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Composition of the genus *Hanleya* (Mollusca: Polyplacophora: Lepidopleurida), with the description of two new species

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An evaluation of all species of the genus *Hanleya* showed that they only inhabit the Atlantic Ocean, occurring from off Brazil (25°44′S) to the Barents Sea (74°27′N). The majority of records refer to *H. nagelfar* which ranges from 9°03′8″N to 74°27′N in coastal waters of North America, Europe and Africa. There are six Recent species of *Hanleya*: *H. tropicalis* Dall, 1881, *H. brachyplax* Jardim and Simone, 2010b, *H. harasewychi* sp. nov, *H. mediterranea* sp. nov, *H. hanleyi* (Bean in Thorpe, 1844) and *H. nagelfar* (Lovén, 1846). The phylogenetic relationship of *H. hanleyi* and *H. nagelfar* has long been questioned. New data on age variability of *Hanleya nagelfar* are provided. *Hanleya hanleyi* is the only species of the genus that also occurs in the intertidal zone. All other members of *Hanleya* inhabit mainly bathyal or sublittoral depths: *H. nagelfar* (28–1680 m), *H. tropicalis* (230 m), *H. brachyplax* (250–408 m), *H. harasewychi* (73–115 m), *H. mediterranea* (50–200 m).

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Keywords: *Hanleya*; new species; taxonomy; age variability; Atlantic Ocean

Introduction

Polyplacophora, known generally as chitons, is a class of exclusively marine molluscs with the shell formed of eight articulating plates. Chitons inhabit hard substrata on the sea floor from intertidal zones to hadal depths. These molluscs are grazers and feed on detritus, marine algae, small animals and sunken wood. There is one group, the genus *Hanleya* Gray, 1857, which includes at least one species (*Hanleya nagelfar* (Lovén, 1846)) that feeds on sponges (Waren and Klitgaard 1991; Todt et al. 2009). *Hanleya* comprises chitons that occupy an intermediate position between the most primitive Recent order of chitons, Lepidopleurida (without shell insertion plates), and the more developed chitons of the order Chitonida (with well-developed, slitted insertion plates). *Hanleya* spp. have unslitted insertion plates or their primordium on the valves. *Hanleya* is the only genus in the family Hanleyidae Bergenhayn, 1955 (Sirenko 2006a). All species currently referred to the genus *Hanleya* are confined to the Atlantic Ocean and its adjacent seas (Figure 1). The species described as *Hanleya spicata* Berry, 1919 and *H. sinica* Fengshan, 1990, both from the northern Pacific Ocean, have recently been transferred to the genus *Deshayesiella* Carpenter in Dall, 1879 (Sirenko 1997; Sirenko and Clark 2008). The species from Plover Bay

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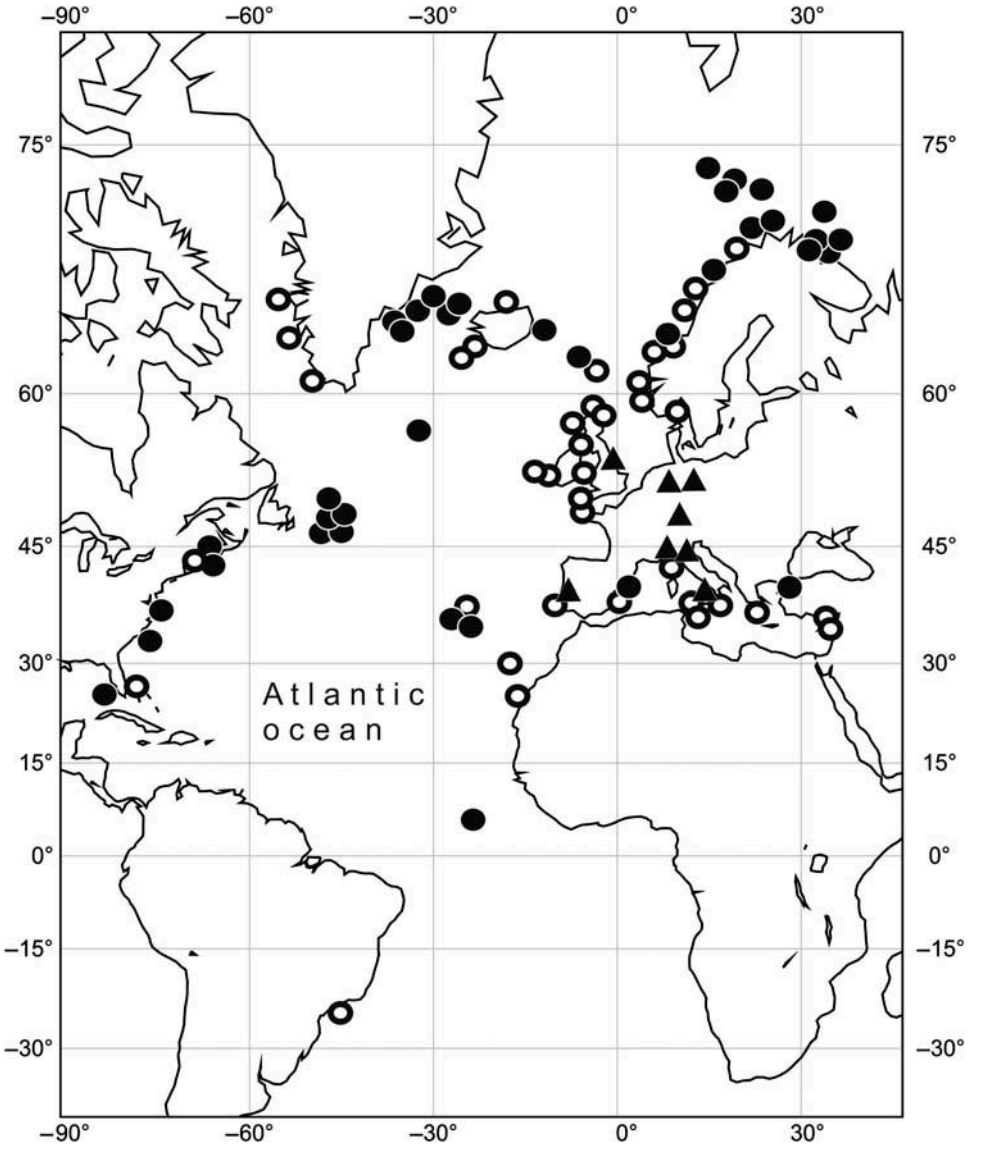


Figure 1. Distribution of the genus *Hanleya.* Black circle: specimens studied by author; empty circle: literature data; triangle: fossil specimens.

(northwestern Pacific, Russia) that was attributed to *Hanleya* by Thiele (1909) is *Hanleyella asiatica* Sirenko, 1973, which belongs to the family Leptochitonidae.

Seven species had been attributed to the genus *Hanleya*: *Chiton mendicarius* Mighels and Adams, 1842; *Chiton hanleyi* Bean in Thorpe, 1844; *Hanleya debilis* Gray, 1857; *Hanleya dalli* Kaas, 1957 (nom. nov. for *Lepidopleurus carinatus* Dall, 1927, non Leach,1852); *Chiton nagelfar* Lovén, 1846; *Chiton abyssorum* M. Sars MS, Jeffreys, 1865 and *Hanleya tropicalis* Dall, 1879. *Hanleya debilis* is a junior synonym of *H. hanleyi* (Kaas and Van Belle, 1985).

Of these, Kaas and Van Belle (1985) considered three species, *H. hanleyi*, *H. nagelfar* and *H. tropicalis*, to be valid. These authors synonymised the remaining four species as either *H. hanleyi* or *H. nagelfar*. More recently, *Hanleya brachyplax* Jardim and Simone (2010a) was added to the genus. It should be noted that the taxonomic status and synonymy of several species within this family is still not certain.

After more than a century, the debate over the relationships between *Hanleya hanleyi* and *H. nagelfar* (and its junior synonym *H. abyssorum* G.O. Sars, 1878) continues. Jeffreys (1865) was of the opinion that *H. nagelfar* is only *H. hanleyi* of extraordinary size. He wrote: 'The *C. Nagelfar* of Lovén is *C. Hanleyi* of an extraordinary large size; and so is the *C. abyssorum* of Sars.' Sparre Schneider (1886) reported the absence of differences in the sculpture of the tegmentum of these two species. Pilsbry (1892) considered *H. abyssorum* to be a variety of *H. hanleyi* that differed in being 'more than double the size, having the girdle wider and thicker, spicules shorter, shell narrower with distinct sculpture'.

In a study of the girdle armature and radulae of these species, Thiele (1909) observed that *H. abyssorum* had numerous calcareous spicules of different sizes (>500 μm), with narrow scales about 250 μm long between the spicules, while *H. hanleyi* had mainly long pointed scales that were ribbed on the dorsal side of the girdle and smooth on the ventral side. Thiele (1909) also reported differences in the radula with the first lateral tooth having a broad top in *H. abyssorum* and a pointed top in *H. hanleyi*.

Kaas and Van Belle (1985) concluded: 'In our opinion the differences in shape of the valves and in the girdle armature are convincing enough to justify specific separation of both forms.' However, Waren and Klitgaard (1991) noted: 'We have thus not been able to find any morphologic character, except the size, separating the different forms of *Hanleya.* Indirect evidence, however, suggests that more than one species may be involved and we recommend that whenever separation under different names is possible it should be done'.

When working in the collections at the National Museum of Natural History, Smithsonian Institution in 1999, four samples of *Hanleya* were studied that had previously been identified as *Hanleya* sp. Careful examination of these specimens revealed that they belong to a new species. Re-examination of old samples identified as *Hanleya hanleyi* from the Mediterranean Sea in the collections of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg indicated that they belong to a second new species.

The objectives of this paper were to describe these two new species of the genus *Hanleya*, and to investigate the variability of *Hanleya nagelfar*.

List of abbreviations:

BL – body length.
NHRM – Naturhistoriska Riksmuseet, Stokholm, Sweden.
spm – specimen(s).
stn – station.
TM – Tromsø Museum, Tromsø, Norway.
USNM – National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

ZIM – Zoologisches Museum und Zoologisches Institut der Universität, Hamburg, Germany.
ZISP – Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

Material and methods

The majority of the material examined had accumulated over many years in the Zoological Institute of the Russian Academy of Sciences. These samples had been collected by different Russian expeditions to various parts of the northern Atlantic Ocean, and deposited in the collections of the Zoological Institute. Eight specimens from the USNM, 13 specimens from the TM and two specimens from the ZIM were also studied; as were 38 specimens from the Newfoundland Bank, recently collected by the R/V NEREIDA and sent to the author for identification by Javier Murillo Perez (Centro Oceanográfico de Vigo, Spain). In total, 72 specimens were used in this investigation. Seventeen specimens of *Hanleya nagelfar* of different sizes were used to study age variability.

In this article, traditional measurements and ratios, and several new ones were used. Dorsal elevation is the ratio of the height of the tegmentum of the intermediate valve to the width of this valve (usually valve V) (Kaas and Van Belle 1985). In consideration of age variability, the ratio of the width of valve V to the width of the adjacent girdle was used. Specimens initially preserved in alcohol were consistently used in order to minimise differences of shrinkage. The ratio of head valve length to head valve insertion plate length was also used. Head valve length is defined as the length of the tegmentum without the insertion plate. Perhaps this novel ratio will prove useful not only for the head but also the tail valve. In the present study, colouration of the tegmentum was used as a character. A white tegmentum is very widespread among deepwater chitons especially among primitive representatives of families such as Leptochitonidae and Hanleyidae. Only a few species of these families have colouration in the tegmentum. Thus visible preserved colouration is a good character in cases where, in spite of bleaching in alcohol-preserved specimens, the colour patterns remain visible.

The valves, dorsal and ventral armature of the girdle, and radular features were examined using a Scanning Electron Microscope (SEM). Selected chitons were prepared for SEM by boiling for 10–15 minutes in a 7% KOH solution, followed by rinsing the remaining hard parts with water. For the valves, this alkaline treatment removed any organic materials that obscured tegmental sculpturing. Valves, calcareous particles of girdle armature and radulae were mounted on stubs using glue and observed in high-vacuum mode with a platinum coating.

Systematics

Class **POLYPLACOPHORA** Gray, 1821
Subclass **LORICATA** Schumacher, 1817
Order **LEPIDOPLEURIDA** Thiele, 1909
Suborder **LEPIDOPLEURINA** Thiele, 1909
Family **HANLEYIDAE** Bergenhayn, 1955
Genus ***Hanleya*** Gray, 1857

Type species ***Hanleya debilis*** Gray, 1857 (=*Chiton hanleyi* Bean in Thorpe, 1844), by monotypy.

Stratigraphic range

Upper Oligocene – Recent.

Distribution

Atlantic Ocean and adjacent seas, from southern Greenland and the western Barents Sea (74.27° N) to the Brazilian coast (25.44° S), including the Mediterranean Sea, and the Gulf of Mexico. Bathymetric range extends from the intertidal zone (*H. hanleyi*) to 1680 m (*H. nagelfar*).

Diagnosis

The following diagnosis for the genus *Hanleya* is based on data from Sirenko (1997), Jardim and Simone (2010b), and new data in this publication.

Animal small to large. Insertion plate of head valve well developed, a primordium of insertion plates present in intermediate valves in all species. Insertion plates of tail valve well developed in *Hanleya harasewychi* sp. nov. and *H. brachyplax*, developed to a variable extent in *H. hanleyi, H. nagelfar* and *H. mediterranea* sp. nov., entirely absent in *H. tropicalis*. Tegmentum with large roundish or oval granules, each granule with one megalaesthete surrounded by 8–16 micraesthetes. Girdle covered with spicules or scales and longer, randomly dispersed needles or spines. Heads of major lateral teeth of radula with tridentate cusp, central denticle largest.

Hanleya harasewychi sp. nov.
(Figures 2–5)

Type material

Holotype, USNM 93189, BL = 15.0 mm, now disarticulated, consisting of a mount of the shell, perinotum and radula, and 3 paratypes, USNM 323067, 454683, 454684.

Type locality

22 mi ESE of Cape Hatteras, North Carolina (35.0800° N, 75.0530° W) U.S. Fish Commission Steamer Albatross, Sta. 2595, 1885, in 63 fathoms (115.2 m), sand, temp, 75°F (holotype).

Material examined

Holotype, USNM 93189, BL = 15.0 mm, 22 mi ESE of Cape Hatteras, North Carolina (35.0800° N, 75.0530° W) U.S. Fish Commission Steamer Albatross, Sta. 2595, 1885, in 63 fathoms (115.2 m), sand, temp, 75°F; Paratype 1, USNM 323067, BL = 5.0 mm,

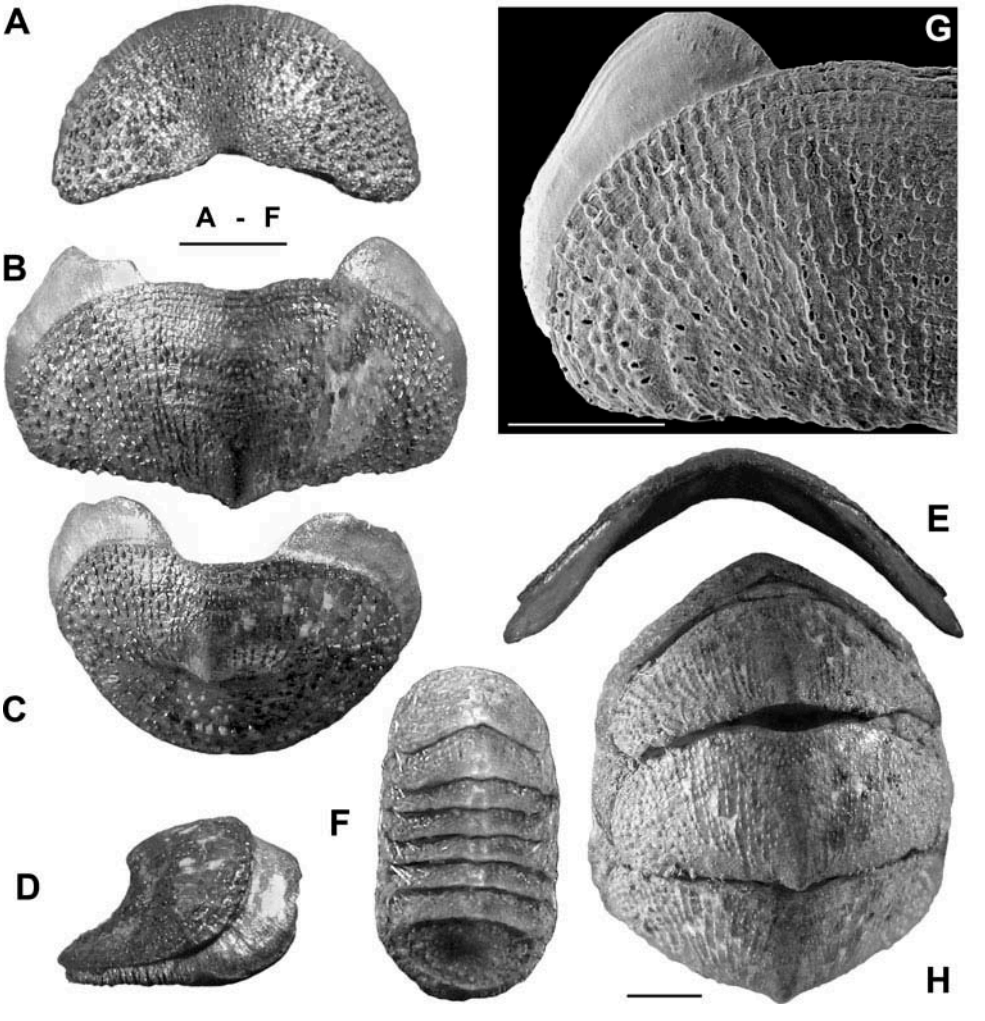


Figure 2. *Hanleya harasewychi* sp. nov., holotype (A–E, G, H) and paratype, USNM 454684, Florida off Foway Light, BL 3 mm (F). (A) valve I, dorsal view; (B) valve V, dorsal view; (C) valve VIII, dorsal view; (D) valve VIII, lateral view; (E) valve V, front view; (F, H) whole specimen, dorsal view; (G) valve V, dorsal view. Scale bars: 1mm.

off Key West, Florida (24.28° N, 81.50° W), U.S. Fish Commission Steamer Albatross, Sta. 2317, 45 fathoms (81.9 m) on coral, 75°F (water column temperature?); Paratype 2, USNM 454683, BL = 3.0 mm, off Fowey Light, Florida (25.35262° N, 80.4508° W), sponges, Eolis Sta. 188, 48 fathoms (87.4 m), Henderson Coll., 1915; Paratype 3, USNM 454684, BL = 3.0 mm, Off Fowey Light, Florida (25.35262° N, 80.4508° W), Eolis Sta. 109, 40 fathoms (72.8 m), Henderson Coll., 1914.

Distribution

Off Cape Hatteras, North Carolina to the Florida Keys, in 73–115 m.

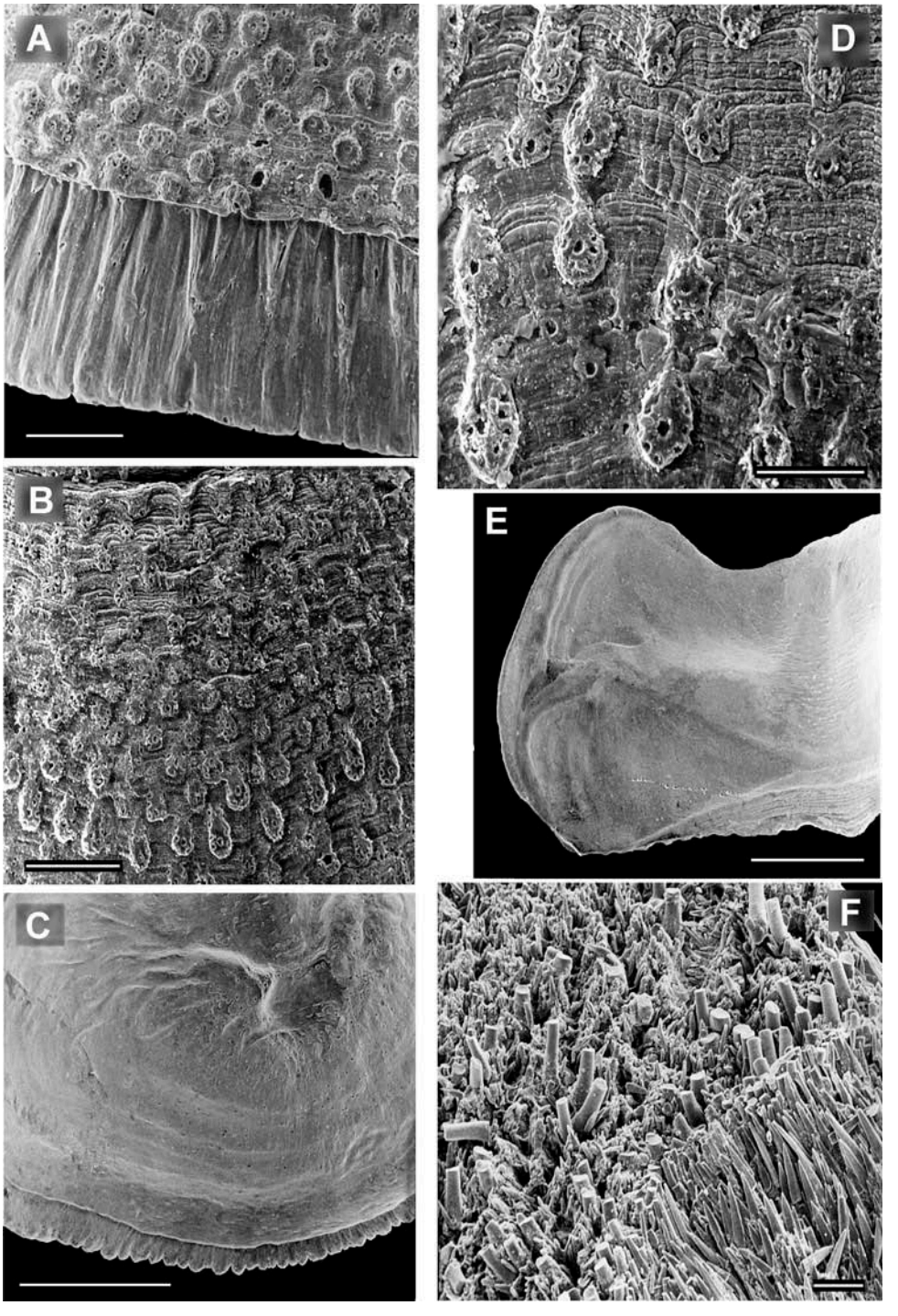


Figure 3. *Hanleya harasewychi* sp. nov., holotype. (A) valve I, front view; (B) valve V, jugal area; (C) valve VIII, ventral view; (D) valve VIII, pleural are; (E) valve V, ventral view; (F) dorsal, marginal and ventral spicules and needles. Scale bars: A, B, D, F: 100 μm; C, E: 1 mm.

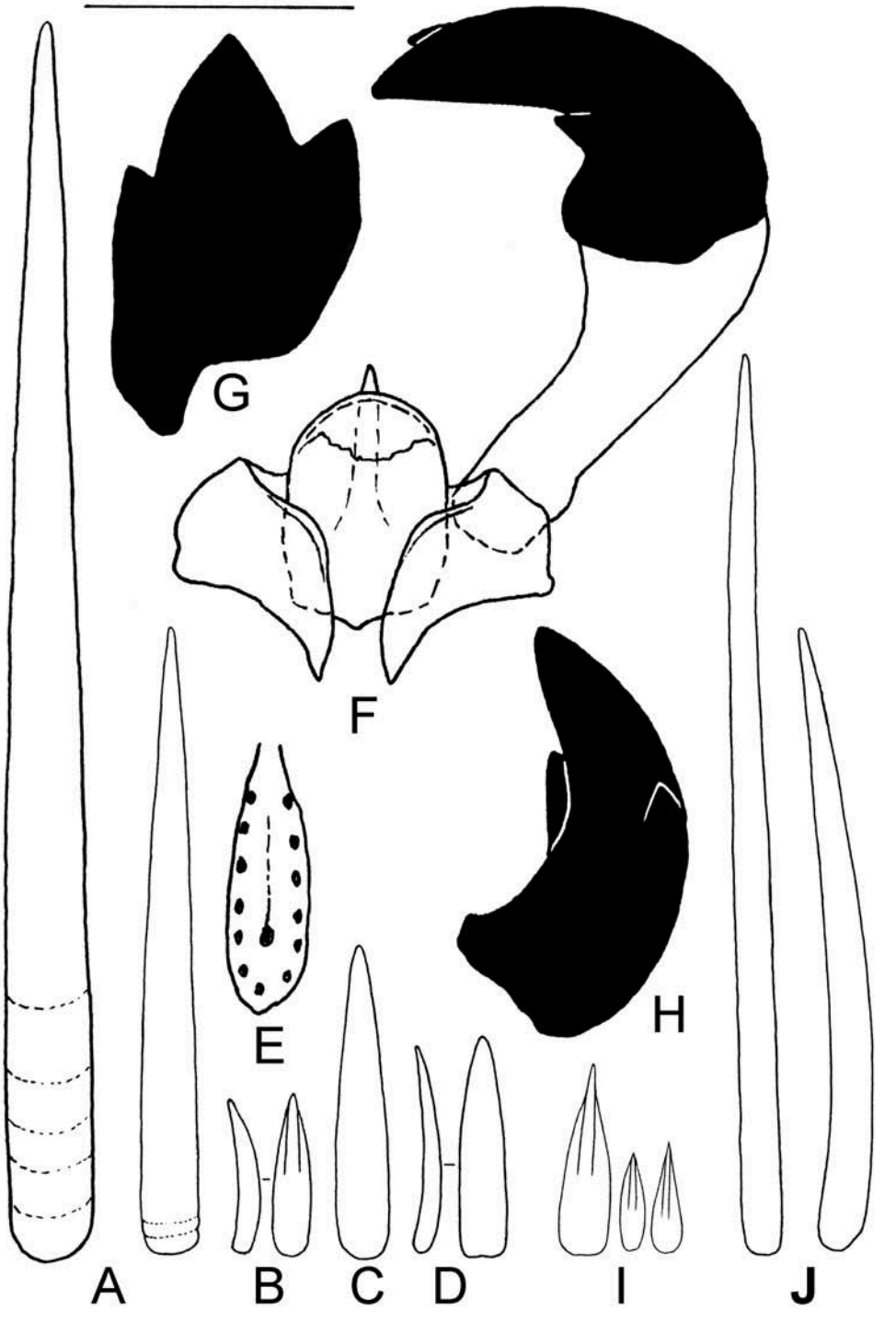


Figure 4. *Hanleya harasewychi* sp. nov., holotype (A–H), paratype, USNM 323067, Florida, off Key West, BL 5.0 mm (I, J). (A) dorsal and marginal needles; (B) dorsal spicules; (C) ventral spicules near margin; (D) ventral spicules; (E) aesthete group; (F) central, first lateral and major lateral teeth of radula; (G, H) head of major lateral teeth of radula; (I) dorsal spicules; (J) dorsal and marginal needles. Scale bars: A–D, F–J: 100 μm.

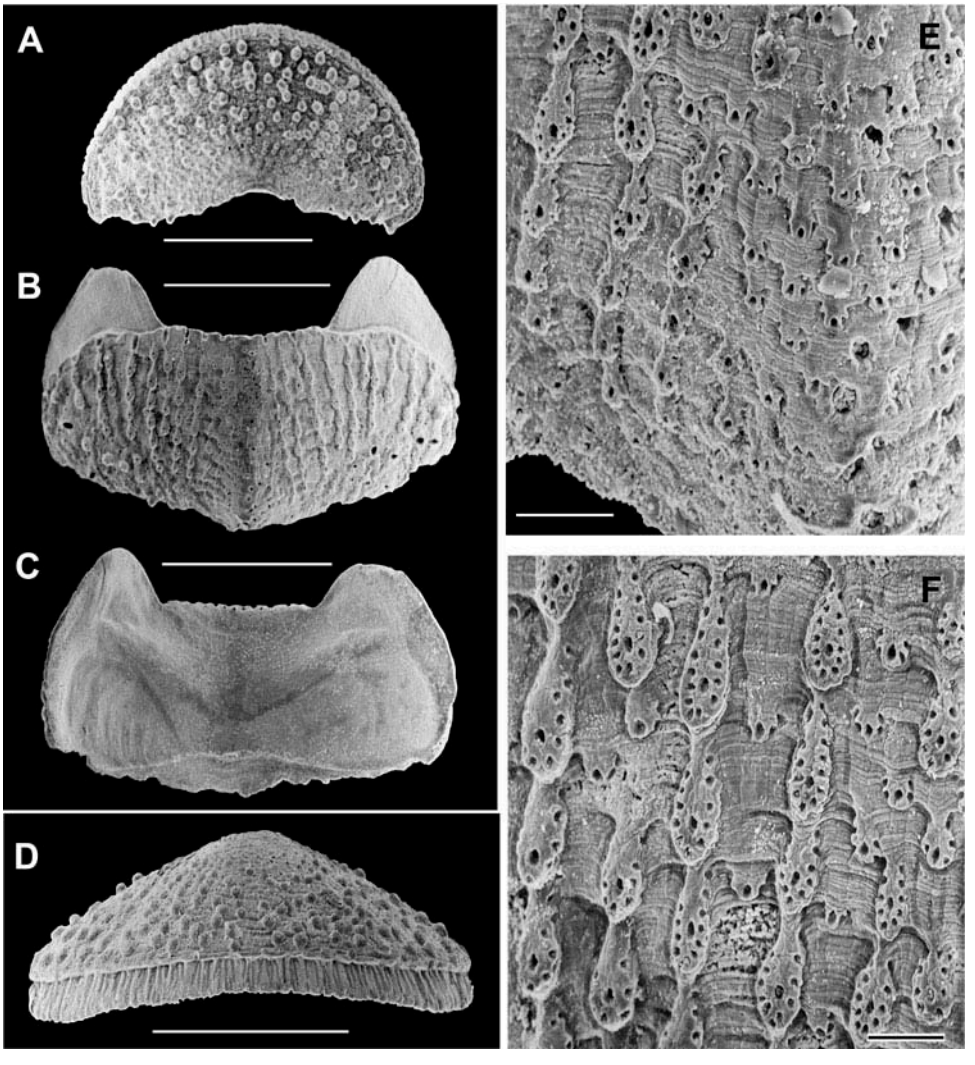


Figure 5. *Hanleya harasewychi* sp. nov., paratype, USNM 323067, Florida, off Key West, BL 5 mm. (A) valve I, dorsal view; (B) valve III, dorsal view; (C) valve III, ventral view; (D) valve I, front view; (E) valve III, jugal and pleural areas; (F) valve III, pleural area. Scale bars: A–D: 1 mm, E, F: 100 μm.

Diagnosis

Animal small (to 15.0 mm), elevated (dorsal elevation of valve V 0.36), back rounded. Head valves, lateral areas of intermediate valves, postmucronal areas sculptured with roundish granules arranged without distinct order, pleural areas of intermediate valves sculptured with long granules, ratio of granule length to granule width in pleural areas, 2.5–3.0; interspaces between rows of granules on pleural areas twice as large as width of granules; width of jugal sinus equal to width of apophyses in intermediate valves; insertion plate of tail valve well

developed and pectinate; each granule contains a single megalaesthete and 12–13 micraesthetes. Valves and girdle buff coloured, spotted with brown and white. Dorsal spicules of girdle flat with one central longitudinal rib distally terminated with sharp beak. Radula with 15 transverse rows of mature teeth; exterior denticle of major lateral teeth of radula half the size of interior one, width of central denticle is equal to its length.

Description

Holotype dry, curled, about 15.0 mm long, 6.0 mm wide when straightened (Figure 2F and H). Valves rounded (Figure 2E). Head valve semicircular (Figure 2A) posterior margin widely V-shaped, tegmentum sculptured with roundish granules arranged without regular pattern. Intermediate valves more or less rectangular (Figure 2B), side margins evenly rounded, posterior margin nearly straight except for a small projecting apex, lateral areas not elevated, with sculpture as in head valve (Figure 2G), pleural areas sculptured with elongated oval granules (about 180 × 60 μm) arranged in longitudinal rows, interspaces nearly twice as broad as width of granules, tegmentum of jugal area sculptured with small, elongated granules arranged without pattern (Figure 3B). Each granule contains a single megalaesthete and 12–13 micraesthetes (Figure 4E). Tail valve as wide as head valve, more or less oval; posterior margin well rounded, anterior margin straight to concave (Figure 2B); mucro central, highly elevated, prominent; length of antemucronal area equal to that of postmucronal area (Figure 2D), the latter deeply concave, sculptured like the head valve; antemucronal area sculptured like central area of intermediate valves (Figure 3D). Tegmentum and girdle buff coloured with white and brown blotches.

Articulamentum white, solid, blotched with rose in front of the central portion. Apophyses wide, long, with primordium of insertion plates extending nearly to end of lateral areas (Figures 3E and 5C), jugal sinus as wide as apophyses. Insertion plates well developed both in head and tail valves (Figure 3A and C) (length of insertion plates 0.4–0.5 mm in head valve, 0.2 mm in tail valve); insertion plates obsoletely striate in head valve, pectinated in tail valve.

Girdle narrow in present condition, densely covered with small, slender, slightly curved, pointed scales (Figures 3E and 4B) each with a single, central, longitudinal rib distally terminated by a sharp beak (≤60–70 × 14–18 μm), as well as randomly dispersed straight to slightly curved needles (Figure 4A) varying in size from 230 × 20 μm to 470 × 30 μm. Marginal needles like dorsal needles (Figure 4C). Ventral scales narrow, sharply pointed, reaching 80 × 17 μm in middle part of girdle, 120 × 20 μm near its margin (Figure 4C and D).

Radula 4.5 mm long, with 15 transverse rows of mineralised mature teeth (total about 20 rows). Central tooth short, almost rectangular, with narrow blade (Figure 4F). Major lateral tooth with tridentate cusp (Figure 4G and H), central denticle largest, as wide as long, exterior denticle smallest, half size of interior denticle.

Gills merobranchial, adanal, without interspace, with 14 ctenidia per side, gills extending from the end of valve VI to anus. It is not possible to find a nephropore or gonopore in these dry specimens.

Age variability

With increasing body size, the width/length ratio of intermediate valves measured using valve V decreases from 2.7 (BL = 5.0 mm) to 2.3 (BL = 15.0 mm), as does the ratio of head valve length/head valve insertion plate length, from 6.0 (BL = 5.0 mm) to 4.6 (BL = 15.0 mm) (Figures 2A, B and 5A, B, D). The smaller paratype (BL = 5.0 mm) has similar dorsal spicules and needles that are slightly shorter and half as wide as those of the holotype (Figure 4I and J). Granules on jugal area in paratype and holotype are similar but on the pleural area of paratype a little bit longer than that of holotype (Figures 2G, 3B, D, 5E, F).

Comparative remarks (Table 1)

Hanleya harasewychi sp. nov. is readily distinguished from its congeners by its buff colour with white and brown blotches, rounded back, longer granules and larger interspaces on pleural areas of valves, fewer rows of mature teeth in the radula, and a shorter central denticle on the major lateral tooth of the radula. The colour of the tegmentum remains visible after preservation and is a reliable taxonomic character.

Hanleya mediterranea sp. nov. has similar dorsal girdle scales, but differs from *H. harasewychi* in having larger, joined granules on the tegmentum (elongate in *H. harasewychi*), as well as similar-sized exterior and interior denticles on the major lateral tooth (very small exterior denticle in *H. harasewychi*).

Hanleya nagelfar, which also has wide apophyses, differs from *H. harasewychi* in having dorsal girdle spicules that are ribbed in young specimens, but nearly smooth and less developed in mature adults, and in lacking a pectinated insertion plate on the tail valve.

Hanleya tropicalis, which also has a small exterior denticle on the major lateral tooth of the radula (Figure 8K), can be distinguished from the new species by its more elevated shell and absence of an insertion plate in the tail valve.

Hanleya brachyplax also has a well-developed insertion plate on the tail valve, but can be separated from *H. harasewychi* by its white colour, shorter granules and fewer interspaces on pleural areas of valves, longer central denticle on the major lateral tooth of the radula, as well as by having longer and narrower apophyses, and a less dorsally elevated shell.

Etymology

This new species honours Dr. M. G. Harasewych, Curator of Marine Molluscs, Department of Invertebrate Zoology, National Museum of National History, Smithsonian Institution for his contributions to malacology and for his help and support during the preparation of this publication.

***Hanleya mediterranea* sp. nov.**
(Figures 6–8A–J)

Hanleya hanleyi – Dell'Angelo, Lombardi and Taviani, 1998:244, Pl. 2, Figures 1–2 (not *H. hanleyi* Bean in Thorpe, 1844), Dell'Angelo and Smriglio, 2001: 85, Pl. 25, E–H, Pl. 26, L–P (partim, non *H. hanleyi* Bean in Thorpe, 1844).

Table 1. Comparison of some important features of shell, girdle, and radula among species of the genus *Hanleya*. The characters of the type species *H. hanleyi* are not included because of incomplete and poor information. The fossil species in the genus are also not included because of the small number and incomplete nature of fossil material.

Features	*H. mediterranea*	*H. nagelfar*	*H. tropicalis*	*H. brachyplax*	*H. harasewychi*
Colour of shell	white	white	white	white	buff spotted with brown and white
Dorsal elevation	0.37–0.43	0.35–0.45	0.47	c. 0.45	0.36
Back	subcarinated	subcarinated to carinated	carinated	?	rounded
Ratio of length of granules on pleural areas of valves to width	c. 1.4–1.7	c. 1.0–2.0	?	c. 1.5–2.0	c. 2.5–3.0
Interspaces between rows of granules on pleural areas of valves	longitudinal rows absent on pleural areas of valves	less than width of granules	less than width of granules	much less than width of granules	twice as large as width of granules
Ratio of width of jugal sinus to width of apophyses in intermediate valves	0.78–0.88	0.75–0.92	0.79	0.74	1.0
Insertion plate in tail valve	weakly developed	weakly developed	absent	well developed	well developed and pectinated
Number of micraesthetes in one granule	9–16	8–12	?	?	12–13
Dorsal scales or spicules of girdle	flat scales	oval in transverse shear spicules	?	?	flat scales

(*Continued*)

Table 1. (Continued).

Sculpture of dorsal scales or spicules of girdle	scales smooth or one longitudinal rib on one side distally terminated with sharp beak	ribbed around whole spicule in small, and smooth in large specimens	?	?	Scales with one central longitudinal rib distally terminated with sharp beak
Number of transverse rows of mature teeth of radula	28–34	25–35	?	?	15
Denticles of head of major lateral teeth of radula	exterior and interior denticles are the same size width of central denticle is shorter than its length	exterior and interior denticles are the same size width of central denticle is shorter than its length	exterior denticle is three times shorter than interior one, width of central denticle is shorter than length	exterior and interior denticles are the same size, width of central denticle is shorter than length	exterior denticle is half the size of interior one, width of central denticle is equal to length

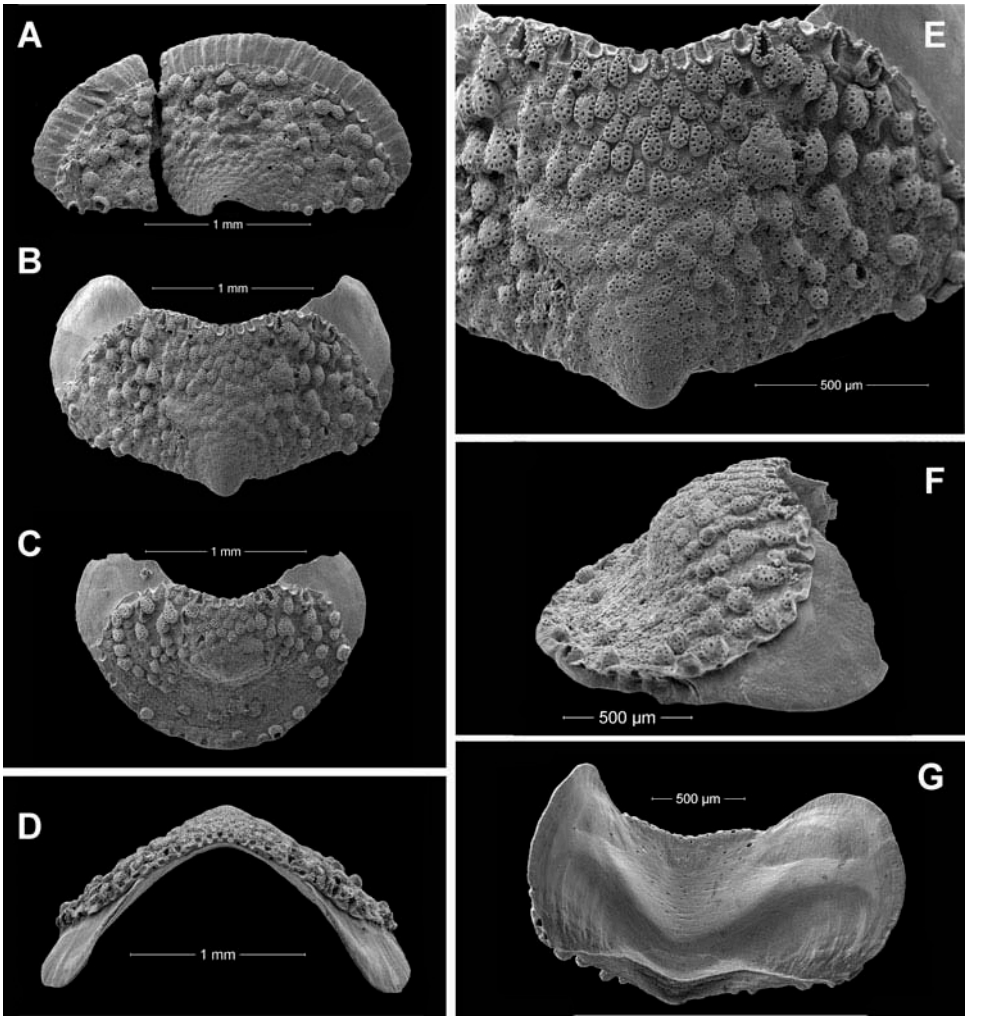


Figure 6. *Hanleya mediterranea* sp. nov., holotype, ZISP 2201, Mediterranean Sea, Spain, Gerona, Bagur, depth 200–300 m, BL 5.4 mm. (A) valve I, dorsal view; (B) valve V, dorsal view; (C) valve VIII, dorsal view; (D) valve V, dorsal view; (E) valve V, central and lateral areas; (F) valve VIII, lateral view; (G) valve IV, ventral view.

Hanleya multigranosa – Sabelli and Taviani, 1979: 161, Figure 4 (non *Chiton multigranosus* Reuss, 1860).

Type material

Holotype, ZISP 2201, BL = 4.7 mm, now disarticulated, consisting of mounts of shell, perinotum and radula, and three paratypes, ZISP 2202.

Type locality

Mediterranean Sea, off Begur, Girona, Spain, in 200–300 m.

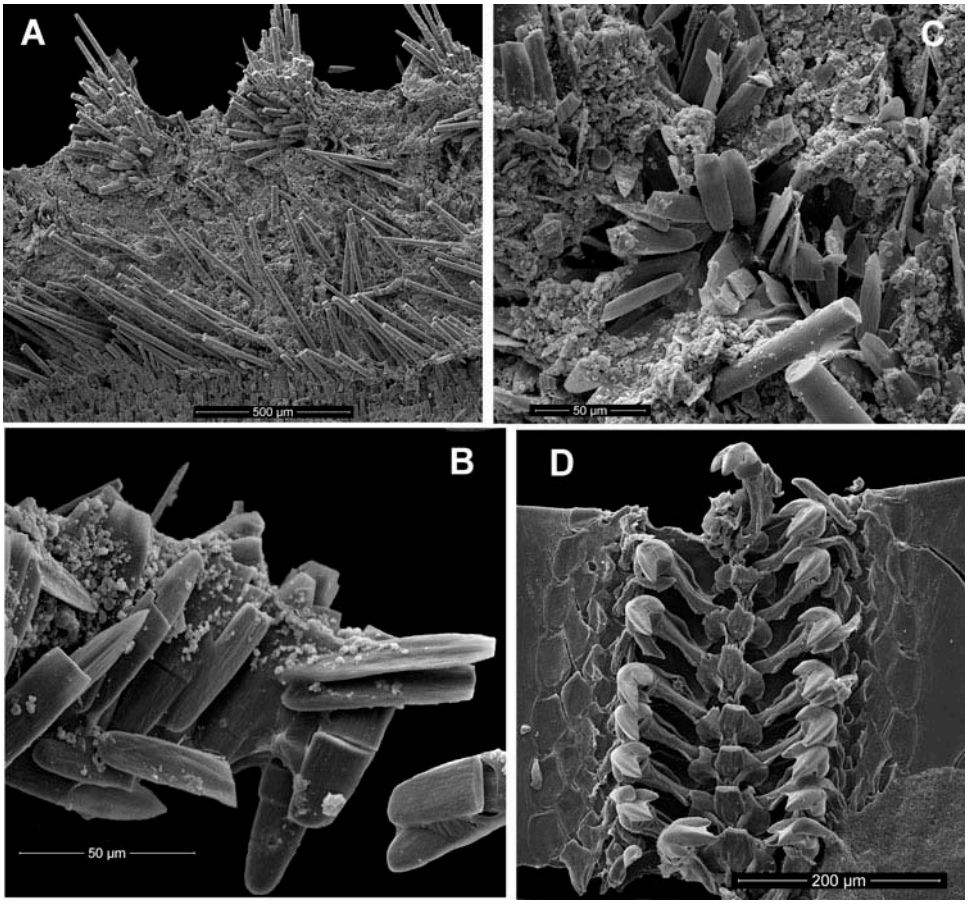


Figure 7. *Hanleya mediterranea* sp. nov., holotype, ZISP 2201, Mediterranean Sea, Spain, Gerona, Bagur, depth 200–300 m, BL 5.4 mm. (A) dorsal marginal and ventral scales and needles; (B, C) dorsal scales and needles; (D) radula.

Material examined

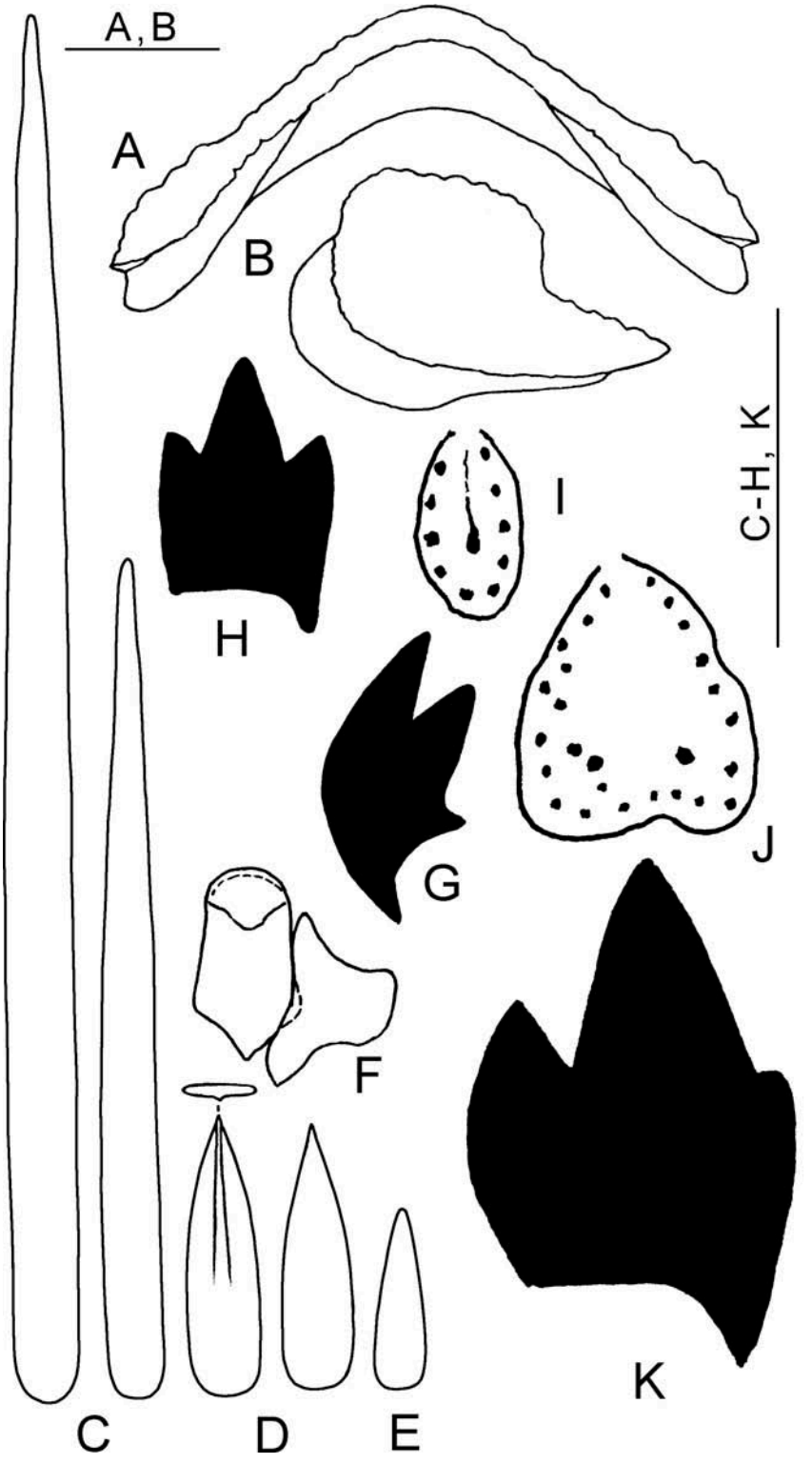
Holotype and three paratypes, ZISP 2202, BL = 4.0–4.7 mm, Mediterranean Sea, off Prinkipo, Turkey , 40.5139° N, 29.0724° E, in 50 m.

Distribution

Mediterranean Sea off Spain and Turkey, in 50–200 m.

Diagnosis

Animal very small, to 4.7 mm long, elevated (dorsal elevation 0.37) subcarinate, valves beaked; anterior margin of intermediate valves splayed laterally, with large inward curve in jugal area. Several granules of tegmentum in pleural areas joined, each granule with single megalaesthete and 9–16 micraesthetes; girdle covered dorsally with long, pointed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A
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scales that are smooth or with one central rib, as well as with numerous long needles. Insertion plates well developed both in head and tail valves.

Description

Holotype small, BL = 4.7 mm. Valves subcarinated, beaked (Figure 6D), shell and girdle white. Head valve semicircular, posterior margin wide, V-shaped, notched in the middle, tegmentum sculptured with roundish granules (diameter 70–80 μm), arranged without pattern (Figure 6A). Intermediate valves trapeziform, anterior margin greatly splayed laterally, with large inward curve in jugal area, posterior margin with small beak, lateral areas sculptured like head valve with rare round granules, jugal area sculptured with oval granules (about 80 × 50 μm) arranged without interspaces or pattern (Figure 6B). Pleural areas sculptured with oval granules (120 × 70 μm) arranged without pattern, several granules join to form larger granules (up to 220 × 160 μm) (Figures 6E and 8I, J). Intermediate valves VI and VII have indistinct, short, longitudinal rows of granules in pleural areas near their posterior margin that are interrupted by large, joined granules in other part of pleural area. Each granule contains one megalaesthete surrounded by 9–16 micraesthetes (Figure 8I). Tail valve narrower than head valve, more or less oval, mucro submedian, clearly indicated, postmucronal slope decidedly concave directly behind mucro, straightening near the posterior margin, antemucronal area sculptured like central area of intermediate valves, postmucronal area like head valve (Figure 6C and F).

Articulamentum strongly developed, insertion plates only on head valve 1/5 the length of the valve, apophyses wide, oriented laterally, connected to primordium of insertion plates in intermediate valves; insertion plates obsoletely striate in head and tail valves (Figure 6G).

Girdle narrow, 1/4 width of intermediate valve, covered dorsally with long pointed scales that may be smooth or with one central rib (50–86 × 23 μm) and numerous long smooth needles (330–550 × 24 μm). Marginal and dorsal needles similar. Ventral scales (50–55 × 18 μm) smooth typically, shorter than dorsal scales (Figures 7A, B, C, and 8C–E).

Radula 2.2 mm long, with 28 transverse rows of mature teeth (total about 34 transverse rows). Central tooth short, nearly rectangular, with narrow blade; major lateral tooth with tridentate cusp, central denticle largest, exterior and interior cusps approximately equal (Figures 7D and 8F–H).

Gills merobranchial, adanal, without interspaces, five ctenidia on each side, gills extending from valve VII to anus.

Etymology

From the Mediterranean Sea, where this species was found.

Figure 8. *Hanleya mediterranea* sp.nov., paratype, ZISP 2202, Prinkipo, Mediterranean Sea, depth 50 m, BL 4.7 mm (A–J). *Hanleya tropicalis* (Dall, 1881), paratype, USNM 95172, Florida, Sands Key Pourtales, depth 230 m, BL 10 mm (K). (A) valve V, frontal view; (B) tail valve, lateral view; (C) dorsal and marginal needles; (D) dorsal scales; (E) ventral scales; (F) central and first lateral tooth of radula; (G, H) head of major lateral tooth of radula; (I, J) aesthete group. Scale bars: A, B: 1 mm, C, H, K: 100 μm.

Comparative remarks (Table 1)

Hanleya mediterranea is distinguished from other species in the genus, including *H. hanleyi*, by its lack of longitudinal rows of granules across the entire pleural area, and by the presence of large granules comprising two or more small granules in pleural areas.

Small specimens of *Hanleya nagelfar*, which have a similar radula, differ from *H. mediterranea* by having dorsal spicules that are oval in transverse section, with six perceptible ribs. In *H. mediterranea* (BL = 4.7 mm) the head valve has more strongly developed insertion plates that are 16–20% the length of the valve, compared with *H. nagelfar*, (BL = 5–7 mm), in which the insertion plates are 3–9% the length of the head valve.

Hanleya tropicalis differs from *H. mediterranea* in having carinated valves, in lacking an insertion plate in the tail valve, and by having a smaller exterior denticle on the major lateral teeth of the radula (Figure 8H and K).

Hanleya harasewychi has similar dorsal scales on the girdle, but differs from *H. mediterranea* by having rounded valves, in the colour of the shell and girdle, by having longer granules on pleural areas of intermediate valves, as well by their arrangement, by a wider jugal sinus, a well-developed and pectinate insertion plate in the tail valve, and by a lower number of mineralised transverse rows of radular teeth as well as in the shape of the head of the major lateral teeth.

Hanleya brachyplax has a similar radula, but differs from *H. mediterranea* in being less elevated, having a well-developed insertion plate in its tail valve, and by its larger size.

Hanleya multigranosa (Reuss, 1860) from Middle Miocene deposits of Bohemia differs from the new species in having a shorter insertion plate on the head valve, a differently shaped tail valve, and smaller and more numerous granules on the tail valve. A single Pleistocene intermediate valve from Parma, Italy, which was identified as *H. multigranosa* by Sabelli and Taviani (1979: Table 1, Figure 4) most likely belongs to *H. mediterranea.* The records of fossil *Hanleya* from the Miocene of Poland, reported as *H. multigranosa* by Sulc (1934) and from the Upper Miocene of Italy, reported as *H. hanleyi* by Dell'Angelo et al. (1999) should be confirmed by comparison of these fossil specimens with the new species described herein. *Hanleya glimmerodensis* Janssen, 1978 from the Upper Oligocene of western Germany differs from *H. mediterranea* in having well-marked longitudinal rows of granules on pleural areas of intermediate valves.

Several publications report *Hanleya hanleyi* as occurring in the Mediterranean Sea (Monterosato 1879; Malatesta 1962; Sabelli 1972, 1974; Dell'Angelo et al. 2004 and references in Dell'Angelo and Smriglio 2001). Among these studies, Sabelli (1972) reported this species to reach a body length of 9 mm, and occur at depths ranging from 35–40 m to 140 m. Sabelli (1974) reported a body length of about 10 mm, while Dell'Angelo and Smriglio (2001) reported a maximum body length of about 13 mm. Dell'Angelo (personal communication) informed me that he has several specimens of *Hanleya hanleyi* collected in the Mediterranean Sea (BL < 7 mm), from depths of 40–120 m and single valves dredged at depths up to 400 m in his collection. Dell'Angelo and Smriglio (2001: pl. 25 C, Figure 36) included several photographs of chitons that have longitudinal rows of granules on central

areas of intermediate valves. Although more than one species of *Hanleya* may inhabit the Mediterranean Sea, I provisionally attribute the above-mentioned records to *H. mediterranea*.

Although the validity of *Hanleya tropicalis* and *H. brachyplax* is not in doubt, the relationship between *H. hanleyi* and *H. nagelfar* has been questioned. It is very difficult to distinguish small specimens of *H. nagelfar* from *H. hanleyi* because they both have a very similar sculpture of the tegmentum (Waren and Klitgaard 1991). As noted in the introduction, the discussion about differences between *H. nagelfar* and *H. hanleyi* has continued since the description of *H. nagelfar*. The relationship between *H. hanleyi* and *H. nagelfar* is further explored by a study of age variability in *H. nagelfar*.

***Hanleya nagelfar* (Lovén, 1846)**
(Figures 9–19)

Chiton nagelfar Lovén, 1846: 158.
Hanleya nagelfar Kaas and Van Belle 1985: 196, Figure 92, map 19 (synonymy); Waren and Klitgaard 1991: 51, Figures 1–6; Dell'Angelo et al. 1998: 244, PL 1, Figure 10.

Type material

Lectotype, NHRM, type collection 1329 (designated by Kaas and Van Belle (1985)).

Type locality

Finnmark, Norway.

Material examined

Barents and Norwegian Seas: R/V *Andrey Pervozvaniy*, 1899, stn 4, 70.0230° N, 31.49° E, 144–178 m, 2 spms; stn 38, 69.58° N, 32.40° E, 230 m, 1 spm; 1900, stn 102, 74.27° N, 22.04° E, 180–211 m, 1 spm (Table 2, No. 8); stn 462, 71.20° N, 33.30° E, 304–280 m, 1 spm; stn 464, 71.21° N, 3159° E, 268 m, 1 spm. R/V *Persey*, 1924, stn 228, 70.3030° N, 31.13° E, 175 m, 1 spm (Table 2, No. 10); 1927, stn 677, 69.31° N, 34.39° E, 173 m, 1 spm; 1935, stn 3337, 71.35° N, 31.464° E, 313 m, 1 spm (Table 2, No. 11).

R/V *SRT4225*, cruise 1, 1955, stn 38/104, 61.308° N, 04.166° E, 300 m, 1 spm. R/V *Sevastopol*. RT-97, cruise 8, 1958, Lofoten Ids., 68.08° N, 13.50° E, 1 spm (Table 2, No. 7); cruise 9, 1958, stn 1453, 62.002° N, 6.146° W, 112 m, 1 spm; stn 1488, 72.291° N, 23.072° E, 335 m, 2 spms. R/V *Maslov*, cruise 5, 1969, stn 180/201, 70.40° N, 17.275° E, 510 m, 1 spm; stn 182/203, 71.30° N, 16.46° E, 300 m, 1 spm (Table 2, No. 13); stn 183/204, 72.02° N; 17.02° E, 360 m, 1 spm (Table 2 No. 12); stn 188/209, 73.20° N, 15.25° E, 500 m, 1 spm. R/V *Tunets*, cruise 105, 1978, stn 4, 70.06° N, 32.325° E, 230 m, 1 spm; stn 11, 70.110° N, 17.350° E, 225 m, 2 spms; stn 12, 70.330° N, 16.540° E, 1100 m, 5 spms. R/V *Dalnie Zelentsi*, cruise, 16.1982, stn 64, 67.559° N, 10.080° E, 280 m, 3 spms. F.D. Behrens, 1948, Lofoten, 2 spm (ZIM). F.D. Saturn,

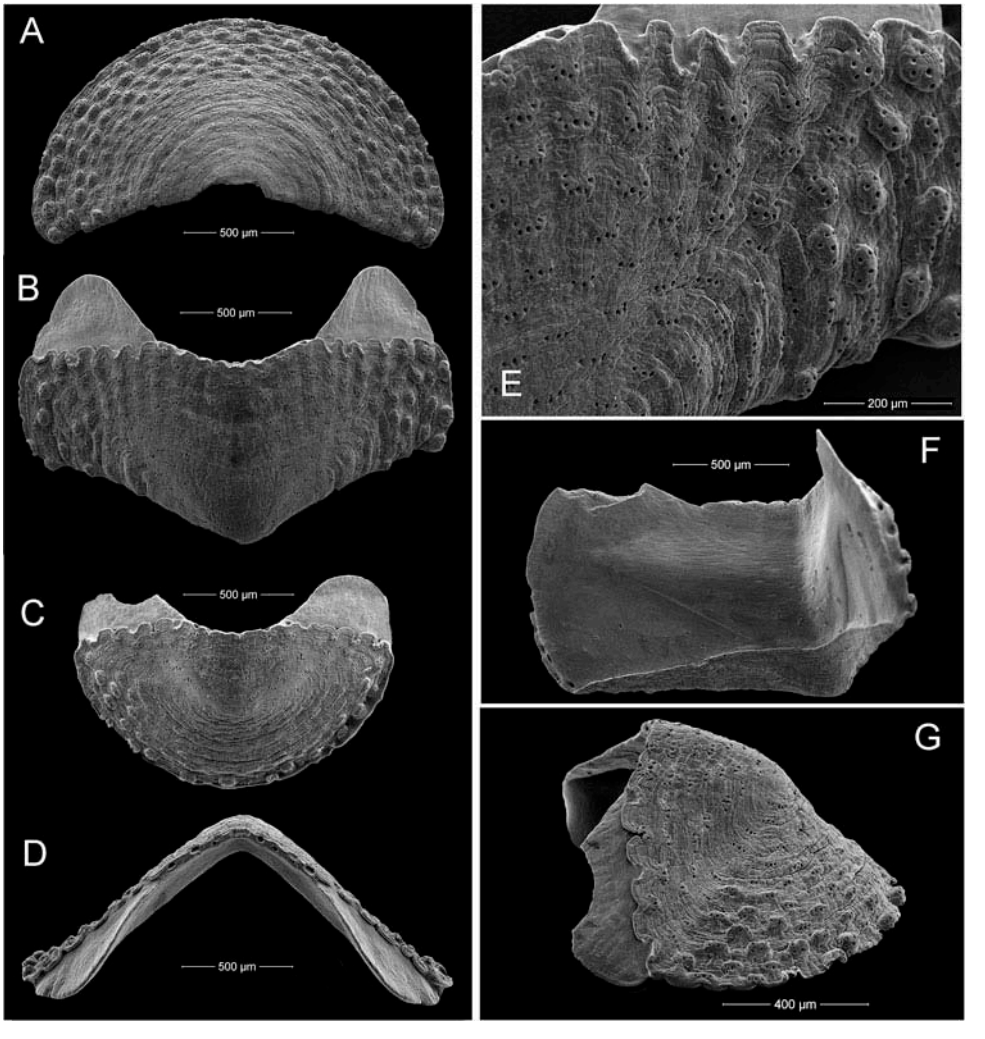


Figure 9. *Hanleya nagelfar* (Lovén 1846), Newfoundland Bank, R/V *NEREIDA*, cruise 0710, stn. 75, 24, depth 1227 m, BL 5.0 mm. (A) head valve, dorsal view; (B) valve V, dorsal view; (C) valve VIII, dorsal view; (D) valve V, front view; (E) pleural and lateral areas of valve V; (F) valve IV, ventral view; (G) tail valve, lateral view.

1958, 64.44° N, 35.06° W, 500 m, 1 spm. (ZIM); 1923, Folden, 50–100 m, 1 spm, (TM 13350); Skattora, Tromso, 54 m, 2 spms, (Table 2, No. 5), (TM 12923); 1951, Senja, Steinavar, 360–365 m, 1 spm, (TM 13335); 1954, Morsdalsfjord, 50–110 m, 1 spm, (TM 13196); 1954, Balsnes, 28 m, 1 spm, (TM 13258); 1954, Brokskar, Rystr, 50–120 m, 1 spm (Table 2, No. 3), (TM 12962); Beiarn, 40–90 m, 1 spm, (TM 13237); 1955, Tjelsund, 60–110 m, 1 spm, (TM 12955); 1955, Holandsfjord, 45–770 m, 1 spm, (TM 13241); 1955, Eiet, 52–58 m, 6 spms, (TM 13001); Masoy, 125–90 m, 2 spms, (TM 13299); 1955, Bjarandfjord, 76–92 m 1 spm, (TM 12997); 1955, Rana, 35–42 m, 1 spm, (TM 13304).

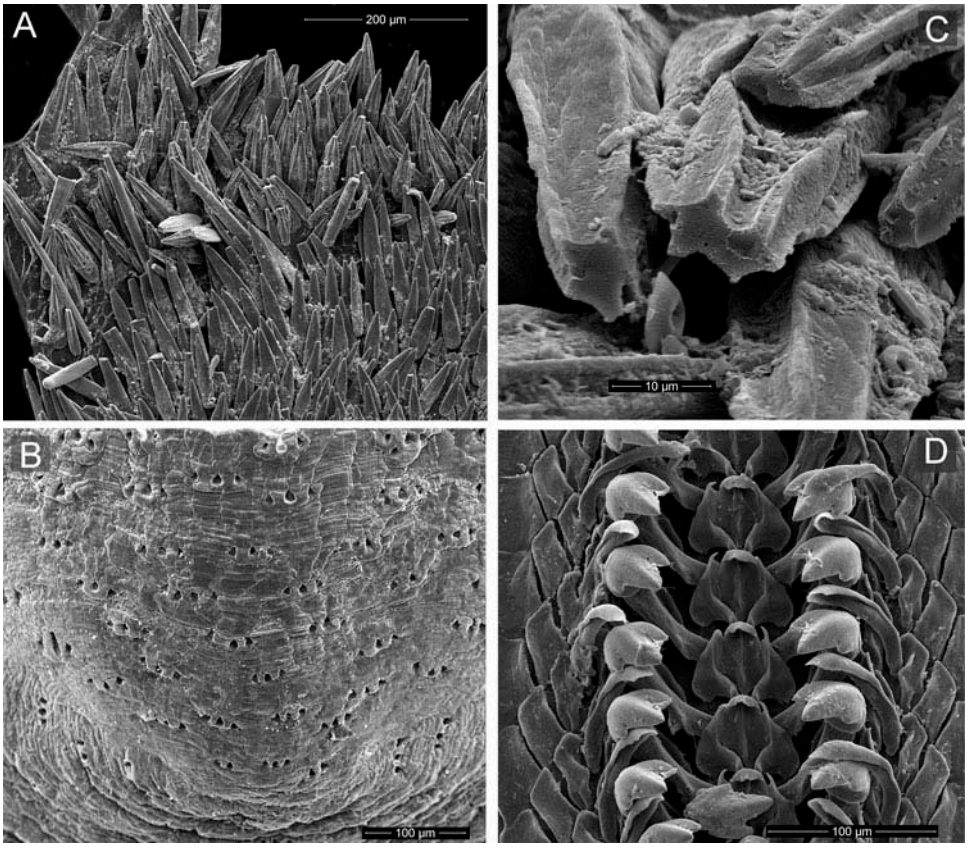


Figure 10. *Hanleya nagelfar* (Lovén, 1846), Newfoundland Bank, R/V *NEREIDA*, cruise 0710, stn. 75, 24, depth 1227 m, BL 5.0 mm. (A) dorsal and ventral spicules and needles; (B) mucro of tail valve; (C) dorsal spicules; (D) radula.

Eastern Greenland Sea: R/V Atlantida, cruise 10, 1973, stn 18/1668, 74.50° N, 16.00° E, 360 m, 1 spm.

Southeastern Greenland: R/V *Sevastopol*, RT-97, cruise 5, 1957, stn 1168, 66.162° N, 31.356° W, 345 m, 2 spms; stn 1609, 65.526° N, 29.586° W, 425 m, 1 spm.

Central and North Atlantic Ocean: R/V *Akademik Keldysh*, cruise 4, 1982 stn 513, 34.261° N, 30.030° W, 690 m, 1 spm; stn 444, 58.208° N, 31.363° W, 1635–1535 m, 1 spm; stn 364, Reykjanes Ridge, 1330 m, 1 spm; st. 385, Reykjanes Ridge, 1680–1800 m, 1 intermediate valve; R/V *Ichtiandr* cruise 8, 1982, stn 39, 09.038° N, 21.101° W, 610–700 m, 1 spm; stn 50, 33.141° N, 29.425° W, 700–740 m, 1 spm.

Newfoundland Bank: R/V *Sevastopol*, RT-97, cruise 16, 1960, stn 2805, 49.477° N, 50.185° W, 318–324 m, 1spm; R/V *Nereida*, 2009, cruise 0509, stn 6, cod 5, 48.2915° N, 44.0609° W, 1348 m, 1 spm; stn 10, cod 54, 48.0005° N, 43.7607° W, 1554 m, 1

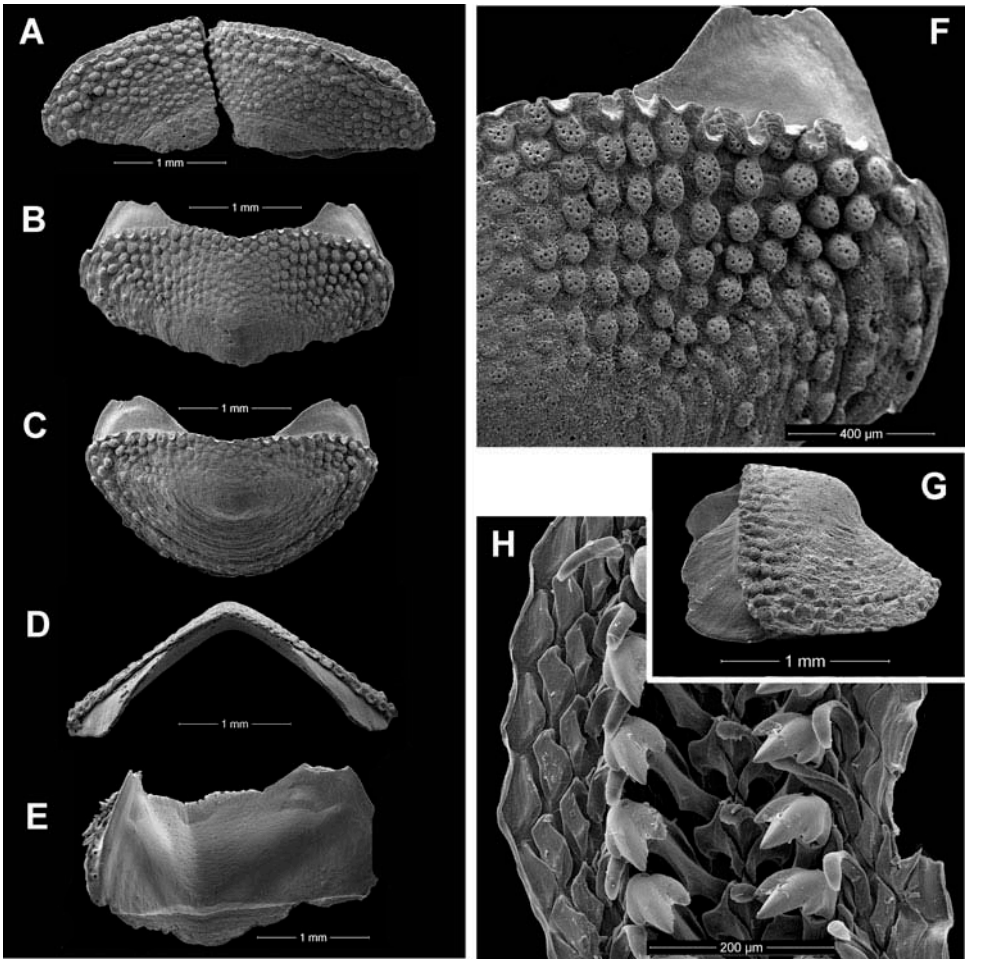


Figure 11. *Hanleya nagelfar* (Lovén, 1846), Newfoundland Bank, R/V *NEREIDA*, cruise 0610, stn. 69, 10a, depth 502–504 m, BL 7.0 mm. (A) valve I, dorsal view; (B) valve V, dorsal view; (C) valve VIII, dorsal view; (D) valve I, front view; (E) valve IV, ventral view; (F) valve V, central and lateral areas; (G) valve VIII, lateral view; (H) radula.

spm; stn 12, cod 16, 47.7772° N, 43.5748° W, 1462 m, 1 spm; stn 19, cod 21, 47.1643° N, 43.5338° W, 1358 m, 2 spms (Table 2, No. 4), stn 22, cod 12, 46.8400° N, 43.6404° W, 956 m, 1 spm (Table 2, No. 6); stn 23, cod 22, 46.7749° N, 43.8651° W, 1127 m, 3 spms; stn 24, cod 27, 46.6942° N, 43.9686° W, 1104 m, 1 spm; 2010, cruise 0610, stn 63, cod 8, 46.3697° N, 44.9944° W, 1406 m, 2 spms; stn 67, cod 7, 46.2677° N, 46.5429° W, 613 m, 1 spm; stn 69, cod 10a, 46.1543° N, 46.4503° W, 502 m, 1 spm; stn 69, cod 10c, 46.1543° N, 46.4503° W, 502 m, 2 spms; stn 71, cod 10, 46.0800° N, 46.3421° W, 888 m, 1 spm; cruise 0710, stn 75, cod. 24, 45.8692° N, 46.8210° W, 1227 m, 1 spm (Table 2, No. 1); stn 96, cod. 30, 43.9894° N, 48.9512° W, 863 m, 1 spm; cruise 0810, stn 99, cod 11, 43.6147° N, 49.0781° W, 548 m, 1 spm; stn 100, cod 12, 43.4844° N, 49.1855° W, 694 m, 2 spm; stn 103, cod 20, 429433° N, 49.5621° W,

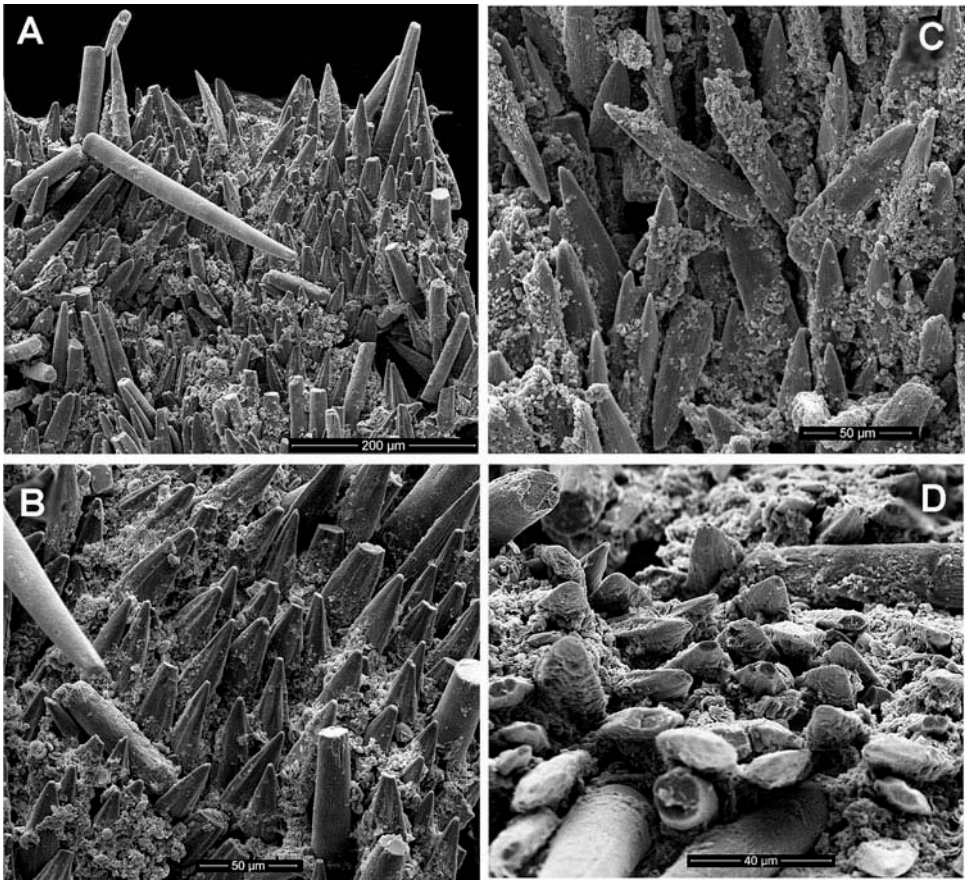


Figure 12. *Hanleya nagelfar* (Lovén, 1846), Newfoundland Bank, R/V *NEREIDA*, cruise 0610, stn. 69, 10a, depth 502–504 m, BL 7.0 mm. (A, B, D) dorsal specules and needles; (C) ventral scales.

1154 m, 1 spm. FN3L, 2006, stn 2, 47.9415° N, 47.3725° W, 411 m, 1 spm; FN3L, 2006, stn 9, 47.9370° N, 47.1883° W, 460 m, 1 spm; FN3L, 2008, stn 37, 47.6480° N, 47.1340° W, 503 m, 2 spms; FN3L, 2008, stn 84, 46.4488° N, 47.2603° W, 396 m, 1 spm; FN3L, 2009, stn 89, 461100° N, 47.3333° W, 1005 m, 2 spms; PLA, 2008, stn 98, 43.6298° N, 48.9907° W, 1436 m, 4 spms (Table 2, No. 9).

North America: Off Eastport, Maine (Jeffreys coll.), 1 spm, (USNM, 177511); Off Martha's Vineyard, Massachussetts, 1 spm, (USNM); Georges Bank, 270 m, 1 spm (USNM); Nova Scotia, 72 m, 1 spm (USNM).

Distribution

North and Central Atlantic Ocean, the Barents, Norwegian and Greenland seas, near southern Greenland, North America, Europe and northern Africa, on Mid-Atlantic

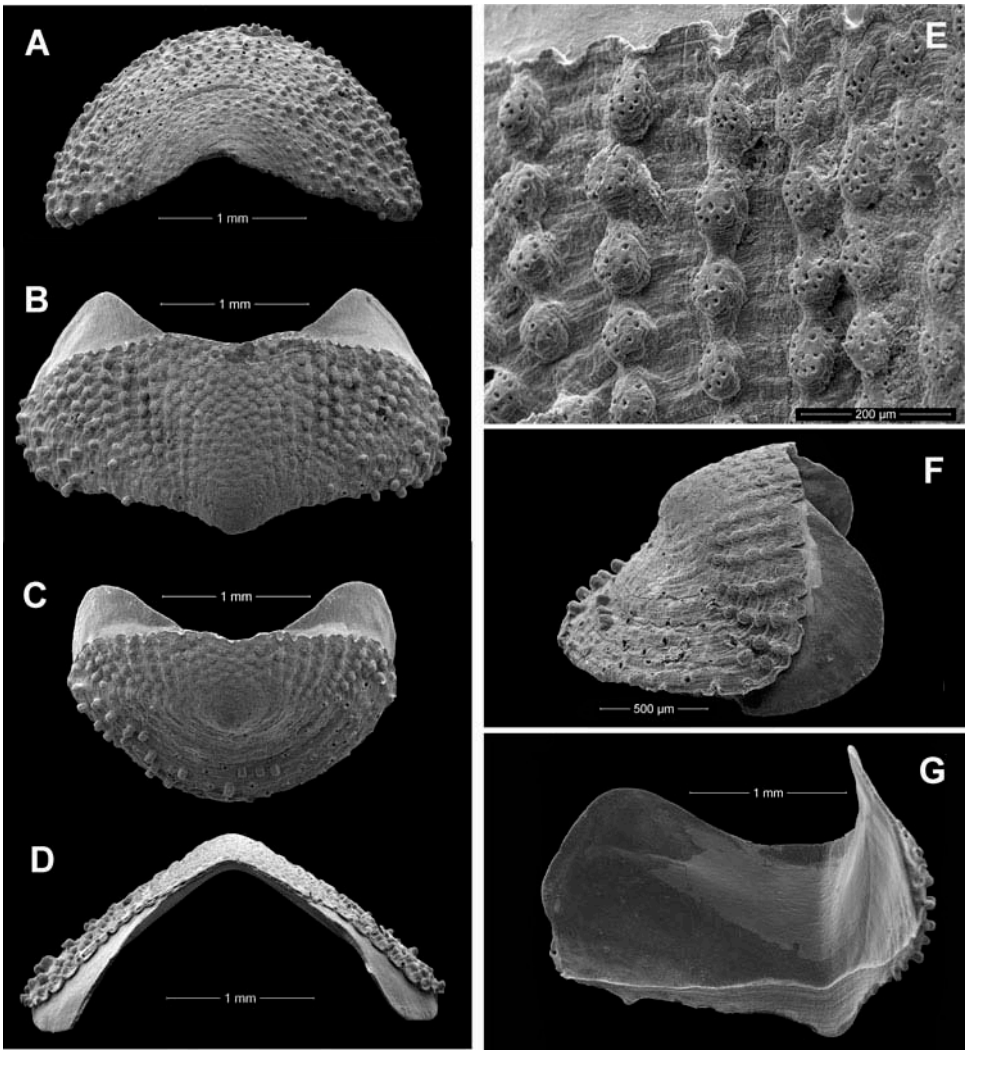


Figure 13. *Hanleya nagelfar* (Lovén, 1846), Northern Norway, depth 52–58 m, BL 7.0 mm. (A) valve I, dorsal view; (B) valve V, dorsal view; (C) valve VIII, dorsal view; (D) valve V, front view; (E) valve V, central area; (F) valve VIII, lateral valve; (G) valve IV, ventral valve.

Ridge from 74.27° N to 09.038° N at depths from 28 to 1680 m, mostly deeper than 200 m.

Large specimens of *Hanleya nagelfar* are easily distinguished from *H. hanleyi* (see Kaas and Van Belle, 1985), but small chitons (<10 mm) are difficult to identify.

In order to study age variability in *H. nagelfar*, seventeen specimens of different sizes (BL = 5.0–73.0 mm), from different regions of the Atlantic Ocean were measured (Table 2, Figures 8–18). These measurements revealed that important changes occur in the shape of the valves, the thickness of the girdle, and the shape, size and ribbing of the dorsal spicules of the girdle.

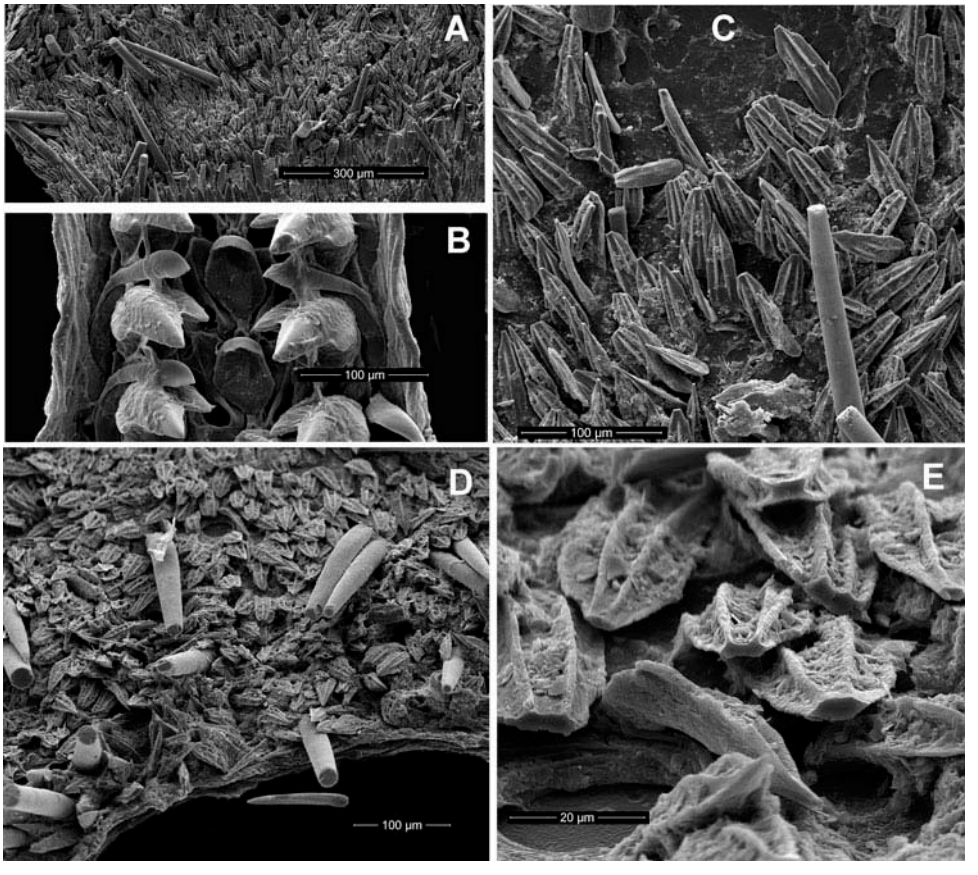


Figure 14. *Hanleya nagelfar* (Lovén, 1846), Northern Norway, depth 52–58 m, BL 7.0 mm. (A) dorsal, marginal and ventral spicules and needles; (B) radula; (C) dorsal spicules and needles.

With increasing body length, the ratio of head valve width/tail valve width decreased from 1.27 (BL = 5.0 mm) to 0.84 (BL = 70.0 mm); the ratio of valve V width/valve V length decreased from 2.56 (BL = 5.0 mm) to 1.36 (BL = 70.0 mm); and the ratio of valve V width/width of adjacent girdle also decreased from 5.9 (BL = 5.0 mm) to 1.36 (BL = 70.0 mm) (Table 2).

Small and medium size specimens (BL = 5.0–29.0 mm) have flattened, short and pointed spicules with 6–7 ribs arranged around the spicule (Figures 10A, C, 12A, B, 14A, C, D, E, 16A–C, 17D, 18A, C). With increasing age (specimen size) the spicules become longer and the ribs become less prominent or obsolete (Figures 18B, D, 19E).

Discussion

Judging from the short descriptions of *H. hanleyi* (Bean in Thorpe 1844; Forbes and Hanley 1850) (see below) this species is very similar to young specimens of *H. nagelfar* in the shape of its shell and the sculpture of the tegmentum.

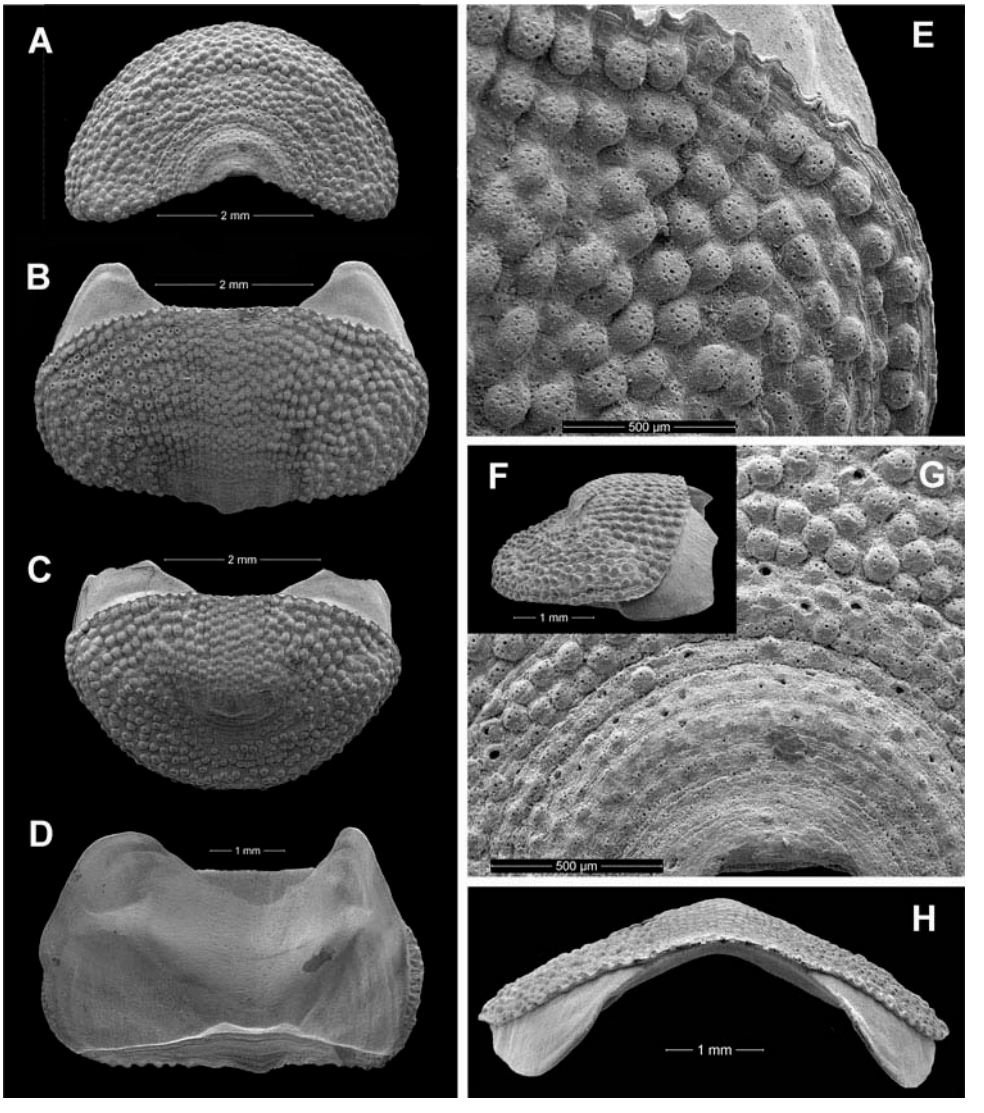


Figure 15. *Hanleya nagelfar* (Lovén, 1846), Reykjanes sea mounts, R/V *Akademik Keldish*, stn. 364, depth 1330 m, BL 14.0 mm. (A) valve I, dorsal view; (B) valve V, dorsal view; (C) valve VIII, dorsal view; (D) valve IV, ventral view; (E) valve V, central and lateral areas; (F) valve VIII, lateral view; (G) valve I, dorsal view; (H) valve V, front view.

Unfortunately, the girdle armature and radula of the type specimen of *H. hanleyi* remain unknown. The information provided by Kaas and Van Belle (1985) on the shell, girdle and radula was based on a study of two specimens of *Hanleya* from Norway rather than from the type locality in England. It may be that the studied specimens were young *H. nagelfar.*

The types of *Chiton hanleyi* were collected in the intertidal zone: 'Only two specimens of this beautiful shell have been met with at Scarborough attached to the

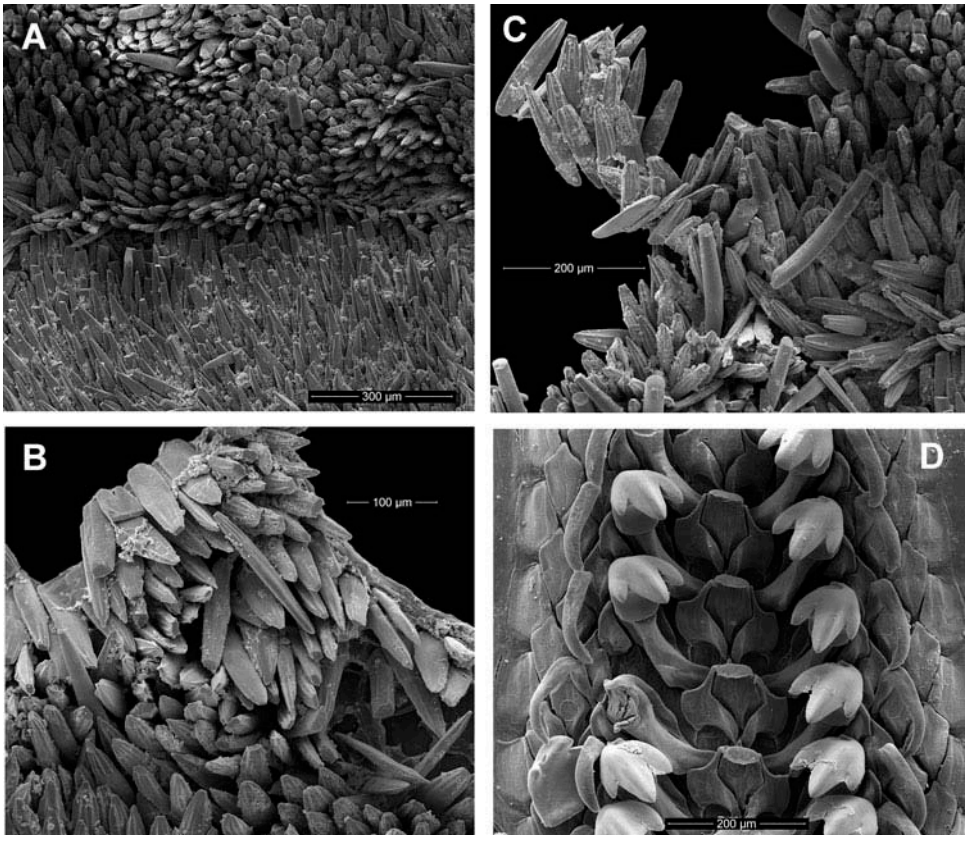
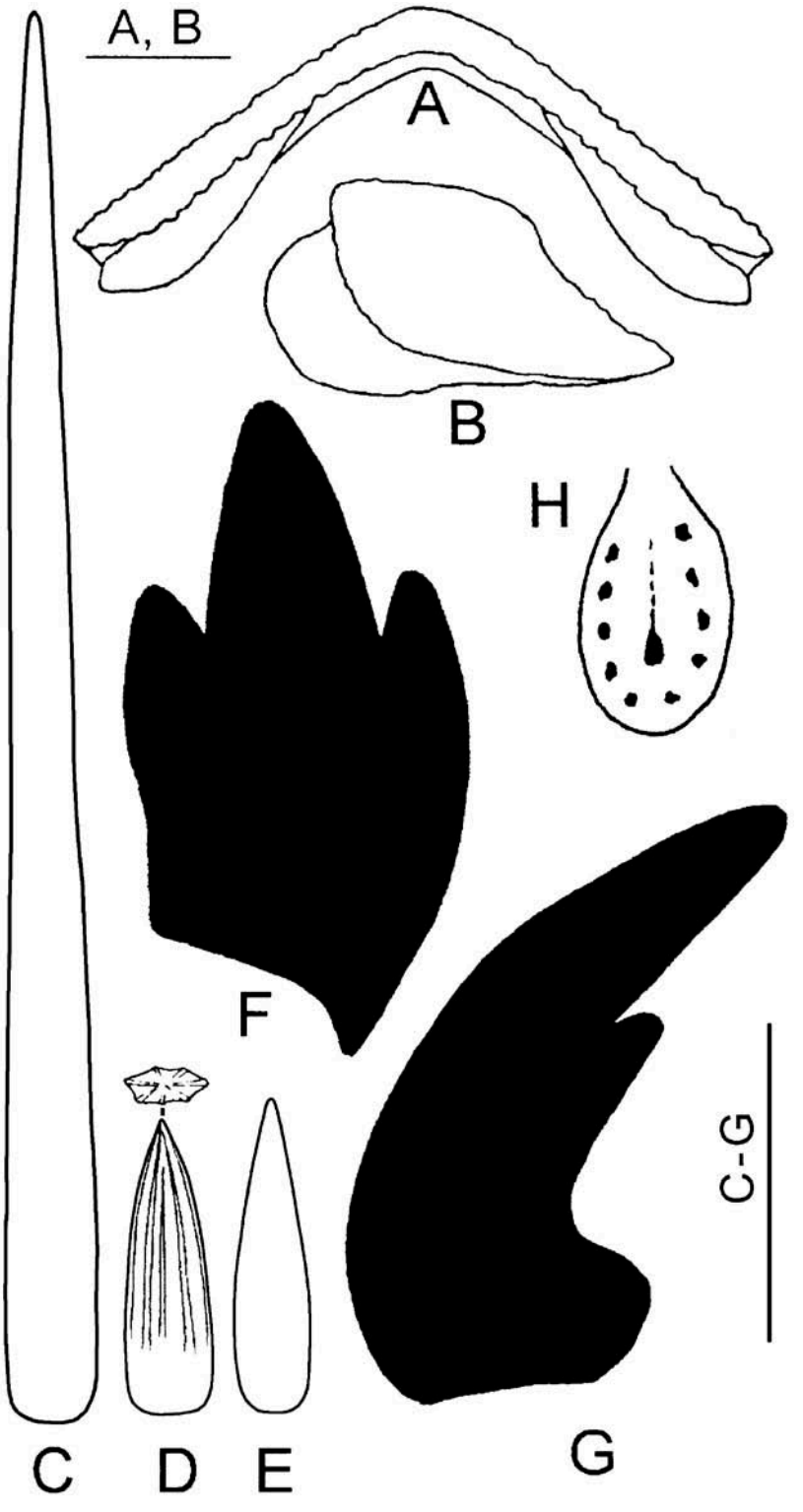


Figure 16. *Hanleya nagelfar* (Lovén, 1846), Reykjanes sea mounts, R/V *Akademik Keldish*, stn. 364, depth 1330 m, BL 14.0 mm. (A) dorsal, marginal and ventral, spicules, needles and scales; (B, C) dorsal spicules and needles; (D) radula.

under sides of rocks at the lowest spring tides.' (Bean in Thorpe 1844, p. 263). The description of *Chiton hanleyi* is short: 'Shell oblong oval narrow, carinated, brownish white, granulated, with the granulations larger towards the margin which is covered with minute spines; inside pale green; length 3 lines (6.3 mm), breadth 1 ½ lines (3.1 mm)' (Bean in Thorpe 1844). In addition, several longitudinal rows of granules are illustrated in figure 57 (Been in Thorpe 1844). Moreover, Forbes and Hanley (1850, p. 398) provided a more detailed interpretation: 'The sculpture is peculiar, and for the size of the shell rather coarse. It consists, upon the central areas, of rather distant and not very numerous longitudinally disposed moniliform rows of granules, that become larger as they recede from the middle of the valves'. Their illustration (Forbes and Hanley 1850: pl. 62, Figure 2) shows the longitudinal rows of granules on the pleural areas. It is not clear whether the description of Forbes and Hanley refers to the type material.

Unfortunately, the type specimens of *Chiton hanleyi* have not been examined in any recent study. The type specimens of *Chiton hanleyi* are kept in the Wood End Museum in Scarborough, England, but were not seen by the author. Data for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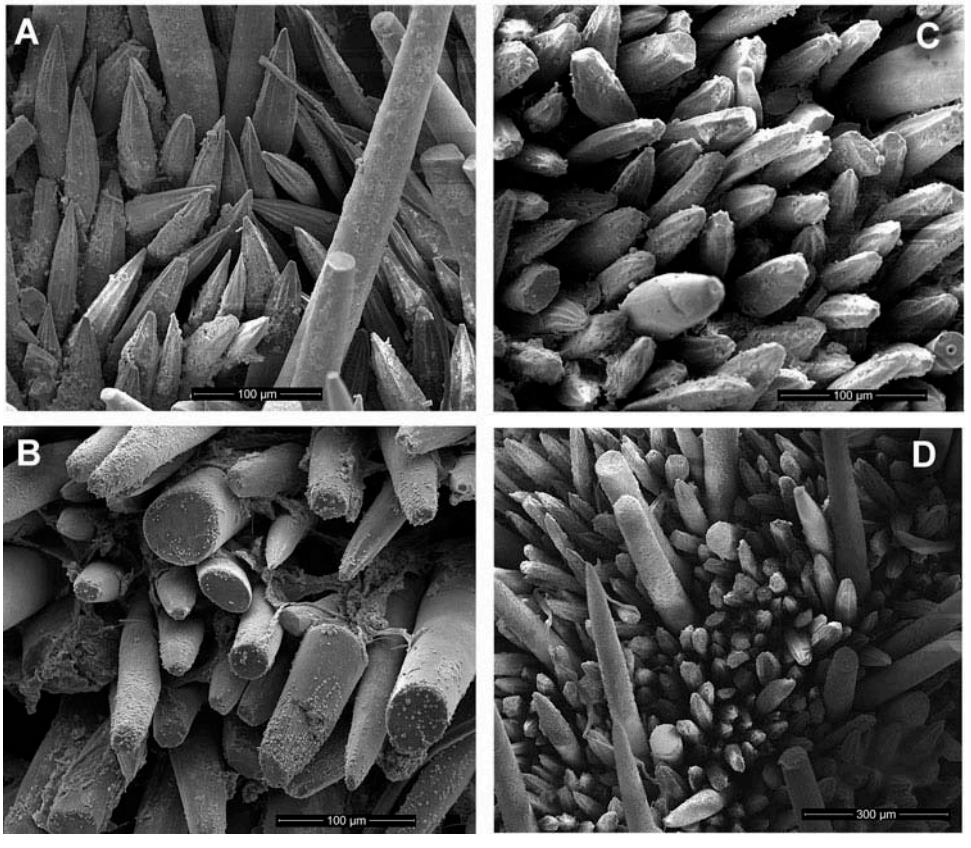

Figure 18. *Hanleya nagelfar* (Lovén, 1846), Northern Norway near Tromsø, depth 54 m, BL 28.0 mm (A); Norway, depth 300 m, BL 70 mm (B); Newfoundland Bank R/V *NEREIDA*, cruise PLA08, stn. 98, depth 1436 m, BL 29.0 mm (C); Central Atlantic, R/V *Ikhtiandr*, st. 50 depth 700–740 m, BL 73 mm (D). (A,D) dorsal spicules and needles.

this species are therefore absent in Table 1. Before a study of type material of *H. hanleyi* it is difficult to determine the potential validity of several synonyms of this species included in Kaas and Van Belle, 1885 (*Hanleya dalli*, *H. debilis*, *Chiton mendicarius*).

Conclusion

All species of *Hanleya* occur only in the Atlantic Ocean and adjacent seas, from off Brazil (25.44° S) to the Barents Sea (74.27° N) (Figure 19). Most records are referable to *H. nagelfar* which ranges from 9.038° N to 74.27° N, from North America to

Figure 17. *Hanleya nagelfar* (Lovén, 1846), Eastport, Maine, USNM 177511, BL 15 mm (A–H); (A) valve V, frontal view; (B) valve VIII, lateral view; (C) dorsal and marginal spicule; (D) dorsal spicule; (E) ventral spicule; (F, G) head of major lateral tooth of radula; (H) aesthete group. Scale bars: A, B: 1 mm, C–G: 100 µm.

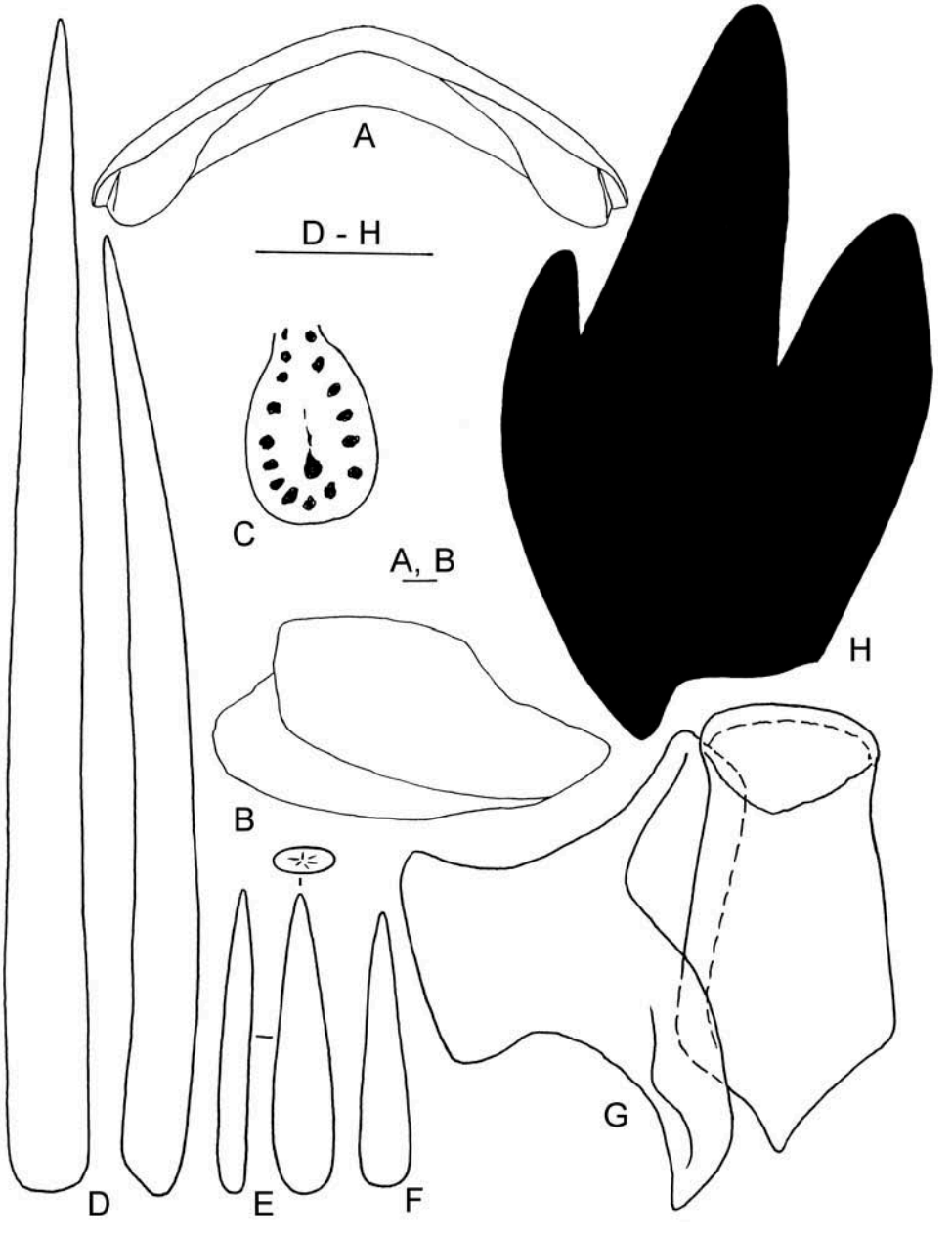

Figure 19. *Hanleya nagelfar* (Lovén, 1846), Southeastern Barents Sea, depth 300 m, BL 36 mm. (A) valve V, frontal view; (B) valve VIII, lateral view; (C) aesthete group; (D) dorsal and marginal needles; (E) dorsal spicules; (F) ventral spicule; (G) central and first lateral tooth of radula; (H) head of major lateral teeth of radula. Scale bars: A, B: 1 mm, D–H: 100 μm.

Table 2. Ratio of width and length of valves and girdle in ontogenesis of *Hanleya nagelfar*. For information for specimens see 'Material examined' in the text, indicated with No. 1–13.

№	BL (mm)	width of valve I	width of valve VIII	width of valve V	length of valve V	width of girdle	Ratio		
							width of valves I/VIII	width/ length of valve V	width of valve V/width of girdle
1	5.0	1.9	1.5	2.05	0.8	0.35	1.27	2.56	5.9
2	14.0	5.0	4.9	5.8	2.7	1.8	1.02	2.15	3.2
3	14.0	4.9	4.8	5.7	2.9	2.6	1.02	1.97	2.19
4	18.0	5.9	5.8	7.0	3.7	3.1	1.02	1.84	2.26
5	24.5	7.0	7.3	8.7	4.9	4.7	0.96	1.78	1.85
6	30.0	7.6	7.7	9.9	5.7	4.0	0.98	1.77	2.5
7	31.0	7.5	8.3	9.8	5.5	5.0	0.90	1.78	1.96
8	33.0	9.1	9.5	11.2	6.3	5.0	0.96	1.78	2.24
9	41.0	10.0	11.9	12.3	6.5	7.0	0.84	1.84	1.76
10	60.0	13.0	15.1	18.0	10.2	–	0.86	1.76	–
11	62.0	13.0	15.0	17.0	9.5	12.0	0.87	1.79	1.42
12	66.0	15.0	17.0	18.9	12.0	12.0	0.88	1.58	1.58
13	70.0	15.8	18.9	19.0	14.0	14.0	0.84	1.36	1.36

Europe and Africa. There are six Recent species of *Hanleya* (*H. tropicalis*, *H. brachyplax*, *H. harasewychi*, *H. mediterranea*, *H. hanleyi* and *H. nagelfar*). The relationship of the last two species is under question. Moreover three fossil species of *Hanleya* were described: *H. glimmerodensis* Janssen, 1978 (Upper Oligocene, W. Germany), *H. multigranosa* (Reuss, 1860) (Middle Miocene, Poland), and *Chiton strigillatum* (S. Wood, 1848) (Lower Pliocene, England). The last species has been synonymised with *H. hanleyi* (Dell'Angelo et al. 2004). *Hanleya hanleyi* is the only species of the genus which has been collected in the intertidal zone. All other members of *Hanleya* inhabit mainly bathyal or rarely sublittoral depths: *H. nagelfar* (28–1680 m), *H. tropicalis* (230 m), *H. brachyplax* (250–408 m), *H. harasewychi* (72.8–118.3 m), *H. mediterranea* (50–200 m).

In order to finally clarify the relationship of *H. hanleyi* and *H. nagelfar*, it will be necessary to study either the type specimen of *H. hanleyi* or a topotype specimen collected in the intertidal zone near Scarborough.

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