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On the presence of anatriaenes in Pachastrellidae (Porifera: Demospongiae): evidence for a new phylogenetic family concept

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Species bearing long-shafted triaenes do not fit the traditional diagnosis of the family Pachastrellidae. However, the present study confirmed the occurrence of anatriaenes in *Characella tripodaria* (= *Sphinctrella linaresi* and *Poecillastra rudiastra*, n. syn.) and *Poecillastra armata*. Although anatriaenes were also formerly described in some specimens of *Characella pachastrelloides*, the results of our re-examination suggest that these spicules are not proper of this species, but foreign material incorporated from the sediment. Because of the presence of anatriaenes in *C. tripodaria* and *P. rudiastra*, the generic diagnoses of *Poecillastra* and *Characella* have been amended. Apart from the taxonomic interest, the present finding requires us to reconsider the possibility that the presence of anatriaenes is ancestral in the Pachastrellidae. Under such an assumption, Pachastrellidae can no longer be considered as a primitive astrophorid family and its calthrops-pseudocalthrops should be regarded as a type of reduced triaenes.

KEYWORDS: anatriaenes, Astrophorida, calthrops, Demosponge phylogeny, spicules.

Introduction

The family Pachastrellidae Carter 1875, as defined by Lévi (1973), contains astrophorids whose tetraxons are calthrops and whose asters are streptasters. The sister family Theneidae Sollas 1886 contains species bearing long-shafted triaenes instead of calthrops (Lévi, 1973).

The idea of a pachastrellid–theneid division has been always accepted among European authors, see Carter (1876), Sollas (1888), Topsent (1894), Lendenfeld (1903) and Dendy (1905). Some alternative family concepts have arisen from mainly non-European authors, but were discarded. For example, the name of Theneidae was used to include all pachastrellid and theneid genera (e.g., Wilson, 1904, 1925; Koltun, 1964), but such use was never adopted generally. Some other authors temporarily followed the family Halinidae erected by de Laubenfels (1934), in which homosclerophorids, pachastrellids and calthropellids were lumped (e.g., Dickinson, 1945; Bergquist, 1968). Nowadays, most authors agree with the family concepts of Pachastrellidae and Theneidae as proposed by Lévi (1973). Nevertheless, many pachastrellid species display skeletal features that, at first sight, do not fit Lévi's diagnosis and this fact can lead to certain ambiguity in assigning some genera into families. For instance, the species *Sphinctrella orthotriaena* Lévi and Lévi, 1983 was originally placed in the family Theneidae instead of Pachastrellidae, probably because it bears orthotriaenes. In general, a few species belonging to the genus *Sphinctrella* Schmidt bear orthotriaenes or plagiotriaenes (e.g., Sollas, 1888; Lebwohl, 1914; Mothes de Moraes, 1978; Lévi and Lévi, 1983; Pulitzer-Finali, 1983; Maldonado,

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1993b). These spicules have rhabdomes significantly shorter than those occurring in Stellettidae, Geodiidae and Theneidae. Therefore, most authors assume that these short-shafted ortho-plagiotriaenes are forms closely related to calthrops ("pseudocalthrops") and, consequently, they consider the genus *Sphinctrella* in the family Pachastrellidae. Similar assumptions are made for the short-shafted dichotriaenes of *Dercitus* Dendy and *Stoeba* Sollas, mesotriaenes of *Yodomia* Lebwhol and *Triptolemus* Sollas, mesotrider desmas of *Brachiaster* Wilson, and so forth.

Under the above assumptions, all those genera bearing calthrops (or calthrops-related tetraxons) along with streptasters have traditionally been considered to be a monophyletic group, i.e. family pachastrellidae (reviewed by Maldonado, 1993a). Pachastrellids, as well as calthropellids, have been regarded as primitive within the order Astrophorida because they bear calthrops which is the spicule type traditionally assumed to be ancestral in Demosponges (Sollas, 1888; Dendy, 1924; Simpson, 1984). However, there are several controversial reports in the literature on species that, apart from the typical pachastrellid spicule set, bear anatriaenes: *Ancorina tripodaria* Schmidt, 1868 (transferred to *Characella* by Topsent, 1938), *Poecillastra armata* Hanitsch, 1895, *Sphinctrella linaresi* Ferrer-Hernández, 1914, and *Poecillastra rudiastra* Pulitzer-Finali, 1983. Anatriaenes were also reported in the holotype of *Characella pachastrelloides* (Carter, 1876), as well as in specimens described by Lévi and Vacelet (1958), but they are not mentioned again in the relatively abundant literature on this species.

Except for *C. pachastrelloides*, most of these 'nominal species' are only known from one record, the holotype. The scarcity of information has led them to a status of unreliable taxonomic validity ('species dubiae') and therefore reports on the presence of anatriaenes in Pachastrellidae had virtually been forgotten. They were considered to be author's mistakes. However, controversy has been reopened when we recently collected three pachastrellid specimens also bearing anatriaenes. The aim of this study is to verify the whole set of records on the presence of anatriaenes in pachastrellids in order to determine the systematic status of this material.

Materials and methods

Sponge specimens were collected from the Alboran Is. slope in 1984 by using trawl nets. Sampling station was a transect located between 70 and 120 m depth, at coordinates 35°54′–35°52′ N / 3°09′–3°05′ W. For further information on sampling and methodology, see Maldonado (1993b) and Templado *et al.* (1993).

Holotypes and other material, as explained in the descriptions, were borrowed from the Museo Nacional de Ciencias Naturales (MNCM, Madrid), Natural History Museum, London (NHM, London), Musée Océanographique (MO, Monaco), and Museo Civico di Storia Naturale 'Giacomo Doria' (MCSN, Genoa).

The skeletal study was made according to the standard procedures of Rützler (1978). Micrographs were taken using a Hitachi S-2300 SEM.

Results

Characella Sollas

Characella tripodaria (Schmidt, 1868)

Three specimens were collected from the slope of the Alboran Is., (CEAB-ALB-8; CEAB-ALB-31; CEAB-ALB-60P), all of them attached to branches of the *Corallium rubrum* (Fig. 1a). They are massive, globose in shape. Their dimensions are $4 \times 2 \times 1{\cdot}5$ cm, $5 \times 3 \times 2{\cdot}5$ cm, and $8 \times 5 \times 5$ cm respectively. The body texture is firm,

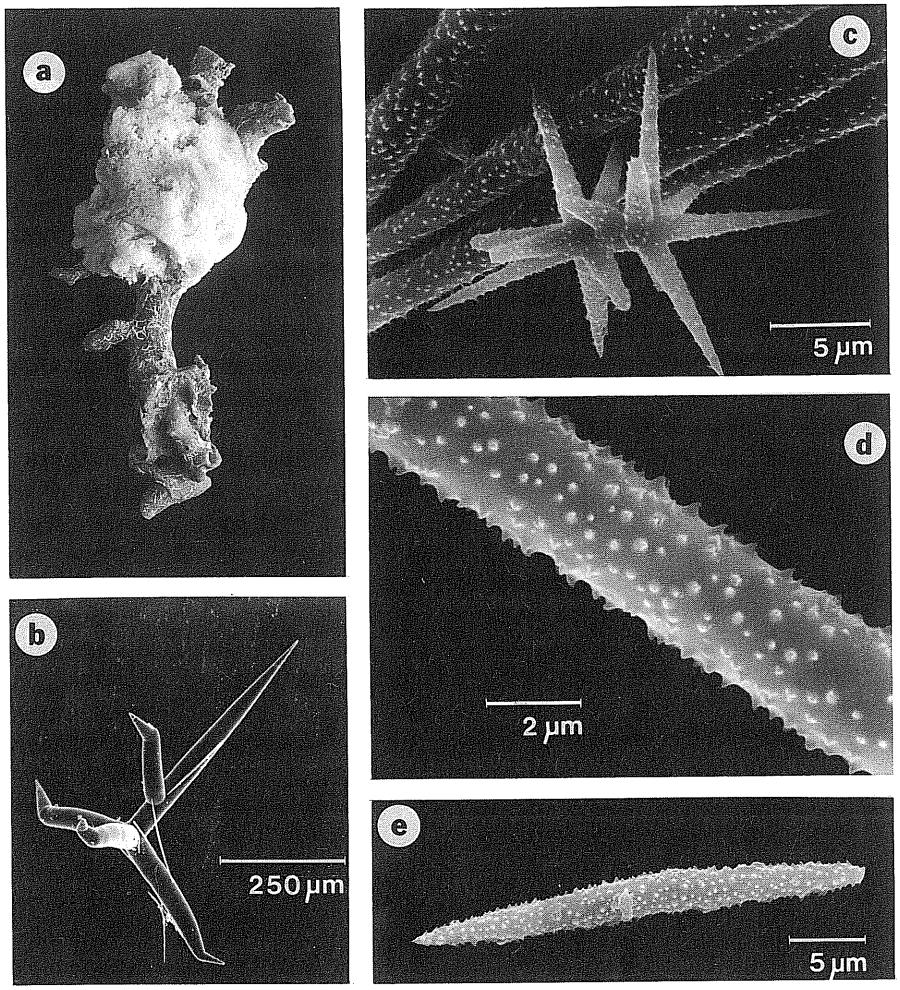

FIG. 1. Features of the specimens collected from the Alboranian slope: (a) general view of the specimen CEAB-ALB-31; (b) malformed pseudocalthrops; (c) sanidaster; (d) ornamentation of microxea-I; (e) microxea-II.

but crumbly when torn. The surface is uneven, rough, and hispid. Oscules, 0·5–1·5 mm in diameter, are sparsely scattered. Ostia are uniporal, most of them grouped in few areas of the specimens but without forming any specialized inhalant structure. Colour in alcohol is ochreous white.

Spicules. Oxeas, stout, fusiform, with attenuated points, occasionally transformed in styles, measuring 900–2430 × 20–58 μm (Fig. 2a). Calthropoid tetraxons, usually with malformations such as under-developed actines, small supplementary actines, or irregular branching (Figs 1b, 2d, 3c); regular actines measure 200–524 × 25–30 μm. Anatriaenes with isodiametric, blunt rhabdomes measuring 1300–3000 × 9–19 μm, and clads 20–75 μm in length which usually have malformations (Figs 2b, c, 3a, b). Microxeas-I, fusiform, faintly microspiny, slightly curved, sharply pointed, and measuring 121–243 × 3–5 μm (Fig. 1d, 2f). Microxeas-II, sharply curved, faintly

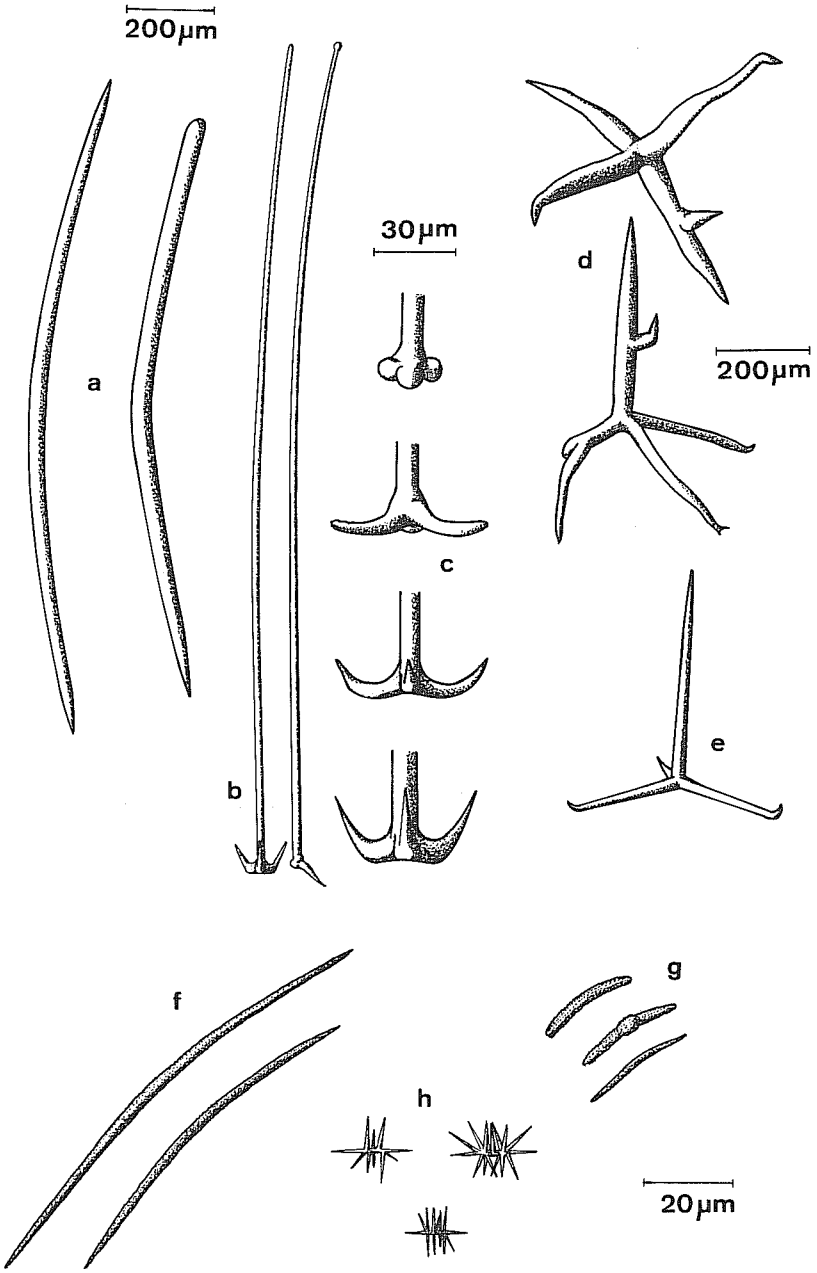

FIG. 2. Spicule set characterizing the Alboranian specimens: (a) oxea and style; (b) anatriaenes; (c) cladomes of anatriaenes; (d, e) malformed calthrops and pseudocalthrops; (f) microxeas-I; (g) microxeas-II; (h) sanidasters.

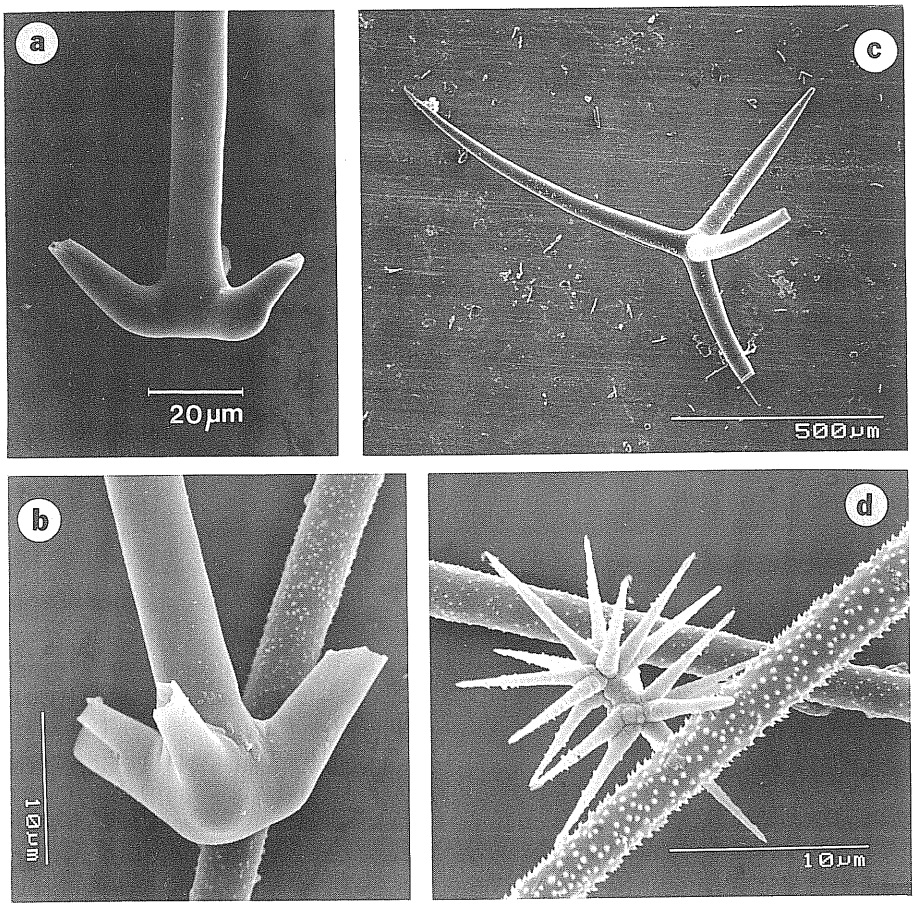

FIG. 3. Spicules of the Alboranian specimens: (a, b) cladomes of anatriaene; (c) pseudocalthrops; (d) sanidaster.

microspiny, usually with one or both ends in a blunt point, and measuring 30–50 × 2–4 µm (Fig. 1e, 2g). Sanidasters, 10–17 µm in length, with a straight central shaft and numerous microspiny actines (Fig. 1c, 2h, 3d).

Skeletal arrangement. The ectosomal skeleton consists of a layer of microxeas-I. The choanosomal skeleton, consisting of abundant oxeas and microxeas-I, is disorganized. Calthrops and anatriaenes are located in the outer choanosome. Anatriaenes, which are relatively scarce, protrude the cladome beyond the sponge surface. Microxeas-II and sanidasters, scarce too, are sparsely scattered in the choanosome.

Remarks

This species was formerly described as *Ancorina tripodaria* Schmidt, 1868 and subsequently regarded as 'species dubia' by Sollas (1888). Anatriaenes and streptasters, originally reported by Schmidt, were not found by Topsent (1938) in a re-examination of a schizotype located in the MNHN of Paris. However, Topsent noticed the presence of spicule fragments which seemed to be part of rhabdomes of anatriaenes and claimed this material as a valid species belonging to the genus *Characella*. My re-examination

Table 1. Summary of the skeletal variability affecting the tetraxonid spicules of *Characella pachastrelloides*. Data are from the examined material (†) or from the literature (‡). '+' = presence of a given spicule type, '−' = absence of a given spicule type. Measurements are in micrometres.

Material	Calthrops	Dichotriaenes	Anatriaenes
Carter 1876 (holotype) (†)	+	−	rare, clads = 100–170
Topsent 1892, 1904, 1928			
St 233 (†)	+	−	−
St 597 (†)	+	−	−
St 1450 (†)	+	−	−
St 2210 (†)	+	−	−
St 2214a (†)	+	+	−
St 2214b (†)	+	+	−
Arnesen 1920 (‡)	−	+	−
Lévi and Vacelet 1958 (‡)	+	−	faintly present, clads = 110
Lévi and Lévi 1989 (‡)	+	−	−
Van Soest and Stentoft 1988 (‡)	+	−	−
Boury-Esnault *et al.* 1994 (†)	+	+	very rare, clads = 105–115

of a slide from the holotype (BNHM: 68:3:2:36) corroborates the existence of scarce anatriaenes and sanidasters, as originally reported by Schmidt (1868). The spicule characterization of this slide is as follows: oxeas, slightly curved, faintly fusiform, with pointed ends, and 1000–1600 × 10–40 μm in size. Calthropoid tetraxons usually malformed, with underdeveloped actines; regular actines measure 180–400 × 15–22 μm. Only one anatriaene was represented in the slide, showing a broken rhabdome (10 μm in diameter) and only one clad developed (25 × 8 μm). Microxeas-I, curved, occasionally centrotylote, entirely microspiny, and measuring 115–180 × 1·5–2·5 μm in size. Microxeas-II, very scarce, sharply bent, hardly fusiform, occasionally centrotylote, with pointed ends and 35–45 × 1·5–2·5 μm in size. Only three sanidasters were found in the slide. They measure 15 μm in length and have numerous microspiny actines.

Characella pachastrelloides (Carter, 1876)

The examined material was as follows: holotype (slides NHM-Porcupine 1840 St. 96. Norman Collection IO.II 1680 and 1681, as *Stelleta pachastrelloides*); specimens collected during the *Prince Albert I* cruises at stations 233, 597, 1450, 2210 and 2214 (Topsent, 1892, 1904, 1928); material collected during the '*Balgim*' Cruise (CP-95.eje-28), recently described by Boury-Esnault *et al.* (1994).

The original descriptions are very accurate (Table 1). The variability in body form and texture of the individuals is unusual (Fig. 4). They range from pyriform to flat masses and from hard to soft textures, respectively. The pattern of hispidity also varies from strongly hirsute to smooth.

Spicules. Oxeas, measuring 1500–4620 × 25–100 μm in global range of size for all individuals. Calthrops and pseudocalthrops, whose clads are 210–1230 × 17–75 μm in global range of size (Fig. 5b); this spicule category was absent in the material described by Arnesen (1920) from the North-Atlantic waters (Table 1). Dichotriaenes, reported only in few specimens (Table 1); the global range of size is 450–1700 × 20–111 μm for rhabdomes, 100–175 × 30–50 μm for protoclads, and 150–500 × 30–50 μm for

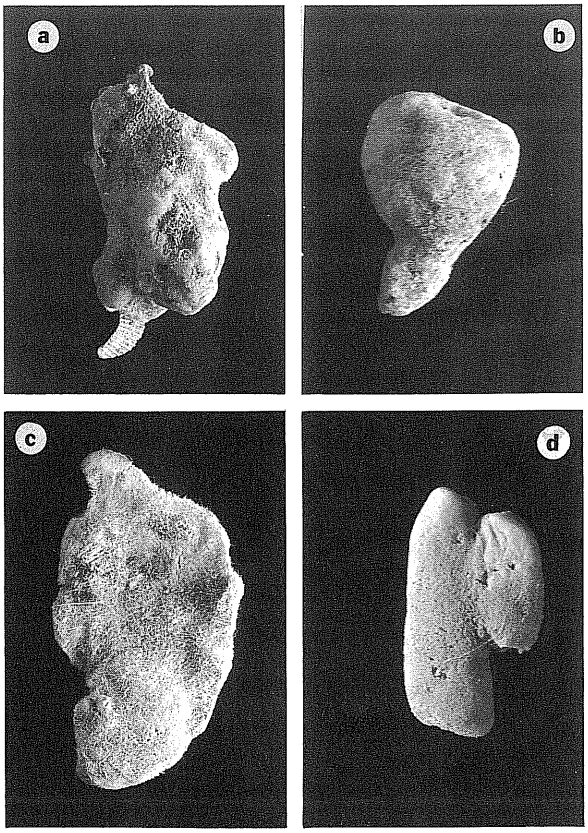

FIG. 4. General view of four Atlanto-Mediterranean specimens of *Characella pachastrelloides*: (a, b, c) specimens collected during the Prince Albert 1 cruises (Topsent 1892, 1904, 1928); (d) specimen collected during the *Balgim* cruise (Boury-Esnault *et al.*, 1994).

deuteroclads. Anatriaenes were reported in the holotype (Carter, 1876) and in material described by Lévi and Vacelet (1958). The presence of anatriaenes in the holotype is corroborated in the present re-examination (Fig. 8c). I have also found few anatriaenes in material recently described by Boury-Esnault *et al.* (1994) (Fig. 5a). These anatriaenes were scarce, with clads measured 100–170 × 18–25 μm in global range (Table 1) and rhabdomes usually broken. Microxeas in two categories, measuring 90–370 × 2–7 μm and 20–60 × 2–6 μm respectively; both entirely and uniformly spiny. The smaller microxeas can be transformed in styles or strongyles in a variable degree, depending on the specimens (Fig. 5c, d, e). Amphiasters, very abundant in all specimens (Fig. 5f, g).

Remarks. There is a significant variability in some of the morphological features of this species as well as in the composition of its tetraxonid spicule set (Table 1). On the one hand, this could suggest that this taxon is actually a species complex but, on the other, microscleres are notably homogeneous in shape and size. Variation in morphology is traditionally assumed to be a result of environmental variation. As for

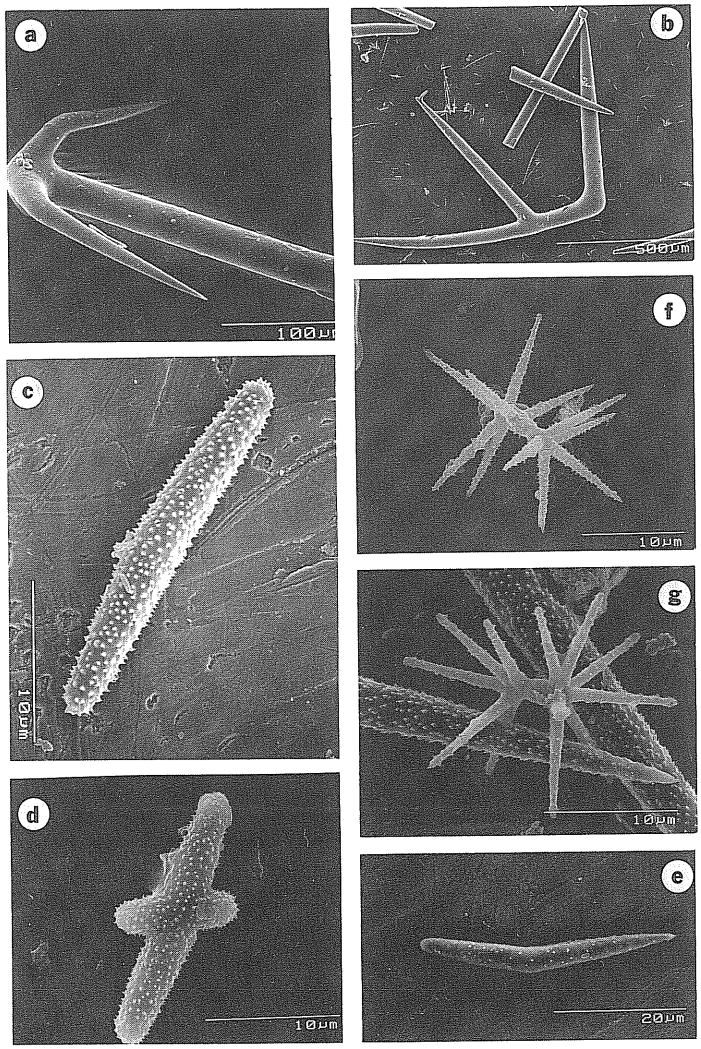

FIG. 5. Spicules of Atlanto-Mediterranean specimens of *C. pachastrelloides*: (a) anatriaene from a specimen collected from the Strait of Gibraltar (Boury-Esnault *et al.*, 1994), being probably a foreign spicule for this species; (b) malformed pseudocalthrops; (c, d) microxeas-II of the Gibraltarian specimen; (e) microxea-II of an Azorian specimen; (f, g) amphiasters.

the variation in the tetraxonid set of spicules, the occasional presence of short-shafted dichotriaenes in some specimens has been traditionally considered as a result of the morphological variability inherent to calthrops-pseudocalthrops, and therefore lacking any taxonomic value (Topsent, 1902, 1904). I could not disprove this old hypothesis in a recent review using parsimony analyses (Maldonado, 1993a) and neither can I from the information gained by the present re-examination.

As for the anatriaenes, they seem to be exogenous elements incorporated into the individuals from the sediment. This theory is supported by three facts: (1) these anatriaenes are similar in shape and size to those known from *Thenea muricata* which is a common species in the epibathyal soft bottoms of the Lusitanian region from

where all reports on anatriaenes arose; (2) the recognized capability of deep-sea sponges to incorporate particles and material from the soft-bottoms on which they usually live unattached (Barthel and Tendal, 1993); and (3) anatrianenes are always scarce and most of them broken relatively near the cladome. Unfortunately, the re-examination of abundant material bearing anatriaenes described by Lévi and Vacelet (1958) could not be accomplished as this material was not available for revision (Lévi, personal communication).

Sphinctrella Schmidt
Sphinctrella linaresi Ferrer-Hernández, 1914

The holotype consists of three massive pieces (MNCN-36). They have a firm texture, but crumbly when torn. Sponge surface is uneven, rough, and finely hispid. Uniporal oscules (1–2 μm in diameter) are observed sparsely scattered on the surface, whereas ostia are not visible.

Spicules. Oxeas, slightly curved, fusiform, with pointed ends, and 1100–1900 × 10–50 μm in size. Calthropoid tetraxons, usually with either aberrant or underdeveloped actines (Fig. 6a); regular actines measure 200–600 × 15–40 μm. Anatriaenes are scarce and characterized by short and usually malformed clads (Fig. 6b); rhabdomes measure up to 1600 × 6–16 μm and clads 25–40 × 6–8 μm. Microxeas-I, slightly or sharply curved, hardly fusiform, with pointed ends, and 120–220 × 2–3·5 μm in size. Microxeas-II, faintly fusiform, sharply curved, usually with one attenuated or blunt end, and 25–45 × 2·5–3 μm in size (Fig. 6f). Sanidasters, scarce, with abundant actines, and 12–19 μm in size (Fig. 6c, d, e).

The skeletal structure is identical to that described in the specimens collected from the Alboran Sea.

Remarks

Although this specimen was originally assigned to the genus *Sphinctrella*, it actually lacks any of the diagnostic features characterizing that genus, such as the sieve-like exhalant areas, the oxea palisades surrounding the exhalant areas and any trace of ringed ornamentation in the microxeas. It is also important to note that, although the microxeas-II were overlooked in the origin description by Ferrer-Hernández (1914), they are abundant in the specimen.

Poecillastra Sollas
Poecillastra armata Hanitsch, 1895

Nowadays, no material of this species exists. According to I. Wallace (Curator of the Liverpool Free Museum; personal communication), the holotype was discarded by the Liverpool University Zoology Museum sometime between 1900 and 1950. Thus, the only available data are from the literature (Hanitsch, 1895): 'Sponge massive, irregular, measuring 10 × 5 × 5 cm. Surface uneven, rough to touch. Oscula 1 mm in diameter, scattered. Examined in dried condition.'

Spicules. 'Oxeas, of huge dimensions, somewhat slantingly arranged towards the surface, straight, or only slightly curved, measuring 3000 × 55 μm. Calthrops, the actines 450 × 45 μm. Orthotriaenes, mostly deformed, rhabdome only slightly longer than cladi, of about the same dimensions as the calthrops. Anatriaenes, fewer in number than the other megascleres, projecting beyond the surface of the sponge, with wide and

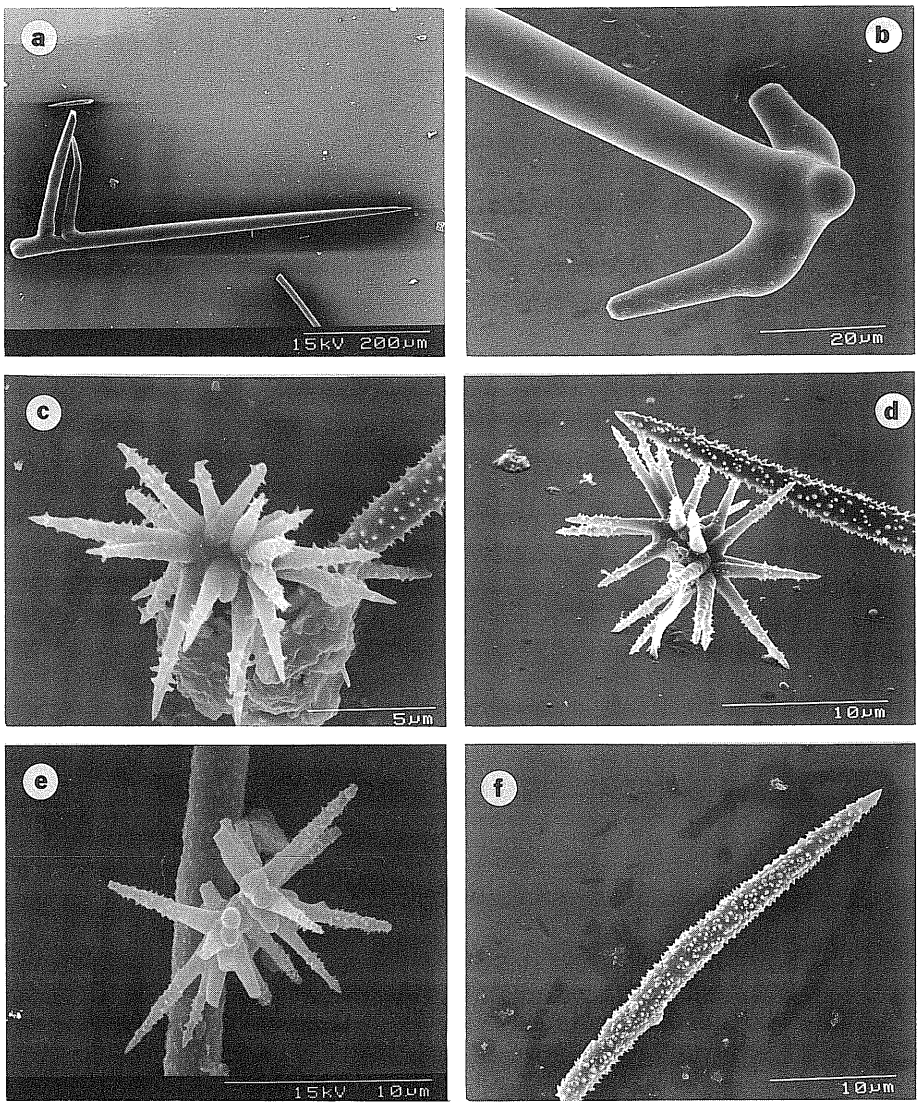

FIG. 6. Spicules of the holotype of *Sphinctrella linaresi*: (a) malformed pseudocalthrops; (b) cladome of anatriaene; (c, d, e) sanidasters; (f) microxea-II.

distinct axial canal in rhabdome and cladi, the rhabdome measuring 2500 × 20 μm, the cladi 9 × 2 μm. Smooth microxeas, present in vast numbers and forming a felted mass throughout the whole sponge, 170 × 3·5 μm. Spirasters, 20 μm in length.'

Remarks

This above description of *P. armata* is similar to those of the holotypes of *Sphinctrella linaresi* and *Charcella tripodaria*, as well as to those of the specimens collected from the Alboranian slope (Table 2). Although the category of smaller microxeas was not reported by Hanitsch in the original description, it might actually

Table 2. Summary of spicule measurements of *C. tripodaria* specimens collected from the Alboran slope (ALB-#) and holotypes of *S. linaresi*, *C. tripodaria* and *P. armata*, after the present re-examination. Measurements are length × width (in micrometers), except for sanidasters where only total length is given '?' = unknown information.

	ALB-8	ALB-31	ALB-60P	*Spinctrella linaresi*	*Characella tripodaria*	*Poecillastra armata*
oxeas	1572–2430 × 28–62	900–2400 × 20–58	1300–2200 × 20–55	1100–1900 × 10–50	1000–1700 × 10–40	3000 × 55
calthrops	238–476 × 25–35	200–524 × 25–35	200–500 × 20–35	200–600 × 15–40	180–400 × 15–22	450 × 45
anatriaenes					one only	
rhabdome	2124–3428 × 18–25	1857–2975 × 9–19	1300–3000 × 10–18	> 1600 × 6–16	> 1000 × 10–12	2500 × 20
clads	40–50 × 10	20–40 × 10–12	50–75 × 9–13	25–40 × 6–8	25 × 8	9 × 20
microxeas-I	153–205 × 4·5–8	121–243 × 4·5–8	150–220 × 3–5	120–220 × 2–3·5	105–180 × 1·5–3	170 × 3·5
microxeas-II	30–45 × 3–4	30–50 × 3–4	35–50 × 2–3	25–45 × 2–3	35–45 × 1·5–2·5	??
sanidasters	10–15	12–17	10–15	12–19	15	20

occur, since such spicules were also overlooked by Ferrer-Hernández (1914) and Schmidt (1868) in their original descriptions, as corroborated in this re-examination.

Poecillastra rudiastra Pulitzer-Finali, 1983

The holotype re-examination was made on slide MSNG-C.E.47161. 'The specimen was a small fragment, shapeless, of firm consistency, whitish in spirit' (Pulitzer-Finali, 1983), which was entirely used for spicule preparations.

Spicules. Oxeas, curved, fusiform, often with a central, irregular knob, occasionally transformed into styles or strongyles, and measuring 700–1250 × 16–25 μm (Fig. 7a). Calthrops, scarcely present, with frequent malformations; regular clads measure 120–650 × 25–37 μm (Fig. 7b). One dichotriaene was reported by Pulitzer-Finali, but not was found in this re-examination. Anatriaenes, scarce, with slightly curved rhabdomes, wider in the basal portion and measuring 1000 × 12–18 μm; cladomes resembled those typical of Spirophorida, with a small beak at the end and clads 30–45 × 8–15 mm in size (Figs. 7d, 8a, b). Microxeas, straight or diversely curved, finely spiny, showing a vague ringed pattern at the mid of the spicule (Fig. 7d). They measure 75–150 × 2–3·5 μm. Streptasters in three categories: (1) Spirasters, 18–25 μm in length, with a thick axis showing two or three spires and numerous short actines; actines are usually as long as the thickness of the central axis (Fig. 7h). (2) Metasters, 18–25 μm in length, with a thin central axis showing an incomplete spire (revolution); actines range between six and 12 in number and are always longer than the thickness of the central axis (Fig. 7f). Transitional morphologies between this category and the above mentioned spirasters were occasionally found (Fig. 7g). (3) Amphiasters and plesiasters, uncommonly large, finely microspiny, showing between two and 6 actines which sometimes are reduced into blunt tubercles (Fig. 7e). Some amphiasters are reduced to diactinal form. Regular actines are 15–25 × 2–2·5 μm in size whereas reduced actines are 5–25 × 3–4 μm.

Remarks

There is no doubt about the validity of this species, since apart from the anatriaenes, its large amphiasters and plesiasters are distinctive traits.

Despite having anatriaenes, this species is not related to the species complex of *Characella tripodaria* (Table 2). Anatriaenes of *P. rudiastra* and *C. tripodaria* are notably different. Besides, the microsclere set clearly points to the former species as belonging to the genus *Poecillastra*. The shape of the cladome of the anatriaenes is closer to those occurring in Spirophorida than to any astrophorid anatriaene, although, unlike anatriaenes of Spirophorida, the rhabdome is not hair-like distally.

In my view, dichotriaenes reported by Pulitzer-Finali may have been foreign. They look similar to those of *Erylus*.

Discussion and conclusions

A remarkable similarity in skeletal and morphological features made evident a multiple synonymy involving the species *C. tripodaria*, *S. linaresi* and *P. armata* (Table 2). The name *Characella tripodaria* (Schmidt, 1868) has priority over *Sphinctrella linaresi* and *Poecillastra armata*. *Characella tripodaria*, so defined, is characterized by the presence of oxeas, scarce and malformed pseudocalthrops, scarce anatriaenes with malformed clads, very scarce sanidasters and two categories of uniformly spiny microxeas. Our specimens collected from the Alboran Is. slope constitute the second

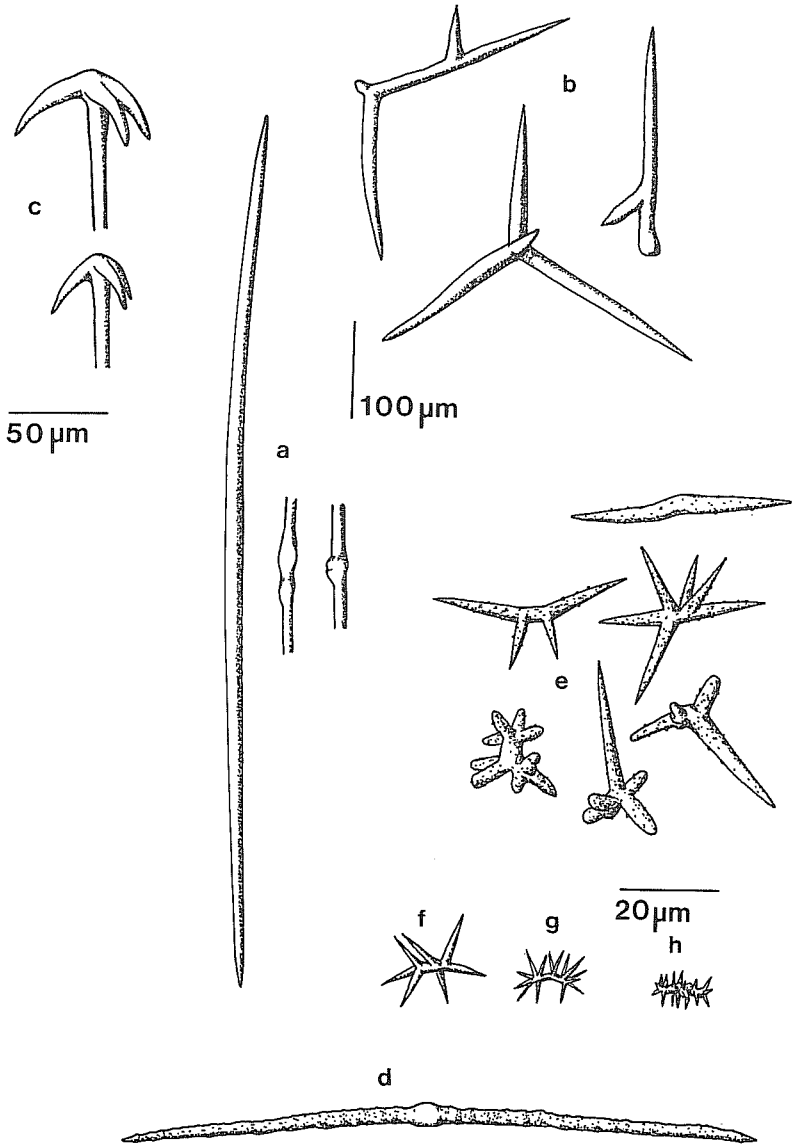

FIG. 7. Spicule set of the holotype of *Poecillastra rudiastra*: (a) regular and centrotylote oxeas; (b) calthrops and pseudocalthrops; (c) cladomes of anatriaene; (d) microxea; (e) regular and malformed amphiasters and plesiasters; (f) metaster; (g) transitional morphology between metaster and spiraster; (h) spiraster.

Mediterranean record for this rare species whose biogeographical area seems to be limited to the Lusitanian region and the Alboran Sea.

Characella pachastrelloides is concluded to lack anatriaenes, although there are two facts indicating that this point deserves special attention in future studies: (1) specimens with anatriaenes reported by Lévi and Vacelet (1958) could not be re-examined herein; and (2) significant morphological and skeletal variability was revealed in the Atlanto-Mediterranean specimens examined. This variability suggests

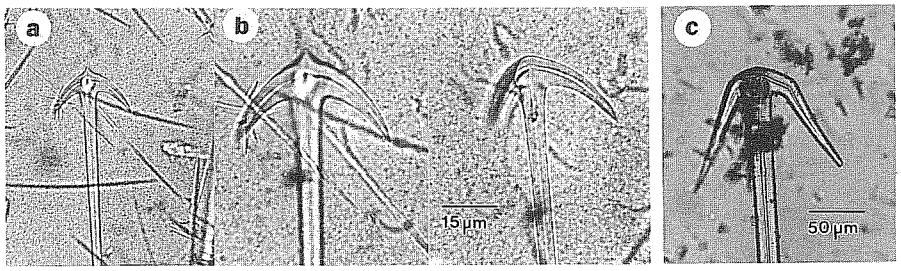

FIG. 8. Anatriaenes through the compound microscope: (a, b) anatriaenes of *Poecillastra rudiastra* (scale bar for 'a' is equal to that in 'c'); (c) anatriaene found in slides of the holotype of *Characella pachastrelloides*; probably a foreign spicule.

that this taxon could actually be a species complex. Besides the presence-absence of anatriaenes, *C. pachastrelloides* and *Characella tripodaria* are distinguishable by their streptasters: the former has abundant amphiasters whereas the latter has scarce sanidasters with numerous actines. This feature, that at first sight might seem unreliable, has been confirmed to be remarkably constant through the whole material reexamined.

Poecillastra rudiastra is a valid species bearing anatriaenes. Its other skeletal features are typical of the genus *Poecillastra*, as chosen by Pulitzer-Finali (1983).

Because of the presence of anatriaenes in *P. rudiastra* and *C. tripodaria*, the generic diagnoses of *Poecillastra* and *Characella* have to be amended, as follows: (1) *Poecillastra* Sollas, 1888 = Pachastrellidae whose megascleres are oxeas, calthrops or pseudocalthrops, and occasionally anatriaenes. Calthrops and pseudocalthrops are present in the inner and outer parts of the sponge choanosome. Microscleres consist of microxeas in a single category along with several types of streptasters in which spirasters are always present. (2) *Characella* Sollas, 1888 = Pachastrellidae with a set of megascleres similar to that of *Poecillastra*, but where tetraxons are restricted to subectosomal locations. Microscleres consist of microxeas and streptasters. Microxeas are in two size categories. Strepasters are found in several shapes, always characterized by having a straight central axis (i.e. amphiasters or sanidasters).

As for the family diagnosis, it seems obvious that the traditional concept of a pachastrellid-theneid division based on the presence or absence of long-shafted triaenes is not consistent. If we agree with the fusion of both families, then the name Pachastrellidae Carter, 1875 has precedence over Theneidae Sollas, 1886. On the other hand, we still can preserve the pachastrellid-theneid division by defining Pachastrellidae for genera where clathrops and triaenes co-occur and Theneidae for genera where only true long-shafted triaenes occur. I prefer this last option only because the current taxonomic system remains unaltered.

Besides the taxonomic interest, the presence of anatriaenes in these species has another important aspect, its phylogenetic significance. If we consider the family Pachastrellidae, anatriaenes occur in only two species. Then, these anatriaenes might be interpreted as a recent evolutionary acquisition in the family. However, if we make an outgroup analysis for the family Pachastrellidae, we find that anatriaenes are present in Spirophorida and in most of the astrophorid families (both in the euastrose and streptastrose lines). Thus, we have to consider the possibility that this could also be the ancestral condition in Pachastrellidae and even in the Order Astrophorida. This theory is consistent with findings of very ancient, but highly specialized triaenes in the fossil record (van Kempen, 1990). On this basis, the streptastrose line of Astrophorida can

be interpreted as subjected to a process of skeletal reduction during which most of the long-shafted triaenes were either lost or reduced to a variety of scarce, malformed pseudocalthrops, which is the present-day condition of this family. Some genera bearing streptasters along with euasters, such as *Stryphnus* Sollas (with relatively short-shafted ortho-plagiotriaenes) and *Asteropus* Sollas (without tetraxons), although traditionally considered within the euastrose line, could be also understood as a result of this reductive skeletal trend.

If we accept the above theory, then the Pachastrellidae can no longer be considered to be a primitive astrophorid family. That is, its calthrops and pseudocalthrops cannot be considered homologous to those of Calthropellidae, but reduced triaenes. This hypothesis also agrees with the result of a recent study in which 'mesotriaenes' of Calthropellidae and Pachastrellidae were demonstrated to be non-homologous spicules (Maldonado, 1993b).

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