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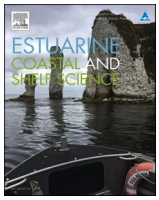

Deep-sea echinoids from the Avilés Canyons System (Cantabrian Sea: North Atlantic Ocean)

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ABSTRACT

The Avilés Canyons System (ACS) is located in the South of the Bay of Biscay (Northern Spain, Cantabrian Sea) and covers a total of 3,390 km^2. It is composed of three canyons, reaching the abyssal plain at 4700 m depth. The mixing of diverse water masses generates gyres and upwellings that contribute to the enrichment in nutrient concentration at different depth and favour the settlement of benthic communities. The ACS has been declared Site of Community Importance (SCI: C ESZZ12003) within the Natura 2000 Network and recognized as a Vulnerable Marine Ecosystem where echinoderms play an important ecological role in benthic communities and habitats.

The aim of the present study is to inventory and review the echinoid fauna collected during the INDEMARES project in the ACS, compare the new findings with previous studies Official Spanish Checklist (IEEM: "Inventario Español de Especies Marinas", 2017, 2020) and update our knowledge of the diversity and distribution of echinoid species.

During the surveys carried out within the project LIFE + INDEMARES-Avilés Canyons System (2010–2012), a total of 287 specimens of echinoids were sampled at 35 stations and depth ranging between 510 and 1476 m. Twelve species of echinoids were identified, the most frequent being *Araeosoma fenestratum* (Thomson, 1872*)* *(*48.57%), *Cidaris cidaris* (Linnaeus, 1758) (42.85%) and *Phormosoma placenta* Thomson, 1872 (28.57%). One species should be considered as a new record in Spanish waters, *Gracilechinus affinis* (Mortensen, 1903) and the species *Echinocardium flavescens* expands its known bathymetric range (from 325 to 552 m*)*.

1. Introduction

The Avilés Canyons System (ACS) (43.87°N and −6.10°W) begins on the continental slope of the Biscay Bay, in the Cantabrian Sea (Northeast Atlantic Ocean), within the Spanish Exclusive Economic Zone (EEZ: Sánchez et al., 2014). It is composed of three canyons of tectonic compressive origin: the Avilés Canyon (AC), El Corbiro Canyon (CC) and La Gaviera Canyon (GC), covering a total surface of 3,390 km^2 (Cristobo et al., 2010; Sánchez et al., 2014; Orejas et al., 2010). The ACS has been declared by the Spanish Ministry of Agriculture, Food and Environment (2014) as a Site of Community Importance (SCI: C ESZZ12003) within the Natura 2000 Network (Ministry of AgricultureFood and Environment, 2014), and recognized as a Vulnerable Marine Ecosystem (EMV: follow OSPAR Convention for the Protection of the Marine environment of the North-East Atlantic (https://www.ospar.org/convention/text)).

The Cantabrian Sea is characterized by different water masses: the East North Atlantic Central Water (ENACW), Labrador Sea Water (LSW), the deepest and cold North Atlantic Deep Water (NAWD), and the Mediterranean water (MW) that comes to the Biscay Bay through the Gibraltar Strait. Finally, the Cantabrian Sea is reached by Caribbean waters, which are warm and shallow waters of the Gulf Stream. As a consequence, marine species of the Cantabrian Sea could have different biogeographic origins (Arias and Crocetta, 2016).

The study area is rich in nutrients at different depths, due to gyres and upwellings favored by local geomorphology and water currents (Sánchez et al., 2014). Seasonal upwellings make this area an important place for the settlement of benthic communities in which echinoderms play an important ecological role (Sánchez et al., 2014).

Echinoids from the ACS were collected during former and ancient oceanographic campaigns and recorded by Agassiz (1881) (*M.S*

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Challenger); Perrier, 1885 (*Travailleur and Talisman*); Koehler (1895) (*Caudan*); Koehler (1909), 1921a (*Princesse Alice*; and *Hirondelle*); Morgan (1913) (*Huxley*); Grieg (1932) (*Michael Sars*); Mortensen (1903), 1907 (*Danish Ingolf-expedition*); Cherbonnier (1969) (*Thalassa*); Monteiro Marques (1980) (*Hespérides* 76); Laubier and Monniot (1985) (*Biogas*) and López-Ibor (1987) (*Cantábrico 83*); Louzao et al. (2010) (COCACE). More recently, the INDEMARES and INTEMARES projects were developed to undertake new campaigns in the ACS and update our knowledge of the diversity of benthic fauna, as well as characterize and classify benthic habitats.

The aim of the present study is to inventory and review the echinoid fauna collected during the INDEMARES project in the ACS and compare the new findings with previous studies (Official Spanish Checklist) (IEEM, 2017 and updated in 2020, among others) to update our knowledge on the diversity and distribution of echinoid species.

2. Material and methods

2.1. Sampling

The LIFE + INDEMARES-ACS project consisted in five multidisciplinary oceanographic surveys undertaken from 2010 to 2012 in the Cantabrian Sea onboard four research vessels: RVs *Vizconde de Eza*, *Thalassa*, *Ramon Margalef* and *Angeles Alvariño*. During these surveys, specimens of echinoids were collected at a total of 35 stations distributed between 510 and 1476 m depth (Table 1, Fig. 1). Sampling was done using different gears: a Rock dredge (DR) (opening 0.8 m wide and 0.3 m high, mesh size 10 mm), a beam trawl Bou de vara (V) (opening 3.50 m wide and 0.65 m high, mesh size of 10 mm), a beam trawl GOC-73 (GOC) (opening 19.44 ± 0.59 m wide and 2.68 ± 0.12 m high, mesh size of 10 mm), and a suprabenthic sledge (TS) (two nets of mesh size 0.5 mm). Sampling was completed by using a Remote Operated Vehicle (ROV) *Liropus* 2000 equipped with 5 video cameras, 2 hydraulics hands, a collector by suction and a box to keep samples.

2.2. Systematics, distribution areas and bathymetric ranges

Echinoids were sorted onboard and fixed in 70% ethanol for further investigations. The identification of species was performed based on the observation of diagnostic, morphological characters following Bell (1892), Mortensen (1903, 1907, 1927, 1928, 1935, 1943a, 1943b, 1948, 1950 and 1951), Koehler (1921b), and Schultz (2005, 2009, 2011). All taxon names were checked for relevance and synonymies based on the original descriptions. Echinoid classifications and new species records were checked through the World Register of Marine Species (WoRMS). AphiaID (urn:lsid:marinespecies.org:taxname) Kroh and Mooi (2021) were included for consulting and referring to synonymies. Morphological notations follow Kroh and Smith (2010).

New records were compared to the known distribution of species using the IEEM (Manjón-Cabeza et al., 2017, 2020) related to the North Atlantic Spanish Marine Sub-Division (NAMD) (see polygon at Fig. 1∗) and supported by other open access databases: GBIF.org (2021), Muséum national d'histoire naturelle (2021), Ocean Biogeographic Information System (2021), and USNM Invertebrate Zoology Collection (Smithsonian National Museum of Natural History, 2021), as well as other sources as Perrier (1881) or Pawson et al. (2009) among others.

3. Results

In the ACS, two thousand and eighty-seven specimens of echinoids were collected and identified. They belong to 12 species (Table 2), 6 families, and 4 orders comprising irregular (1 species) and regular (8 species) Euechinoids, as well as Cidaroids (3 species). The family Echinidae is by far the richest family (5 species), and *Gracilechinus* the richest genus (4 species). The most frequent species (percentage of occurrence per station) were *A. fenestratum* (Thomson, 1872) (48.57%), *C. cidaris* (Linnaeus, 1758) (42.85%) and *P. placenta* Thomson, 1872 (28.57%).

One species represent a new record for the Cantabrian Sea (Table 2): *G. affinis* (Mortensen, 190). A later species, *E. flavescens* (O.F. Müller, 1776), extends the known species bathymetric range (from 325 to 552 m depth).

3.1. Systematics

Class Echinoidea Leske, 1778
Subclass Cidaroidea Smith, 1984
Order Cidaroida Claus, 1880
Family Cidaridae Gray, 1825
Genus *Cidaris* Leske, 1778
Cidaris cidaris (Linnaeus, 1758). AphiaID: 124257 (Fig. 2 a-h).

Material examined. 40 specimens collected at stations A410DR12, A410DR4, A710DR14, A710DR7, A11DR11, A11DR10, A11DR7, A11DR5, A11DR4, A11DR3, A11G06, A11G04, A11G02, A11V06, A11T6.

Diagnosis. *Cidaris cidaris* is characterized by the presence of non-crenulate primary tubercles, scrobicular tubercles well-differentiated from surrounding secondary spines, and the absence of pits or grooves on the corona. In *C. cidaris*, test shape is variable but usually spherical (Fig. 2a, b, c). The apical disc is larger than the peristome, about half the test diameter (Fig. 2a and b). Ambulacra are distinctly sinuate. Interambulacra are covered with many granules in between primary tubercles. Oral primary spines are not serrated (Fig. 2d). Aboral primary

Table 1
Geographical position and depth of the sampling stations. **ST**: Station, **LAT:** latitude (decimal grade), **LON:** longitude (decimal grade), **D:** depth (m).

ST	LAT	LON	D	ST	LAT	LON	D
A11DR3	43.92	−5.77	776	A11V06	44.02	−5.47	1228
A11DR4	43.99	−5.73	593	A11V07	43.98	−5.48	984
A11DR5	43.99	−5.78	908	A410DR3	43.95	−5.83	893
A11DR7	43.88	−5.91	551	A410DR4	43.93	−5.76	700
A11DR10	43.77	−6.23	931	A410DR8	43.78	−6.20	844
A11DR11	43.74	−6.11	560	A410DR12	43.86	−6.43	828
A11G02	43.92	−6.25	1051	A410DR17	43.94	−6.45	1476
A11G03	43.96	−6.47	1464	A410DR18	44.00	−5.58	767
A11G04	43.96	−5.76	535	A410DR19	43.96	−6.60	533
A11G05	43.89	−6.13	578	A710DR8	43.76	−6.19	800
A11G06	44.02	−5.46	1244	A710DR13	43.97	−5.79	769
A11G07	43.98	−5.48	990	A710DR14	44.02	−5.71	772
A11T4	43.96	−5.77	530	A710DR15	43.99	−5.81	1228
A11T6	44.02	−5.47	1238	A710DR16	44.03	−5.72	928
A11V02	43.92	−6.25	1008	A710DR7	43.75	−6.15	621
A11V03	43.96	−6.47	1473	A412ROV7	43.88	−5.91	487
A11V04	43.95	−5.77	510	A912ROV3	43.75	−6.19	748
A11V05	43.89	−6.13	552				

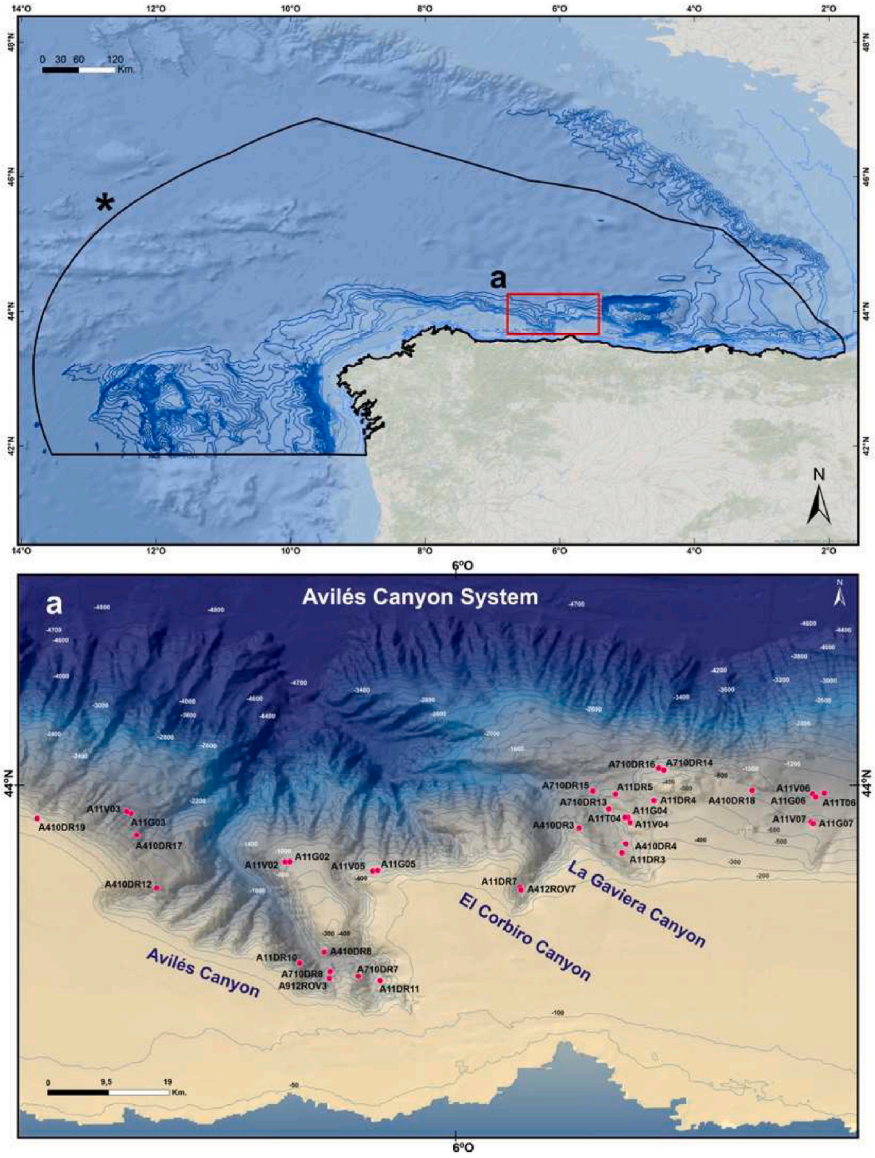

Fig. 1. Study area. a. ACS sampling stations with presence of Echinoids. ⋆ North Atlantic Spanish Marine Sub-Division (NAMD) polygon.

spines are slender and very long (2–2.5 the test diameter), with the base swollen (Fig. 2e). The shaft is covered in granules organized in 12–16 sharp ridges, with cortical hairs present in between ridges (Fig. 2f). Scrobicular, secondary spines are well-differentiated from other secondary spines: they are flattened with a round tip (Fig. 2f). Other secondaries are smaller, pointed and erected (Fig. 2g). As other species of the genus, *C. cidaris* has globiferous pedicellariae ending with a single long terminal tooth (Fig. 2h). The colour is white-yellowish (Fig. 2a).

Geographical distribution. Atlantic Ocean, Norwegian Sea, North Sea, Bay of Biscay, Galician coast, South and North of Azores, North West Atlantic, Fundy Bay. Morocco coast, south of The Canary Island (south of El Hierro), Gulf of Guinea, North of Angola coast, West of South Africa, Mediterranean Sea, East and West Mediterranean Sea.

Bathymetric range. 33–2338 m depth (USNM E 15671 NMNH identified by Pawson et al., 2009; OBIS database). Present study: 535–1244 m depth.

Remarks. There are six known species of the Genus *Cidaris* worldwide. *Cidaris cidaris* is the only one recorded in the ACS. It distinguishes from other species of the genus by the presence of large, flattened and rounded scrobicular spines at the tip, a sphaerical test shape, a large apical system, and long, slender aboral primary spines with sharp ridges. It may be confused with the species *Stylocidaris affinis* (Philippi, 1845). However, *C. cidaris* is larger, has longer primary spines (2–2.5 the test diameter against 1 to 1.5 in *S. affinis*) and is more uniform in colour. The presence of a single long tooth at the end of globiferous pedicellariae is also a feature that distinguishes *C. cidaris* from *S. affinis*, in which globiferous pedicellariae end with small teeth. *Cidaris cidaris* differs from *Histocidaris purpurata* (Thomson, 1872) by the colour of the test, which is white in *C. cidaris* and purple in *H. purpurata* when preserved. *Histocidaris purpurata* does not have globiferous pedicellariae and primary tubercles are crenulate.

Genus *Stereocidaris* Pomel, 1883

Stereocidaris ingolfiana Mortensen (1903). AphiaID: 124267 (Fig. 2 i-m).

Material examined. 31 specimens from stations A11G06, A11G03, A11V06, A11V03.

Diagnosis. As a species of *Stereocidaris*, first or second uppermost primary tubercles in interambulacra are rudimentary and carry no functional spine (Fig. 2i). *Stereocidaris ingolfiana* distinguishes from other species of the genus by primary spines having strong rows of spinules fused into keels with serrated edges (Fig. 2j). In ambulacra, perradial tubercles are small and irregularly arranged (Fig. 2i). Oral

Table 2
Echinoid taxa identified from the Avilés Canyons System. Systematics follows Kroh and Smith (2010).

Order	Family	Species
Cidaroida Claus, 1880	Cidaridae Gray, 1825	*Cidaris cidaris* (Linnaeus, 1758)
		Stereocidaris ingolfiana Mortensen (1903)
	Histocidaridae Lambert, 1900	*Histocidaris purpurata* (Thomson, 1872)
Echinothurioida Claus, 1880	Echinothuriidae Thomson, 1872	*Araeosoma fenestratum* (Thomson, 1872)
		Calveriosoma hystrix (Thomson, 1872)
	Phormosomatidae Mortensen, 1934	*Phormosoma placenta* Thomson, 1872
Camarodonta Jackson, 1912	Echinidae Gray, 1825	*Echinus melo* Lamarck, 1816
		Gracilechinus acutus (Lamarck, 1816)
		Gracilechinus affinis (Mortensen, 1903)
		Gracilechinus alexandri (Danielssen & Koren, 1883)
		Gracilechinus elegans (Düben & Koren, 1844)
Spatangoida L. Agassiz, 1840	Loveniidae Lambert, 1905	*Echinocardium flavescens* (O. F. Müller, 1776)

primary spines are short and serrated (Fig. 2k). Scrobicular spines are flattened (Fig. 2l, m). Globiferous pedicellariae are present with terminal opening surrounded by small teeth. The colour of the test is usually light brown and the collar of spines is pinkish (Fig. 2i, l).

Geographical distribution. Atlantic Ocean, South of Iceland, South of Nova Scotia, Cape Verde, Georgia coast, East and South Florida, Gulf of Mexico, Caribbean Sea.

Bathymetric range. 37–1745 m depth (USNM E 9731 NMNH identified By Cutress, 1959; Mortensen, 1927). Present study: 1228–1473 m depth.

Remarks. There are 18 species of *Stereocidaris* recorded worldwide but there are no other species that could be confused with the specimens from Cantabrian Sea. Interestingly, the tests of collected specimens were relatively flatter (Fig. 2i) than it usually occurs in populations of the Caribbean Sea (Schultz, 2011).

Family Histocidaridae Lambert, 1900

Genus *Histocidaris* Mortensen, 1903.

Histocidaris purpurata (Thomson, 1872). AphiaID: 513337 (Fig. 2 n-r).

Material examined. 14 specimens from stations A11G06, A11G03, A11V06, A11V02.

Diagnosis. As other members of the family Histocidaridae, in *H. purpurata* primary tubercles are perforate and strongly crenulated. In *H. purpurata*, the test is flattened apically and orally (Fig. 2n). Primary spines are long and cylindrical (2–2.5 is the test diameter) with the shaft covered in very fine spinules arranged into longitudinal ridges and a long collar (Fig. 2n, o). Secondary spines are slender and flattened, scrobicular are broader than other secondaries and erect at the base of primary spines, not appressed (Fig. 2p, q). Oral primary spines are finely serrate laterally (Fig. 2r). As in other species of Histocidaridae, globiferous pedicellariae are lacking, tridentate pedicellariae are present and typically possess only two valves. Colour of the test is white, slightly brown and purple (Fig. 2n, o).

Geographical Distribution. Atlantic Ocean, British Island, The Canary Islands, East of Florida, Caribbean Sea, Indian ocean, Andaman Sea, Pacific Ocean, Tasman Sea, North and South New Zealand.

Bathymetric range. 565–1800 m depth (OBIS database; Schultz, 2011) Present study: 1008–1464 m depth.

Remarks. There are 16 species worldwide assigned to the genus *Histocidaris* Mortensen, 1903. Only *H. purpurata* is present in the Cantabrian Sea. In some specimens, crenulation of primary tubercles may not be not visible. There are not any other species in the area that could be confused with it.

Subclass Euechinoidea Bronn, 1860

Order Echinothurioida Claus, 1880

Family Echinothuriidae Thomson, 1872.

Genus *Araeosoma* Mortensen, 1903.

Araeosoma fenestratum (Thomson, 1872). AphiaID: 149880 (Fig. 3 a-e).

Material examined. 55 specimens from stations A410DR19, A410DR18, A410DR12, A410DR8, A410DR4, A410DR3, A710DR16, A710DR14, A710DR8, A710DR7, A11DR7, A11DR5, A11DR4, A11G07, A11G06, A11V07, A412ROV7.

Diagnosis. The test is round in living specimens (Fig. 3a). In the apical system, the madreporite is conspicuous and genital pores open outside the genital plates in membranous gaps (Fig. 3b). Plates of the corona are not in contact with each other on the oral side and are separated by conspicuous interstices (Fig. 3c). The peristome has many plates and two rows of pore-pairs in ambulacra (Fig. 3d). On the aboral side, primary spines are thorny (Fig. 3b). As in all Echinothuriidae, there is a distal hoof at the tip of oral primary spines (Fig. 3e). It has dactylous pedicellariae with deeply sinuate edge. The colour of the test is dark purple or brown (Fig. 3a).

Geographical distribution. Atlantic Ocean, South Iceland, British Islands, Bay of Biscay, Florida coast, Gulf of Mexico, Caribbean Sea, South Azores.

Bathymetric range. 145–1400 to 1800 m depth (Mortensen, 1927; Serrano et al., 2017). Present study: 533–1244 m depth.

Remarks. There are 19 species of *Araeosoma* Mortensen, 1903 recorded worldwide. *Araeosoma fenestratum* is the only one present in the ACS, *A. fenestratum* and *Calveriosoma hystrix* (Thomson, 1872) overlapping geographically with each other. The two species can be difficult to differentiate. Basically, *A. fenestratum* differs by the presence of dactylous pedicellariae with a deeply sinuate edge, whereas *C. hystrix* lacks dactylous pedicellariae and pedicellariae do not have deeply sinuate edge. In addition, the test of *A. fenestratum* is dark purple or brown when preserved in alcohol, while in *C. hystrix* it keeps red in colour.

Genus *Calveriosoma* Mortensen, 1934

Calveriosoma hystrix (Thomson, 1872). AphiaID: 124338 (Fig. 3 f-j).

Material examined. 15 specimens at stations A11G06, A11V06.

Diagnosis. The test is usually flat or hemispherical (Fig. 3f). On the apical system, ocular and genital plates are large and in contact with each other (Fig. 3g). Ambulacra have longitudinal rows of primary tubercles from the peristome to the apex, and many secondary tubercles (Fig. 3h). Ambulacral plates are not in contact aborally but orally (Fig. 3h and i). Oral primary spines end with a conical hoof (Fig. 3j). Tridentate pedicellariae are present without sinuate edge. The colour of the test is bright red in living specimens as well as in specimens preserved in alcohol (Fig. 3f).

Geographical distribution. Atlantic Ocean, South of Iceland, British Island, Bay of Biscay, Azores, The Canary Islands, Caribbean Sea (Yucatan Channel, In front of Quintana Roo).

Bathymetric range. 360–2338 m depth (Schultz, 2011; OBIS database). Present study: 1228–1244 m depth.

Remarks. There are 2 species of the Genus *Calveriosoma* Mortensen, 1934. *Calveriosoma gracile* (A. Agassiz, 1881) and *C. hystrix*. *Calveriosoma gracile* occurs in the Pacific Ocean and is characterized by the presence of wide bare bands aborally and test yellow in colour so that the two species cannot be confused with each other. *Calveriosoma hytrix* is very similar in morphology to *A. fenestratum* also present in the ACS (see before).

Family Phormosomatidae Mortensen, 1934

Genus *Phormosoma* Thomson, 1872.

Phormosoma placenta Thomson, 1872. AphiaID: 124343 (Fig. 3 k-n).

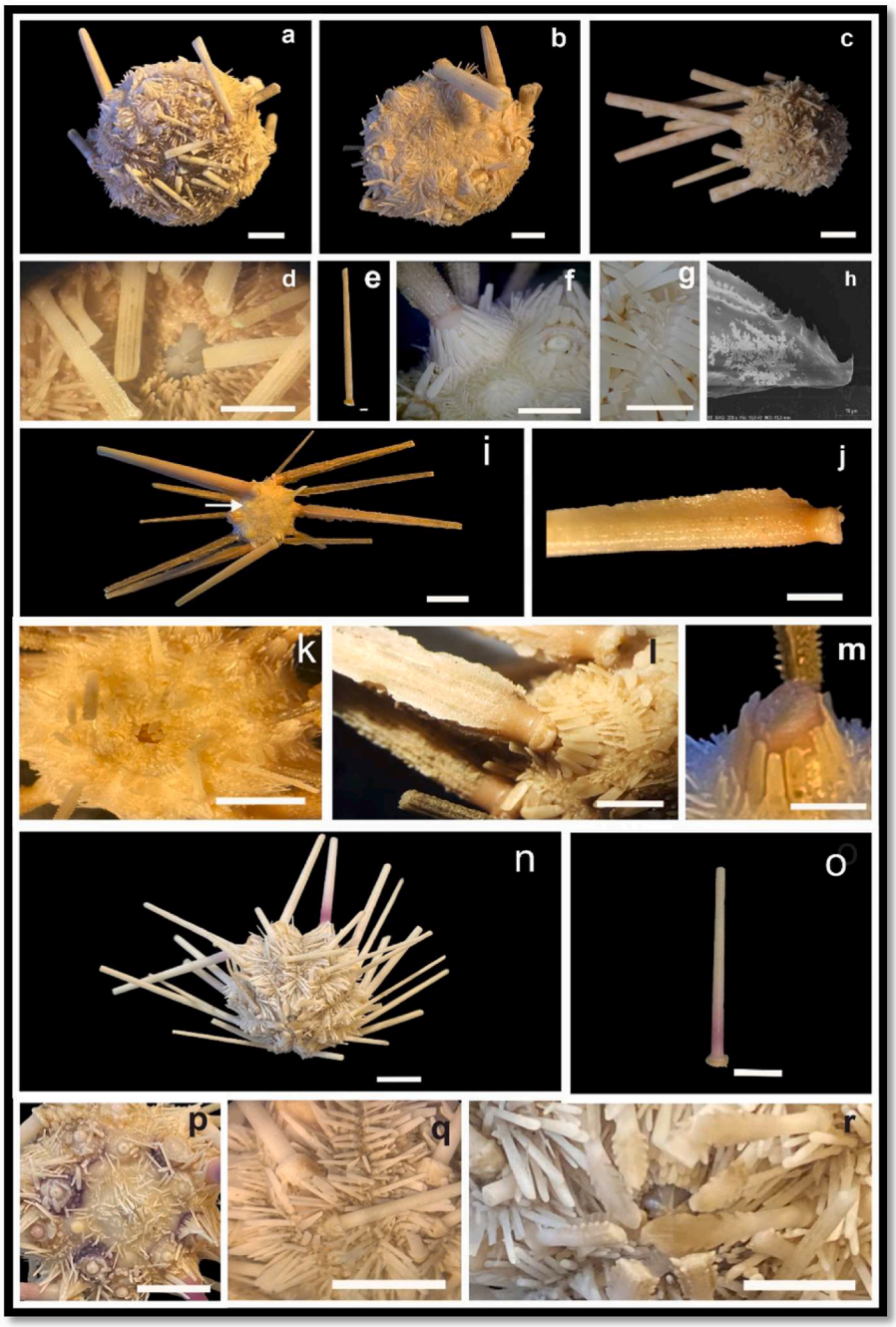

Fig. 2. *Cidaris cidaris*: **a.** Oral view. Scale bar: 10 mm. **b.** Aboral view. Scale bar: 10 mm. **c.** Test and primary spines, general view. Scale bar: 10 mm. **d.** Detail of oral spines. Scale bar: 5 mm. **e.** Primary spine Scale bar: 5 mm. **f.** Detail of scrobicular spines and base of primary spine. Scale bar: 5 mm. **g.** Detail of ambulacral naked area with erect secondary spines. Scale bar: 1.25 mm. **h.** Globiferous pedicellaria. Scale bar: 70 μm. ***Stereocidaris ingolfiana***: **i.** Aboral general view. **Arrow:** Rudimentary primary tubercle with no spine. Scale bar: 10 mm. **j.** Detail of primary spine with lateral keel. Scale bar: 5 mm. **k.** View of oral primary spines. Scale bar: 5 mm. **l.** Aboral primary and scrobicular spines. Scale bar: 2.5 mm. **m.** Detail of scrobicular spines at the base of a broken primary spine. Scale bar: 2.5 mm. ***Histocidaris purpurata***: **n.** General view. Scale bar: 10 mm. **o.** Primary spine. Scale bar: 10 mm. **p.** Apical system. Scale bar: 10 mm. **q.** Detail of scrobicular, secondary and primary spines. Scale bar: 10 mm. **r.** Detail of oral primary spines. Scale bar: 5 mm.

Material examined. 116 specimens from stations A710DR13, A11G07, A11G05, A11G04, A11G02, A11V07, A11V05, A11V03, A11V02, A912ROV3.

Diagnosis. The test is low hemispherical (Fig. 3k). The apical disc is less wide than the peristome (Fig. 3k and l). The oral side presents demiplates located at the outer (adradial) edge and covered on most of its surface by deepened areoles (Fig. 3m, n), the aboral side lacks deepened areoles (Fig. 3k). As in other Phormosomatidae, oral primary spines are simple with fleshy skin bags at their distal end, and not hoof (Fig. 3n). Aboral primary spines are straight, and not curved. There are tridentate pedicellariae. Colour of the test is usually light brown (Fig. 3k).

Geographical distribution. Atlantic Ocean, Iceland, British Island, Bay of Biscay, South of Spain and Portugal, coast of Morocco, South-East of Liberia, South-East of Ivory coast, Gulf of Guinea, Labrador Sea, East coast of North America from Nova Scotia to Florida, Gulf of Mexico, Caribbean Sea, North of Guyana, Brazilian coast (Spirito Santo coast, Salvador de Bahía).

Bathymetric range. 38–4100 m depth (Gondim et al., 2018; Mironov, 2014). Present study: 535–1473 m depth.

Remarks. There are 4 species of the Genus *Phormosoma* Thomson, 1872 recorded worldwide. *Phormosoma placenta* only occurs in the ACS. *Phormosoma placenta* differs in morphology from other echinothuriids of the Cantabrian Sea by the absence of terminal hoof at the end of oral primary spines but the presence of a fleshy distal bag of skin.

Order Camarodonta Jackson, 1912.

Family Echinidae Gray, 1825

Genus *Echinus* Linnaeus, 1758

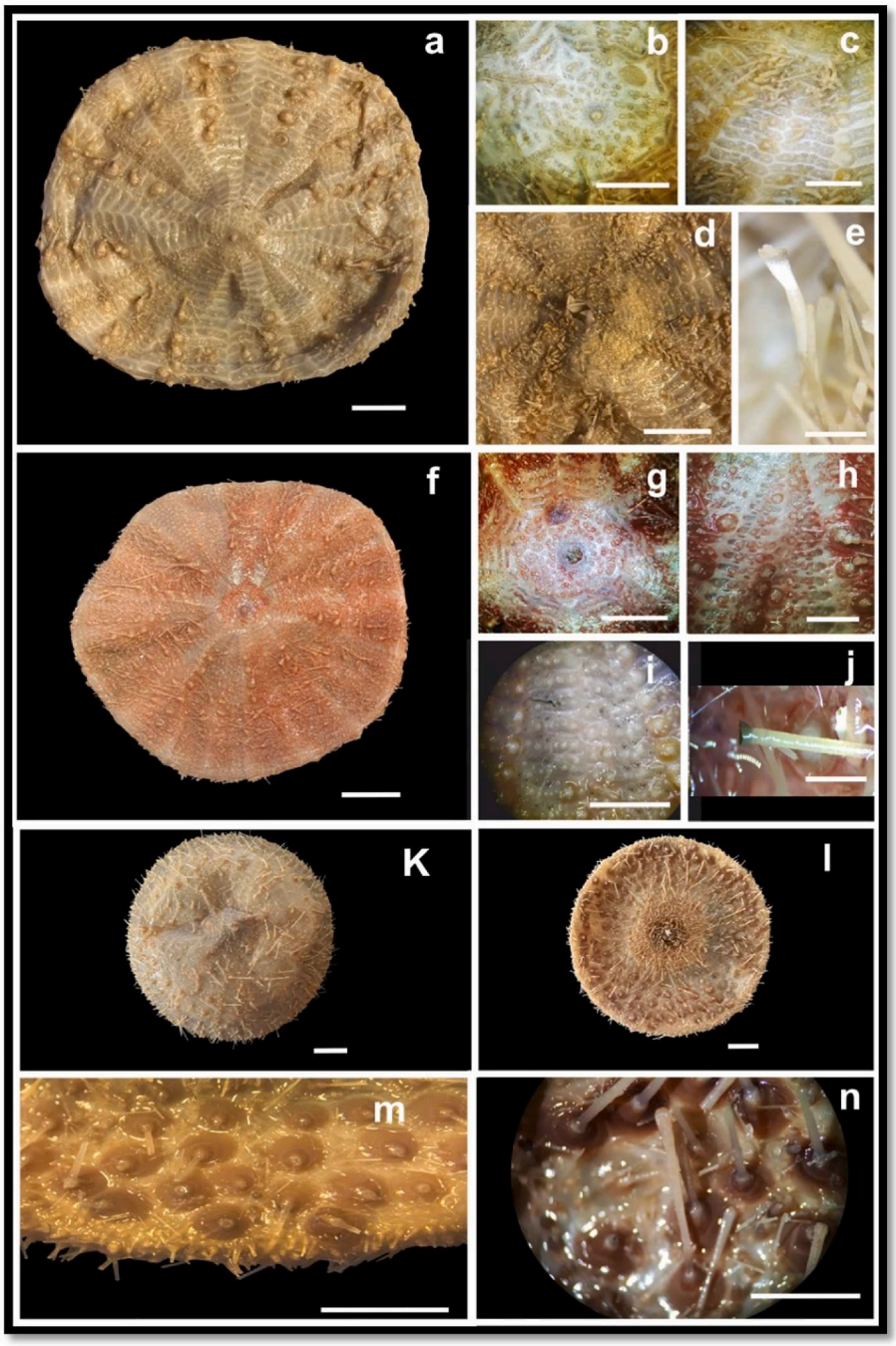

Fig. 3. *Araeosoma fenestratum*: **a.** Aboral view. Scale bar: 10 mm**. b.** Detail of apical system. Scale bar: 5 mm. **c.** Detail of adoral part of ambulacrum. Scale bar: 5 mm. **d.** Focus on peristome. Scale bar: 10 mm. **e**. Detail of an oral spines showing the long, conical hoof at the end. Scale bar: 0.625 mm. ***Calveriosoma hystrix:*** **f.** Aboral view. Scale bar: 10 mm. **g.** Focus on apical system. Scale bar: 5 mm. **h.** Detail of adoral part of one ambulacrum. Scale bar: 2.5 mm. **i.** Detail of aboral part of one ambulacrum. Scale bar: 2.5 mm. **j**. Detail of an oral spine showing the short terminal hoof. Scale bar: 1.25 mm. ***Phormosoma placenta:*** **k.** Aboral view. Scale bar: 10 mm. **l**. Oral view. Scale bar: 10 mm. **m**. Detail of oral tubercles with well-developed areoles Scale bar: 10 mm. **n.** Detail of oral spines with fleshy skin bag at the end. Scale bar: 5 mm.

3.1.1. General remarks on the morphology of the genus Echinus and Gracilechinus

Both genera are very alike in morphology. Fell and Pawson (1966) erected the genus *Gracilechinus* based on the presence of primary tubercles on every compound ambulacral plate. In contrast, the genus *Echinus* Lamarck, 1816 is restricted to species with a primary tubercle developed on every second or third compound ambulacral plate only. However, the species *G. acutus* (Lamarck, 1816) seems like an exception with primary tubercles developed on every second or third plate only questioning the taxonomy of the species, if not of both genera.

Echinus melo Lamarck, 1816. AphiaID: 124294 (Fig. 4 a-d).

Material examined. Only one specimen from station A11G02.

Diagnosis. The test is globular in shape (Fig. 4a). The apical system shows a prominent madreporite and the periproct carries few plates, which are variable in size (Fig. 4b). As for all species of the genus, ambulacra present a primary tubercle developed only on every second or third compound plate (Fig. 4c). Interambulacra have a small primary tubercle in the middle of every second plate (Fig. 4c). The peristome is small and not sunken (Fig. 4d). The primary spines are slender and longer than secondaries (Fig. 4a). Tridentate pedicellariae are present. The colour is usually greenish or yellow-brown (Fig. 4a).

Geographical distribution. Atlantic Ocean, Bay of Biscay, South of Azores, West of Morocco, West of Portugal, West Mediterranean Sea.

Bathymetric range. 25–1100 m depth (Schultz, 2005). Present study: 1051 m depth.

Remarks. There are 6 recognized species of the genus *Echinus* worldwide. *Echinus melo* and *E. esculentus* Linnaeus, 1758, are very similar in morphology. *Echinus melo* shows a globular test and only one

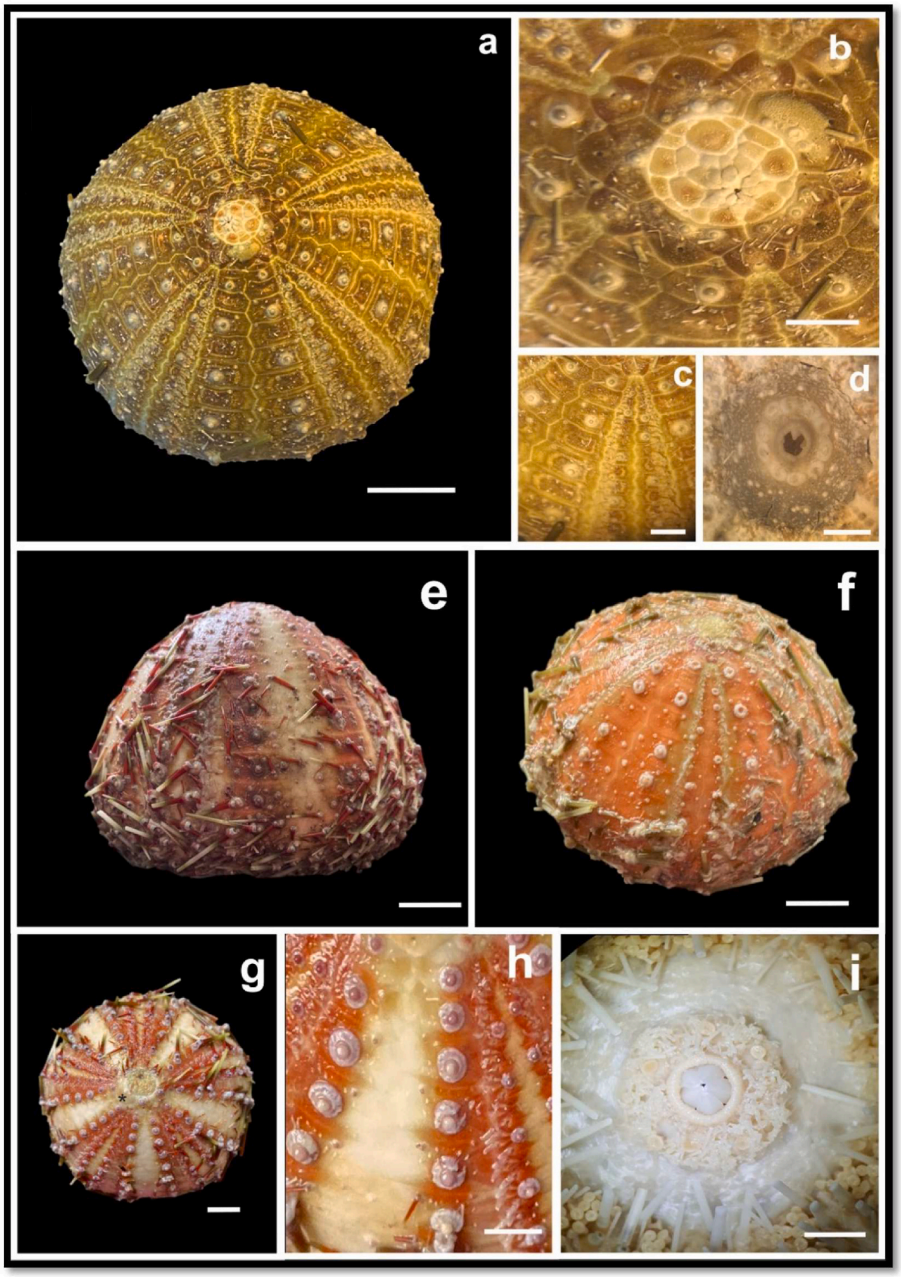

Fig. 4. *Echinus melo*. a. General aboral biew. Scale bar: 10 mm. **b**. Detail of apical system. Scale bar: 2,5 mm. c. Ambulacrum II showing the echinoid plate pattern and interambulacra 1 showing the presence of one primary tubercle every two plates. Scale bar: 2,5 mm. d. View of peristome showing the ten buccal plates with no spines. Scale bar: 5 mm. *Gracilechinus acutus*. e. Corona of *Gracilechinus acutus acutus* in lateral view. Scale bar: 10 mm. f. *Gracilechinus acutus* var. *flemingii* in oblique view. Scale bar: 10 mm. g. *Gracilechinus acutus* var. *norvergicus*, in apical view. Scale bar: 10 mm. h. Ambulacra and interambulacra showing the occurrence of primary tubercles on every plate. Scale bar: 5 mm. i. Peristome. Scale bar: 5 mm.

primary tubercle present on every second plate in interambulacra, while in *E. esculentus* the test is usually subconical and one primary tubercle is present on every plate in interambulacra. The species of *Gracilechinus* are also very similar, such as *G. acutus* (Lamarck, 1816), but differ by the presence of primary tubercles on every ambulacral plate. *Echinus melo* is very recognizable by its globular test shape, weak tuberculation, and arrangement of primary tubercles in ambulacra and interambulacra.

Genus *Gracilechinus* Fell and Pawson 1966.

Gracilechinus acutus (Lamarck, 1816). AphiaID: 532031 (Fig. 4 e-i).

Material examined. 3 specimens from stations A11G05, A11G02, A11V04.

Diagnosis. The test shape is very variable in profile, from low to conical or globular (Fig. 4e, f, g). The apical system is dicyclic (all ocular plates exsert) and variable in size, the madreporite is slightly enlarged, and the periproct is covered with many small plates (Fig. 4g). There is one primary tubercle on every second or third compound plate in ambulacra (Fig. 4h). Interambulacra present one primary tubercle on each plate (Fig. 4h). The peristome is usually small (20% test diameter) but variable in size, there are no spines on buccal plates (Fig. 4i). Primary spines are short but longer than secondary ones (Fig. 4e). Tridentate pedicellariae are present. Test colour is variable, from red to light yellow, with lighter stripes in pore zones (Fig. 4e, f, g).

Geographical distribution. Atlantic Ocean, Norwegian Sea (Norway coast from south until north), North Sea, Iceland, British Islands, Bay of Biscay, Maine coast, New York coast, Gabon coast, Congo coast, middle Angola coast, West of Namibia, West of South Africa, Mediterranean Sea, West Mediterranean Sea, Sea of Crete.

Bathymetric range. 20–1280 m depth. (Mortensen, 1927). Present study: 510–1051 m depth.

Remarks. The species is very variable in test shape, size, and arrangement of tubercles in both ambulacra and interambulacra. Two subspecies of *G. acutus* are currently recognized to date: *G. acutus acutus* (Lamarck, 1816) and *G. acutus norvergicus* (Düben & Koren, 1844). The two varieties *G. acutus mediterraneus* Mortensen, 1906, and *G. acutus*

flemingii Forbes, 1841 are considered as synonymous of *G. acutus* (Kroh and Mooi, 2022). There are 11 species assigned to the Genus *Gracilechinus* worldwide. *Gracilechinus acutus* and *G. elegans* (Düben & Koren, 1844) are very alike but differ in the apical system, with larger genital plates in *G. elegans* compared to *G. acutus*. *Gracilechinus acutus* is also very similar to *E. esculentus,* which has numerous equal-size secondary tubercles present in interambulacral, hardly differentiable from primary tubercles, while in *G. acutus* secondary tubercles are smaller, scarce, and irregularly arranged. Hybridization between the two species is common (Schultz, 2005).

Gracilechinus affinis (Mortensen, 1903). AphiaID: 532039. **New record** (Fig. 5 a-d).

Material examined. 1 specimen from station A11T4.

Diagnosis. The test is usually subconical (Fig. 5a). In the apical disc, genital plates are covered with several primary tubercles, ocular plates present either one tubercle or no tubercle, the periproct has many small plates and there is no suranal plate visible (Fig. 5b). In ambulacra, primary tubercles are present on every compound plate, secondary tubercles are scarce (Fig. 5c). Interambulacra have large and robust primary tubercles present adapically to the apex, secondary tubercles are mainly present on the oral side (Fig. 5a). Primary tubercles decrease in size from the ambitus towards the peristome and the apical system (Fig. 5a, d). The peristome lacks spine on buccal plates. Primary spines are robust (Fig. 5c). Tridentate pedicellariae are present. Colour of the test is greenish to purple, primary spines are light green or purple at the base (Fig. 5a).

Geographical distribution. Atlantic Ocean, British Islands, Ireland, South of Iceland, Azores, In front of Saint John of Terranova, from Nova Scotia to North Carolina, Florida, Gulf of Mexico, Mediterranean Sea: West of Sicily.

Bathymetric range. 241–3136 m depth (Pawson et al., 2009). Present study: 530 m depth.

Remarks**.** *Gracilechinus affinis* is very similar in shape to *G. alexandri* (Danielssen & Koren, 1883) and both species often co-occur (Schultz, 2011). *Gracilechinus affinis* differs by the irregular size and arrangement of ambulacral tubercles decreasing towards the apical system and the

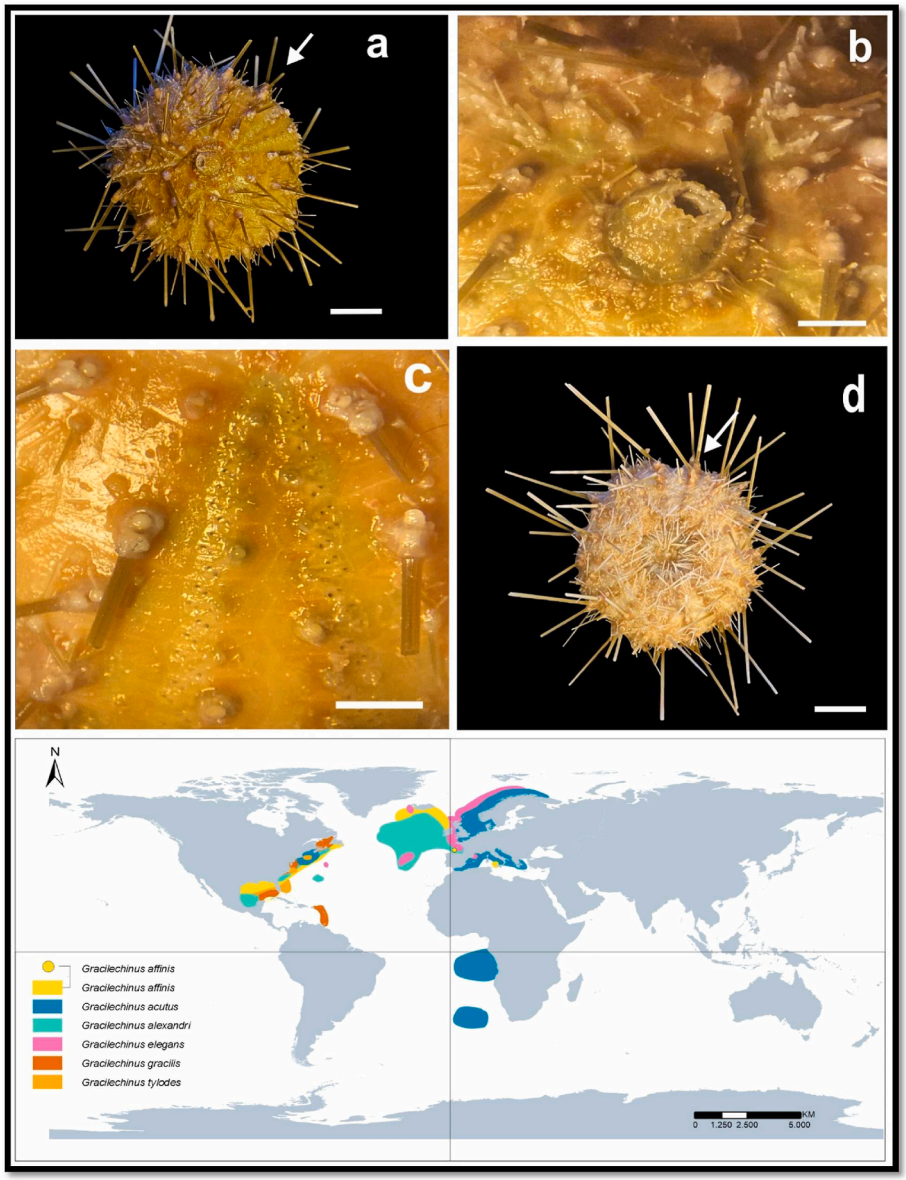

Fig. 5. *Gracilechinus affinis* (new record): **a**. Aboral view. Scale bar: 10 mm. **Arrow:** Tubercles decreasing in size towards the apex. **b**. Detail of apical system. Scale bar: 5 mm. **c**. Detail of one ambulacrum and interambulacrum showing primary tubercles and pore-pairs patterns. Scale bar: 5 mm. **d**. Oral general view. Scale bar: 10 mm. **Map.** World distribution map of species of *Gracilechinus*.

peristome. In *G. alexandri*, ambulacral tubercles are more homogeneous in size.

Gracilechinus alexandri (Danielssen & Koren, 1883). AphiaID: 532032 (Fig. 6 a-f).

Material examined. 1 specimen from station A710DR15.

Diagnosis. The test is low, flattened orally and aborally (Fig. 6a). The apical system has inner part of genital plates well tuberculated, the outer part is naked, and the periproct is large (larger than genital plates) showing numerous small plates and large suranal plate (Fig. 6b). Ambulacra present primary tubercles regular in size, smaller in the aboral side, which is also covered with less miliary tubercles than in the oral side (Fig. 6a, c). One primary tubercle is developed on every compound plate (Fig. 6d). Interambulacra have regular series of primary tubercles and secondary tubercles present on every plate, sparser on the aboral side (Fig. 6d). The peristome presents many large plates (Fig. 6e). Globiferous and tridentate pedicellariae are present. Colour of the test is white, spines are red or yellow (Fig. 6c, f).

Geographical distribution. Atlantic Ocean, South of Iceland, Faroes Channel, (exceptionally Norway and Lofoten), British Islands, Bay of Biscay, middle of North Atlantic Ocean, North West of Azores, North East American coast from Maine to North Carolina, coast of Georgia, Florida and Gulf of Mexico.

Bathymetric range. 365–4700 m depth (Schultz, 2011; David and Sibuet, 1985). Present study: 1228 m depth.

Remarks. The species is morphologically very close to *G. affinis* (see before) and *G. elegans* (Düben & Koren, 1844). *Gracilechinus elegans* differs by the size of genital plates that are as large as the periproct, while genital plates are smaller than the periproct in *G. alexandri*. Also, in *G. alexandri,* the aboral side is less tuberculated than in *G. elegans*.

Gracilechinus elegans (Düben & Koren, 1844). AphiaID: 532035 (Fig. 6 g-k).

Material examined. 8 specimens from stations A410DR17, A410DR4, A410DR3, A710DR15, A710DR13, A11V04.

Diagnosis. The test is variable in shape, from subconical or flattened (Fig. 6g and h). In the apical system, the periproct is small, it shows almost the same size as the madreporite, and has many small plates (Fig. 6i). Ambulacra present many miliary tubercles and one robust primary tubercle developed on each plate but it is smaller than inter-ambulacral tubercles (Fig. 6j). Interambulacra have strong primary tubercles, larger than ambulacral ones, and many secondary (smaller aborally) and miliary tubercles (Fig. 6g, h, j). The peristome shows many plates (Fig. 6k). Spines are long (1/2 to 2/3 test diameter) and solid (Fig. 6g and h). Globiferous and tridentate pedicellariae are present. Colour of test is white (Fig. 6g and h).

Geographical distribution. Atlantic Ocean, Norwegian Sea, North Sea, West Iceland, British Islands, Bay of Biscay, Azores Islands, East of Rhode Island, Mediterranean Sea, Catalonia coast, West African coast.

Bathymetric range: 50–2000 m depth (Mortensen, 1927). Present study: 510–1476 m depth.

Remarks. *Gracilechinus elegans* is very similar in morphology to

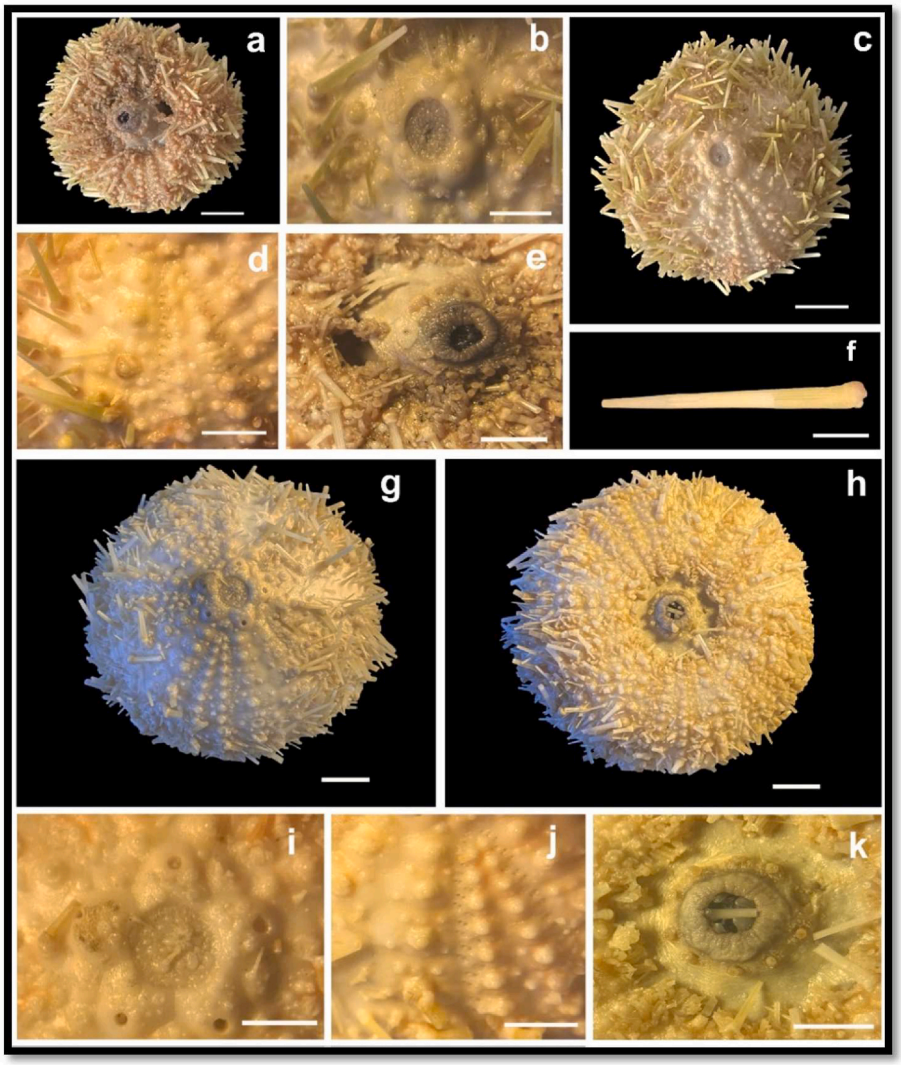

Fig. 6. *Gracilechinus alexandri*: **a**. Oral general view. Scale bar: 10 mm. **b**. Detail of apical system. Scale bar: 5 mm. **c**. Aboral general view. Scale bar: 10 mm. **d**. Detail of one ambulacrum and interambulacrum. Scale bar: 5 mm. **e**. Detail of peristomial membrane. Scale bar: 5 mm. **f**. Primary spine. Scale bar: 2.5 mm. ***Gracilechinus elegans***: **g**. Aboral general view. Scale bar: 10 mm. **h**. Oral general view. Scale bar: 10 mm. **i**. Detail of apical system. Scale bar: 5 mm. **j**. Detail of one ambulacrum and interambulacrum showing primary tubercles and pore-pairs patterns. Scale bar: 5 mm. **k**. detail of peristome. Scale bar: 5 mm.

G. alexandri and *G. affinis*. The apical system is the main distinctive feature of *G. elegans* that differs from other species of the genus by genital plates almost as large as the periproct, while they are smaller in *G. alexandri* and *G. affinis*.

Order Spatangoida L. Agassiz, 1840

Family Loveniidae Lambert, 1905

Genus *Echinocardium* Gray, 1825

Echinocardium flavescens (O.F. Müller, 1776). AphiaID: 124394. New contribution for North Atlantic Spanish Marine Sub-Division (NAMD) (Fig. 7 a-c).

Material examined. 2 specimens from station A11V05.

Diagnosis. Species of the genus are loveniid echinoids characterized by the almost absence of large aboral primary spines, the presence of both a subanal and anal fasciole, and a short labral plate. *Echinocardium flavescens* is a small species that differs from other species of the genus by a fragile, relatively high test with a very faint or absent frontal notch (Fig. 7a), large primary tubercles with longer spines on the aboral side in interambulacra (Fig. 7a and b) and two series of widely spaced pore pairs present in the frontal ambulacrum. Paired petals are also almost flush with the test. The posterior end of the test is vertical. In addition, the inner fasciole is broad (Fig. a, c), the anal fasciole is incomplete (open aborally) and join the subanal branch adorally. Colour of test is whitish to light brown (Fig. 7a).

Geographical distribution. Atlantic Ocean, Northwest of Russia, South of Svalbard, Norwegian Sea, North Sea, West of Iceland, British Islands, Faroe Islands, Azores Islands, Mediterranean Sea, North of Sicily.

Bathymetric range. 5–325 m depth (Mortensen, 1927). Present study: **552 m** depth**.** The deepest record for this species so far**.**

Remarks. Seven species of the Genus *Echinocardium* Gray, 1825 are currently recognized worldwide (De Ridder and Saucède, 2020). Four of them were recorded in the vicinity of the ACS: *E. cordatum* (Pennant, 1777), *E. mortenseni* Thiéry, 1909, *E. pennatifidum* Norman, 1868 and *E. flavescens. Echinocardium flavescens* differs by showing larger interambulacral tubercles that are well-developed aborally, the anal fasciole is incomplete and joint to the subanal branch, and the inner fasciole is broad and short. In *E. mortenseni*, the frontal ambulacrum is flush with the test, and large aboral tubercles are present anteriorly in interambulacra only. In *E. cordatum,* the frontal ambulacrum is deeply sunken and the sulcus extends adapically up to the apical disc, large aboral tubercles are present anteriorly inside the fasciole only, the inner fasciole is long, and the subanal fasciole is typically shield-shaped, and separated from the anal branch. *Echinocardium pennatifidum* is very close to *E. flavescens* and both species have known hybrids (Schultz, 2005). However, in *E. pennatifidum*, there is no larger tubercles in the interambulacral area, the inner fasciole is thin, and the subanal fasciole is not in contact with the anal fasciole.

3.2. Database and distribution

Echinoid IEEM collect 23 echinoid species present in NAMD between 510 and 1476 m depth. Eleven out of twelve species collected in the study area were already recorded in this checklist, *Gracilechinus affinis* being a new contribution. In contrast, 13 species registered in NAMD were not found in the present study: *Aeropsis rostrata* (Norman, 1876), *Brissopsis lyrifera* (Forbes, 1841), *Echinocardium mediterraneum* (Forbes,

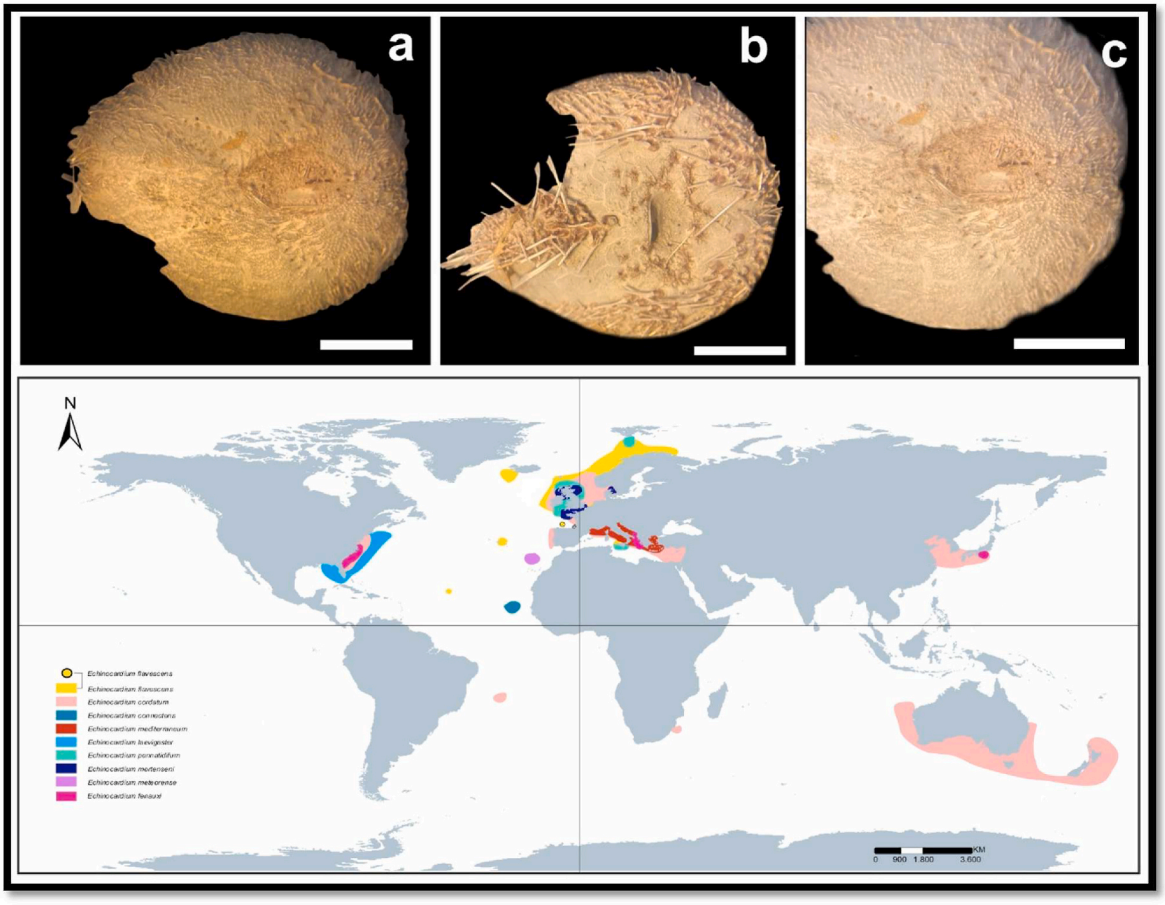

Fig. 7. *Echinocardium flavescens*: **a**. Aboral view. Scale Bar: 5 mm. **b**. Oral view. Scale bar: 5 mm **c.** Focus on apical side. Scale bar: 5 mm. **B:** Map of nominal *Echinocardium* species' distribution worldwide. The species *Echinocardium connectens* and *Echinocardium laevigaster* are poorly known from few fragments and doubtful (De Ridder and Saucède, 2020).

1844), *Echinocyamus pusillus* (O.F. Müller, 1776), *E. esculentus* Linnaeus, 1758, *Hygrosoma petersii* (A. Agassiz, 1880), *Neolampas rostellata* A. Agassiz, 1869 *Pourtalesia miranda* A. Agassiz, 1869, *Salenocidaris profundi* (Duncan, 1877), *Spatangus purpureus* O.F. Müller, 1776, *Spatangus raschi* Lovén, 1869, *Sperosoma grimaldii* Koehler, 1895, *Tromikosoma uranus* (Thomson, 1877).

4. Discussion

A recent study on Asteroids from the ACS (García-Guillén et al., 2022) underlined the scarcity of studies assessing deep-sea echinoderm fauna in the study area, despite the many benthos surveys previously undertaken, mostly in shallow waters or/and at very local spatial scale. In any case, some echinoid checklists have been published in IEEM (Manjón-Cabeza et al., 2017, 2020) by the Ministry for the Ecological Transition and the Demographic Challenger due to the assignment by the European Union.

Based on this dataset, three species of echinothurioids were missed in the ACS according to our results: *H. petersii* (A. Agassiz, 1880), *S. grimaldii* Koehler, 1895 and *T. uranus* (Thomson, 1877). *Hygrosoma petersii*, and *S. grimaldii* are two species collected in nearer waters into the NAMD (Galician Bank, based on personal data), but were never recorded in the ASC. On the other hand, *T. uranus* is present in the IEEM dataset as a species under revision. It is a rare species usually misidentified with other species of the same order, either belonging to the same genus, *Araeosoma* Mortensen, 1903, or to *Sperosoma* Koehler, 1895, despite species of *Sperosoma* clearly differ in the morphology of pedicellariae (Mortensen, 1927).

Other species that were not sampled in our study are *B. lyrifera* (Forbes, 1841), *E. mediterraneum* (Forbes, 1844), *E. pusillus* (O.F. Müller, 1776), *P. miranda* A. Agassiz, 1869, *S. purpureus* O.F Müller, 1776, *S. raschi* Lóven, 1869, *N. rostellata* A. Agassiz, 1869, all belonging to the Infraclass Irregularia Latreille 1825. These species are associated with soft and sedimentary bottoms with varying proportions of sands, silts or muds. Some of them were collected on the Aviles shelf but were never collected in the ACS due to the prevalence of rocky bottoms. The irregular echinoid *E. flavecens* is an exception as the only irregular echinoid sampled in the ASC. This may be related to the presence of local sandy bottoms developed on some canyon terraces favoring the settlement of the species.

5. Conclusions

Echinoids herein sampled in the ACS are typical of deep-sea rocky bottom communities. They are mainly represented by three groups: Echinothurioida, Camarodonta and Cidaroida. Our results improve our knowledge of echinoid distribution providing a new record for the NADM *G. affinis*. This work also highlights some possible mistakes in the taxonomic identification of the IEEM, which should also be revised taking into account species distribution records.

CRediT authorship contribution statement

Laura M. García-Guillén: Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Thomas Saucède:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation. **Pilar Ríos:** Writing – review & editing, Writing – original draft, Methodology, Investigation. **M. Eugenia Manjón-Cabeza:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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