A reconsideration of the relationship between polyaxonid and monaxonid spicules in Demospongiae: new data from the genera *Crambe* and *Discorhabdella* (Porifera)

M. J. URIZ AND M. MALDONADO

Centro de Estudios Avanzados de Blanes, Camino de Santa Bárbara s/n 17300-Blanes, Girona, Spain

The relationships between different spicule lineages of Demospongiae are revised through the ontogenetic study of the main spicules of the genera *Crambe* and *Discorhabdella*. The presence of terminal orifices in the basal spines of the asterose acanthostyles of *Discorhabdella*, and the actines of the desmas of *Crambe* have been shown by examining young spicules under high magnification. Thus, the polyaxonid origin of both spicule types is hereby supported by the ontogenetic information, and their homology is also supported by their equivalent arrangement in the skeleton. The current differences in shape between both spicule types are considered the result of a divergent morphological evolution from an ancestral polyactinal corpuscle, by the atrophy/hypertrophy of a different number of actines. Arguments are also presented to support the homology of these two spicule types with the sphaeroclons of *Vetulina*, and other fossil genera. Moreover, the presence of axial canals inside the tubercles of the tuberose tylostyles of *Discorhabdella* and *Crambe tuberosa* indicates that the tubercles are actually atrophied actines as in the case of the hadromerid genus *Terpios*. According to the ontogeny, the tuberose morphology of these spicules may correspond to the retention of an ancestral characteristic in the Poecilosclerida and Hadromerida; in this case, a monophyletic origin, is suggested between both taxa. From the overall results here presented, the tetraxonid spicule, presently considered by most authors as the primitive morphotype, as well as some monaxons, could be considered as evolving from a polyaxial form.

ADDITIONAL KEY WORDS:–Demosponges – evolution – polyaxonid spicules.

CONTENTS

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INTRODUCTION

Spicule shape is considered as one of the most conservative features in sponges (Lévi, 1973). These skeletal elements are nowadays the major character used to support the Systematics of the Phylum (Lévi, 1973; Bergquist, 1978; Hartman, 1981). Thus, taxonomic groups are based on the shared skeletal homologies. The primary perception of a homology becomes more difficult when no morphological similarity is, at first sight, noticed among the elements involved, as in the case of homologies of the type named 'transformational homologies' (*sensu* Pinna, 1991). In these cases, complementary information can be obtained from other sources, such as the ontogenetic development of those spicule types suspected to be homologous. It is commonly accepted that the symmetry axes of a spicule are predetermined by the presence of axial canals (Simpson, 1984; Simpson *et al.*, 1985). So far, spines and similar accessory structures have mostly been noticed as anaxial (De Pomar, 1973; personal observation). However, some authors have reported the existence of a branch of the axial canal in processes that they named 'spines' of birotules and oxeas of freshwater sponges (Drum, 1968; Garrone *et al.*, 1981; Simpson, 1984) and sterrasters of *Geodia* (Simpson, 1989). We have also noticed the presence of axial canals in the 'spines' of the cladotyles of *Acarnus* Gray, 1867 (personal observation). Nevertheless, all these spicules seem to be derived from streptasterose corpuscles (Volkmer-Ribeiro & Watanabe, 1983; Simpson, 1989; Volkmer-Ribeiro, 1990) and, thus, the so-called 'spines' would actually be actines.

Tetractine, diactine and monactine spicules have been assumed to constitute three different states of an ordered evolutionary series whose polarization is subject to debate. This series would reflect to a certain extent the phylogenetic derivation of the major groups of Demosponges (Schulze, 1880; Dendy, 1921, 1924; Brien, 1968; Simpson, 1990; Gruber, 1993). In contrast, it has also been suggested that many monaxonid groups may never have been related to the tetraxonid assemblage (Lévi, 1958; Reid, 1970). However, there is little evidence for the position that a polyaxonid morphology would include such a hypothetical evolutionary series. This paper is intended to cast some light on the relationships between the polyaxonid and monaxonid spicule lineage through the study of the ontogeny of some peculiar spicules belonging to the genera *Crambe* Vosmaer, 1880 and *Discorhabdella* Dendy, 1924, whose morphology, at first sight, does not fit either the tetraxonid or the monaxonid pattern.

MATERIAL AND METHODS

The material studied of the genera *Crambe* and *Discorhabdella* consisted of holotypes of *Discorhabdella tuberosocapitata* (Topsent, 1892) (Monaco Museum, MN-040323), *Discorhabdella incrustans* Dendy 1924 (British Museum of Natural History, BMNH: 1923.10.1.157), *Discorhabdella hindei* Boury-Esnault *et al.*, 1992 (Museum National d'Histoire Naturelle de Paris, MNHN-LBIM, D-NBE-1991-1), *Crambe tuberosa* Maldonado & Benito, 1991 (Centro de Estudios Avanzados de Blanes, CEAB-ALB-44-C), and *Crambe erecta* Pulitzer-Finali, 1993 (Museo Civico di Storia Naturale 'Giacomo Doria', Genova, MSNG

48311). Specimens of *C. acuata* (Lévi, 1958) from Namibia (Benguela-VI and VII cruises, 1984; see Uriz, 1988), *C. taillezi* Vacelet & Boury-Esnault, 1982 from NE Spain (Ecopharm-I cruisse, see Uriz *et al.*, 1992) and the Alboran Island (Fauna-I cruisse, see Templado *et al.*, 1993; Maldonado, 1993) were also examined. For comparative purposes, a skeletal study was also carried out on specimens of *Terpios hoshinota* Rützler & Muzik, 1993, *Phorbas fictitus* (Bowerbank, 1866), *Microciona gradalis* (Topsent, 1925), *Myxilla rosacea* (Lieberkühn, 1859), and *Eurypon coronula* (Bowerbank, 1874).

Micrographs were taken through a Hitachi scanning electron microscope, after being cleaned, dehydrated and coated with gold-palladium as habitual (e.g. Boury-Esnault *et al.*, 1992).

RESULTS

Structures with axial canal

The main spicules of the genera examined consisted of tuberose tylostyles and asterose desmoids in the species of the genus *Crambe* (Figs 1a–c & 2a, b), and tuberose tylostyles along with asterose acanthostyles in those of the genus *Discorhabdella* (Figs 1d, e & 2c, d). Immature spicules, whose silification was unfinished, were abundantly found in different species of both genera. Scanning observation of such young spicules under high magnification revealed terminal orifices in some spine-like or tubercle-like processes, testifying to the previous presence of an axial filament inside them.

Asterose desmoids

The youngest stages of these spicules were observed in *Crambe tuberosa*. They were aster-like corpuscles, 4 μm in diameter, with equal length actines (Fig. 3a). More advanced stages, 50–60 μm in diameter, already exhibited the actines split, according to their size, shape and direction, into two categories, as in the mature spicules (Fig. 3b, c). In these young stages, as well as in young desmoids of *C. tailliezi*, holes were found at the end of both short and long actines (Fig. 3d). Through growth, short actines maintained spine-like appearance whereas long actines became spiny, sometimes branched, arms with distal zygome plates.

Fossil spicules, closely resembling the desmoids of the living species of *Crambe* were reported by Hinde & Holmes (1892) from Tertiary sponge-beds in Oamaru (New Zealand) (Fig. 4). Such remains, interpreted as sphaeroclons, were used by the authors to erect a new fossil species named *Vetulina oamaruensis* Hinde & Holmes, 1892. The similarity between the fossil desmas from Oamaru and those present in *Crambe tuberosa* indicates that the fossil remains more probably belong to a fossil species of the genus *Crambe* than to one of the genus *Vetulina*.

Asterose acanthostyles

The youngest stages of this spicule type were found in *Discorhabdella incrustans*. They consisted of forms, 20 μm in length, exhibiting a comparable but a more slender shape than that of the mature spicules. They still lacked distal spines but the sub-proximal 'spines' were incipient and arranged in an
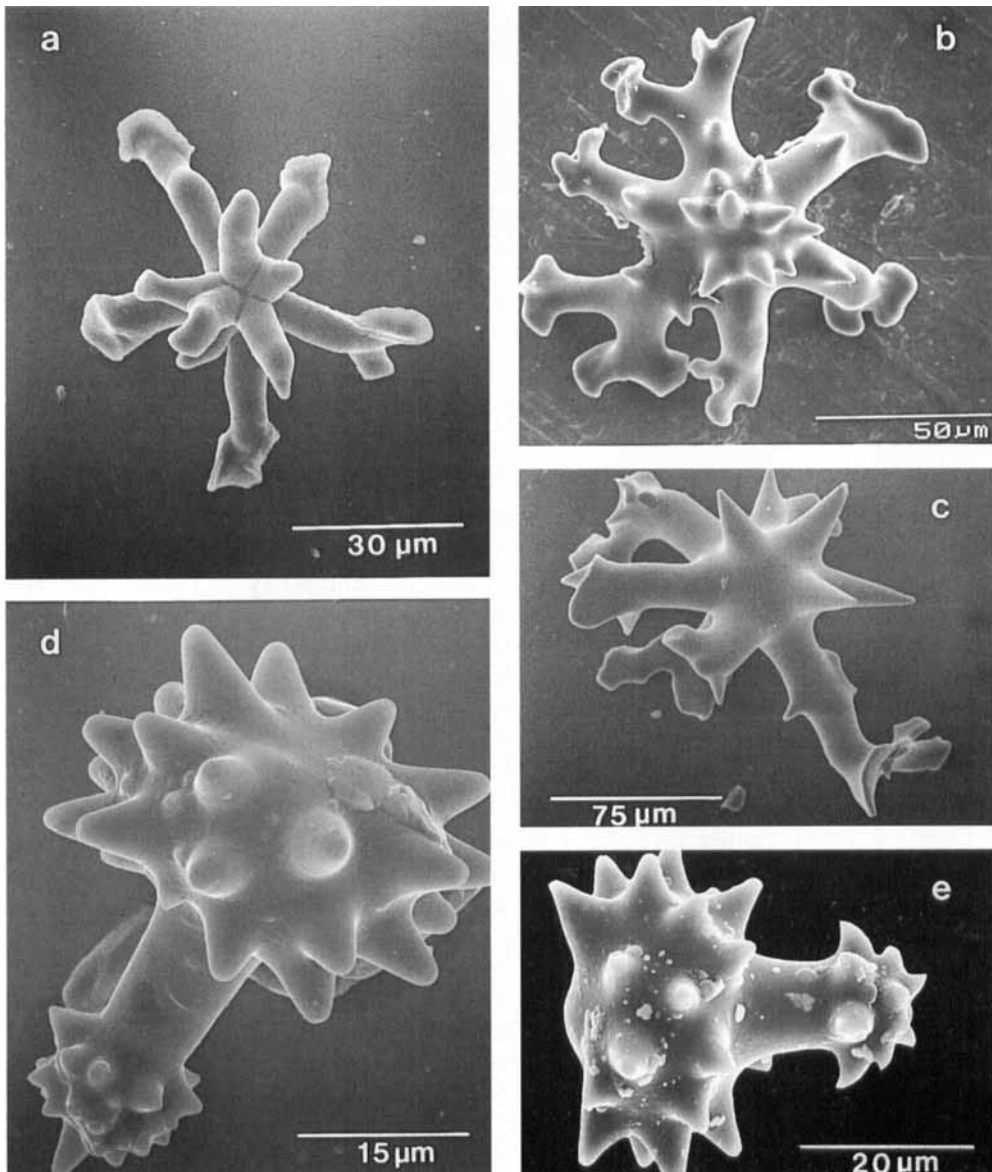
Figure 1. Basal spicules of the genera *Crambe* and *Discorhabdella*. Mature desma of (a) *C. taillezi*, (b) *C. tuberosa* and (c) *C. acuata*; mature asterose acanthostyle of (d) *D. hindei* and (e) *D. incrustans*.

almost radial fashion (Fig. 5b). Such 'spines' showed wide orifices at their tips (Fig. 5a, b), the occurrence of which demonstrates their actinal nature. Young stages exhibiting orifices at the tip of the sub-proximal 'spines' were also found in the asterose acanthostyles of *Discorhabdella hindei* and in the acanthostyles of *Discorhabdella tuberosocapitata* which display a typical, non-
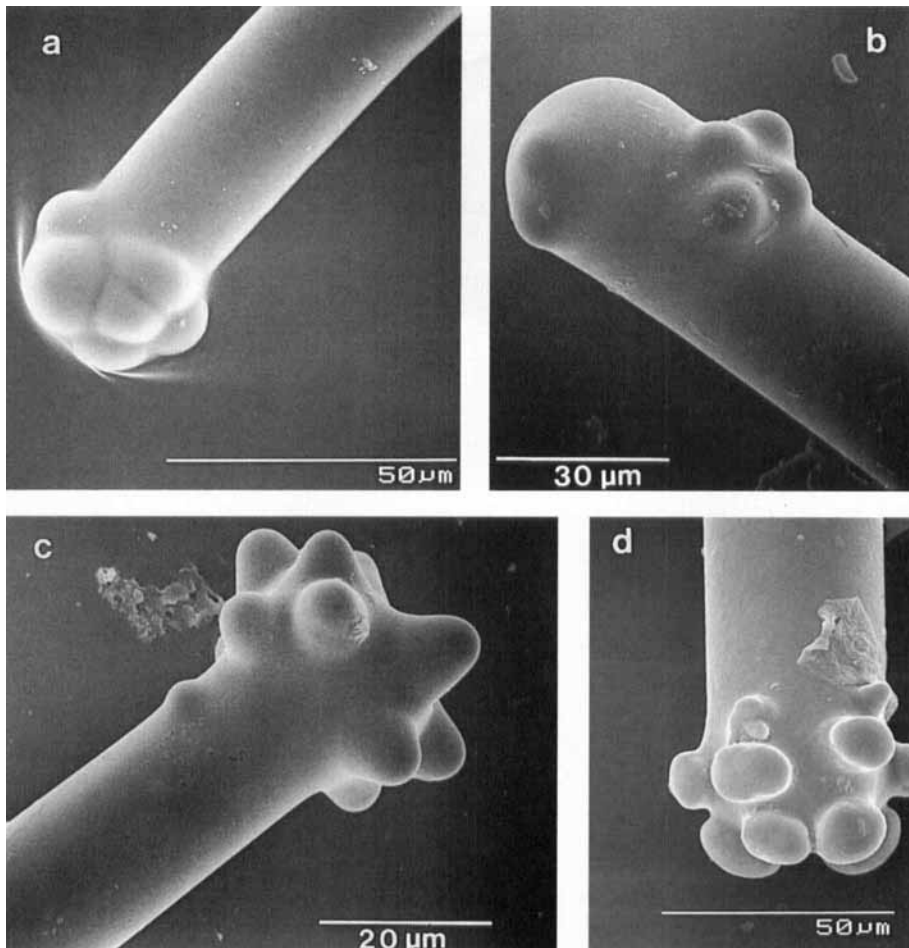
Figure 2. Tuberose tylostyles of the genera *Crambe* and *Discorhabdella*. Tylostyle of (a) *C. tuberosa*, (b) *C. taillezi*, (c) *D. hindei* and (d) *D. incrustans*.

asterose appearance (Fig. 5c, d). In contrast, orifices were never noted at the end of the distal spines in any phase of the spicule growth. Nor were they found during the development of the scarce spines ornamenting the spicule shaft or the proximal spine-like actines.

Tuberose acanthostyles

The tubercles of the young tuberose acanthostyles of *Crambe tuberosa* and *Discorhabdella incrustans* were radially arranged structures, conical in shape, perforated by a central canal (Fig. 6a–c). Through development, their terminal orifices were covered by secondary silica deposition and these structures became rounded (Fig. 2d).

The polyaxonid origin of the asterose desmoids of *Crambe* and the asterose acanthostyles of *Discorhabdella* is hereby supported by the ontogenetic
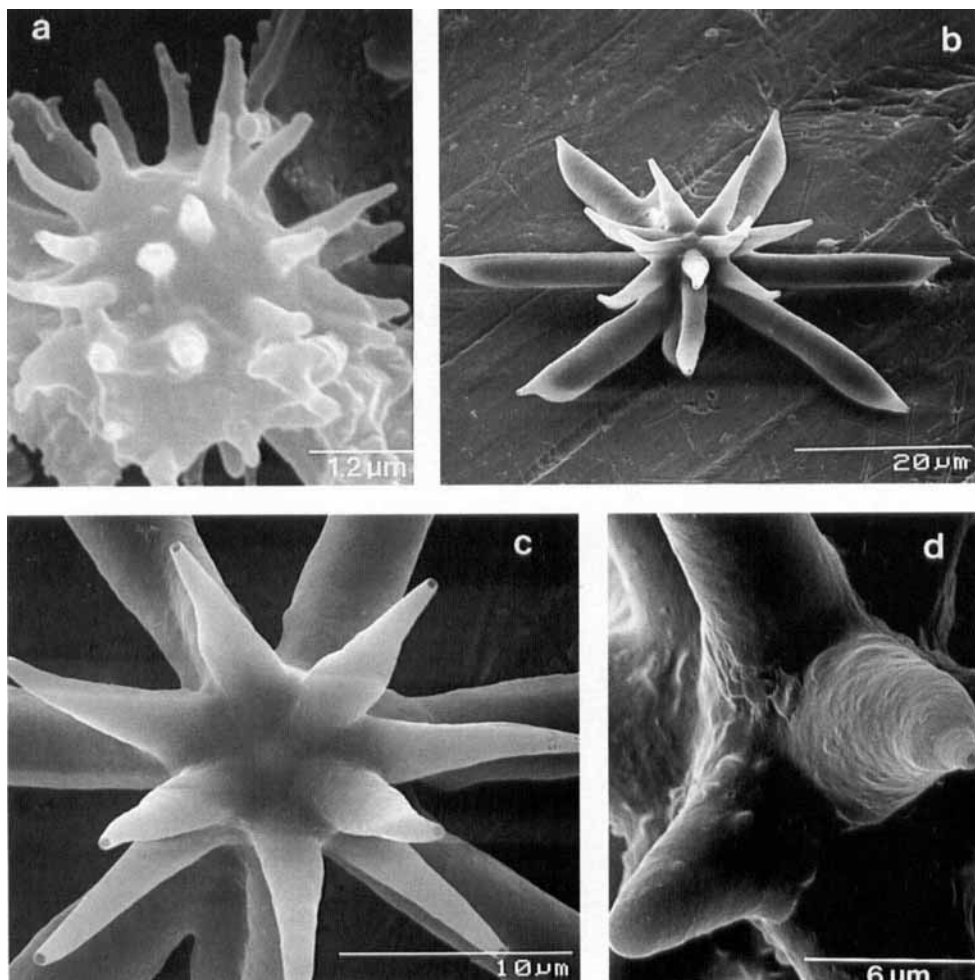
Figure 3. Immature desmata of *Crambe*: (a) small corpuscle of a very young desma of *C. tuberosa*; (b & c) immature desmata of *C. tuberosa* showing a terminal orifice in both the long and short actines; (d) terminal orifice in an actine of a desma of *C. taillezi*.

information. The presence of orifices at the tip of the structures traditionally considered as 'ornamental spines' reveals that they are actually actines.

Common spicule types

Orifices like those of the odd spicule types of *Crambe* and *Discorhabdella* described above were also found in other actinal structures of more common spicules, such as calthrops (Fig. 6d) anatriaenes, oxeas (Fig. 6e), and in the shaft of the isochelae.

Structures without an axial canal

Orifices showing the existence of an axial filament during the formation of the spines were not found in the acanthostyles of *Phorbas fictitius, Microciona gradalis, Myxilla rosacea,* and *Eurypon coronula*.
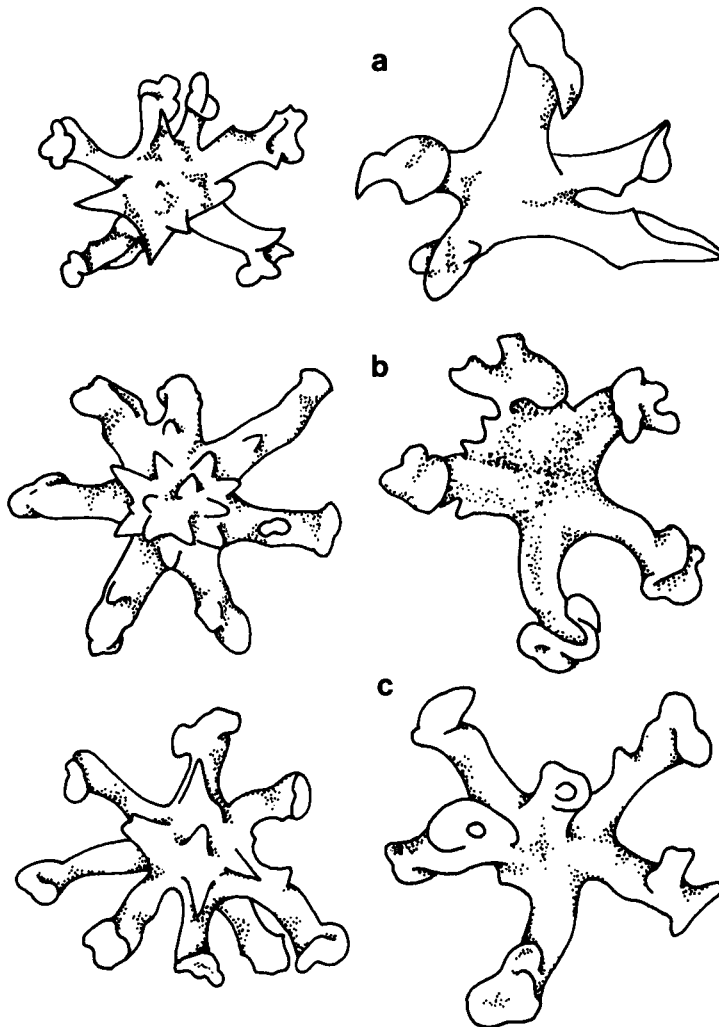
Figure 4. (a) Fossil sphaeroclons from Oamaru sponge beds attributed to the genus *Vetulina* (redrawn from Hinde & Holmes, 1892); (b) asterose desmata of *C. tuberosa*; (c) asterose desmata of *C. acuata*.

Orifices were also not found at the tip of the spines in the oxydiscorhabds of *Discorhabdella incrustans* nor in the acanthorhabds of *Crambe tailliezi* and *Crambe acuata*. Thus, both microrhadoid microscleres seem to belong to the monaxonid spicule type, despite the fact that oxydiscorhabds display their spines arranged in two subterminal whorls.

Similarly, no terminal orifices were observed in stages of the desmas with incipient spines, zygome plates and bifurcated arms, all characteristic features of the mature spicules. In fact, spines, zygomes, as well as the most distal part of the arms, lacked an axial filament. According to Lévi (1991), the shape of the zigomatic-plates seems to result from a morphological coupling with the spines and zigomatic-plates of the neighbouring desmas to produce the articulate skeleton (Fig. 7).
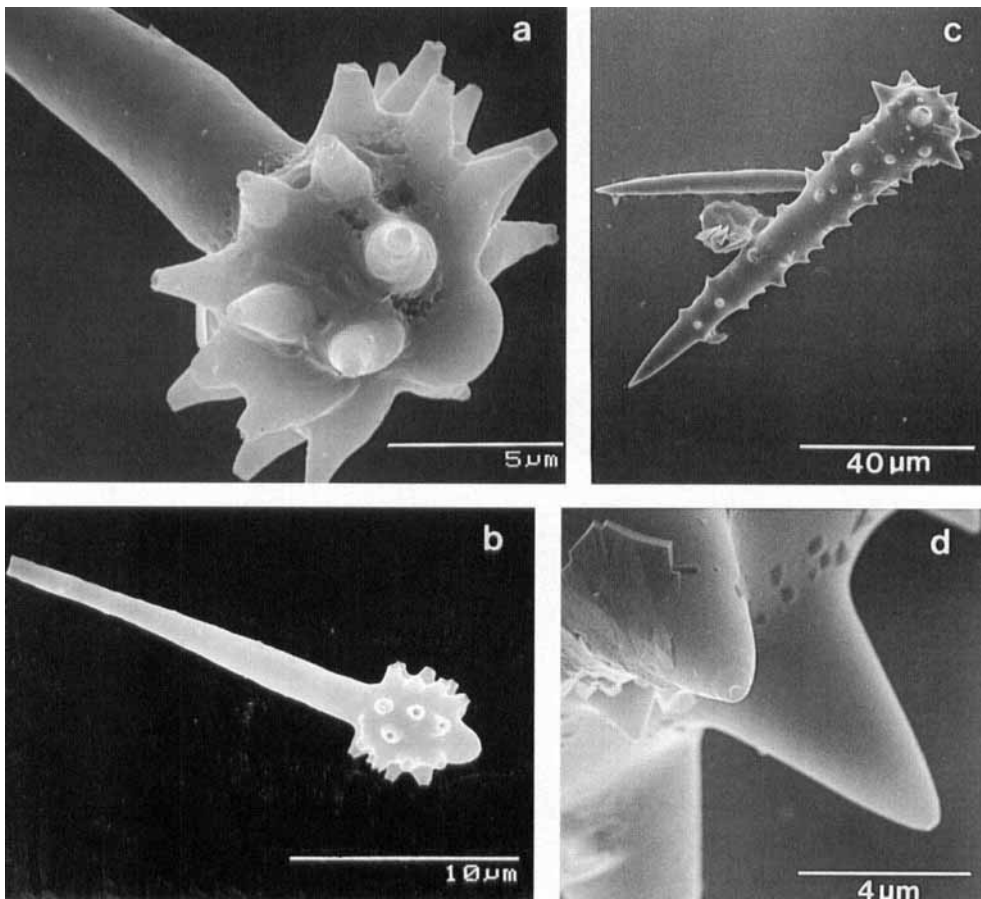
Figure 5. Acanthostyles of *Discorhabdella*: (a & b) immature acanthostyles of *D. incrustans* showing a terminal orifice in each of the basal 'spines'; (c) mature acanthostyle of *D. tuberosocapitata*; (d) terminal orifice in a basal 'spine' of a young acanthostyle of *D. tuberosocapita*.

DISCUSSION

Fossil and recent aster-like desmas and desmoids

As far as we know, no fossil material has been described under the generic name of *Crambe*. However, the fossil spicules, closely resembling the desmoids of the living species of *Crambe* (Fig. 6) reported by Hinde & Holmes (1892) from Tertiary sponge-beds in Oamaru (New Zealand) more probably belong to a species of the genus *Crambe*. Similar sphaeroclons have also been found in other fossil genera, such as *Cladodia* Moret, 1925 and *Exodictia* Moret, 1925. Sphaeroclons have traditionally been postulated to be aster-like desmas lacking an axial canal in their arms (Schmidt, 1879; Schrammen, 1910; Reid, 1970; Gruber, 1993). Arms of these desmas are interpreted, therefore, not to be true actines (Reid, 1970). Nevertheless, the existence of canals inside the arms of sphaeroclons has been known for a long time but earlier interpreted as either the remains of a cell or secondary opened canals filled by air (e.g. Schmidt, 1879; Schrammen, 1910; Sollas, 1888), and, in any case, non-
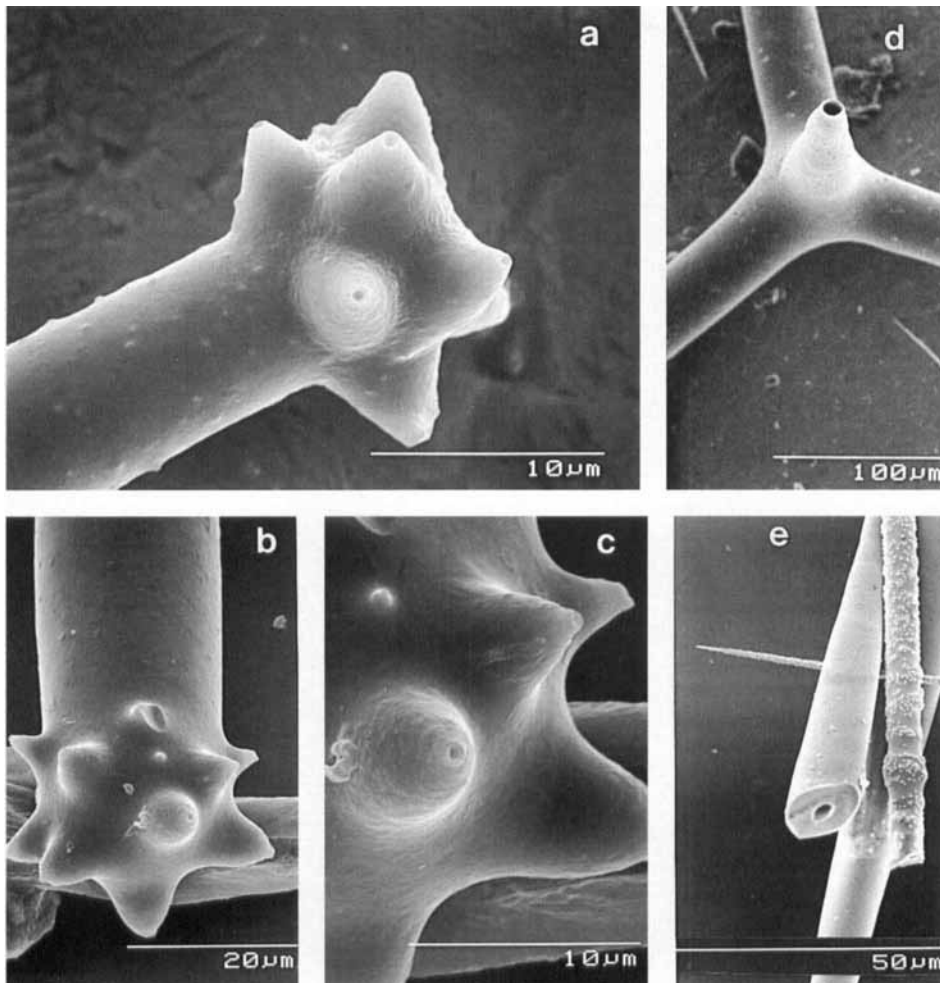
Figure 6. Terminal orifices indicating the presence of axial filaments. Young tuberose tylostyle of (a) *C. tuberosa*, (b & c) *D. incrustans*; (d) young caltropose; (e) axial conduct of an oxea.

homologues to the axial canals. Later, Moret (1925) also described the existence of canals in the arms of fossil sphaeroclons, but he also regarded them as being non-homologous to the axial canals: "cette cavité suit d'ailleurs les divisions du spicule et peut donner l'illusion de canaux axiaux élargis par dissolution" (Moret, 1925).

Some of these earlier authors had also noticed a relationship between the so-called 'cavity of air' of the sphaeroclons and that found in young sterrasters of *Geodia* Lamarck, 1915 (Sollas, 1888; Moret, 1925) which definitively corresponds to a true axial canal enlarged by erosion (Rützler & Macintyre, 1978; Simpson *et al.*, 1985). In fact, various studies suggest that virtually all silica spicules examined to date are elaborated within a membrane-limited cavity that contains a thin, proteinaceous axial filament. The existence of an axial filament is viewed to be especially relevant in determining a fixed geometry of the spicule shape (Garrone *et al.*, 1981; Simpson, 1984, 1990;
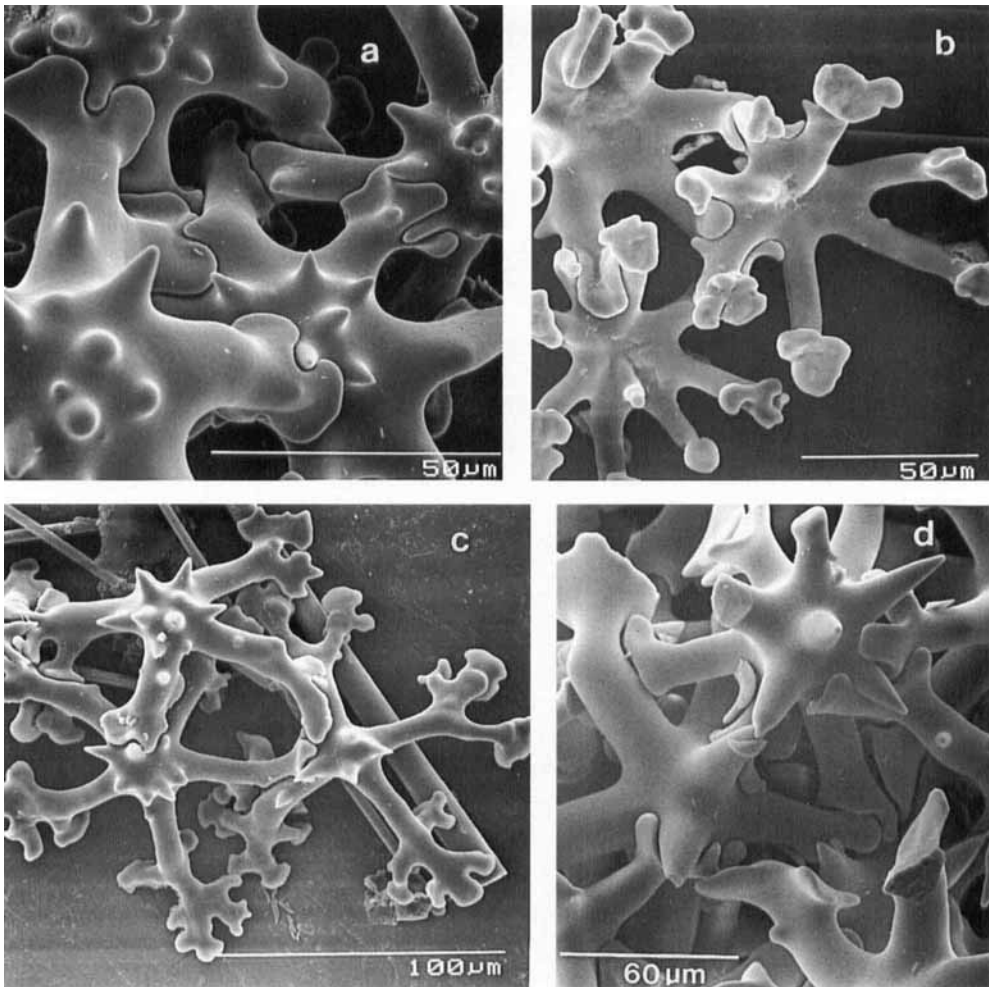
Figure 7. Articulate desmal skeleton of *Crambe*. Sphaeroclons of (a) *C. tuberosa* from Alboran, upper face, (b) *C. tuberosa*, lower face and (c) *C. taillezi* from Alboran; (d) desmas of *C. acuata* from Namibia.

Simpson *et al.*, 1985; Donadey *et al.*, 1990). The persistence of a fixed shape through time has been recorded in most spicule types of Demosponges, sphaeroclons included (e.g. Rauff, 1893; De Laubenfels, 1955; Reid, 1970; Van Kempen, 1990). The variability observed in the final shape of the crepidal desmas and the morphological coupling required for articulating them have been suggested to be the result of a secondary silification subsequent to that associated with the growth of the axial filament (Lévi, 1991). Thus, if sphaeroclons were anaxial spicules, an unpredictable and highly changing shape would be expected, which is not the case. The traditional interpretation given for the canals found in fossil desmas is unrealistic. In fact, all evidence tends to support that aster-like desmoids of *Crambe* and the so-called sphaeroclons of *Vetulina* Schmidt, 1879, and those of other fossil genera are polyaxonid, homologous spicules.

Homology between asterose acanthostyles and desmoids

The polyaxonid origin of the asterose desmoids of *Crambe* and the acanthostyles of *Discorhabdella* supports the hypothesis of homology between these two spicule types. Such a hypothesis is also supported by the equivalent arrangement of both spicule types in the skeleton (Dendy, 1924; Lévi, 1960, 1963; Vacelet & Boury-Esnault, 1982; Uriz, 1988; Maldonado & Benito, 1991; Boury-Esnault *et al.*, 1992). The current differences in shape between both spicule types could be explained by considering these two elements as being the result of a divergent morphological evolution brought about by an actinal atrophy or hypertrophy from an ancestral polyactinal corpuscle. Divergence in shape would be determined by the evolutionary fixation of the atrophy/hypertrophy of a different number of actines in each case. The process suggested here would be similar to that traditionally postulated for explaining the origin of triaenes from calthrops (Reid, 1970). Thus, all evidence led to the conclusion that asteroid desmas (sphaeroclons *s.l.*) and asterose acanthostyles are in fact the same structure under different morphological expressions, i.e. states of a 'transformational homology'. Moreover, the existence of other asterose acanthostyles such as those described in *Hymeraphia spinispinosa* Topsent, 1892, and other polyactinal spicules such as those of *Cyamon* Gray, 1867, and *Trikentrion* Ehlers, 1870, besides reinforcing the proposed relationships between monaxonid and polyaxonid morphologies, would concur with the hypothesis that hypertrophy has been evolutionarily fixed in a different number of axes, yielding a morphological diversity (from polyactinal to monactinal) in the resulting forms.

The relationship proposed here between some monaxonid and polyaxonid morphologies was intuitively claimed by Dendy (1921), who, however, regarded all these 'pseudopolyact' forms, the desmoids of *Crambe* included, as evolving from acanthostyles.

Tuberose tylostyles vs non-tuberose monactines

The presence of axial canals inside the young tubercles of the tuberose tylostyles of *Discorhabdella* and *Crambe tuberosa* indicates that the tubercles are actually atrophied actines. Lumps on the tyle, corresponding to vestigial tubercles, have occasionally been described in spicules of specimens of *C. tailliezi* (see Maldonado, 1993, present study) and *C. acuata* (Lévi, 1958) [*Folitispa acuata*]. Tuberose tylostyles have also been described in species of other living genera such as *Rotuloplocamia* Lévi, 1952, and *Terpios* Duchassaing & Michelotti, 1864, as well as in the fossil *Rhopaloconus* Sollas, 1880. A polyaxonid origin has explicitly been claimed for the tuberose tylostyles of different species of *Terpios* Duchassaing & Michelotti, after demonstrating the occurrence of a radial pattern of canals inside the tyle (Rützler & Smith, 1993).

According to the ontogenetic evidence, the tuberose morphology of these monactines may correspond to the retention of an ancestral morphology of the evolutionary transformation series of the main monactines of the poecilosclerid and hadromerid lineage. However, the occurrence of this character in a few, relatively unrelated species and genera suggests that this

feature may sometimes crop up as a paedomorphosis phenomenon, rather than as a sign of a true ancestral status of these species. Unfortunately, such a matter cannot be solved with the currently available information. Whether all the main monactines (styles-tylostyles, acanthostyles) of Poecilosclerida and Hadromerida, or even those of other orders of Demospongiae also have a polyaxonid origin or not is another question unsolved in the current state of knowledge.

Taxonomic and evolutionary implications

The evidence of the homology between the sphaeroclons of *Crambe* and the asterose acanthostyles of *Discorhabdella* suggests a closer taxonomic relationship between both genera than traditionally thought. Moreover, species of such genera have recently been supposed to be Tethyan or very ancient relicts (Boury-Esnault *et al.*, 1992; Maldonado & Uriz, 1993).

In a similar way, Poecilosclerida and Hadromerida would display a monophyletic origin, if the main monactine spicules of both groups would evolve from an ancestral polyaxonid form. This interpretation would cast some doubt on the actual separation of the subclasses Ceractinomorpha and Tetractinomorpha in Demospongiae (Lévi, 1973), supporting the opinion of Reiswig (1971) based on other skeletal evidence. By generalising from the results and arguments hereby presented, the tetraxonid (calthropoid) forms, commonly assumed to be the primitive spicule of Demospongiae since Dendy's study (1921), could be thought now to be a morphological type evolved from a polyaxonid form. In this way, the existence of tetraxonid morphotypes in Homosclerophorida, Astrophorida, Spirophorida, as well as in several hadromerid and poecilosclerid genera such as, for instance, *Timea* Gray, 1867 (see Maldonado, 1992), *Cyamon*, and *Trikentrion* (see Hooper, 1991) would be more easily explainable. However, the palaeontological evidence does not help to make a decision on the ancestral spicule type since the most ancient spicules recorded to date are both Cambrian oxeas (Finks, 1970) and tetraxons (van Kempen, 1990).

The formation of ornamental spines (without canal axial) seems to result from a secondary phase of the spicule silification, starting when the growth conducted by the axial filament has been completed. Actually, the occurrence of spines can take place in polyaxonid, tetraxonid, and monaxonid spicules. Sometimes the presence of spines brings about a morphological convergence between true monactines never related to polyaxonid forms, and monactine-like spicules evolved from polyaxonid forms by atrophy of all axis but one.

From a conservative point of view, it must be conceded that ontogeny is an important but insufficient clue for corroborating any homological proposition because such information can be deceptive when it is not palingenetic. Hence, it is necessary to test the congruence between this ontogenetic information and complementary data obtained from other sources in a wide taxonomic array (Weston, 1988; Pinna, 1991; Kitching, 1992). Consistency and congruence tests of all skeletal and taxonomic relationships emerging from this study are being conducted.

ACKNOWLEDGEMENTS

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