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***Henricia* spp. (Echinodermata: Asteroidea: Echinasteridae)
of the White Sea: morphology, morphometry and synonymy**

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1 *Henricia* spp. (Echinodermata: Asteroidea: Echinasteridae) of the White Sea: morphology,
2 morphometry and synonymy

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Draft

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16 Abstract

17 Though sea stars of the genus *Henricia* Gray, 1840 are widely used in biological studies, their species diversity in the
18 Arctic is poorly understood. We conducted a taxonomic revision of the genus *Henricia* from the White Sea and examined
19 381 specimens of *Henricia* sea stars deposited in the collection of the Zoological Institute of the Russian Academy of
20 Sciences (St Petersburg), the type collection founded by A. M. Djakonov, and our own collection. Following Madsen
21 (1987) and Djakonov (1950), we identified six species in the White Sea: *H. eschrichti* (Müller and Troschel, 1842), *H.*
22 *perforate* (O. F. Müller, 1776), *H. scabrior* (Michailovskij, 1903), *H. solida* Djakonov, 1950, *H. sanguinolenta* (O. F.
23 Müller, 1776) and *H. pertusa* (O. F. Müller, 1776). Updated descriptions, identification keys and distribution data of these
24 species are provided. Statistical analysis based on the set of individual characters confirmed the validity of the species *H.*
25 *scabrior*. Synonymy of *Henricia* species according to Djakonov (1950) and Madsen (1987) is discussed.

26

27 Keywords: *Henricia*, sea stars, species identification, tabular key, Russian Arctic.

28 Introduction

29 The genus *Henricia* Gray, 1840 (Asteroidea: Echinasteridae) comprises approximately 50 nominal species
30 (European Register of Marine Species; Clark and Downey 1992; Hansson 2001; Eernisse et al. 2010; Clark and Jewett
31 2010). These sea stars, widely distributed in the Arctic, the Atlantic and the Pacific Ocean, are popular objects of
32 zoological, faunistic, biochemical and genetic studies.

33 Identification of species within the *Henricia* complex is notoriously difficult (Clark and Downey 1992; Madsen
34 1987; Djakonov 1950; Xiao and Liao 2011). The difficulties are associated with the following: (i) many descriptive
35 characters are highly variable (Fisher 1911; Mortensen 1927; Heding 1935; Clark and Downey 1992); (ii) these sea stars
36 tend to form local morphologies (Djakonov 1950; Madsen 1987); and (iii) their life history is poorly studied (Mercier and
37 Hamel 2008). Due to the lack of stable discriminating morphological characters the taxonomy of this genus remains
38 confusing. The same species name has often been applied to *Henricia* sea stars with different morphological characters
39 (Heding 1935, 1936; Djakonov 1950; Rasmussen 1965; Brun 1976; Madsen 1987, etc.). For instance, the name *Henricia*
40 *sanguinolenta* has been commonly used as a catchall for *Henricia* sea stars from different regions of the North Atlantic.

41 A large contribution to the faunistic studies of the genus *Henricia* in the North Atlantic was made by the Danish
42 researcher F. Madsen. In his re-evaluation of the *Henricia sanguinolenta* species complex from the Norwegian Sea and
43 adjacent waters (Madsen 1987), Madsen reviewed the history of the study of this genus and compiled detailed species
44 descriptions and identification keys. These materials are commonly used in studies of echinoderms from the North-Atlantic
45 and other areas. Madsen proposed many morphological characters that had never been used for the identification of sea
46 stars before. He also advocated the analysis of metric characters though he did not use statistical analysis.

47 Based on the differences in skeleton arrangement, the shape of skeletal elements (plates and spines) and the texture
48 of the surface integument, Madsen distinguished two groups of species within the genus *Henricia*: *H. perforata* group and
49 *H. pertusa* group.

50 The *H. perforata* group is characterised by (i) irregular transverse rows and weakly differentiated longitudinal
51 series of the actinal skeleton elements; (ii) large, stout and blunt abactinal spines sheathed in a thick soft integument and
52 occurring singly or in a group (pseudopaxillae). This group comprises three species: *H. eschrichti* (J. Müller and Troschel,
53 1942), *H. oculata* (Pennant, 1777) and *H. perforata* (O. F. Müller, 1776).

54 The *H. pertusa* group is characterised by (i) regular transverse rows and well differentiated longitudinal series of
55 the actinal ossicles; (ii) minute and slender abactinal spines covered by a thin skin layer, their distal ridge extended into
56 several thorns (following the terminology of Madsen, 1987); these spines are always arranged in pseudopaxillae. The *H.*

pertusa group comprises six species: *H. cylindrella* (Sladen, 1883), *H. hedingi* Madsen, 1987, *H. lisa ingolfi* Madsen, 1987, *H. pertusa* (O. F. Müller, 1776), *H. sanguinolenta* (O. F. Müller, 1776) and *H. spongiosa* (O. Fabricius, 1780).

Working with European collections of sea stars, Madsen synonymised many species described by Heding (1936), Clark and Downey (1992), Mortensen (1927), Djakonov (1950). The only omission in his revision of the *Henricia* genus was the species proposed by Rasmussen (1965).

Henricia sea stars inhabiting the Russian Arctic had been invariably identified as *Henricia* sp. or *H. sanguinolenta* until 1950, when Djakonov showed that several species from this genus, in fact, occurred there. He described two new species, *H. skorikovi* and *H. solida*, in the White Sea, and also recorded there *H. eschrichti* (J. Müller and Troschel, 1842 sensu Djakonov) (Djakonov 1950). At the Barents Sea, he recorded altogether six species, including three new ones: *H. sanguinolenta* (O. F. Müller sensu Djakonov), *H. eschrichti* (J. Müller and Troschel, 1842 sensu Djakonov), *H. scabrior* (Michailovskij, 1902) (originally described from the North Atlantic), *H. knipowitschi* Djakonov, 1950, *H. skorikovi* Djakonov, 1950, and *H. solida* Djakonov, 1950.

Madsen, who was familiar with Djakonov's study but not with the Russian Arctic collections of sea stars, noticed considerable affinities of *H. skorikovi* and *H. solida* with *H. perforata* group and synonymised these species with *H. eschrichti*. He also synonymised *H. scabrior* with *H. perforata*. As the result, he added the records of species described by Djakonov to the data on the distribution of *H. eschrichti* and *H. perforata* (Madsen 1987).

In this paper, we present the results of our comprehensive examination of the sea stars from the genus *Henricia* from the White Sea. It was based on our own collections, the collections of the Zoological Institute of the Russian Academy of Science (St Petersburg) and Djakonov's type collection (Zoological Institute of the Russian Academy of Science, St Petersburg) of *Henricia* species. Our aim was to determine the main morphological and morphometrical characters required for the identification of *Henricia* species and to synonymise several *Henricia* species from the White Sea and the North Atlantic. In this way, we attempted to fill the gap in the existing revision of the genus *Henricia* (Madsen 1987).

Both morphological and morphometric characters to be examined were chosen according to different authors (Heding 1935, 1936; Djakonov 1950; Madsen 1987) and complemented by us. Statistical analysis was used to evaluate the significance of the chosen characters.

84   Material and methods

85   *Material.* Our study was based on the examination of 381 specimens of sea stars from the genus *Henricia*: 197 specimens
86   collected by scuba divers under the direction of O. Bratova near the Keret' Island Archipelago (Kandalaksha Bay, White
87   sea) at a depth of 5–12 m in 2003–2007, 174 specimens from the collections of the Zoological Institute of the Russian
88   Academy of Sciences (collected in different sites of the White Sea at a depth of 15–200 m by trawling and dredging in late
89   19th — early 20th century) and 10 samples from the type species collection of sea stars stored in the Zoological Institute
90   (described as *H. knipovitchi*, *H. solida*, *H. scabrior*, and *H. scorikovi*; Djakonov, 1950). The distribution of the examined
91   *Henricia* species across the collection sites is shown in Fig. 1 a, b. All specimens were preserved in 70% ethanol.

93   *Characters and measurements.* Sea stars (fixed specimens) were examined under stereo microscopes MBS-10 (LOMO),
94   Leica M205C, an inverted light microscope Nikon Eclipse TS100, an electron scanning microscope Zeiss SUPRA 40VP,
95   and photographed using a variety of digital cameras. Species identification was based on characters suggested by various
96   authors (Heding 1935, 1936; Diakonov 1950; Madsen 1987) as well as several previously unmentioned characters.

97   Characters identified during examination of intact fixed sea stars under stereo microscopes:

- 98   - Ray radius (*R*): the length (mm) of one arm per sea star.
- 99   - Disc interradius (*r*): one measurement (mm) per sea star.
- 100   - Integument thickness: thick (spines enclosed in the sheath of the integument, Fig. 5e) or thin (spines only webbed together
101   basally by the integument, Fig. 7e).
- 102   - Number of abactinal spines per pseudopaxilla: the average number in 10–15 pseudopaxilla per sea star disc.
- 103   - Arrangement of abactinal spines per pseudopaxilla: single or arranged in a group, row, or circle.
- 104   - Density of abactinal spines: the average value of three measurements of the number of spines per 9 mm² of the abactinal
105   disk surface outside the madreporit and the anus in a sea star; the obtained values were subsequently recalculated for 1
106   mm².
- 107   - Number and arrangement of spines per adambulacral plate at the arm base: in the first 10 plates from the arm base in one
108   arm per sea star.
- 109   - Number of spines per actinal (actinolateral, inferomarginal, and superomarginal) plate at the arm base: in the first 10
110   plates from the arm base in one arm per sea star.
- 111   - Number of papulae per mesh of the abactinal side: 10 or more meshes per sea star.
- 112   - Differentiation of longitudinal and transverse rows of the actinal skeleton plates: well or weakly differentiated.

Examination of the actinal skeleton (cleaned from spines with the help of dissecting needles) under the stereomicroscope:

- Extension of actinolateral plate series (Fig. 2): 1/3, 1/2, 3/4 of the length or the entire length of an arm.

- Shape of actinal (actinolateral, inferomarginal, and superomarginal) plates: examination of all plates in one arm per sea star.

Examination of 0.5 cm² area of the skin prepared from the abactinal disk surface (not including the madreporit and anus) under inverted light and scanning electron microscopes (see below for the preparation procedure):

- Length (mm) and shape (distal ridge blunt or extended in crown-forming thorns) of abactinal spines: more than 15 spines per sea star.

- Size of skeletal reticulum meshes: the average value of three dimensions (mm) of meshes per sea star with $R > 20$ mm.

- Intermediate plates in skeletal reticulum meshes: presence or absence.

- Degree of spine tubercle development: well-defined (as a distinct articular tubercle, Fig. 3c), weakly-defined (as a knoll on the plate surface, Fig.5c) or undefined.

- Shape of abactinal skeleton plates.

In some specimens from the collections of the Zoological Institute some identification characters could not be verified because of the damage due to long-term storage in alcohol.

Preparation of skeletal elements. To facilitate the observation of skeletal plates and spines, pieces of asteroid derma were cleaned of the tissue using two methods of dissolving: 1, traditional technique with sodium hypochlorite solution (Madsen 1987); 2, advanced technique with trypsin solution in borax buffer (Tiago et al. 2005). After rinsing off the solvent in several portions of distilled water, pieces of skeleton were mounted on microscope glass slides using Canada balsam or on the sticky surface of specimen holders for scanning electron microscopy (SEM). The method of dissolving tissues with trypsin gave better results and was usually used to prepare skeletal elements for SEM. Skeletal elements (plates and spines) were coated with silver and examined under an electron scanning microscope Zeiss SUPRA 40VP.

Species identification. Species were generally identified according to Madsen (1987) based on the set of characters described above. Identification keys of Heding (1935, 1936) and Djakonov (1950) were also taken into account. Most of the examined characters were pooled to construct the tabular key (Table 1). They were arranged in the following order: main characters for group identification, additional characters for group identification, main characters for species identification, and additional characters for species identification.

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Statistical analysis. Numerical data were analysed by different tests (software: Open Office 3.1, Statistica 6.0, Statistical Package for the Social Sciences 9.0) to assess whether there were differences between species in the *H. perforata* group. The *t*-test was used to compare the averages of the number of abactinal spines per 1 mm², the number of abactinal spines per pseudopaxilla. The following characters were used as a data matrix for the principal component analysis (PCA): the number of abactinal spines per 1 mm², the number of abactinal spines per pseudopaxilla, the mesh size and the number of spines per inferomarginal plate. The number of abactinal spines per 1 mm², the number of abactinal spines per pseudopaxilla, the mesh size were also used in two-way analysis of variance (ANOVA) followed by the Tukey's honest significant difference (HSD) test. The differences between data were considered statistically significant if the *p*-values were <0.05.

Results

The examined specimens of sea stars could be clearly divided into two morphologically different groups: *H. perforata* group and *H. pertusa* group following Madsen (1987). Species from *H. perforata* group were identified as *Henricia eschrichti*, *H. perforata*, *H. scabrior* and *H. solida*. Sea stars of *H. pertusa* group were identified as *H. sanguinolenta* and *H. pertusa*. The distribution of these species across the sampling sites is shown in Fig. 1.

The examined specimens were different in size, the length of ray radii varying from 7–20 mm (juveniles) to 100 mm (adults). It was difficult to identify the species of juveniles because their skeleton elements were underdeveloped: abactinal plates lay close to each other, skeleton reticulum always had small meshes and the number of spines per pseudopaxilla was incomplete. However, it was possible to identify the group of species to which juveniles might belong on the basis of the shape and the arrangement of abactinal and actinal spines.

Complete descriptions of the investigated species are given below. They were made according to the same scheme: type locality, holotype, distribution, synonyms, material examined, diagnosis, description, new records and taxonomic remarks.

H. perforata group

Description: Abactinal skeleton represented by irregular reticulum of plates with relatively big meshes (0.5–2.0 mm). Integument covering spines thick and soft. Abactinal spines large (0.5–0.8 mm), rather stout and blunt. Actinal plates arranged in more or less distinct transverse rows but not in regular longitudinal series.

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Henricia eschrichti (Müller and Troschel, 1842)

Fig. 3, Table 1

Echinaster eschrichti J. Müller and Troschel, 1842:25. Type locality: SW Greenland (Madsen 1987).

Henricia sanguinolenta: Rasmussen, 1965: 176; Syn. n. Type locality: North Sea.

Henricia skorikovi: Djakonov, 1950: 93-94, Figs 51-54, 194. Syn. n. Type locality: White Sea.

Henricia eschrichti: Madsen, 1987: 257-263, Figs. 3b, 46-50.

Holotype: specimen in alcohol, $R = 55$ mm, $r = 13$ mm, Zoological Museum, Humboldt University, Berlin (Madsen 1987).

Distribution: NE Atlantic: Denmark Strait, Greenland Sea, Norwegian Sea. NW Atlantic (SW Greenland). Arctic:

Canadian Coast (Foxe Bay and Gulf of St. Lawrence), Barents Sea, White Sea. Depth: 12–400 m (Madsen 1987; Djakonov 1950).

Material examined: our collection, 20 specimens; ZIN collection, 37 specimens; type collection, 1 type and 4 syntype specimens (*Henricia skorikovi*).

Diagnosis. Abactinal skeleton represented by irregular reticulum of plates with relatively big meshes. Pseudopaxillae consisting of 6–12 (rarely 3–6) spines arranged in double row. Abactinal spines stout, with blunt, rough distal end. Inferomarginal plates pronounced, usually bearing 12–16 spines in double row.

Description: External morphology. Body rather stout (Fig. 3a). Arms nearly cylindrical along most of their length, tapering gradually. Typical R/r ratio varying from 2.8 to 4.8. In largest specimen $R=100$ mm and $r=25$ mm ($R=4r$). Colour in life pinkish-violet. Moderately thick integument sheathing the spines (Fig. 3e).

Abactinal side. Abactinal skeleton represented by uniform reticulum composed of small and narrow oval plates. Each plate with a well-defined tubercle (Fig. 3b-c). Skeletal meshes large, 0.7–1.3 mm in length, more open on disk and basal arms. Large meshes containing loose intermediate plates (Fig. 3c). Each mesh with one or two papulae (Fig. 3e). Spines large (0.4–0.8 mm), nearly cylindrical, with blunt distal ends (Fig. 3d). Spines grouped in pseudopaxillae, each with 6–12 spines (rarely 3–6) in double row (Fig. 3e). Spines arranged densely, about 17 spines per mm².

199 *Actinal side*. Actinal skeleton organized in weakly defined longitudinal rows of plates. Transverse rows also poorly defined
200 (Fig. 3f). Size of plates and number of spines diminishing towards arm end. Spines of each adambulacral plate grouped in
201 double row. Actinolateral plates small, four-lobed, bearing 6–8 spines in basal parts of arms. Inferomarginal plates
202 elongated, four-lobed, bearing pseudopaxillae with 12–16 spines in single or double row. Inferomarginal plates arranged in
203 more or less distinct longitudinal series. Superomarginal plates small, comparable-sized with abactinal plates, bearing
204 pseudopaxillae with 6–8 spines. Superomarginals hardly distinguishable from abactinal plates. Actinolateral plates
205 extending for about three-fourth of distance to arm tip. Papulae lying singly between actinolateral and marginal plates as
206 well as between actinolateral and adambulacral plates.

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208 *New records*: White Sea, coordinates: 66°17'25"N 33°40'47"E, 66°17'23"N 33°38'02"E, 66°19'29"N 33°32'45"E,
209 66°18'04"N 33°50'47"E, 66°18'52"N 33°53'15"E, 66°17'42"N 33°38'20"E, 66°19'26"N 33°40'26"E, 66°20'56"N 33°51'15"E,
210 64°01'00"N 36°39'04"E, 64°54'00"N 35°48'30"E, 64°54'00"N 35°20'30"E, 65°16'46"N 36°88'11"E, 65°55'85"N 39°66'06"E,
211 66°21'50"N 33°35'56"E, 65°01'00"N 35°20'30"E, 66°20'56"N 33°51'15"E, 65°55'85"N 39°66'06"E, 64°13'59"N
212 37°21'32"E, 66°06'71"N 44°11'01"E, 64°16'00"N 36°11'50"E (Fig. 1), at 5 – 150 m.

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214 *Taxonomic remarks*: Description of *Henricia sanguinolenta* by Rasmussen is completely identical with that of *H. eschrichti*
215 by Madsen. See Discussion for synonymy of species described by Madsen and Djakonov.

216
217 ***Henricia perforata*** (O. F. Müller, 1776)

218 Fig. 4, Table 1

219 *Asterias perforata* O. F. Müller, 1776: 234. Type locality: Between southern Norway and Denmark, in the region of
220 Skagerrak/Kattegat (Madsen 1987).

221 *Henricia knipowitchi*: Djakonov, 1950: 93. Syn.n. Type locality: Barents Sea.

222 *Henricia perforata*: Madsen, 1987: 243-254, Figs. 3a, 31-43.

223 *Type*: lost (Madsen 1987).

224 *Neotype*: dried specimen, $R=61\text{mm}$, $r=11\text{mm}$, Zoological Museum, University of Copenhagen (Madsen 1987).

225 *Distribution*: NE Atlantic: Greenland Sea, North Sea (from the northern British Coast and the Kattegat and Skagerrak to the
226 Norwegian Coast), and Norwegian Sea. NW Atlantic: Baffin Sea, Hudson Bay, Labrador Coast. Arctic: Barents Sea, Kara
227 Sea, Laptev Sea, East Siberian Sea. Depth: 2–1200 m (Madsen 1987, Djakonov 1950).

Material examined: our collection, 57 specimens; type collection, 1 type specimen (*Henricia knipowitchi*).

Diagnosis: Abactinal skeleton represented by an irregular meshwork with relatively large meshes. Abactinal spines grouped in pseudopaxillae, 3 – 8 spines in each. Abactinal spines large, stout, with serrated, although slightly blunt distal ends. Inferomarginal plates well-defined, usually bearing 6 – 8 spines in a single or double row.

Description: External morphology. Body shape greatly variable (Fig. 4a-b). Arms sometimes tapering gradually from comparatively large base to blunt tip. In some specimens disk smaller and arms cylindrical, usually stout, rarely slender. R/r ratio varying from 2.7 to 5.8. In largest specimen $R=80$ mm and $r=19$ mm ($R=4.2r$). Arm angles usually acute, with interbranchial depressions extending just up on disk. Colour in life varying from lilac to purple and violet. Entire body covered with thick integument (Fig. 4f).

Abactinal side. Skeleton represented by irregular meshwork with relatively large meshes. Meshes in basal part of arm measuring 0.7–1.8 mm in length. Abactinal plates oval, four-lobed, each with a well-defined tubercle. Ends of abactinal plates often overlapping. Several small intermediate plates present in some large meshes, loose or connecting into group of secondary plates subdividing the mesh (Fig. 4c). Papulae in almost every mesh, single (Fig. 4f) or in groups of 2–4. Spines large, stout, with serrated, although slightly blunt distal ends (Fig. 4d), 0.3–0.7 mm in length. Spines grouped in pseudopaxillae, 3–8 spines in each, groups of 6–8 spines occurring rarely (Fig. 4e-f). Secondary (intermediate) plates bearing fewer spines than basic plates. Spines in pseudopaxillae arranged in irregular double row. Density of spines arrangement about 11 spines per mm^2 .

Actinal side. Skeleton irregular, weakly differentiated (Fig. 4g). Longitudinal arrangement indistinct, except for series of plates adjacent to adambulacral series. Adambulacral spines grouped in double row. Actinolateral plates small, four-lobed, bearing 5–6 spines. Inferomarginal plates elongated, four-lobed, bearing pseudopaxillae with 6–8 spines in single or double row. Inferomarginal plates arranged in more or less distinct longitudinal series. Superomarginal plates suboval, three- or four-lobed, bearing pseudopaxillae, 4–6 spines in each. Superomarginal plates similar in size to abactinal plates and poorly distinguishable from latter. Actinolateral plates usually extending up to $3/4$ of arm length rather than to the arm tip. Papulae lying singly between actinolateral and marginal plates as well as between actinolateral and adambulacral plates.

256 New records: White Sea, coordinates: 66°17'25"N 33°40'46"E, 66°20'1"N 33°39'45"E, 66°17'22"N 33°38'2"E, 66°19'28"N
257 33°32'45"E, 66°18'51"N 33°53'14"E, 66°18'49"N 33°50'47"E, 66°17'66"N 33°39'61"E, 66°17'4"N 33°36'17"E, 66°19'25"N
258 33°40'26"E, 66°20'56"N 33°51'15"E (Fig. 1), at 5–15 m.

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260 *Taxonomic remarks:* See Discussion for synonymy of species described by Madsen and Djakonov.

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262 ***Henricia scabrior*** (Michailovskij, 1903)

263 Fig. 5, Table 1.

264 *Cribrella sanguinolenta forma scabrior* Michailovskij, 1903: 478. Type locality: Svalbard.

265 *Henricia scabrior*: Heding, 1935: 31. Type locality: Norwegian Sea (Djakonov 1950).

266 *Henricia perforata*: (partly) Madsen, 1987: 250, Fig. 40. Syn. n. Type locality: East Greenland, North Iceland.

267 *Type*: lost.

268 *Neotype*: specimen in alcohol, $R=50$, $r=15$ from the Barents Sea; Zoological Institute of the Russian Academy of Sciences,
269 St Petersburg.

270 *Distribution*: NE Atlantic: Greenland Sea, Norwegian Sea. Arctic: Barents Sea, Kara Sea. Depth: 2–1200 m (Djakonov
271 1950).

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273 *Material examined*: our collection, 18 specimens; ZIN collection, 35 specimens; type collection, 3 type specimens
274 (*Henricia scabrior*).

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276 *Diagnosis*: Abactinal skeleton represented by irregular meshwork with large meshes. Spines single or grouped in
277 pseudopaxillae, 2–4 spines in each. Abactinal spines large, not serrated, with slightly blunt distal ends. Inferomarginal
278 plates indistinguishable, usually bearing 4–6 spines in single or double row.

279

280 *Description: External morphology*. Body rather stout (Fig. 5a). Arms sometimes tapering gradually from rather large disk
281 to blunt tip. R/r ratio varying from 3.8 to 5.3. In largest specimen $R=60$ mm and $r=15$ mm ($R=4r$). Arm angles acute.
282 Colour in life yellow, pinkish-violet. Entire body covered with thick integument (Fig. 5e).

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284 *Abactinal side.* Skeleton represented by irregular meshwork with relatively large meshes (Fig. 5b). Meshes on basal ends of
285 arms 1.0–1.5 mm in length. Abactinal skeleton composed of oval, elongated, four-lobed plates, each with weakly-defined
286 tubercles (Fig. 5c). Spines large (0.5–0.8 mm), not serrated, with slightly blunt distal ends (Fig. 5d). Spines single or rarely
287 grouped in pseudopaxillae, 2–4 spines in each (Fig. 5c, e). Density of spines arrangement rather low, about 9 spines per
288 mm².

289 *Actinal side.* Skeleton irregular. All actinal series indistinct except adambulacral one (Fig. 5f). Adambulacral spines
290 grouped in single irregular row. Actinolateral plates small, four-lobed, bearing 1–4 spines. Inferomarginal plates elongated,
291 with 4–6 spines. Superomarginal plates suboval, three- or four-lobed, bearing pseudopaxillae with 3–4 spines. Actinolateral
292 plates usually extending up to 3/4 of arm length rather than to the arm tip. Papulae lying singly between actinolateral and
293 marginal plates as well as between actinolateral and adambulacral plates.

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295 *New records:* White Sea, coordinates: 66°17'25"N 33°40'47"E, 66°20'1"N 33°39'45"E, 66°17'23"N 33°38'2"E, 66°19'28"N
296 33°32'45"E, 66°18'51"N 33°53'14"E, 66°17'66"N 33°39'61"E, 66°17'42"N 33°36'17"E, 66°19'25"N 33°40'26"E, 65°65'50"N
297 34°40'30"E, 64°95'61"N 34°90'36"E, 66°64'43"N 34°40'92"E, 65°01'00"N 35°20'30"E, 66°06'71"N 44°11'01"E, 64°48'30"N
298 35°02'59"E, 66°57'45"N 32°98'01"E (Fig. 1), at 5–15 m.

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300 *Taxonomic remarks:* According to Djakonov (1950), the descriptions of *Cribrella sanguinolenta* forma *scabrior*
301 Michailovskij, 1903 and *Henricia scabrior* Heding, 1935 were identical; he united these species into *Henricia scabrior*.
302 Madsen (1987) mentioned that some specimens of *H. perforata* collected in East Greenland and North Iceland had
303 extremely open abactinal skeleton, with very large meshes and many loose plates. We suggest that these specimens could
304 be *H. scabrior*. See Discussion for synonymy of species described by Madsen and Djakonov.

305
306 ***Henricia solida*** Djakonov, 1950

307 Fig. 6, Table 1

308 *Henricia solida* Djakonov, 1950: 94–95, Fig. 50. *Type locality:* White Sea (Djakonov 1950).

309 *Type:* lost.

310 *Neotype:* specimen in alcohol, *R*=50, *r*=15 from the White Sea; Zoological Institute of the Russian Academy of Sciences, St
311 Petersburg.

312 *Distribution:* Arctic: White Sea, Barents Sea. Depth: 15–290 m (Djakonov 1950).

313

314 *Material examined:* ZIN collection, 6 specimens collected in 1911; type collection, 1 type specimen (*Henricia solida*).

315

316 *Diagnosis:* Abactinal skeleton represented by meshwork consisting of cruciform and elongated plates. Abactinal spines
317 single or, rarely, grouped in pseudopaxillae, 2–4 spines in each. Abactinal spines large, serrated, blunt. Inferomarginal
318 plates well-defined, usually bearing 4–6 spines in single or double row.

319

320 *Description: External morphology.* Body rather stout, with broad disk and slender, tapering arms (Fig. 6a). R/r ratio varying
321 from 3.6 to 5.0. In largest specimen $R=53\text{mm}$ and $r=13\text{mm}$ ($R=4r$). Arm angles acute. Colour in life yellow or pinkish-
322 violet. Entire body covered with thick integument (Fig. 6b).

323 *Abactinal side.* Skeleton represented by irregular meshwork with relatively large meshes. Abactinal skeleton composed by
324 cruciform (in nodes) and elongated (between nodes) plates; spine tubercles undefined. Secondary plates absent. Meshes on
325 arm bases 0.5–0.8 mm in length. Papulae almost in each mesh, single or in groups of two. Spines large, with serrated,
326 although blunt distal ends. Spines single or grouped in pseudopaxillae, 2–4 spines in each (Fig. 6b). Acceptable preparation
327 of spines could not be made because of unsatisfactory preservation of specimen.

328 *Actinal side.* Actinal skeleton irregular (Fig. 6c). Actinal series of plates not defined except adambulacrals. Adambulacral
329 spines grouped in single irregular row. Actinolateral plates small, four-lobed, bearing 1–3 spines. Inferomarginal plates
330 elongated, with 4–5 spines. Superomarginal plates suboval, three- or four-lobed, bearing pseudopaxillae of 3–4 spines.
331 Actinolateral plates not reaching arm tip, usually terminating in mid arm.

332

333 *New records:* White Sea, coordinates unknown.

334

335 *Taxonomic remarks:* The validity of this species has been questioned. *H. solida* described from the White Sea by Djakonov,
336 1950 was attributed to *H. eschrichti* (Madsen, 1987). However, *H. solida* is probably a distinct species because of the
337 specific arrangement and number of abactinal spines (see Discussion).

338

339 ***H. pertusa* group**

340 *Description:* Abactinal skeleton represented by irregular meshwork with relatively small meshes (0.2–0.4 mm, rarely 0.5
341 mm). Integument covering spines thin. Abactinal spines minute (0.25–0.45 mm), their distal ridge extended into more or

less conspicuous, crown-forming thorns. Actinal skeleton organized in regular transverse and longitudinal rows (Fig. 2).
Actinolateral plates extending to arm tip.

Henricia sanguinolenta (O. F. Müller, 1776)

Fig. 2, 7, Table 1

Asterias sanguinolenta O.F. Müller, 1776: 234. Type locality: Southern Norwegian Coast (Madsen 1987).

Henricia sanguinolenta: Madsen, 1987: 209-218, Figs. 1, 2a-b, 4-9.

Type: lost (Madsen 1987).

Neotype: dried specimen, $R=24$ mm, $r=6$ mm, from Norwegian Skagerrak coast. Zoological Museum, University of Copenhagen (Madsen 1987).

Distribution: NE Atlantic: North Sea (from the NE British Coast to the Norwegian Coast), Norwegian Sea. Arctic: Barents Sea, White Sea. NW Atlantic: the USA Coast from Massachusetts to the Bay of Fundy. Depth: 0–150 m (usually less than 50 m) (Madsen 1987; Djakonov 1950).

Material examined: our collection, 82 specimens; ZIN collection, 120 specimens.

Diagnosis: Abactinal skeleton represented by irregular meshwork with small meshes. Spines always grouped in pseudopaxillae, 5 – 20 spines in each. Abactinal spines small, with crown-forming distal thorns. Actinal skeleton organized in regular transverse and longitudinal rows.

Description: External morphology. Body stout (Fig. 7a). Shape of arms on cross sections varying from conical to more or less cylindrical; arms always blunt. R/r ratio varying from 2.5 to 5.1. In largest specimen $R=45$ mm and $r=9$ mm ($R=5r$). Arm angles usually acute, with interbranchial depression extending almost halfway on disk. Colour in life varying from lilac to purple. Integument thin, with spines visible through skin (Fig. 7e).

Abactinal side. Abactinal skeleton composed of small angular or (sub)oval plates, some of them with well-defined tubercles (Fig. 7b). Skeleton represented by uniform regular meshwork with very small meshes (0.05–0.4 mm). Conspicuous papulae occurring singly. Spines always grouped in pseudopaxillae, 5–20 spines in each (Fig. 7e). Abactinal spines of three types (Fig. 7c, d): spines with three short distal thorns, spines with five long distal thorns and spines with five and more crown-forming thorns. Spines more or less uniform in size (0.25–0.4 mm). Spines arranged very densely, about 31 spines per mm^2 .

371 *Actinal side*. Skeleton organized in regular transverse and longitudinal rows (Fig. 2). Adambulacral spines grouped in
372 double row. Actinolateral plates small, squarish, each bearing 6–8 spines. Inferomarginal plates elongated, four-lobed,
373 bearing pseudopaxillae of 12–14 spines (rarely, as many as 20), grouped in single or double row. Superomarginal plates,
374 similarly to abactinal plates, small but easily distinguishable from latter. Superomarginal plates bearing pseudopaxillae of
375 8–12 spines. Actinal papulae always single, lying between actinolateral and marginal plates as well as between actinolateral
376 and adambulacral plates, especially numerous between actinolateral and inferomarginal plates.

377

378 *New records*: White Sea, coordinates: 66°17'25.5"N 33°40'46.98"E, 66°20'1.1"N 33°39'45.206"E, 66°17'22.942"N
379 33°38'2.11"E, 66°19'28.64"N 33°32'45.279"E, 66°18'51.643"N 33°53'14.91"E, 66°18'49.477"N 33°50'47.357"E,
380 66°19'25.8"N 33°40'26.22"E, 66°20'56.1"N 33°51'15.261"E, 64°49'55"N 34°58'15"E, 64°54'00"N 35°48'30"E, 64°13'59"N
381 37°21'32"E, 64°13'06"N 36°18'04"E, 64°27'55"N 35°13'10"E, 64°14'09"N 36°18'47"E, 66°50'22"N 42°01'21"E,
382 65°02'15"N 35°01'08"E, 64°40'09"N 36°40'00"E, 66°06'71"N 44°11'01"E, 64°16'00"N 36°11'50"E, 65°01'00"N 35°20'30"E,
383 64°57'36"N 34°44'25"E, 64°55'00"N 36°24'30"E, 64°20'02"N 36°26'14"E, 66°29'21"N 41°21'09"E (Fig. 1), at 5–75 m.

384

385 ***Henricia pertusa*** (O. F. Müller, 1776)

386 Table 1

387 *Asterias pertusa* O. F. Müller, 1776: 234. Type locality: Southern Norwegian Coast (Madsen 1987).

388 *Henricia eschrichti*: Djakonov 1950: 90–91. Syn.n. Type locality: White Sea.

389 *Henricia pertusa*: Madsen, 1987: 223–231, Figs. 2 c–d, 14–20.

390 *Type*: lost (Madsen 1987).

391 *Neotype*: dried specimen, $R=60\text{mm}$, $r=8\text{mm}$, Zoological Museum, University of Copenhagen (Madsen 1987).

392 *Distribution*: NE Atlantic: Greenland Sea (Faroes areas, around Iceland, W Greenland), Norwegian Sea, North Sea. Arctic:
393 Barents Sea. Depth: 100–1400 m (Madsen 1987; Djakonov 1950).

394 *Material examined*: ZIN collection, 1 specimen.

395

396 *Diagnosis*: Abactinal skeleton represented by irregular meshwork with small meshes. Spines always in pseudopaxillae of
397 15 – 30 spines. Abactinal spines small, expanding upwards with 3 (rarely 5) distal thorns.

398

Description: External morphology. Disk small, arms slender and tapering. In examined specimen $R=35$ mm, $r=5$ mm ($R/r=7$). Arm angle acute. Integument thin, spines visible through skin.

Abactinal side. Skeleton represented by uniform regular meshwork with very small meshes (0.1 – 0.3 mm). Each mesh containing 1–2 papulae. Abactinal pseudopaxillae bearing 15–30 spines. Spines enlarging upwards, bearing 3 (sometimes 4 or 5) thorns.

Actinal side. Skeleton organized in regular transverse and longitudinal rows.

New records: White Sea, coordinates: 66°29'21"N 41°21'09"E (Fig. 1), 50 m.

Taxonomic remarks: ZIN collection contains a single heavily damaged specimen. For detailed description, see Madsen (1987).

Morphometric data

In order to reveal significant differences between species within *H. perforata* group, we applied the *t*-test to the means of the following characters: density of spines (number of abactinal spines per 1 mm²), number of abactinal spines per pseudopaxilla and mesh size (Table 2). The statistical analysis included the data on *H. eschrichti*, *H. perforata* and *H. scabrior*; *H. sanguinolenta* was used as an outgroup. The density of spines was significantly different in pairs *H. eschrichti* – *H. perforata*, *H. eschrichti* – *H. scabrior*, *H. eschrichti* – *H. sanguinolenta* but not significantly different in *H. scabrior* and *H. perforata*. The average number of spines per pseudopaxilla was significantly different in pairs *H. eschrichti* – *H. scabrior* and *H. perforata* – *H. scabrior* but not significantly different in pairs *H. eschrichti* – *H. perforata* and *H. eschrichti* – *H. sanguinolenta*. A significant difference in the mesh size was found only for the pair *H. perforata* – *H. scabrior*.

Number of abactinal spines per 1 mm², number of abactinal spines per pseudopaxilla, mesh size and number of spines per inferomarginal plate were used as a data matrix for the principal component analysis (PCA). Forty sea stars were used in this analysis: 7 specimens of *H. scabrior*, 14 specimens of *H. perforata* and 19 specimens of *H. eschrichti*. PCA showed that two principal components (PC) accounted for most (84%) of the total variance. The first principle component explained 58.05% of the variability, while the second explained 25.67% (Fig. 8a, b). The highest loadings giving the greatest contribution to PC1 were the density of abactinal spines arrangement, number of spines per inferomarginal plate and number of abactinal spines per pseudopaxilla. PC2 mainly depended on the length of the skeletal mesh. The PCA

428 scores corresponding to *H. eschrichti*, *H. scabrior* and *H. perforata* were grouped in slightly-overlapping neighbouring
429 regions (Fig. 8c). Some scores were located between these regions; they were *Henricia perforata* with the largest number
430 of abactinal spines per pseudopaxilla and *H. eschrichti* with the largest meshes of the abactinal skeleton. This illustrates
431 the broad variability of characters in *Henricia* species. In our opinion, the chosen set of parameters could be used for
432 distinguishing species within *H. perforata* group.

433 The ANOVA test demonstrated significant differences in the number of abactinal spines per 1 mm²
434 ($F(2.37)=13.436, p=0.00004$), the number of abactinal spines per pseudopaxilla ($F(2.37)=17.434, p=0.000001$), the mesh
435 size ($F(2.37)=4.22, p=0.02241$) in *H. eschrichti*, *H. scabrior* and *H. perforata*. According to the Tukey's HSD test,
436 *H. eschrichti* significantly differed from *H. scabrior* and *H. perforata* by the number of abactinal spines per 1 mm²; sea
437 stars of these three species could also be distinguished by the number of abactinal spines per pseudopaxilla; and *H. scabrior*
438 differed from *H. eschrichti* and *H. perforata* by the mesh size (Table 3).

439

440 Discussion

441 Based on the analysis of morphological and morphometric data, we distinguished the main characters that can be
442 used for identification of groups and species of sea stars from the genus *Henricia* and additional characters, which can be
443 used to confirm the attribution of a sea star to a particular group and species. The main characters for the identification of
444 each group are: 1, integument thickness; 2, differentiation of longitudinal rows of the actinal skeleton; 3, size of abactinal
445 skeleton mesh; 4, shape of abactinal spines. Size of abactinal spines, arrangement of abactinal spines in pseudopaxillae and
446 extension of actinolateral plates series are additional characters for group identification. The main characters for separation
447 of related species within *H. perforata* group are: 1, number of abactinal spines per pseudopaxilla; 2, size of skeleton mesh;
448 3, number of inferomarginal spines per pseudopaxilla; 4, differentiation of longitudinal series of inferomarginal plates.
449 Additional characters for species identification are: 1, presence of intermediate plates in meshes; 2, degree of expression of
450 abactinal plate tubercle; 3, number of papulae per mesh on the abactinal side; 4, arrangement of adambulacral spines; 5,
451 number spines per actinolateral and superomarginal plates (Table 1).

452 Madsen divided the genus *Henricia* in two groups: *perforata* and *pertusa* (Madsen 1987). According to our
453 findings, species from *H. perforata* group and those from *H. pertusa* group differ in the mesh size of the skeletal reticulum,
454 the thickness of integument, the shape of spines and the arrangement of the actinal skeleton. We showed that the mesh size
455 could be considered as an important identification character though Madsen did not consider it as such. Species of *H.*
456 *perforata* group are characterised by large meshes of the abactinal skeleton. The largest mesh size among the investigated

specimens was 1.8 mm and the smallest was 0.5 mm. Sea stars from *H. pertusa* group have small meshes: the largest mesh was 0.4 mm long and the smallest was 0.05 mm. The abactinal skeleton of species from *H. pertusa* group was sometimes so compact that the mesh could not be seen without magnification.

In the identification key to *H. perforata* group, Madsen (1987) noted that abactinal spines occurred singly or in small groups. We showed that sea stars from *H. perforata* group often had pseudopaxillae with many spines (for instance, 6–12 in *H. eschrichti*). Thus, the small number of spines in pseudopaxillae cannot be regarded as a characteristic feature of this group.

Madsen (1987) also used the arrangement of the adambulacral spines for the identification of groups: adambulacral spines in one or two irregular rows in *H. perforata* group and in two to four rows in *H. pertusa* group. Our analysis showed that the number of spines and their arrangement depended on the overall density of spines. The higher the density of spines in the abactinal pseudopaxillae, the more spines were found in the actinal pseudopaxillae and the more ordered was actinal arrangement (Table 1). Thereby, the arrangement of the adambulacral spines is useful only as an additional character for species identifications within the *H. perforata* group.

Some researchers used the shape of abactinal spines as an important species character (Madsen 1980, Djakonov 1950, Clark and Jewett 2010). Indeed, the shape of spines is quite different between *H. perforata* and *H. pertusa*. However, spine shape is very similar in related sea stars from *H. perforata* group, such as *H. eschrichti*, *H. perforata* and *H. scabrior*. We analysed more than 100 samples of abactinal spines in these three species and established that some sea stars had spines of transitional shapes alongside with spines with a shape typical of the species. Thus, the shape of spines cannot be regarded as a stable character for an unambiguous identification of species within *H. perforata* group.

All examined specimens of *H. sanguinolenta* had abactinal spines of highly variable shape: straight spines with three thorns, expanding spines with three thorns, spines with three to five long thorns and spines with numerous short thorns. All these types of abactinal spines could be found in one and the same sea star. Madsen (1987) speculated that different shapes of abactinal spines in *H. sanguinolenta* were associated with their development: as a spine grows, the number of its thorns increases. However, we ascertained that spines with three short thorns were not always small; they were often of the same size or larger than spines with numerous thorns. In addition, several very small sea stars ($R=1$ cm) from our collections had spines with only three thorns as well spines with multiple thorns. All the other morphological characters in these sea stars corresponded to those of *H. sanguinolenta*. This indicates that the shape of spines in *H. sanguinolenta* is naturally variable and does not depend on the developmental stage.

Initially, we identified all the collected material according to Madsen (1987). In general, it was easy to identify *H. sanguinolenta*, *H. eschrichti* and *H. perforata* using Madsen's key. In some case, however, the identification was problematic. For example, according to Madsen (1987) *H. sanguinolenta* is characterized by 10–15 spines per abactinal pseudopaxilla. In our material, there were specimens with 7–9 spines grouped together. Formally, according to Madsen's key they would have had to be attributed to *H. lisa ingolfi*. It was only after careful comparison of descriptions of these two species that these specimens could be correctly identified as *H. sanguinolenta*. Thus, a certain caution is necessary during identification of *Henricia* sea stars with the use of Madsen's keys.

One specimen from the ZIN collection originated from the White Sea Throat. Although poorly preserved, it was identified as *H. pertusa*. This species is common in the Barents Sea and the Norwegian Sea at a depth of more than 100 m (Djakonov 1950, Madsen 1987). This indicates that the occurrence of *H. pertusa* in the deep water areas of the White Sea is possible.

In our collection, there were many sea stars from *H. perforata* group that had big meshes and single spines (sometimes groups of three spines) of the abactinal skeleton. Heding (1935) described this form as *H. scabrior*. Djakonov (1950) and Brun (1976) also considered it as a distinct species. However, Madsen (1987), who found a similar sea star in the Greenland Sea, considered it as a local morphology of *H. perforata*. We showed that *H. scabrior* has its own set of species-specific characters: abactinal spines single or rarely grouped in pseudopaxillae, 2–4 spines in each; papulae in nearly each mesh, single or in groups of 2–4; adambulacral spines grouped in single irregular row. Therefore, in our opinion, it is a valid species.

As shown by morphometric analysis, species from *H. perforata* group cannot be correctly separated based on just one character. For instance, *H. eschrichti* differs from *H. perforata* and *H. scabrior* in the density of spines on the abactinal surface, while the main difference of *H. scabrior* from *H. eschrichti* and *H. perforata* is in the number of spines in pseudopaxillae. PCA, ANOVA and Tukey's HSD tests confirmed these intraspecific differences in some characters. It is only using a set of individual characters that one can reliably separate species of *H. perforata* group. This set of characters comprised: i, the density of spines on the abactinal surface; ii, the number of abactinal spines per pseudopaxilla; iii, the number of spines on the inferomarginal plate and; iv, the mesh length of the abactinal skeleton.

Synonymy of northern *Henricia* species described by A. M. Djakonov and G. J. Madsen

There are certain discrepancies in the descriptions of some *Henricia* species made by Madsen (1987) and Djakonov (1950). According to Madsen *H. knipovitchi* (Djakonov 1950) and *H. scabrior* (Michailovski, 1903) are

synonyms of *H. perforata* (O.F. Müller, 1776); *H. solida* (Djakonov, 1950) and *H. skorikovi* (Djakonov, 1950) are synonyms of *H. eschrichti* (J. Müller and Troschel, 1842), and *H. sanguinolenta* (O.F. Müller, 1776) is a synonym of *H. pertusa* (O.F. Müller, 1776). Madsen also considered that the sea stars which Djakonov identified as *H. eschrichti* were *H. sanguinolenta*. These discrepancies are probably rooted in the fact that Madsen had no opportunity to analyse Djakonov's collection of *Henricia* and relied purely on his papers.

The descriptions of *H. eschrichti* made by Madsen and Djakonov were completely different. According to Djakonov, sea stars of this species were characterised by well-defined rows of the actinal skeleton, with sharp spines not covered by skin. On the contrary, Madsen (1987) defined *H. eschrichti* as a species with actinal skeleton that did not form distinct rows and possessed blunt spines covered by thick skin. Based on the revision of Djakonov's collection, we may conclude that *H. eschrichti* by Djakonov (J. Müller and Troschel, 1842, sensu Djakonov, 1950) should be considered as *H. pertusa* by Madsen (O.F. Müller, 1776, sensu Madsen, 1987), and *H. skorikovi* (Djakonov, 1950) is identical to *H. eschrichti* (J. Müller and Troschel, 1842, sensu Madsen, 1987). The sea stars identified by Djakonov as *H. sanguinolenta* (O.F. Müller, 1776, sensu Djakonov, 1950) fit the description of *H. sanguinolenta* by Madsen (O.F. Müller, 1776, sensu Madsen, 1987).

Djakonov (1950) based his description of *H. solida* (Djakonov, 1950) on only 6 specimens. He noted that the validity of this species had not been established yet. We also analysed these specimens and could not accurately assign them to any of the species described by Madsen, Heding and others.

Our examination of *H. scabrior* (Michailovskij, 1903) and *H. knipovitchi* Djakonov, 1950 showed that these sea stars differed in the number of spines per pseudopaxilla and in the size of the skeleton mesh (see above). We conclude that *H. scabrior* is an independent species, while *H. knipovitchi* is a synonym of *H. perforata*.

Conclusions

Identification of *Henricia* species in the White Sea is problematic due to the absence of a unified set of morphological characters. We propose a set of morphological and morphometric characters for differentiation of the species within *H. perforata* group. In this set, we distinguish the main characters for group identification, additional characters for confirmation of group identification, the main characters for species identification within the group and additional characters for confirmation of species identification within the group. We present diagnoses and a tabular key for identification of six *Henricia* species from the White Sea: *H. eschrichti*, *H. perforata*, *H. scabrior*, *H. solida*, *H. sanguinolenta*, *H. pertusa*. After an analysis of northern *Henricia* species described by A. M. Djakonov (1950) and G. J.

543 Madsen (1987), we come to a conclusion that: (i) *H. skorikovi* Djakonov, 1950 is a new synonym for *H. eschrichti* (Müller
544 and Troschel, 1842; sensu Madsen, 1987); (ii) *H. knipowitchi* Djakonov, 1950 is a new synonym for *H. perforata* (O. F.
545 Müller, 1776; sensu Madsen, 1987); (iii) *H. scabrior* (Michailovskij, 1903; sensu Djakonov, 1950) is a valid species; (iv)
546 *H. solida* Djakonov, 1950 is a distinct species and cannot be attributed to *H. eschrichti* as Madsen (1987) suggested; (v)
547 *H. eschrichti* Djakonov 1950 is a new synonym for *H. pertusa* (O. F. Müller, 1776; sensu Madsen, 1987).

548

549

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559

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588   Chinese waters. Zootaxa, **3115**: 1-20. doi: 10.5281/zenodo.279350.

589 Table 1. Tabular key to the White Sea species of the genus *Henricia*.

Species \ characters	<i>H. eshrichti</i> n=62	<i>H. perforata</i> n=58	<i>H. scabrior</i> n=54	<i>H. solida</i> n=7	<i>H. sanguinolenta</i> n=202	<i>H. pertusa</i> n=1	
<i>Henricia</i> group	<i>H. perforata</i> group				<i>H. pertusa</i> group		
integument	thick	thick	thick	thick	thin	thin	Main characters for identification of the group
differentiation of longitudinal rows of the actinal skeleton plates	weakly differentiated	weakly differentiated	weakly differentiated	weakly differentiated	well differentiated	well differentiated	
size of abactinal skeleton mesh, mm (min-max); R, mm (min-max)	large 0.7-1.3 (R=1.5-6) n=19	large 0.7-1.8 (R=2.3-6.5) n=14	large 1.06-1.6 (R=2.4-6.3) n=7	medium 0.5-0.8 (R=1.5-3) n=6	small 0.05-0.4 (R=1.4-4.5) n=56	small 0.05-0.3 (R=3.5) n=1	
shape of abactinal spines	nearly cylindrical with blunt distal ends	stout with blunt distal ends	not serrated, with slightly blunt distal ends	with serrated, although blunt, distal ends	with 3 short or 5 long or > 5 distal thorns forming a crown	enlarged upwards with 3 (sometimes 4-5) thorns	
size of abactinal spines, mm (min-max); R, mm (min-max)	large 0.4-0.6 (R=3-6) n=10	large 0.3-0.7 (R=2.3-6.5) n=12	large 0.5-0.8 (R=2.4-6.3) n=8	large —	small 0.25-0.4 (R=2.2-4.5) n=14	small —	Additional characters for identification of the group
arrangement of abactinal spines in pseudopaxillae	in a double row	in irregular double row	single or in groups of 2-4 spines	in groups of 2-4 spines	in a circle	in a circle	
extension of actinolateral plates series	3/4 of the distance to the arm tip	3/4 of the distance to the arm tip	3/4 of the distance to the arm tip	3/4 of the distance to the arm tip	all the way to the arm tip	all the way to the arm tip	
shape of abactinal skeleton plates	small and narrow oval	oval and four-lobed	oval, elongated, four-lobed	cruciform (in nodes), elongated (between nodes)	small angular or (sub)oval	small angular or (sub)oval	
number of abactinal spines per pseudopaxilla (min-max); R, mm (min-max)	6-12 (R=1.5-10) n=62	3-8 (rarely 6-8) (R=1.1-7.1) n=58	1 (rarely 2-4) (R=2.4-6.3) n=54	2-4 (R=1.5-3) n=7	5-20 (R=1.4-4.5) n=202	15-30 (R=3.5) n=1	

average number of abactinal spines per pseudopaxilla $\pm$ SE; <i>R</i> , mm (min-max)	5.54 $\pm$ 0.98 (<i>R</i> =1.5-10) <i>n</i> =25	3.85 $\pm$ 0.29 (<i>R</i> =2.3-6.5) <i>n</i> =16	1.85 $\pm$ 0.26 (<i>R</i> =2.4-6.3) <i>n</i> =9	—	7.35 $\pm$ 0.37 (<i>R</i> =2.2-4.5) <i>n</i> =21	—	Main characters for species identification
density of abactinal spines (average spines number in 1 mm ² $\pm$ SE); <i>R</i> , mm (min-max)	17.45 $\pm$ (<i>R</i> =1.5-10) <i>n</i> =25	10.98 $\pm$ 1.2 (<i>R</i> =2.3-6.5) <i>n</i> =16	8.83.3-6.5(<i>R</i> =2.4-6.3) <i>n</i> =9	—	31.26 $\pm$ 2.44 (<i>R</i> =2.2-4.5) <i>n</i> =21	—	
average size of skeleton mesh $\pm$ SE, mm); <i>R</i> , mm (min-max)	1.01 $\pm$ 0.07 (<i>R</i> =1.5-6) <i>n</i> =19	0.95 0.07 (<i>R</i> =2.3-6.5) <i>n</i> =14	1.37.3.07(<i>R</i> =2.4-6.3) <i>n</i> =7	—	—	—	
number of inferomarginal spines per pseudopaxilla (min-max); <i>R</i> , mm (min-max)	12-16 (<i>R</i> =1.5-10) <i>n</i> =25	6-8 (<i>R</i> =2.3-6.5) <i>n</i> =16	4-6 (<i>R</i> =2.4-6.3) <i>n</i> =9	4-5 (<i>R</i> =1.5-3) <i>n</i> =6	12-14 (<i>R</i> =2.2-4.5) <i>n</i> =30	—	
differentiation of longitudinal series of inframarginal plates	more or less differentiated	more or less differentiated	undifferentiated	undifferentiated	well differentiated	well differentiated	
presence of intermediate plates in meshes	only in the biggest mesh	sometimes	often present	absent	absent	absent	
degree of tubercle development on abactinal plates	well-defined	well-defined	weakly-defined	undefined	well-defined	—	
number of papulae per mesh on the abactinal side (min-max); <i>R</i> , mm (min-max)	1-2 (<i>R</i> =1.5-10) <i>n</i> =62	2-4 (<i>R</i> =1.1-7.1) <i>n</i> =58	2-4 (<i>R</i> =2.4-6.3) <i>n</i> =54	1-2 (<i>R</i> =1.5-3) <i>n</i> =7	1 (<i>R</i> =1.4-4.5) <i>n</i> =202	1 (<i>R</i> =3.5) <i>n</i> =1	Additional characters for species identification
arrangement of adambulacral spines	in double row	in double row	in single irregular row	in single irregular row	in double row	in double row	
number of actinolateral spines per plate (min-max); <i>R</i> , mm (min-max)	6-8 (<i>R</i> =1.5-10) <i>n</i> =25	5-6 (<i>R</i> =2.3-6.5) <i>n</i> =16	1-4 (<i>R</i> =2.4-6.3) <i>n</i> =9	1-3 (<i>R</i> =1.5-3) <i>n</i> =6	6-8 (<i>R</i> =2.2-4.5) <i>n</i> =30	—	
number of superomarginal spines per pseudopaxilla (min-max); <i>R</i> , mm (min-max)	6-8 (<i>R</i> =1.5-10) <i>n</i> =25	4-6 (<i>R</i> =2.3-6.5) <i>n</i> =16	3-4 (<i>R</i> =2.4-6.3) <i>n</i> =9	3-4 (<i>R</i> =1.5-3) <i>n</i> =6	8-12 (<i>R</i> =2.2-4.5) <i>n</i> =30	—	
<i>R</i> / <i>r</i> (min-max)	2.8-4.8 <i>n</i> =62	2.7-5.8 <i>n</i> =58	3.8-5.3 <i>n</i> =54	3.6-5.0 <i>n</i> =7	2.5-5.1 <i>n</i> =202	7 <i>n</i> =1	

590

591

Abbreviations: '—' - no data; 'n' - number of sea stars examined; 'R' – ray radius; 'r' – disc interradius; 'SE' - Standard Error.

592 Table 2. Statistical analysis: the principal component analysis (Fig. 8) and the *t*-test.

	Spines number in 1 mm ² (N(s))		Spines number in pseudopaxillae (z)		Length of the mesh, mm (<i>L</i>)		Spines number in inferomarginal plate (Hm)	
	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>
<i>Henricia sanguinolenta</i>	31.26±2.44	21	5.54±0.98	25	--	--	--	--
<i>H. eschrichti</i>	17.45±1.04	25	3.85±0.29	16	1.01±0.07	19	10±0	19
<i>H. perforata</i>	10.98±1.2	16	1.85±0.26	9	0.95±0.09	15	8±0	15
<i>H. scabrior</i>	8.83±1.37	9	7.35±0.37	21	1.37±0.1	7	6±0	7

Means of spines number in 1 mm² compared by *t*-test.

<i>H. perforata</i>	4.12*	
<i>H. sanguinolenta</i>	5.72*	
<i>H. scabrior</i>	4.71*	1.11
	<i>H. eschrichti</i>	<i>H. perforata</i>

Means of spines number in pseudopaxillae compared by *t*-test.

<i>H. perforata</i>	1.42	
<i>H. sanguinolenta</i>	1.63	
<i>H. scabrior</i>	2.26*	4.55*
	<i>H. eschrichti</i>	<i>H. perforata</i>

Means of length of the mesh compared by *t*-test.

<i>H. perforata</i>	0.52	
<i>H. scabrior</i>	0.17	2.83*
	<i>H. eschrichti</i>	<i>H. perforata</i>

593 *- values indicated significant (*P*< 0.05) differences.

594 Abbreviations: ‘*n*’ - number of sea stars examined; ‘SE’ - Standard Error.

595 Table 3. Statistical analysis: the Tukey's HSD test.

Spines number in 1 mm ²		
<i>Henricia perforata</i>	0.0005*	
<i>H. scabrior</i>	0.0006*	0.7284
	<i>H. eschrichti</i>	<i>H. perforata</i>
Spines number in pseudopaxillae		
<i>H. perforata</i>	0.0015*	
<i>H. scabrior</i>	0.0001*	0.0569
	<i>H. eschrichti</i>	<i>H. perforata</i>
Mesh size		
<i>H. perforata</i>	0.8868	
<i>H. scabrior</i>	0.0401*	0.0226*
	<i>H. eschrichti</i>	<i>H. perforata</i>

596 *- values indicate significant ($P < 0.05$) differences.

597

598 Figure captions

599 Fig. 1. The White Sea (a) and the Keret' Archipelago (b) of the White Sea, with distributions of *Henricia* species. Star – *H.*
600 *eschrichti*, triangle – *H. scabrior*, square – *H. sanguinolenta*, circle – *H. perforata*, diamond – *H. pertusa*.

601 Fig. 2. Scheme of the actinal skeleton of the sea star (*Henricia sanguinolenta* is taken as an example): 1, mouth place; 2,
602 adambulacral plates; 3, actinolateral plates; 4, inferomarginal plates; 5, superomarginal plates; 6, intermarginal plates; 7,
603 angle of the mouth formed by two oral plates.

604 Fig. 3. *Henricia eschrichti*: light (a, e, f) and scanning (b, c, d) microscopy. a, abactinal view; b, part of abactinal skeleton
605 with spines; c, part of abactinal skeleton without spines, note a plate with a well-defined tubercle (white arrow) and
606 intermediate plates (white arrowhead); d, abactinal spines from the basal arm; e, part of abactinal side, note papulae (white
607 arrow); f, part of actinal side, note inferomarginal spines arranged in rows (white arrow). Scale bar: a, 1 sm; b, c, 500 μ m;
608 d, 50 μ m; e, f, 1 mm.

609 Fig. 4. *Henricia perforata*: light (a, b, f, g) and scanning (c-e) microscopy. a, b, abactinal view; c, part of abactinal
610 skeleton, note secondary plates which subdivide the meshes (white arrow); d, abactinal spines from the basal arm; e, part of
611 abactinal skeleton with partially preserved integument and pseudopaxillae, note the secondary plate (white arrow); f, part of
612 abactinal side, note single papulae (white arrow); g, part of actinal side, inferomarginal spines arranged in rows are
613 indicated by white arrows. Scale bar: a, b, 1 cm; c, e, 500 μ m; d, 50 μ m; f, g, 1 mm.

614 Fig. 5. *Henricia scabrior*: light (a, e, f) and scanning (b-d) microscopy. a, abactinal view; b, part of abactinal skeleton, note
615 secondary plates (white arrow); c, abactinal plate with tubercle and four spines; d, abactinal spines from the basal arm; e,
616 part of abactinal side, note single spines covered with thick skin (white arrow), papulae (white arrowhead); f, part of actinal
617 side.

618 Fig. 6. *Henricia solida*: light microscopy. a, abactinal view; b, part of abactinal side, note single spines covered with thick
619 skin (white arrow); b, part of actinal side.

620 Fig. 7. *Henricia sanguinolenta*: light (a, d, e) and scanning (b, c) microscopy. a, abactinal view; b, part of abactinal skeleton
621 without spines, note plates with well-defined tubercles (white arrow); c, d, abactinal spines from the basal arm; e, part of
622 abactinal side.

623 Fig. 8. The principal component analysis. a, b, c, data of load distribution factor. N(s) – spines number in 1 mm² of
624 abactinal surface; z – spines number in pseudopaxillae; Hm – spines number in inferomarginal plate, L – length (mm) of
625 the mesh, star – *Henricia eschrichti*, circle – *H. scabrior*, triangle – *H. perforata*.

626

Fig. 1. The White Sea (a) and the Keret' Archipelago (b) of the White Sea, with distributions of *Henricia* species. Star – *H. eschrichti*, triangle – *H. scabrior*, square – *H. sanguinolenta*, circle – *H. perforata*, diamond – *H. pertusa*.

173x234mm (300 x 300 DPI)

Fig. 2. Scheme of the actinal skeleton of the sea star (*Henricia sanguinolenta* is taken as an example): 1, mouth place; 2, adambulacral plates; 3, actinolateral plates; 4, inferomarginal plates; 5, superomarginal plates; 6, intermarginal plates; 7, angle of the mouth formed by two oral plates.

83x55mm (300 x 300 DPI)

Fig. 3. *Henricia eschrichti*: light (a, e, f) and scanning (b, c, d) microscopy. a, abactinal view; b, part of abactinal skeleton with spines; c, part of abactinal skeleton without spines, note a plate with a well-defined tubercle (white arrow) and intermediate plates (white arrowhead); d, abactinal spines from the basal arm; e, part of abactinal side, note papulae (white arrow); f, part of actinal side, note inferomarginal spines arranged in rows (white arrow). Scale bar: a, 1 sm; b, c, 500 μ m; d, 50 μ m; e, f, 1 mm.

173x192mm (300 x 300 DPI)

Fig. 4. *Henricia perforata*: light (a, b, f, g) and scanning (c-e) microscopy. a, b, abactinal view; c, part of abactinal skeleton, note secondary plates which subdivide the meshes (white arrow); d, abactinal spines from the basal arm; e, part of abactinal skeleton with partially preserved integument and pseudopaxillae, note the secondary plate (white arrow); f, part of abactinal side, note single papulae (white arrow); g, part of actinal side, inferomarginal spines arranged in rows are indicated by white arrows. Scale bar: a, b, 1 cm; c, e, 500 μ m; d, 50 μ m; f, g, 1 mm.

173x182mm (300 x 300 DPI)

Fig. 5. *Henricia scabrior*: light (a, e, f) and scanning (b-d) microscopy. a, abactinal view; b, part of abactinal skeleton, note secondary plates (white arrow); c, abactinal plate with tubercle and four spines; d, abactinal spines from the basal arm; e, part of abactinal side, note single spines covered with thick skin (white arrow), papulae (white arrowhead); f, part of actinal side.

173x171mm (300 x 300 DPI)

Fig. 6. *Henricia solida*: light microscopy. a, abactinal view; b, part of abactinal side, note single spines covered with thick skin (white arrow); c, part of actinal side.

83x157mm (300 x 300 DPI)

Fig. 7. *Henricia sanguinolenta*: light (a, d, e) and scanning (b, c) microscopy. a, abactinal view; b, part of abactinal skeleton without spines, note plates with well-defined tubercles (white arrow); c, d, abactinal spines from the basal arm; e, part of abactinal side.

173x193mm (300 x 300 DPI)

Fig. 8. The principal component analysis. a, b, c, data of load distribution factor. N(s) – spines number in 1 mm2 of abactinal surface; z – spines number in pseudopaxillae; Hm – spines number in inferomarginal plate, L – length (mm) of the mesh, star – *Henricia eschrichti*, circle – *H. scabrior*, triangle – *H. perforata*.

197x158mm (300 x 300 DPI)