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Hanleya hanleyi (Bean in Thorpe, 1844) (Mollusca, Polyplacophora) and the influence of the Gulf Stream System on its distribution

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ABSTRACT. The polyplacophoran genus *Hanleya* contains two similar species in the Northeast Atlantic, *H. hanleyi* (Bean in Thorpe, 1844) and *H. nagelfar* (Lovén, 1846), which were primarily differentiated by dramatic difference in size but also in part by distribution and minor morphological and ecological features. The question of whether these two names represent two species or whether *H. nagelfar* is merely a name for *H. hanleyi* that have grown to extraordinary size, has been raised repeatedly since 1865. The problem was protracted by inaccessibility of the type specimen for the senior species name, and a lack of material collected near the type locality of *H. hanleyi*, both issues which we resolved in the course of this study. We examined the details of valves, girdle armature, and radula in specimens of *Hanleya hanleyi* from the Mediterranean Sea and Scotland. The similarity of relevant features among small specimens of *H. hanleyi* and *H. nagelfar* from Scotland, the Mediterranean Sea, Norway and Newfoundland Bank and the type specimen of *Hanleya hanleyi* suggests the two species are synonymous. *Hanleya nagelfar* is a junior synonym of *H. hanleyi*. Finally we note the eggs of *H. hanleyi* contain an unusual large drop of lipid that may increase their floatation. We propose that the eggs and larvae of *H. hanleyi* have an extended pelagic distribution and this extended dispersal period may connect populations from bathyal habitats in the slope of Newfoundland Bank via surface currents of the Gulf Stream System to northward and eastward in the Atlantic ocean.

Introduction

The chiton *Hanleya hanleyi* was described by Bean in Thorpe [1844] from Scarborough, England in the intertidal zone. Since that time the species was described redundantly several more times [*fide* Kaas, Van Belle, 1985]: *Lepidopleurus carinatus* Dall, 1927 = *Hanleya dalli* Kaas, 1957, from Gulf of Maine, USA, 22 m; *Hanleya debilis* Gray, 1857 with type locality unknown; *Chiton mendicarius* Mighels et Adams, 1842, from Casco Bay, Maine, USA. There are six presently accepted species in the genus *Hanleya* [*fide* Sirenko, 2014]: *H. hanleyi* (Bean in Thorpe, 1844); *Hanleya debilis* Gray, 1857; *H. dalli* Kaas, 1957, *H. nagelfar* (Lovén, 1846), *H. tropicalis* Dall, 1879, and *H. harasewychi* Sirenko, 2014. These include two species – *H. nagelfar, and H. hanleyi* – that have been the subject of extensive previous comparisons [Jeffreys, 1865; Kaas, Van Belle, 1985; Warén, Klitgaard, 1991; Sirenko, 2014].

The key difference between *H. nagelfar* and *H. hanelyi* is size. *Hanleya hanleyi* is relatively small, typically around 2 cm long, whereas *H. nagelfar* is the largest chiton in the order Lepidopleurida and regularly over 8 cm long. The fine details of the relevant features used in chiton taxonomy, particularly the valve sculpture and microstructure of the cuticular girdle armature, are strongly similar in both taxa. And previous authors have noted that small specimens of *H. nagelfar* are exceedingly rare [e.g. Kaas,Van Belle, 1985; Warén, Klitgaard, 1991]. As almost all small specimens are identifiable as *H. hanleyi*, and all large specimens as *H. nagelfar*, there is persistent doubt about whether these represent two species or simply large and small individuals of one taxon.

Since Jeffreys [1865], who considered *H. nagelfar* as merely *H. hanleyi* of extraordinary size, the discussion about validity of two or three species (*H. hanleyi, H. nagelfar* and *H. abyssorum*) has continued. *Hanleya nagelfar* (Lovén, 1846) was originally described from Finmark, Norway. Shortly afterward, that species was described a second time as *Chiton abyssorum* M. Sars MS, Jeffreys, 1865, from Bergen, Norway, 270-360 m, recognised as a junior synonym by Kaas and Van Belle [1985].

Sparre Schneider [1878] reported the absence of differences in the sculpture of the tegmentum of *H. hanleyi* and *H. nagelfar* and considered them to be the same. Pilsbry [1892] considered *H. abys-*

sorum to be a variety of *H. hanleyi*. By contrast Thiele [1909] found differences in calcareous spicules and radula of *H. hanleyi* and *H. nagelfar* and considered them separate species. Kaas and Van Belle [1985] considered the two species, *H. hanleyi* and *H. nagelfar* both to be valid, with *H. abyssorum* being a junior synonym of *H. nagelfar*. This has been the generally accepted taxonomic *status quo* since that publication, but even then they wrote: "So the last word on Scandinavian *Hanleya* species has not yet been spoken" [Kaas, Van Belle, 1985: 199]. Warén and Klitgaard [1991] devoted a substantial article on *H. nagelfar*, to examine its life history and particularly the feeding ecology. They compared *H. nagelfar* with *H. hanleyi* and decided to consider both species as valid but with an ecological question and noted intermediate population of *Hanleya* living on dead *Lophelia* branches. Todt *et al*. [2009] expanded the ecological understanding of *H. nagelfar* and noted its presence on multiple sponge hosts. Most recently Sirenko [2014] showed age variation of dorsal spicules and width of girdle of *H. nagelfar.*

In order to resolve the question of true taxonomic comparison between *H. hanleyi* and *H. nagelfar,* it was necessary to examine the type of *H. hanleyi* and to obtain detail features of *H. hanleyi* collected near the type locality. The availability of appropriate material including the syntype of *H. hanleyi* in the present study made this possible for the first time.

Materials and Methods

We have examined extensive materials of *Hanleya hanleyi* and *H. nagelfar*, including the lectotype of *H. nagelfar* and material of both species from the NE Atlantic in the collections of Naturhistoriska Riksmuseet (Stockholm, Sweden, NHRM) and the National Museum Wales (Cardiff, UK, NMWZ) including additional material attributed to both species from the Irish Sea, and the Zoological Institute, Russian Academy of Sciences (St. Petersburg; ZISP).

We studied the type specimen of *H. hanleyi* from Scarborough, England held by the Scarborough Museums Trust, Woodend, Scarborough, UK. The syntype is damaged but we were able to capture images of the shell, radula, and long needles of the girdle in the syntype though not small spicules. Destructive sampling of the type of *H. hanleyi* was not permitted by the institutional authority, therefore it could only be examined superficially. The specimen was preserved dry, with the foot, gills, and viscera removed, but the radula left *in situ*. We removed the specimen from the card by dissolving the attaching glue and removed and rehydrated a section of the radula for SEM imaging. The specimen was superficially cleaned to remove dust and debris; in the course of gentle cleaning some spicules were dislodged and these were mounted for examination via SEM.

Detailed descriptions were prepared for two additional key specimens. One specimen of the genus *Hanleya* was collected in Secche della Meloria, the Mediterranean Sea, at depth of 120 m (ZISP 2266). One more specimen was collected in Scotland historically (1889) by I. Skvortsovsky (ZISP 2267). These specimens were preserved dry.

In preparation for SEM imaging of specimens, the valves, armature of girdle and radula were boiled for 15 minutes in 7% KOH solution to remove all organic material, for further examination with a Scanning Electron Microscope (FEI Quanta 250). To examine the oocytes, gonad was dissected from preserved specimens of *H. nagelfar* and examined under a microscope (Leica DME).

Six samples of *H. nagelfar*, collected from the slope of the Newfoundland Bank collected by the R/V *Nereida* from Javier Murillo Peres, were examined in order to study egg morphology and time of reproduction.

Systematics

Class Polyplacophora Gray, 1821
Order Lepidopleurida Thiele, 1909
Family Hanleyidae Bergenhayn, 1955

Genus *Hanleya* Gray, 1857

Type species: *Hanleya debilis* Gray, 1857 (type by monotypy).

Genus distribution and range: Atlantic Ocean, from 25° S (Brazil) to 74° N (Greenland), including the Mediterranean Sea, and Gulf of Mexico. Upper Oligocene-Recent.

Hanleya hanleyi (Bean in Thorpe, 1844) (Figs. 1-10)

Chresonymy, after Kaas and Van Belle [1985] and Sirenko [2014].

?Chiton mendicarius Mighels, Adams, 1842: 42, pl. 4, fig. 8 (type lost); Clench, Turner, 1950: 308, pl. 42, fig. 6.

Chiton hanleyi Bean *in* Thorpe, 1844: 263, fig. 57; Sparre Schneider, 1886: 96.

Chiton nagelfar Lovén, 1846: 158; Jeffreys, 1865: 216; G.O. Sars, 1878: 110.

Hanleya debilis Gray, 1857: 186.

Chiton abyssorum M. Sars MS, Jeffreys, 1865: 216 (nom. nud.); M. Sars MS, G.O. Sars, 1878:109, pl. 7, fig. 4, pl. 34, fig. 3; Sparre Schneider, 1886: 96; Oskarsson, 1944: 9, fig. 1.

Hanleya abyssorum. — Dall, 1879: 319; Thiele, 1893: 388, pl. 31, fig. 39; Burne, 1896: 4, figs l-3, pl. 2, figs 1-3; Thiele, 1909: 14, pl. 2, fig. 4; Dons, 1933: 151, fig. 3;

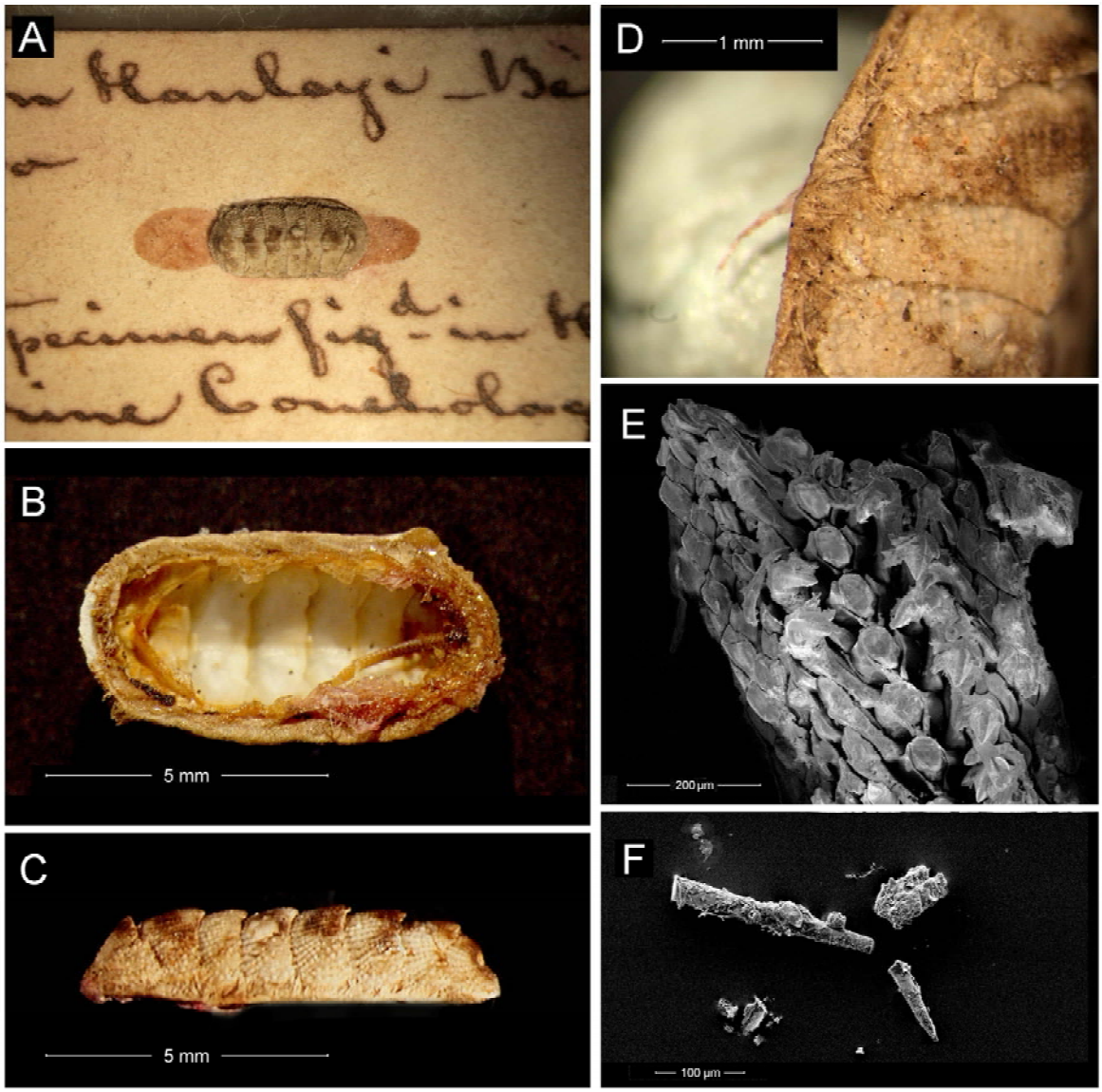

FIG. 1. *Hanleya hanleyi* (Bean in Thorpe, 1844). Syntype, Scarborough, Yorkshire, England, intertidal, body length (BL) – 7.6 mm. **A.** Whole specimen, dorsal view; **B.** Whole specimen, ventral view; **C.** Whole specimen, lateral view; **D.** Head valve, three intermediate valves and girdle, dorsal view; **E.** Part of radula; **F.** Needle of dorsal part of girdle.

РИС. 1. *Hanleya hanleyi* (Bean in Thorpe, 1844). Синтип, Скарборо, Йоркшир, Англия, литораль, длина тела (BL) – 7.6 мм. **A.** Целый экземпляр, вид сверху; **B.** Целый экземпляр, вид снизу; **C.** Целый экземпляр, вид сбоку; **D.** Головной щиток, три промежуточных щитка и перинотум, вид сверху; **E.** Часть радулы; **F.** Дорсальная игла.

Knudsen, 1949: 4; Muus, 1959: 41.

Acanthopleura hanleyi. — Monterosato, 1879: 27.

Hanleya hanleyi var. *abyssorum*. — Pilsbry, 1892: 18, pl. 4, figs 74-77; Nierstrasz, Hoffmann, 1929: 30.

Hanleya hanleyi. — Dautzenberg, Fischer, 1912: 21 (bibliography and synonymy); Nierstrasz, Hoffmann, 1929: 29, figs 26a-g, 52; Leloup, Voltz, 1938: 11, fig. 11; Knudsen, 1949: 4; Jakovleva, 1952: 59, fig. 20, pl. 2, fig. 2; Muus, 1959: 40, fig. 23; Malatesta, 1962: 153, figs 9-10; Knudsen, 1970: 3; Sabelli, 1972: 97, figs 1-6; 1974, figs 1-13; Laghi, 1977: 99, figs 5-9; Kaas, 1979: 25; McKay, Smith, 1979: 2; Dell'Angelo, Forli, 1995: 225; Dell'Angelo, Giusti, 1997: 51, fig. 2; Dell'Angelo, Smriglio 1999: 85, pls 25-26, figs 34-36 (*partim*); Dell'Angelo *et al*. 2004: 30, pl. 2, fig. 8; 2013: 76, pl. 3, figs D-F.

Lepidopleurus carinatus Dall, 1927:11 (not of Leach, 1852).

Hanleya nagelfar. — Dons, 1933: 151, figs 1-2; Kaas, Van Belle, 1985: 196, fig. 92, map 19 (synonymy); Warén, Klitgaard, 1991: 51, figs 1-6; Bellomo, Sabelli 1995: 201, fig. 1; Dell'Angelo *et al*., 1998: 244, pl. 1, fig. 10; Dell'Angelo *et al*., 2015: 231, pl. 4, figs 10-12.

Hanleya dalli Kaas, 1957: 83 (nom. nov. pro *L. carinatus* Dall).

Laminoplax dalli. — Ferreira, 1981: 190, figs 1-6.

Hanleya sp. — Dell'Angelo *et al*. 2004: 30, pl. 3, fig. 1.

Material examined. **Type material:** syntype of *H. hanleyi*: Scarborough Museums Trust, Woodend, Scarborough, UK. Scarborough, Yorkshire, England; intertidal. Lectotype of *H. nagelfar* (NHRM, type coll. 1329: Finmark, Norway).

Other material: specimens of *H. hanleyi* from the Mediterranean (ZISP 2266: Secche della Meloria, 120 m), Scotland (ZISP 2267: coll, I. Skvortsovsky 1889), Irish Sea (NMWZ 1991.076,1174: Irish Sea Survey 1991 stn 72) and

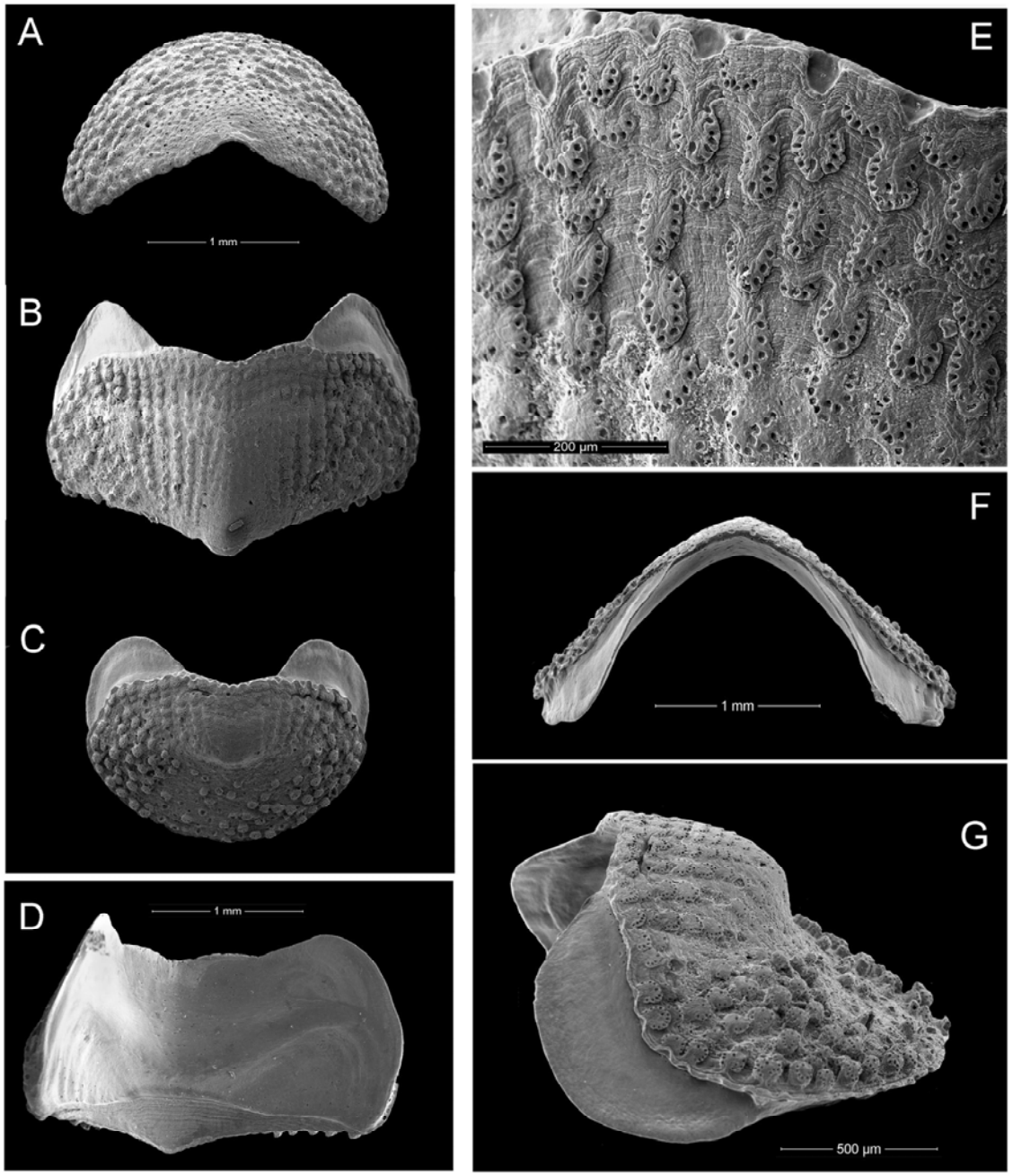

FIG. 2. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2266, Secche della Meloria, the Mediterranean Sea, depth 120 m, BL – 5.7 mm. **A.** Head valve, dorsal view; **B.** Valve V, dorsal view; **C.** Valve VIII, dorsal view; **D.** Valve IV, ventral view; **E.** Valve V, central area; **F.** Valve V, rostral view; **G.** Valve VIII, lateral view.

РИС. 2. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2266, Сече делла Мелория, Средиземное море, глубина 120 м, BL – 5.7 мм. **A.** Головной щиток, вид сверху; **B.** Щиток V, вид сверху; **C.** Щиток VIII, вид сверху; **D.** Щиток IV, вид снизу; **E.** Щиток V, центральное поле; **F.** Щиток V, вид спереди; **G.** Щиток VIII, вид сбоку.

Norway (NMWZ 2000.101.0015: Gullfaks Oilfield A, Norway, 129-137 m), and other material included by Sirenko [2014].

Original Description and type specimen

Chiton Hanleyi – Bean.—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 [6.4 mm], *breadth 1½ lines* [3.2 mm].

Only two specimens of this beautiful shell have been met with at Scarborough attached to the under sides of rocks at the lowest spring tides. We have great pleasure in naming it after the author of "a Descriptive Catalogue of recent Shells". Bean in Thorpe [1844: 263].

Only a single specimen is retained by the Scarborough Museums Trust (Fig. 1); the fate of the second specimen referred to by Bean is unknown. The colour of the tegmentum is white in the type

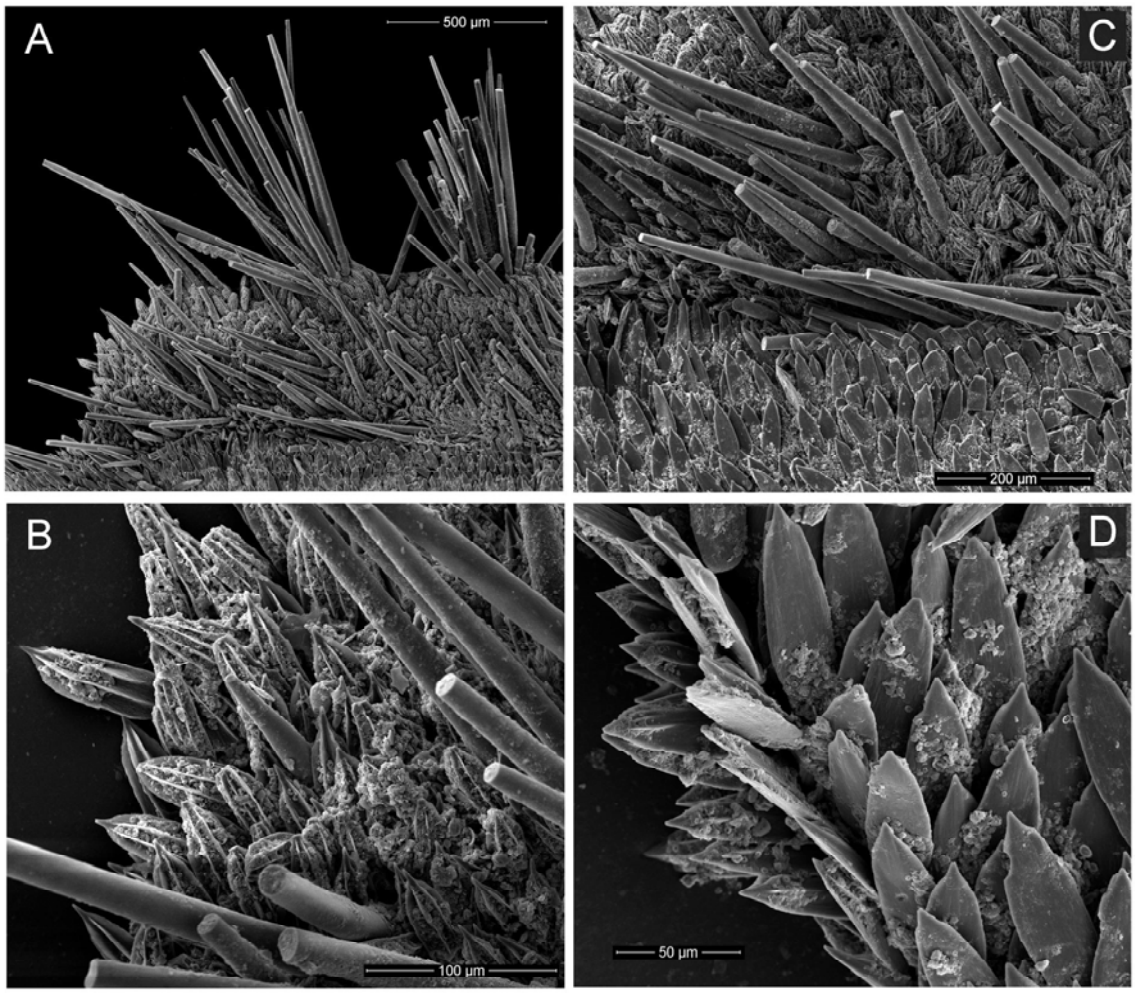

FIG. 3. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2266, Secche della Meloria, the Mediterranean Sea, depth 120 m, BL – 5.7 mm. **A, C.** Dorsal and marginal needles and dorsal spicules and ventral scales; **B.** Dorsal needles and spicules; **D.** Ventral scales.

РИС. 3. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2266, Сече делла Мелория, Средиземное море, глубина 120 м, BL – 5.7 мм. **A, C.** Дорсальные и маргинальные иглы и дорсальные спикулы и вентральные чешуйки; **B.** Дорсальные иглы и спикулы; **D**. Вентральные чешуйки.

specimen and in all other known specimens of *H. hanleyi* (not green as stated by Bean). The syntype is slightly larger than the measurements indicated in the original description.

Diagnosis: Animal of small to large size, syntype 7.6 mm, other individuals over 80 mm long, elongate oval, little elevated (dorsal elevation on intermediate valves c. 0.30). Intermediate valves subcarinate, with distinct central keel, side slopes straight, with clear posterior beak. Tegmentum sculpted with longitudinal rows of oval granules forming radiating pattern. Girdle spiculose, relative width increasing over ontogeny.

Description: The following features can be definitively described from the syntype specimen: Body length 7.6 mm, elongate oval, little elevated (dorsal elevation on intermediate valves c. 0.30). Valves subcarinate, with distinct central keel, side slopes straight, with clear posterior beak.

Head valve semicircular with apical notch; tail valve with central protruding rounded mucro, postmucronal slope straight. Tegmentum of head valve, lateral areas of intermediate valves and postmucronal area of tail valve uniformly sculptured with numerous, oval granules, increasing in size and spacing towards the outer margins; pleural areas and antemucronal area of tail valve sculptured with smaller granules, in longitudinal rows, fine and close set on the jugum, getting larger and posteriorly converging towards the side margins.

Perinotum with straight spicules, including fewer long needle-like spicules, stalked in short chitinous cups, over 250 ìm long up to 470 ìm.

Central radula tooth tall and broad, with a thin blade, major lateral cusps tridentate, central denticle much larger than others, all denticles sharply pointed.

Distribution: North and Central Atlantic Ocean including the Mediterranean, near southern Green-

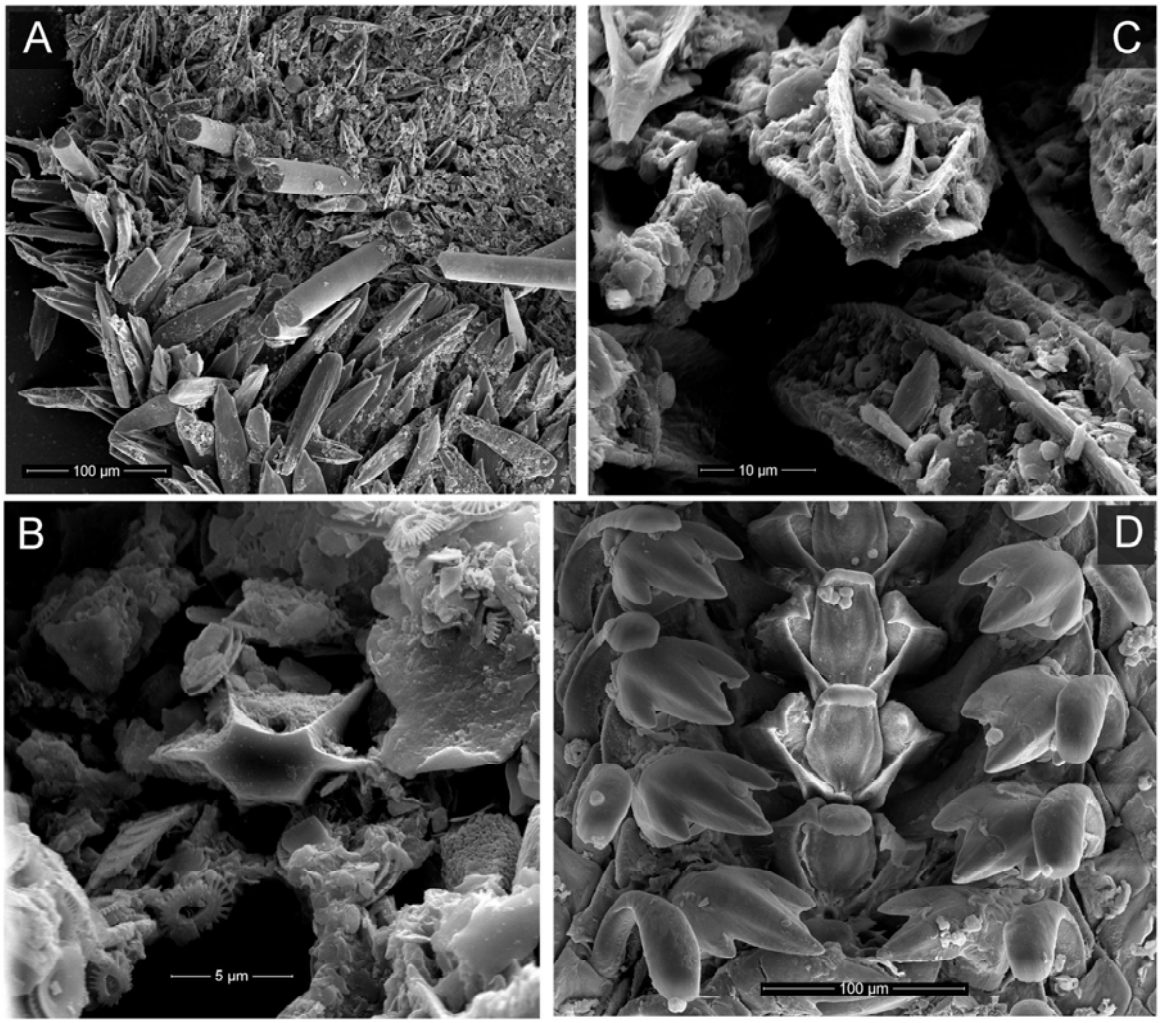

FIG. 4. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2266, Secche della Meloria, the Mediterranean Sea, depth 120 m, BL – 5.7 mm. **A.** Dorsal needles and spicules, marginal needles and ventral scales; **B, C.** Dorsal spicules; **D.** Radula.

РИС. 4. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2266, Сече делла Мелория, Средиземное море, глубина 120 м, BL – 5.7 мм. **A.** Дорсальные иглы и спикулы, маргинальные иглы и вентральные чешуйки; **B, C.** Дорсальные спикулы; **D.** Радула.

land, North America, Europe, Canary Islands and northern Africa, at depths from intertidal (rare) to 1680 m, mostly 35–300 m.

Comparative descriptions

Specimen of *H. hanleyi* from the Mediterranean Sea (ZISP 2266) (Figs. 2-4).

Body length of the dry specimen 5.7 mm, its radula 3.1 mm long with 32 transverse rows of mature teeth. The detailed examination of this specimen (Figs 2-4) revealed its similarity to shell and radula of *H. hanleyi* [Fig 1; Kaas and Van Belle 1985]. The Mediterranean specimen has the similar longitudinal rows of oval granules on the valves, similar teeth of radula, and long needles on dorsal part of girdle.

The Mediterranean specimen has similarity to single valves illustrated in Dell'Angelo and Smriglio, [2001: plate 25A–D] and to valves, girdle armature and radula of juvenile specimens of *Hanleya nagelfar* from Newfoundland and Norway with body length 5-7 mm, previously illustrated by Sirenko [2014: figs. 9–14].

Specimen of *H. hanleyi* from Scotland (ZISP 2267) (Figs. 5-7).

Body length of the dry specimen 7.5 mm, its radula is 3.7 mm long with 30 transverse rows of teeth. All features of the specimen are very similar to those of the Mediterranean specimen and above-mentioned specimens identified both as *Hanleya hanleyi* [in Dell'Angelo, Smriglio, 2001] and as *H. nagelfar* [in Sirenko, 2014].

Remarks: Based on the similarity of small spec-

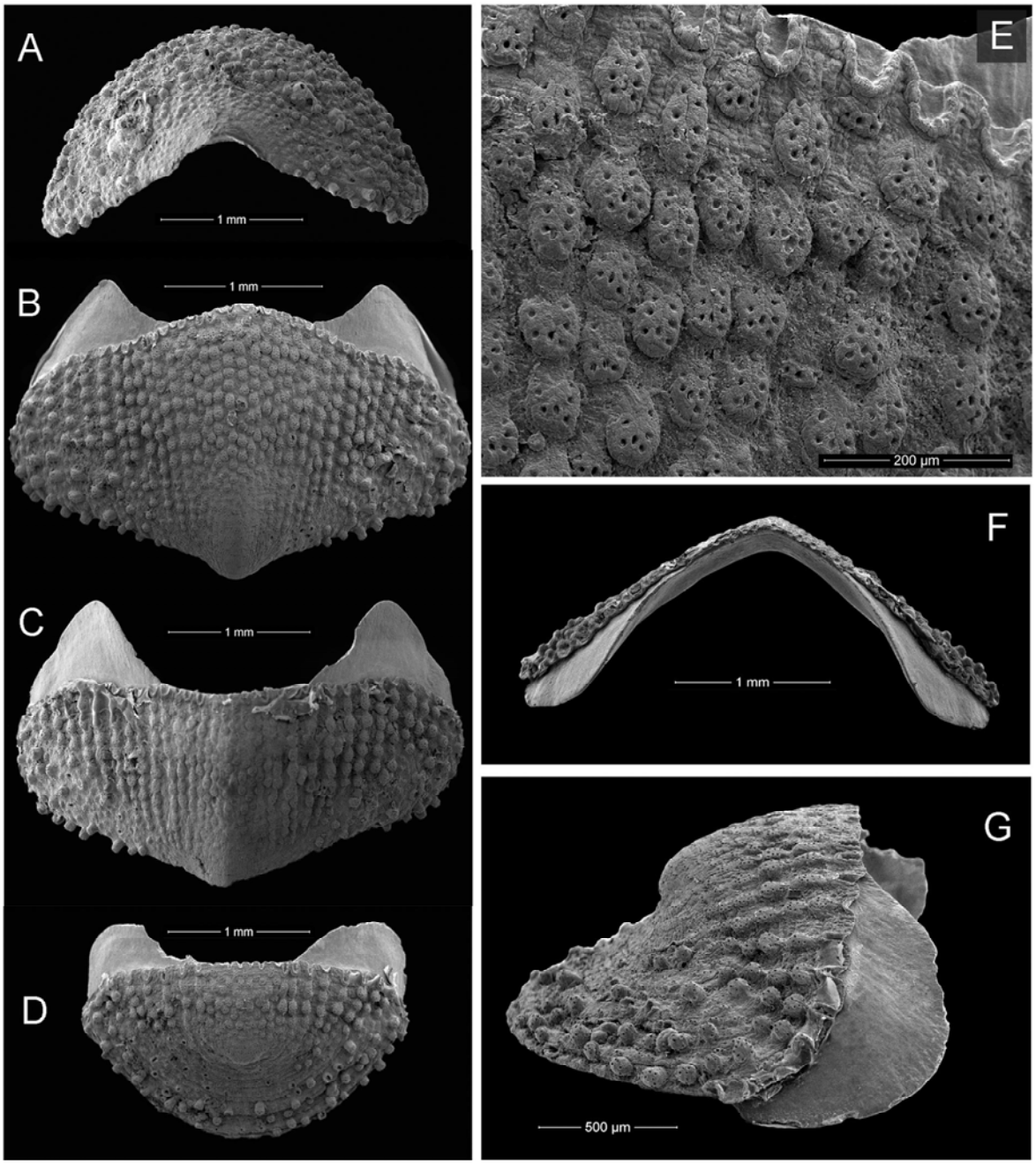

FIG. 5. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2267, Off Scotland, BL – 7.5 mm. **A.** Head valve, dorsal view; **B.** Valve II, dorsal view; **C.** Valve V, dorsal view; **D.** Valve VIII, dorsal view; **E.** Valve II, central area; **F.** Valve V, rostral view; **G.** Valve VIII, lateral area.

РИС. 5. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2267, у Шотландии, BL – 7.5 мм. **A.** Головной щиток, вид сверху; **B.** Щиток II, вид сверху; C. Щиток V, вид сверху: **D**. Щиток VIII, вид сверху; **E.** Щиток II, центральное поле; **F.** Щиток V, вид спереди; **G.** Щиток VIII, вид сбоку.

imens attributed to *H. nagelfar* to the definitive description of *H. hanleyi*, we consider *H. nagelfar* to be a name attributed to large specimens of the same species and that epithet is a junior synonym of *H. hanleyi*.

A number of features of chitons are variable with environmental conditions and animal age, these include the dorsal elevation of individuals, and aesthete density.

Chiton mendicarius Mighels et Adams, 1842 is an older name that *Chiton hanleyi* Bean in Thorpe, 1844, and according to principle of priority (ICZN, 1999, Art. 23) should be used as valid name. But this name was used only in 8 or 9 published works, whereas *C. hanleyi* has been used in more than 100 works since its description in 1844 and at the same time *C. mendicarius* was considered as synonym of *C. hanleyi*. We consider that the use of the older

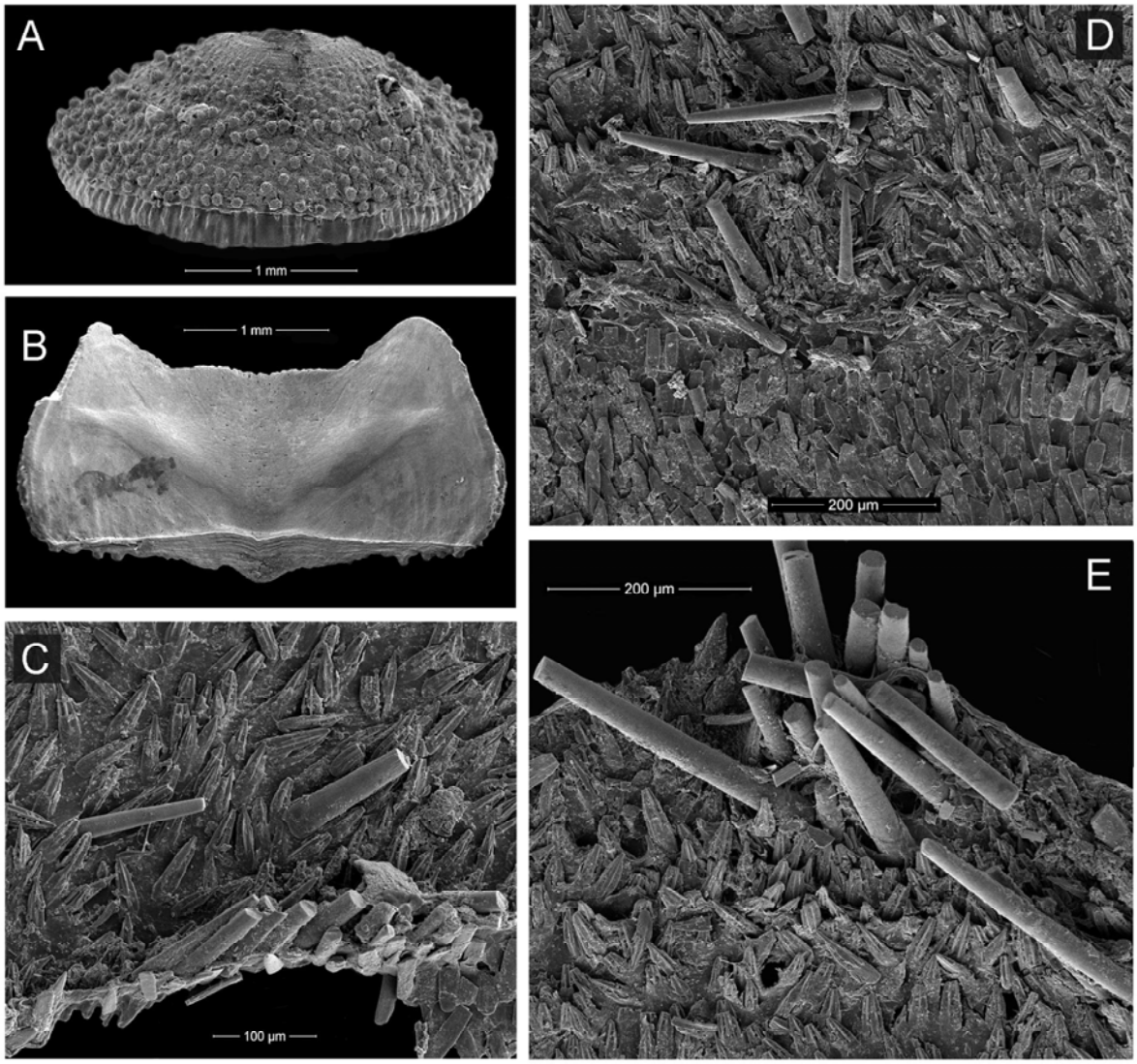

FIG. 6. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2267, Off Scotland, BL – 7.5 mm. **A.** Head valve, rostral view; **B.** Valve IV, ventral view; **C, D.** Dorsal needles and spicules, marginal needles and ventral scales; **E.** Dorsal needles and spicules.

РИС. 6. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2267, у Шотландии, BL – 7.5 мм. **A.** Головной щиток, вид спереди; **B.** Щиток IV, вид снизу; **C, D.** Дорсальные иглы и спикулы, маргинальные иглы и вентральные чешуйки; **E.** Дорсальные иглы и спикулы.

synonym (*C. mendicarius*) would threaten stability and cause confusion, and so wish to maintain use of the junior synonym (*C. hanleyi*). We will refer the matter to the International Commission for Zoological Nomenclature for a ruling under plenary power. While the case in under consideration use of the junior name is to be maintained (ICZN, 1999, Art. 23.9.3).

Discussion

The Mediterranean represents the southern aspect of the range of *H. hanleyi* and is outside the recorded range of *H. nagelfar* [Kaas, Van Belle, 1985]. The northern part of the UK (Scotland) represents the southern aspect of the range of *H. nagelfar* and is in the middle part of the recorded range of *H. hanleyi* [Kaas, Van Belle 1985; Sirenko, 2014]. Thus the two small specimens from the Mediterranean Sea and off Scotland described here are important to assess potential differences between the two species. Yet these specimens share similar features of valves, girdle armature and radula. It is important that all small specimens we examined from Newfoundland Bank, and off Norway [Sirenko, 2014] and these two small specimens from the Mediterranean Sea and off Scotland have the same dorsal ribbed spicules, with ribs not only on one side but around whole spicule. Among the material described in detail here, the specimen from Scotland was collected from nearest to type locality (Scarborough, England), and it has similar features

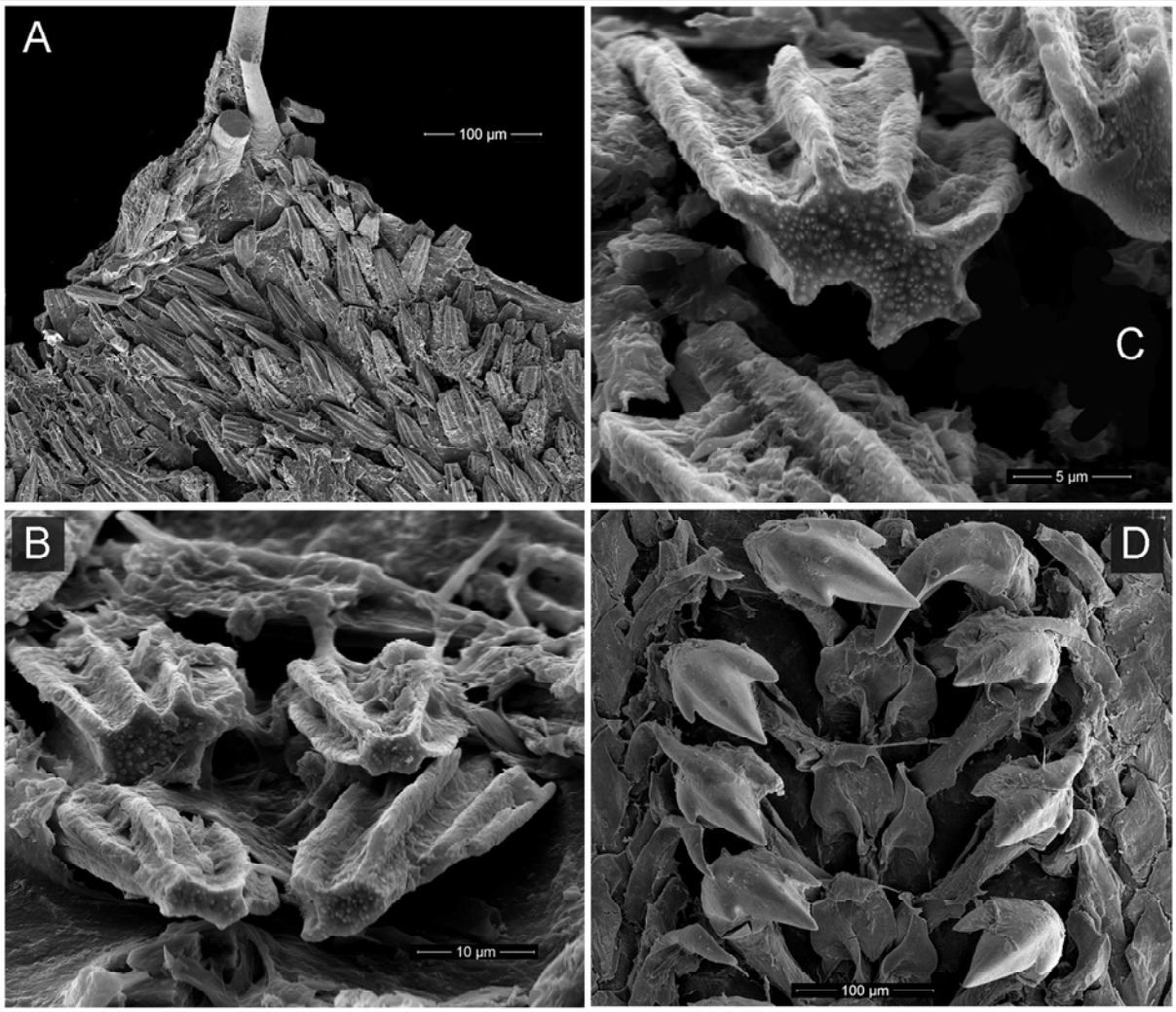

FIG. 7. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2267, Off Scotland, BL – 7.5 mm. **A.** Dorsal needles and spicules; **B, C.** Dorsal spicules; **D.** Radula.

РИС. 7. *Hanleya hanleyi* (Bean in Thorpe, 1844). ZISP 2267, у Шотландии, BL – 7.5 мм. **A.** Дорсальные иглы и спикулы; **B, C.** Дорсальные спикулы; **D**. Радула.

to the type specimen of *Hanleya hanleyi*. Most probably all specimens studied herein belong to species *H. hanleyi*. In such an event, taking into account age variability of girdle armature in *Hanleya nagelfar* [Fig. 8; Sirenko, 2014] we have to recognize a strong overlap and identity of features between the two species *H. hanleyi* and *H. nagelfar.*.

The distribution and morphology of this species suggests two different ecotypes [Warén, Klitgaard 1991]. If larvae are recruiting into similar habitats to the slope of the Newfoundland Bank (ecosystems with large sponges) we infer they will grow up to big size typical of *H. "nagelfar"* at depths > 100 m in the NE Atlantic, in the western Barents Sea, off Norway, southern Greenland, Iceland, Azores, Canary and Cape Verde Islands. If larvae settle in shelf habitats, which are less typical of this species overall, they will stay small in size like typical *H. hanleyi* off Great Britain and in the Mediterranean Sea.

Hanleya 'nagelfar' has been reported on taxonomically diverse sponges [Todt *et al*., 2009], which may indicate that while they are sponge-feeding but not evidentially specialist. Sponges have extensive chemical and physical defenses against predation. That *Hanleya* feeds on species in at least three separate taxonomic orders of sponges in European North Atlantic [Morrow, Cárdenas, 2015] and could indicate a generalist feeding strategy of the chiton that could extend to other prey taxa as available.

In the course of this study we studied three female specimens and two males from of the slope of Newfoundland Bank collected in the beginning of September 2009 with mature gonads. The females (body lengths 16, 30 and 40 mm) had eggs of diameter 250-300 µm including the egg hull. The

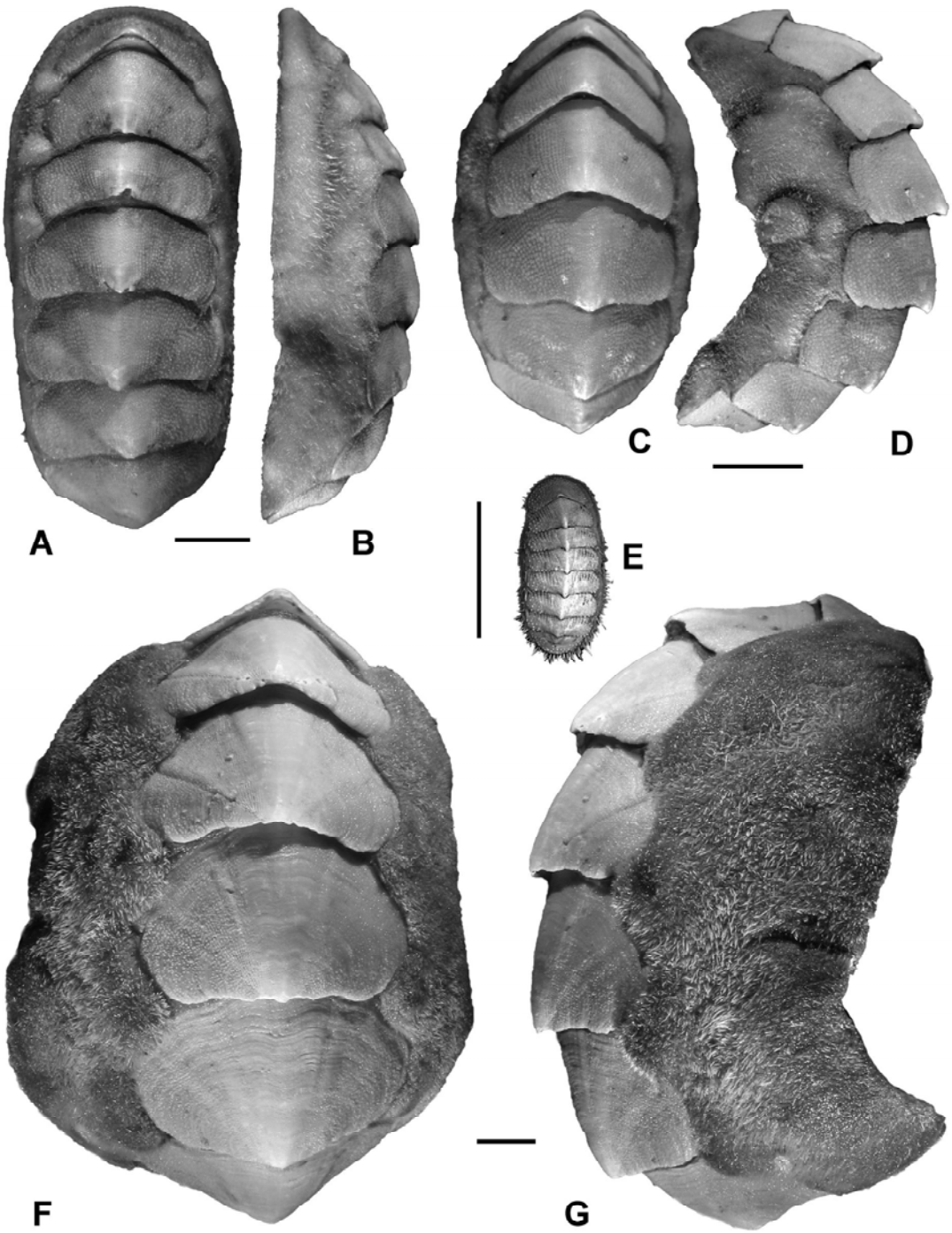

FIG. 8. *Hanleya hanleyi* (Bean in Thorpe, 1844), age variation. **A, B.** BL-35 mm, the western Barents Sea, 268 m; **C, D.** BL-29 mm, slope of the Newfoundland Bank, 1137 m; **E.** BL-7 mm, off northern Norway, 50-100 m; **F, G.** BL-75 mm, the eastern Norwegian Sea, 360 m. Scale bar 5 mm.

РИС. 8. *Hanleya hanleyi* (Bean in Thorpe, 1844), возрастная изменчивость. **A, B.** BL-35 мм, запад Баренцева моря, 268 м; **C, D.** BL-29 мм, склон Ньюфаундлендской банки, 1137 м. **E.** BL-7 мм, у Норвегии, 50-100 м; **F, G.** BL-75 мм, восток Норвежского моря, 360 м. Масштаб: 5 mm.

smallest female (16 mm) had several hundred eggs and the largest one (40 mm) had several thousand eggs. This extends the range of sexual maturity to smaller specimens than the previously observed minimum of approximately 30 mm body length [Warén, Klitgaard, 1991]. The eggs were covered with an egg hull which consist of small, flattened, weakly raised, round pustules (20-25 μm) (Fig. 9). Within each egg is yolk and a distinct large drop of transparent fat. We emphasize that such large drop of fat inside the eggs were observed for the first time and have not been reported in any other chi-

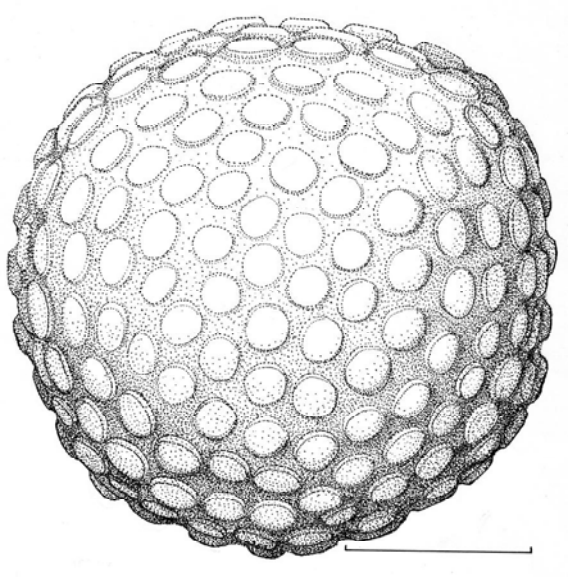

FIG. 9. Egg of *Hanleya hanleyi* (Bean in Thorpe, 1844), slope of the Newfoundland Bank, BL of female – 16 mm, R/V *Nereida*, stn 10, cod 54, 48.0005°N, 43.7607°W, 1554 m. Scale bar 100 μm.

РИС. 9. Яйцо *Hanleya hanleyi* (Bean in Thorpe, 1844), склон Ньюфаундлендской банки, BL самки – 16 mm, э/с *Нереида*, ст. 10, код 54, 48.0005°N, 43.7607°W, 1554 м. Масштаб: 100 мкм

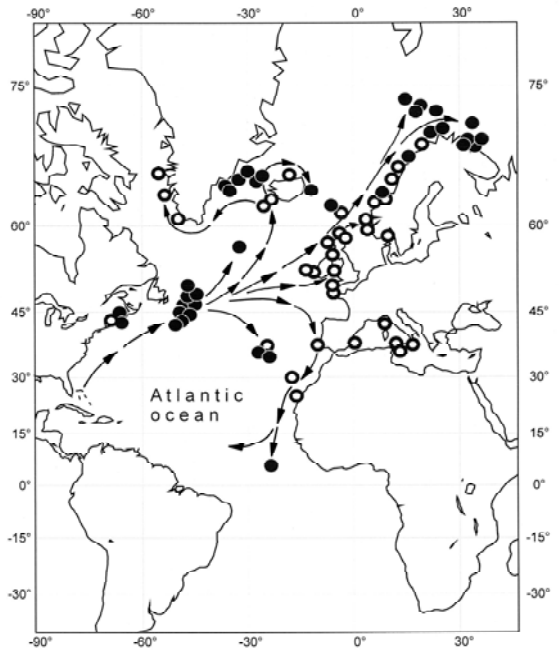

FIG. 10. Distribution of *Hanleya hanleyi* (Bean in Thorpe, 1844), and comparison with the influence of the Gulf Stream System. Black circles: specimens studied by the authors; empty circle: literature data; arrows: currents of the Gulf Stream System.

РИС. 10. Распространение *Hanleya hanleyi* (Bean in Thorpe, 1844), и влияние на него Системы Гольфстрим. Черные круги: экземпляры, изученные автором; пустой круг: литературные данные; стрелки: течения Системы Гольфстрим.

tons. Usually eggs of chitons have small dropules of fat or do not have fat; where lipid spaces have been observed they are small [e.g. Ituarte, Arellano, 2015: fig. 2H]. The lipid content of *H. hanelyi* eggs could increase their positive buoyancy. Based on comparisons with the general mode of spawning in other chiton species, we infer that fertilization occurs in the sperm cloud in close proximity to the adults, and the fertilized eggs then disperse and can float higher into the water column. For animals living entirely in sponges, such as *H. 'nagelfar'* there is no impediment to this mode of reproduction so long as the male and female individuals are in close proximity, certainly the sponge currents could help to expel fertilised eggs into the water column. There is no anatomical or observational evidence of brooding in *H. hanleyi*, in either ecotype.

The distribution of *H. hanleyi sensu lato* can be speculatively compared to circulating branches of the Gulf Stream System. The Gulf Stream passes over a large population of *H. hanleyi* inhabiting the slope of the Newfoundland Bank in the Western Atlantic. Further to the north, the Gulf Stream is divided into several branches: the North Atlantic current, Norwegian current, Canara current, Irwinger current, and West Greenland current [Gorshkov 1977]. Practically each current covers the places where *H. hanleyi* has been recorded (Fig. 10). Taking into account our speculation on the apparent positive buoyancy of eggs of this species, we may suppose that some fertilized eggs of this mainly bathyal species (411-1554 m in the slope of the Newfoundland Bank) float to the surface and are ciculated by the waters of the Gulf Stream. This comparison suggests that the Gulf Stream could maintain connectivity between the populations of *H. hanleyi* on both sides of the Atlantic, and intermediate populations in the mid Atlantic [Sirenko 2014]. This suggests a hypothesis of population connectivity that could be tested in future by investigating population genetic patterns.

There are other species of deep-sea molluscs with eggs and larvae that float or move higher in the water column and are distributed with faster-moving near-surface currents [Rex *et al*., 2005; Young *et al.,* 2012]. Surface currents are also warmer, which substantially decreases the expected larval duration of lecithotrophic (yolk-feeding) larvae like chitons, so long-distance dispersal of deeper benthic populations may be more relevant over multigenerational timescales [Yearsley, Sigwart, 2011]. For coastal species larval recruitment is known to be predominantly local to the adult population [Ebert, Russell 1988].

In the case of *H. hanleyi* it may be that long-distance dispersal of buoyant eggs and larvae underlies some of the observed disparity of the *hanleyi* / *nagelfar* ecotypes. Other chiton species have a pelagic larval duration of 4-14 days [Pearse, 1979] and modelling results suggest potential pelagic larval durations of up to over 100 days in deep, cold (2°C) water [Yearsley, Sigwart, 2011]. The average speed of the Gulf Stream is 4 miles per hour (6.4 km/hour). The surface waters cover the distance of about 3500 km between the Newfoundland Bank and Great Britain in 46-47 days [Gorshkov, 1977]. The lipid content of *H. hanleyi* eggs makes them positively buoyant and could also provide additional food resource for the lecithotrophic larvae.

Our supposition about distribution of eggs or larvae from Newfoundland population with the Gulf Stream could even explain the rarity of young specimens of *H. "nagelfar"* in Norway [Warén, Klitgaard, 1991], if recruitment in that locality is primarily from a source population further west. Indeed, small specimens in Norway and the western Barents Sea are rare, perhaps because there is limited local recruitment, but the local population consists mainly of long-lived founders. Other chitons are known to live over 15 years [Lord, 2012]. In contrast to Norway, there are abundant young specimens of *H. hanleyi* in the Newfoundland Bank slope: 18 of 23 samples contained chitons with body length less than 25 mm, and 5 samples contain young chitons with body length less than 10 mm, despite sampling by dredge with large-mesh net. It is not clear whether this segregation in demographics, with separate populations of large and small individuals, is due to the local conditions or differential recruitment. While our new results provide new evidence that this complex represents a single species, *H. hanleyi*, there is still scope for further investigation of the biology and natural history of this animal.

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References

Bean W. 1844. A supplement of new species. In: Thorpe C., *British marine conchology; being a descriptive catalogue, arranged according to the Lamarckian system, of the salt water shells in Great Britain.* Edward Lumley, London: 263-267.

Bellomo E., Sabelli B. 1995. A new addition to the Mediterranean Pleistocene "Boreal Guests": *Hanleya nagelfar* (Lovén, 1864) (Mollusca, Polyplacophora from Calabria (S. Italy). *Bollettino della Società Paleontologica Italiana*, 34: 201-204.

Burne R.H. 1896. Notes on the anatomy of *Hanleya abyssorum* M. Sars. *Proceedings of the Malacological Society of London*, 2: 4-13.

Clench W.J., Turner R.D. 1950. The Western Atlantic marine mollusks described by C.B. Adams. *Occasional Papers on Mollusks*, 1(15): 233-403, pls 29-49.

Dall WH. 1879. Report on the limpets and chitons of the Alaskan and Arctic regions, with descriptions of genera and species believed to be new. *Proceedings of the US National Museum*, 1: 281-344. doi:10.5479/si.00963801.1-48.281

Dall WH. 1927. Diagnoses of undescribed new species of mollusks in the collection of the United States National Museum. *Proceedings of the US National Museum*, 70: 1-11.

Dautzenberg P., Fischer H. 1912. Mollusques provenant des campagnes de l'*Hirondelle* et de la *Princesse-Alice* dans les Mers du Nord. *Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier*, 37: 1-598, pls.1-11.

Dell'Angelo B., Forli M. 1995. I Polyplacophora del Pleistocene inferiore di Riparbella (Pisa) con elenco dei molluschi rinvenuti. *Bollettino Malacologico*, 30: 221-252.

Dell'Angelo B., Giuntelli P., Sosso M., Zunino M. 2015. Polyplacophora from the Miocene of North Italy. Part 1: Leptochitonidae, Hanleyidae, Ischnochitonidae and Callistoplacidae. *Rivista Italiana di Paleontologia e Stratigrafia*, 121: 217-242.

Dell'Angelo B., Giusti F. 1997. I Polyplacophora di una tafocenosi profonda. *La Conchiglia*, 29 (283): 51-58.

Dell'Angelo B., Landau B., Marquet R. 2004. Polyplacophora from the Early Pliocene of Estepona (Málaga, southwest Spain). *Bollettino Malacologico*, Suppl. 5: 25-44.

Dell'Angelo B., Lombardi C., Taviani M. 1998. Chitons (Mollusca, Polyplacophora) collected during cruise CS96 in the Strait of Sicily. *Giornale di Geologia*, 3 (60): 235-252.

Dell'Angelo B., Smriglio C. 1999. *Chitoni viventi del Mediterraneo.* Edizioni Evolver, Roma, 256 p. (English Ed., 2001: *Living chitons of the Mediterranean*).

Dell'Angelo B., Sosso M., Prudenza M., Bonfitto A. 2013. Notes on fossil chitons. 5. Polyplacophora from the Pliocene of Western Liguria, Northwest Italy. *Rivista Italiana di Paleontologia e Stratigrafia,* 119: 65-107.

Dons C. 1933. Zoologiske Notiser XVIII. Om utbredelsen av *Hanleya nagelfar*. *Det Kgl Norske Videnskabers Selskabs Forhandlinger*, 5(39): 151-153.

Ferreira A.J. 1981. *Laminoplax*, a new genus of chitons and the taxonomic position of *Hanleya dalli* Kaas, 1957 (Polyplacophora: Afossochitonidae). *The Nautilus*, 95: 189-193.

Gorshkov S.G. (Ed.) 1977. *Atlas of Oceans. Atlantic and Indian Ocean*. USSR, Ministry of Defence, Navy, Moscow, 306 p.

Gray J.E. 1857. Guide to the systematic distribution of Mollusca in the British Museum. I, Polyplacophora. Taylor & Francis, London: 176-188.

ICZN (*International Code of Zoological Nomenclature*). 1999. 4th Edition. International Trust for Zoological Nomenclature, London, 232 pp.

Ituarte C., Arellano F.E. 2015. Structural study of the ovary, oogenesis and brooding in *Tonicia lebruni* (Polyplacophora, Chitonida) from Patagonia. *Acta Zoologica* (Stockholm). 00: 000-000.

Jakovleva A.M. 1952. Shell-bearing mollusks (Loricata) of the seas of the USSR. Opredeliteli po faune SSSR 45: 1-107, pls 1-11 [in Russian]. (Translated in English by the Israel Program for Scientific Translations, Jerusalem, 1965).

Jeffreys J.G. 1865. *British conchology, or an account of the Mollusca which now inhabit the British Isles and the surrounding seas*. 3. London, 393 p., 8 pls.

Kaas P. 1957. Notes on Loricata 5. On some preoccupied names. *Basteria*, 21: 83-87.

Kaas P. 1979. On a collection of Polyplacophora (Mollusca, Amphineura) from the bay of Biscay. *Bulletin du Muséum national d'Histoire Naturelle,* section A, série 4, 1: 13-31.

Kaas P, Van Belle R.A. 1985. *Monograph of living chitons (Mollusca: Polyplacophora). Vol. 1. Order Neoloricata: Lepidopleurina*. Leiden-London-Koln-Kobenhavn, Brill E.J./Backhuys W., 240 p., 95 figs, 45 maps.

Knudsen J. 1949. Amphineura. In: *Zoology of Iceland*. Munksgaard, Copenhagen and Reykjavik, 4(59): 1-11.

Knudsen J. 1970. Amphineura. *Zoology of the Faroes*, 51: 1-8.

Laghi G.F. 1977. Polyplacophora (Mollusca) neogenici dell'Appennino settentrionale. *Bollettino della Società Paleontologica Italiana,* 16: 87-115, pls 1-4.

Leloup E., Volz P. 1938. Die Chitonen (Polyplacophoren) der Adria. *Thalassia*, 2: 1-63.

Lord J.P. 2012. Longevity and growth rates of the Gumboot chiton, *Cryptochiton stelleri*, and the black leather Chiton, *Katharina tunicata*. *Malacologia* 55(1): 43-54.

Lovén S.L. 1846. Index molluscorum litora Scandinaviae Occidentalia habitantium. *Öfversigt af Kungliga. Vetenskaps-Akademiens Forhandlingar Stockholm*, 3: 134-160.

Malatesta A. 1962. Mediterranean Polyplacophora Cenozoic and Recent. *Geologica Romana*, 1: 145-171.

McKay D.W., Smith S.M. 1979. *Marine Mollusca of East Scotland*. Royal Scottish Museum, Edinburgh: viii+185 p.

Mighels J.W., Adams C.W. 1842. Descriptions of twenty four species of the shells of New England. *Boston Journal of Natural History*, 4: 37-54.

Monterosato M.T.A. 1879. Enumerazione e sinonimia delle Conchiglie mediterranee. Monografia dei Chitonidi del Mediterraneo. *Giornale di Scienze Naturali ed Economiche*, 14: 9-31.

Morrow C.C., Cárdenas P. 2015. Proposal for a revised classification of the Demospongiae (Porifera). *Frontiers in Zoology*, 12(1):2-27.

Muus B.J. 1959. Skallus, sotaender, blaeksprutter [Amphineura, Scaphopoda and Cephalopoda]. *Danmarks fauna*, 65: 1-239.

Nierstrasz H.F., Hoffmann H. 1929. Aculifera Placophora. *Die Tierwelt der Nord- und Ostsee*, 9A: 26-64.

Óskarsson I. 1944. Saeskeldýrarannsóknir i Eyjafirdi. *Nattúrufraedingurinn*, 14: 1-21.

Pearse J.S. 1979. Polyplacophora. In: Giese A.C, Pearse J.S (Eds). *Reproduction of marine invertebrates, Volume 5: Pelecypods and lesser classes*. New York, Academic Press: 27-85.

Pilsbry H.A. 1892-1894. Monograph of the Polyplacophora. In: Tryon G.W. (Ed.). *Manual of Conchology.* Academy of Natural Sciences, Philadelphia, 14:1–128, pls 1–30 (1892); i-xxxiv, 129–350, pls 31–68 (1893); 15:1– 64, pls 1–10 (1893); 65-133, pls 11–17 (1894).

Rex M.A, McClain C.R, Johnson N.A, Etter R.J, Allen J.A, Bouchet P., Warén A. 2005. A sourcesink hypothesis for abyssal biodiversity. *American Naturalist*, 165: 163-178.

Sabelli B.A. 1972. Sulla presenza e distribuzione di *Hanleya hanleyi* in Mediterraneo. *Conchiglie*, 8: 97-100.

Sabelli B.A. 1974. *Hanleya hanleyi* (Bean, 1844). *Schede malacologiche del Mediterraneo*, scheda n° 44: 1-6.

Sars G.O. 1878. Bidrag til kundskaben om Norges arktiske fauna: 1. Mollusca regionis Arcticae Norvegiae. *Christiania, Brøgger,* 466 p.

Sirenko B.I. 2014. Composition of genus *Hanleya* (Mollusca, Polyplacophora, Hanleyidae) with description of two new species. *Journal of Natural History*, 48: 2913-2945.

Sparre Schneider J. 1886. Undersøgelser af dyrelivet I de arktiske fjorde. 3 Tromsøsundets Molluskfauna. *Tromsø Mus. Aarsh*. 8: 44-112 (1885).

Thiele J. 1893. Das Gebiss der Schecken zur Begrundung einer naturlichen Classification. In: Troschel F.H., *Polyplacophora, Lepidoglossa, Schuppenzungler*. Berlin, 2: 353-401, pls 30-32.

Thiele J. 1909. Revision des Systems der Chitonen, Part I. *Zoologica Stuttgart*, 22:1-70.

Thorpe C. 1844. *British marine conchology; being a descriptive catalogue arranged according to the Lamarckian system of the salt water shells of Great Britain. By Charles Thorpe assisted by several distinguished conchologists and illustrated with numerous delineations of the rarer and unfigured species by G.B. Sowerby and W. Wood*. Edward Lumley, London, 267 p.

Todt C., Cárdenas P., Rapp H.T. 2009. The chiton *Hanleya nagelfar* (Polyplacophora, Mollusca) and its association with sponges in the European Northern Atlantic, *Marine Biology Research*, 5, 408-411.

Warén A., Klitgaard A. 1991. *Hanleya nagelfar*, a sponge-feeding ecotype of *H. hanleyi* or a distinct species of chiton? *Ophelia*, 34(1): 51-70.

Yearsley J.M, Sigwart J.D. 2011. Larval Transport Modeling of Deep-Sea Invertebrates Can Aid the Search for Undiscovered Populations. *PLoS ONE*, 6(8): e23063. doi:10.1371/journal.pone.0023063

Young C.M, He R., Emlet R.B., Li Y., Qian H., Arellano S.M., Van Gaest A., Bennett K.C., Wolf M., Smart T.I., Rice M.E.. 2012. Dispersal of deep-sea larvae from the intra-American seas: Simulations of trajectories using ocean models. *Integrative and Comparative Biology*, 52(4): 483-496.

Hanleya hanleyi (Bean in Thorpe, 1844) (Mollusca, Polyplacophora) и влияние системы Гольфстрим на ее распространение

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РЕЗЮМЕ. Хитоны рода *Hanleya* содержат два сходных вида в Северной Атлантике, *H. hanleyi* (Bean in Thorpe, 1844) и *H. nagelfar* (Lovén, 1846), которые главным образом различали по их размерам, а также частично их распространением и мелкими морфологическими и экологическими признаками. Вопрос о том, представляют ли эти два названия виды или *H. nagelfar* является просто *H. hanleyi*, которая вырастает до значительных размеров, поднимался неоднократно начиная с 1865 года. Решение проблемы затягивалось из-за недоступности типового экземпляра вида со старшим названием и отсутствием материала, собранного вблизи типовой местности вида *H. hanleyi*. Оба этих вопроса были решены в ходе наших исследований. Мы исследовали детали щитков, вооружение перинотума и радулы у экземпляров *H. hanleyi* из Средиземного моря и Шотландии. Сходство существенных черт среди мелких экземпляров *H. hanleyi* и *H. nagelfar* из Шотландии, Средиземного моря, Норвегии и Ньюфаундлендской банки, а также типового экземпляра *H. hanleyi* предполагает, что оба вида конспецифичны. *Hanleya nagelfar* является младшим синонимом *H. hanleyi*. Мы заметили, что яйцо *H. hanleyi* содержит необычно большую каплю жира, что может увеличивать его пловучесть. Мы предположили, что яйца и личинки *H. hanleyi* могут долго находиться в планктоне и это расширяет перенос и может связывать популяции через поверхностные течения Системы Гольфстрим от батиального местообитания на склоне Ньюфаундлендской банки до северной и западной частей Атлантического океана.