August 1997. The two specimens found here were taken in one of three replicate grab samples in April.

Table 1. Available locality and environmental information on the three salmon farms in which specimens of the new species have been found. (A - Rysjedalsvika, B - Fjelbergøy, C - Skorposen). General description of sediment: Sand with a little silt (A), well-sorted sand-silt (B), and rather coarse shell sand and gravel with much silt (C).

Locality	A	B_1	B_2	C
Area	Sogneffj.	Hardangerfj.		Outer coast
Collecting date	March 1995	March 1997	April 1997	April 1997
Depth (m)	34	34	34	54
Number of grab stations	5	3	3	1
Number of sampling occasions	2		4	5
Total number of grab hauls	30		36	15
Sediment vol. (l)	2	3	4	15
% sand and gravel	80	62	65	54
% loss on ignition	4.2	3.2	2.3	10.1

SYSTEMATICS

Family Xylodisculidae Warén, 1992
Genus *Xylodiscula* Marshall, 1988

Type species. *Xylodiscula vitrea* Marshall, 1988, by original designation. Type locality: deep water off New South Wales, on sunken driftwood.

Diagnosis. Subdiscoidal shell, transparent, fragile, and smooth, small (diameter to 3.9 mm, but most species < 2.0 mm). Hyperstrophic protoconch (in species with planktotrophic development). Animal with anteriorly shallowly bifid foot, long, slender tentacles with small eyes in their base, short, cylindrical snout and two palial tentacles of which the anterior one is much longer. Radula formula: 2-1-0-1-2. Lateral teeth roughly fan-shaped with a narrow base, broad, serrated edge and outer, smooth side folded forwards. Inner marginal tooth broader, paddle shaped with inner side and broad, rounded top finely serrated. Outer marginal claw-shaped with inner side serrated for a short distance close to point. Jaws apparently absent. (Warén 1992).

Xylodiscula planata sp. nov.

Type locality. Rysjedalsvika in the municipality of Hyllestad, on the northern shore of the outer parts of Sognefjorden, 61°06.9'N, 05°16.4'E. 34 m, silty sand.

Type material. Holotype (on a SEM-stub) ZMBN (Zoological Museum Bergen Norway) 66812, Paratype, SEM-stub of protoconch and radula, SMNH (Swedish Museum of Natural History) 5188.

Material examined. The holotype and the paratype from the type locality, five specimens from Fjelbergøy, south of Halsnøy in Klosterfjorden, 59° 45.5'N, 05° 41.0'E,



Fig. 2. Scanning electron micrograph of shell of holotype of *Xylodiscula planata* sp. nov. Dorsal view. Scale bar 100 μ m.

and two from Skorposen west of Sotra, 60°20'N, 04°56'E. (Some of these destroyed in failed attempt to make radula preparation).

Etymology. *Planatus* (Latin), flat

Description. Holotype was originally 1.7 mm in diameter, but a small portion of the outer lip has since broken off. Shell (Figs 2-5) thin, fragile and completely transparent. Essentially planispiral, and no sculpture except for fine, close-set, slightly sinuous growth lines (Fig. 3). Whorls evenly rounded, with a deep and distinct suture. Aperture entire, with a diameter of c. 700 μ m. Slightly more than two, regularly expanding, teleoconch whorls. Protoconch with small, distinctly inrolled tip (Fig. 5). Number of larval whorls difficult to determine, as no clear demarcation of border between larval and teleoconch whorls could be found. Umbilicus wide (umbilical diameter c. 24 % of shell diameter) and deep exposing inner whorls of protoconch. Periostracum thin, colourless to faintly yellowish, transparent, easily seen only in dried specimens (Fig. 3). In most specimens traces of yellow to orange “ferruginous” deposit, present in umbilical opening (Fig. 4), partly covering the protoconch, in suture and in shallow erosion scars on shell (Fig. 5). Operculum slightly yellowish, stiff but fragile, multispiral with (at least) six spiral turns. Scattered small grains of “ferruginous” deposit found also on outer surface of operculum.

The animal, as seen through the shell in alcohol-preserved specimens, almost colourless, except for a couple of opaque, white “blotches” on the right side of the animal, just behind the head/foot complex (Fig. 6A) (probably identical to the pigmented mantle organs men-



Fig. 3. Scanning electron micrograph of shell of holotype of *Xylodiscula planata* sp. nov. Lateral view. Scale bar 100 μ m.

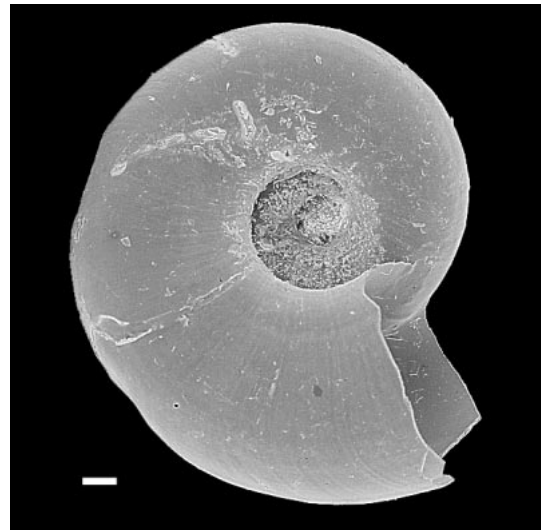


Fig. 4. Scanning electron micrograph of shell of holotype of *Xylodiscula planata* sp. nov. Ventral view. Scale bar 100 μ m.

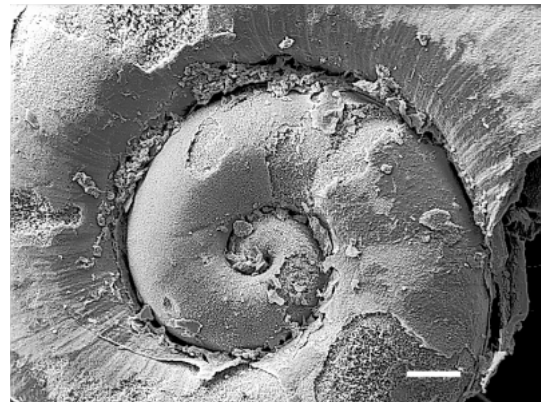


Fig. 5. Scanning electron micrograph of shell of paratype of *Xylodiscula planata* sp. nov. Dorsal view of nuclear whorls. Scale bar 50 μ m. Preparation and photo by Anders Warén.

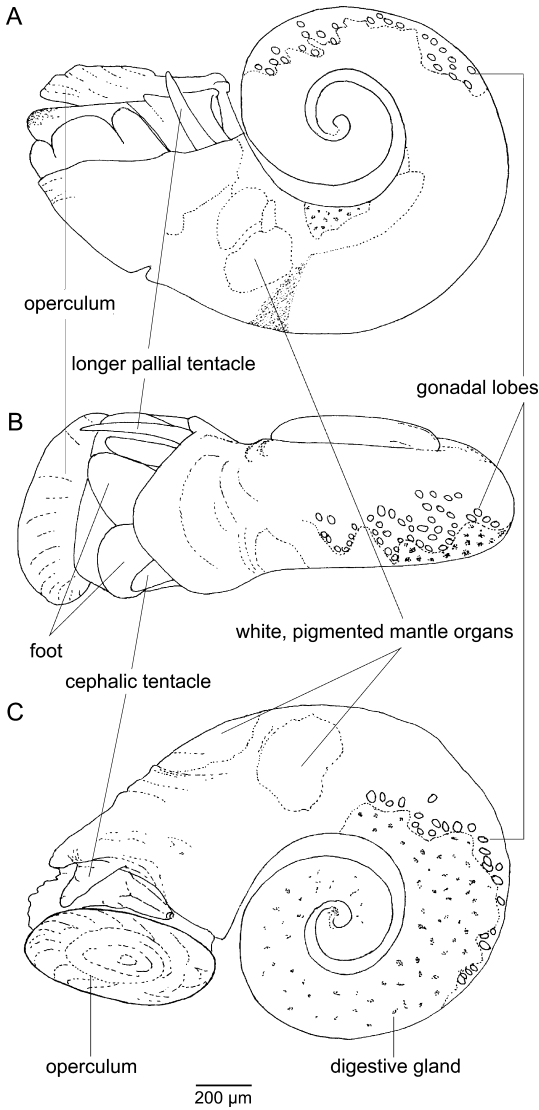


Fig. 6. Drawing of some soft-part features. Composite of two specimens from Fjelbergøy. A) Decalcified animal, right side view; B) Dorsal view; C) Left side view. Scale bar 200 µm.

tioned by Warén (1992) for *Xylodiscula bouchetti*, and the elongated, reddish brown digestive gland, richly spotted with dark brown granules. Gonad and digestive gland sharing the spire, with digestive gland on the outer side of the spiral (Fig. 6 A-C). No pigmented eyes visible through the shell in preserved specimens, but after removal of the shell and mantle, tiny, black, half-moon shaped eyes visible at the base of cephalic tentacles. Cephalic tentacles long and solid, somewhat spatulate at their tips (Fig. 7C), densely covered with cilia. Adja-

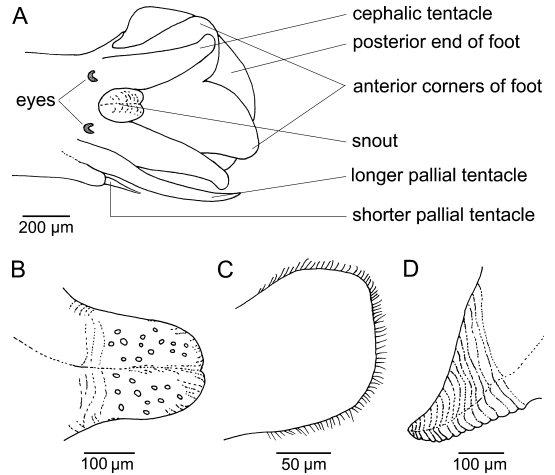


Fig. 7. A) Head-foot complex, with pallial tentacles, after removal of the mantle (Scale bar 200 µm); B) Enlarged view of snout (Scale bar 100 µm); C) Spatulate tip of cephalic tentacle (Scale bar 50 µm); D) Small bipectinate gill (Scale bar 100 µm).

cent to the right-side cephalic tentacle (Fig. 7A) two slender pallial tentacles, the anterior about three times as long as the posterior. Snout short and muscular, with a dense cover of papillae (Fig. 7B). Bipectinate gill (Fig. 7D), attached to the ceiling of the pallial skirt. The investigated specimens had no epipodial tentacles, no penis, no lateral extension of the snout, nor of the posterior or anterior corners of the short foot.

As our own attempts to produce an acceptable radula preparation failed, we appealed to Anders Warén, who succeeded in making a SEM-preparation of the radula, and who is also responsible for the SEM-photos. The preparation happened to fall upside-down on the SEM-stub (Warén pers. commn), so the different radula elements in Fig. 8 are mostly seen from below. Radula with the formula 2 - 1 - 0 - 1 - 2, with at least 16 transverse rows of teeth. Lateral teeth (Fig. 8B) roughly fan-shaped with a narrow base, flat (artificially flattened during preparation?), cutting edge almost straight (slightly wavy), finely, if somewhat unevenly serrated with about 24 thin, fairly long denticles. Cutting edge with smooth, narrow, thickened, winglike extension. Marginal teeth apparently of two kinds, one (Fig. 8D) broad, paddle-shaped with inner side and broad, rounded tip finely serrated with rather short and well separated, denticles which number slightly more than 20. The other (Fig. 8C, upper teeth) slender, “jaw”-shaped, cutting edge long, with numerous, at least 36, close-set, long and “powerful” denticles, having somehow the appearance of the lower jaw of a carnivorous reptile.

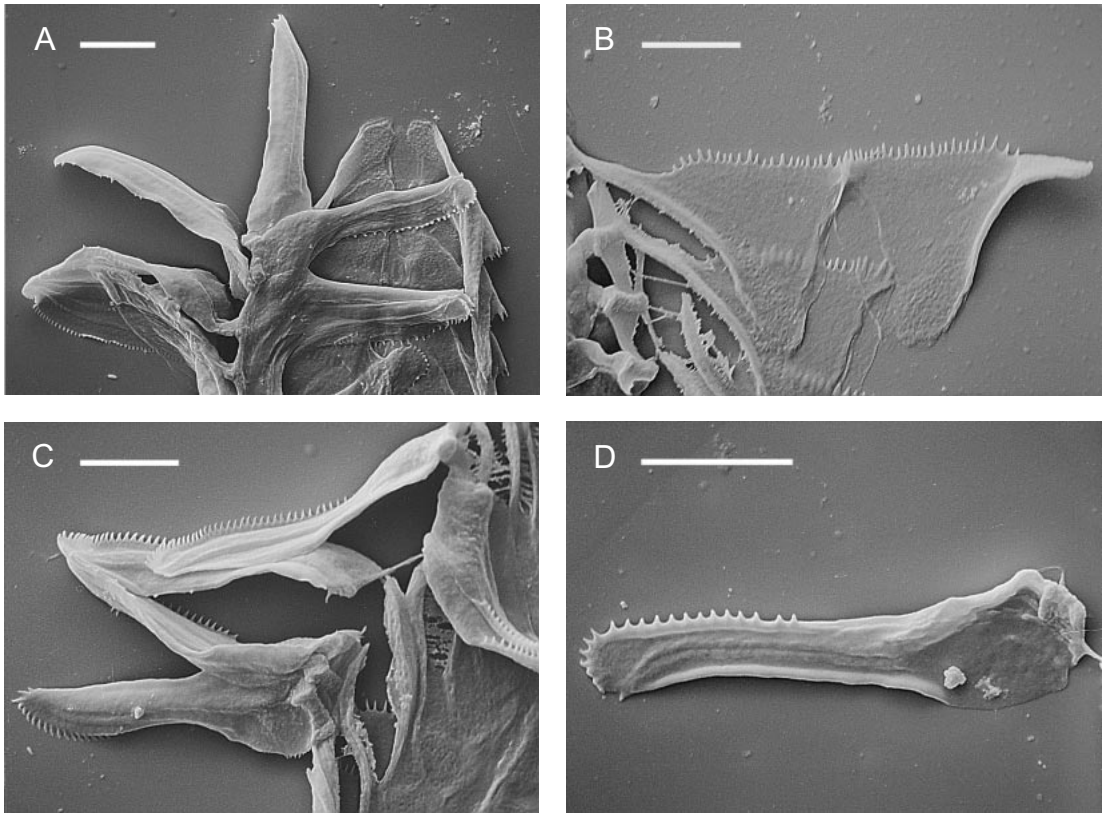


Fig 8. Scanning electron micrograph of radula of paratype of *Xylodiscula planata* sp. nov. Radula mounted upside-down so that all details seen from the under side. A) A number of “paddle-shaped” marginals in different orientations (Scale bar 10 µm). B) Lateral teeth (Scale bar 10 µm). C) Marginals. Uppermost several “jaw-shaped” marginals (Scale bar 10 µm). D) A single, “paddle-shaped” marginal (Scale bar 10 µm). Preparation and photos by Anders Warén.

DISCUSSION

In addition to the typical xylodisculid radula, the discoidal shape of the shell, lack of spire, very deep suture (caused by the narrow contact zone between whorls), widely open umbilicus, and the tiny, inrolled tip of the protoconch, all agree with the generic diagnosis of *Xylodiscula*, and differ in one or more respects from all known alternative genera. Further, a number of soft-part characteristics as described by Warén (1992), such as shape of foot, long and slender tentacles with tiny eyes at their base, short and conical snout, and the two pallial tentacles of different lengths, all agree with similar features in our specimens (see Fig. 6). Two white pigmented mantle organs centrally in the pallial skirt is also a common feature of our specimens and *Xylodiscula boucheti* as described in Warén (1992).

The family Xylodisculidae was erected by Warén, 1992, and further discussed by Warén & Bouchet (1993), and Marshall (1994). The present record represents the

introduction of the family Xylodisculidae to the Norwegian fauna, and to northern Europe in general.

So far this family includes a single genus, *Xylodiscula* Marshall, 1988, with nine described species:

Xylodiscula major Warén & Bouchet, 1993

North Fiji Basin, 2000 m, hydrothermal vent, “La Dame Blanche”.

Xylodiscula analoga Warén & Bouchet, 2001

Mid-Atlantic Ridge, Menez Gwen and Lucky Strike, 850-1728 m, hydrothermal vent.

Xylodiscula osteophila Marshall, 1994

Off Mernoo Bank, Chatham Rise, New Zealand, c. 900 m, from whale bone.

Xylodiscula boucheti Warén, Carrozza & Rochini, 1992

Corsica and Tuscan Archipelago, 90-400 m, from *Posidonia detritus* and in an amphora!



Xylodiscula lens Warén, 1992

Corsica and Tuscan Sea, 90-400 m, from
Posidonia detritus and sunken driftwood.

Xylodiscula vitrea Marshall, 1988

Off Broken Bay, New South Wales, 439-714 m,
on sunken driftwood.

Xylodiscula eximia Marshall, 1988

Off White Island, New Zealand, 1075-1100 m, on
sunken driftwood.

Xylodiscula librata Marshall, 1988

Off White Island, New Zealand, 1075-1100 m, on
sunken driftwood.

Xylodiscula planata n. sp.

Western Norway, 34-56 m, associated with sur-
plus fish feed.

Finally a species presumably closely related to, if not conspecific with, *X. vitrea* Marshall, 1988, has been described (but not named) by Hasegawa (1997), from sunken driftwood in deep water in Suruga Bay on the Pacific coast of Japan.

Xylodiscula planata may be distinguished from *X. major* and *X. analoga* by being much smaller, and lacking a thick ferruginous deposit covering the entire shell. From *X. osteophila* it is distinguished by its complete lack of spire and a wider umbilical opening. *X. librata* has a typical lecithotrophic protoconch. *X. eximia* is perhaps the species most similar as far as shell characters go. According to the original description, however (Marshall 1988), an operculum is absent, and the opercular lobe is very thin, indicating that either the operculum is lacking, or easily lost. This is not the case for *X. planata*.

X. vitrea, the type species of the genus, is relatively wider compared to its height, has a wider umbilicus, and a distinct fold or varix marking the end of the protoconch. Of the two Mediterranean species, *X. lens* has a much wider umbilicus (reported to have a diameter 40 to 45 % of shell diameter), while *X. boucheti* has an umbilicus with a diameter from 30 to 33 % of the shell diameter as compared to the 24 % of *X. planata*. *X. boucheti* may further be distinguished from our new species by its slightly lamellose, brownish periostracum. Another possible diagnostic character is the delimitation of the protoconch. A distinct "check-mark" is clearly seen in fig. 45B in Warén (1992), while the transition from protoconch to teleoconch appears quite smooth in our Fig. 5. It is of course possible that a similar "check-mark" has been destroyed by erosion in our type material, although we regard this as rather unlikely.

Comparison with the radula of *X. boucheti* is complicated by the fact that the illustration and description of its radula is based on a light microscopic examination only (Warén, pers. commn). Based on the drawing

in Warén (1992) (his fig. 43) it may be concluded that: The laterals as seen in Fig. 8B are roughly similar to those in the drawing of Warén, except for the winglike extension on the outside of the anterior edge. In addition, the denticles on the cutting edge are generally longer and more slender than the corresponding denticles of *X. boucheti*. The paddle-shaped marginals are more slender and proportionally longer than in *X. boucheti* (Fig. 8D). The denticles along the inner edge are rather short and well separated, and number slightly more than 20. Far more denticles are seen in the drawing of Warén, and they also appear to be more close-set. If we interpret Fig. 8A correctly, the several very different-looking marginals seen in this photo are actually different orientations of the same radular element. The ones at the right are oriented as in Fig. 8D, while the two upper left ones have been folded over so that their cutting edges are hidden. We interpret the slender jaw-shaped teeth as seen in the upper part of Fig. 8C to represent another kind of marginals, as these are rather conspicuously different from the teeth described above. There are no parallels to these teeth in the drawing of Warén. These marginals may correspond to the outer marginals of *X. boucheti*, but they may alternatively be interpreted as teeth from an early row in the radula, while the paddle-shaped marginals are from one of the later rows.

Both because of the morphological characters mentioned above, and the localities and habitats reported, we conclude that the only species at all likely to be conspecific with our specimens is *X. boucheti*. However, we regard the differences taken together, to be sufficient to classify *X. planata* as a species different from *X. boucheti*. Although not likely, we do not completely rule out the possibility that it is merely a geographical variety (or subspecies) of *X. boucheti*. The final word on the taxonomic status of these gastropods must await further investigations in the North Atlantic and a genetic analysis of populations from several localities. We feel it is proper to introduce a new name for the material at hand, to emphasise the novel characteristics of the radula, as well as the distribution and habitats.

The only species in northern European waters at all likely to be mistaken for *Xylodiscula planata*, are *Noerrevangia fragilis* Warén & Schander, 1993, known from a single specimen from clayey bottom at 43 m in Faroese waters (Warén & al. 1993), *Skeneopsis planorbis*, and perhaps juveniles of *Margarites helicinus* (Phipps, 1774). An enumeration of the differences between the four species seems appropriate.

Compared to *Noerrevangia fragilis*, *X. planata* has more rapidly expanding whorls, is practically planispiral, and has an umbilicus that is more spacious. The suture is deeper, and there is no sign of any flattening



of the adapical surface of the whorls. The most conspicuous difference is probably the complete lack of spire in our specimens. Of three specimens of *X. boucheti* illustrated by Warén (1992), one appears to have a low spire, the other two are completely flat. Our nine specimens are all completely flat-spired, however, and this character alone should suffice to keep *X. planata* apart from *Noerrevangia*.

Skeneopsis has a wax-coloured to brownish, slightly translucent shell. The shell is sturdy and tough, not at all fragile as in *X. planata*. The shell surface is rough, appearing somewhat corroded, and frequently with small algae attached. Inside the colourless operculum, a partial ring of blackish pigment is visible. The whole head-foot complex has a lot of dark pigment, and there are distinct, black eye-spots at the base of the tentacles.

Juveniles of *Margarites helicinus* are conspicuously different from the adults, and have been mistaken for other species in the past. The shells of juveniles are smooth and shiny, and yellowish in colour. However, they do not have a wide open umbilicus, eyes are visible through the shell, spire is present (if low), and the diameter to height ratio is smaller than for *Xylodiscula planata*.

Xylodiscula planata is obviously not a common species. In a total of 34 grab samples taken at the same localities, bottoms and depths, the species was found only in four. It has not been found in several hundreds of grab samples taken over the years, with the same methodology, from similar bottoms and depths in the

outer fjords and coastal area on the west coast of Norway. The grab samples which contained the new species were always the ones with the highest numbers of both individuals and species from the respective sample localities and dates.

The species common to the four samples are listed in Table 2. The sample from Rysjedalsvika containing the type material, was the richest, with 1120 individuals of at least 54 different species, all found in less than two litres of sediment. However, some of the animals found in this grab sample most likely belong to an encrusting community dominated by *Mytilus*. This station was just outside a floating platform on which the fish enclosure nets used to be cleaned of encrusting organisms. The fauna in all four samples was dominated by a number of opportunistic species of small polychaetes, of which *Capitella capitata* (Fabricius, 1780), *Pholoe inornata* (Johnston, 1839), and *Heteromastus filiformis* (Claparède, 1864), (among others) were found in all four grab samples. This combination usually indicates somewhat organically enriched sediment. The only species in addition to the small polychaetes which were constantly present in fairly high numbers was the leptostracan, *Nebalia* sp. (probably *Nebalia borealis* Dahl, 1985).

At all three sampling sites (Table 1), the sediment was dominated by sand-sized particles, although locality C had a high content of shell gravel as well. The content of organic matter was fairly high at all stations, particularly so when the low proportion of particles of

Table 2. The most common species in the four grab hauls in which *X. planata* has been found. Comparison between the sample from Rysjedalsvika (A), the two near Fjelbergøy (B) and the one outside Sotra (C). Numbers in parentheses are from other replicate grab hauls in the same series. All species except *Xylodiscula*, *Nebalia* (Leptostracan crustacean), and *Macoma* (Bivalve) are polychaetes.

Locality	A	B ₁	B ₂	C
Number of species	54	45	22	51
Total abundance	1120	403	361	898
<i>Xylodiscula planata</i>	2	2	3	2
<i>Harmothoe</i> sp.	18	2	1	7
<i>Pholoe inornata</i>	17	13	13	54
<i>Phyllodoce groenlandica</i>	16	0 (9)	2	105
<i>Nereimyra punctata</i>	59	1	1	6
<i>Ophiodromus flexuosus</i>	9	2	0	0
<i>Kefersteinia cirrata</i>	22	1	3	3
<i>Nereis pelagica</i>	18	8	4	4
<i>Malacoceros fuliginosa</i>	13	0 (6)	4	4
<i>Capitella capitata</i>	694	288	230	417
<i>Heteromastus filiformis</i>	5	3	17	58
<i>Owenia fusiformis</i>	0	10	0	1
<i>Cirratulus cirratus</i>	61	2	4	3
<i>Nebalia</i> sp.	14	26	61	15
<i>Macoma calcareo</i>	0	2	1	1



silt and clay is taken into consideration. The small volumes of sediment taken by each grab, except at locality C, may indicate a rather thin sediment layer on top of a rocky slope. From all samples emanated a distinct smell of decaying fish feed, and remnants of fish feed were seen. We find it intriguing that *X. planata* has so far been found only on bottoms where surplus fish feed has been deposited fairly recently.

The eight or nine species of *Xylodiscula* described so far, have been found on hydrothermal vents at depths of more than 2000 m, on decaying whale bone on the deep-sea bottom (c. 1000 m), on sunken drift-wood from bathyal depths (400-1100 m), from *Posidonia* remains in shelf depths (90-120 m) in the Mediterranean, and in this study on decaying surplus fish feed in inshore waters (30-60 m) in western Norway. Species of the genus have not yet been reported from hot or cold seeps. We have not been able to find records of any gastropod genus with a wider range of biogenic and chemoautotrophic habitats. The closest being *Pyropelta* McLean & Haszprunar, 1987, which have been reported from hot vents, as well as whale bones and cold seeps. *Xylodiscula* thus seems to support the “stepping-stone” hypothesis for the colonisation of hydrothermal vents which has been suggested by several authors (see e.g. Distel & al. 2000, and references therein). The genera

of small gastropods having closely related species in both hydrothermal vents, on decaying whale bones, and sunken driftwood, probably all feed on the bacterial populations responsible for the final remineralization of these animal and plant remains. It is only to be expected that some of these groups have species adapted to reducing habitats also in shallow water, as is now demonstrated by the *Xylodiscula* species found on *Posidonia* remains in the Mediterranean, and on surplus fish feed in inshore Norwegian waters.

ACKNOWLEDGEMENTS

We appreciate the participation of Helge B. Botnen, Øyvind F. Tvedten and Kari E. Ellingsen in the field work and the working up of the material. We are grateful to Dr. Anders Warén at SMNH for the radula preparation and SEM-photographs of the radula elements and the protoconch, as well as valuable criticism of the manuscript. The remaining SEM photographs were taken at the Laboratory for Electron Microscopy at the University of Bergen, by Chief Engineer Egil Sev. Erichsen, whose help has been inestimable. Dr. Torleiv Brattegard read and made valuable comments on an early draft of the manuscript. Elin Holm has drawn the map and redrawn all of our rough sketches of soft parts in Figs 6 and 7. An anonymous referee has contributed a lot to a better and more concise manuscript.

REFERENCES

- Distel DL, Baco AR, Chuang E, Morrill W, Cavanaugh C, Smith CR. 2000. Do mussels take wooden steps to deep-sea vents? *Nature* 403:725-726.
- Hasegawa T. 1997. Sunken-wood associated gastropods collected from Suruga Bay, Pacific side of the Central Honshu, Japan with a description of 12 new species. *National Science Museum Monographs Tokyo* 12:59-123.
- Høisæter T. 1986. An annotated check-list of marine molluscs of the Norwegian coast and adjacent waters. *Sarsia* 71:73-145.
- Marshall BA. 1988. Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. *Journal of Natural History* 22:949-1004.
- Marshall BA. 1994. Deep-sea gastropods from the New Zealand region associated with recent whale bones and an Eocene turtle. *The Nautilus* 108:1-8.
- Warén A. 1989. New and little known Mollusca from Iceland. *Sarsia* 74:1-28.
- Warén A. 1991. New and little known Mollusca from Iceland and Scandinavia. Part II. *Sarsia* 76:53-124.
- Warén A. 1992. New and little known “Skeneimorph” gastropods from the Mediterranean Sea and the adjacent Atlantic Ocean. *Bollettino Malacologico* 27:149-247.
- Warén A, Bouchet P. 1993. New records, species, genera and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta* 22:1-90.
- Warén A, Bouchet P. 2001. Gastropoda and Monoplacophora from Hydrothermal Vents and Seeps: New Taxa and Records. *The Veliger* 44:116-231.
- Warén A, Gofas S, Schander C. 1993. Systematic position of three European heterobranch gastropods. *The Veliger* 36:1-15.

Accepted 19 July 2000 – Printed 30 November 2001
Editorial responsibility: Jarl Giske