

Skeletal morphology of two controversial Poecilosclerid genera (Porifera, Demospongiae): *Discorhabdella* and *Crambe*

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ABSTRACT: The genera *Discorhabdella* and *Crambe* are characterized by bearing uncommon spicule types, i.e. pseudoastrose acanthostyles and sphaeroclones, respectively. They have traditionally been considered to be unrelated taxa, but the present reexamination made evident that an important amount of skeletal features are shared by both. Some of these morphological features, such as the ornamentation on the point of the ectosomal subtylostyles, are reported for the first time. The study also revealed that a tuberoso nature of the tytes of the main choanosomal megascleres could be a common ancestral condition in both genera. The morphology of the multi-toothed anchorate chelae showed a gradual transition across the species, suggesting that the morphological diversity in chelae was generated in these genera through a "palmate-anchorate-arcuate" evolutionary sequence. However, the forward or backward direction of this sequence remained unclear from the available evidence. Important levels of skeletal variability were found to affect many of the skeletal characters, especially in the genus *Crambe*. In some cases, this variability transgressed the limits theoretically defining a species, making evident that the traditional procedure just based on comparison of the skeletons becomes unreliable when tackling the taxonomy of these genera. Most of the skeletal variability seemed to correspond to genetic polymorphisms, except in the case of *C. acuata*. In this taxon, the skeletal variability could be a result of the existence of a cryptic species, originated by a misconceived synonymy between *C. acuata* and *C. chelastra*. Besides the skeletal variability, the obscure taxonomic meaning of many skeletal features favored the existence of conflicting taxonomic proposals for the suprageneric location of these genera, depending on the author's criteria. This study made evident that any subsequent attempt of phylogenetic inference should be based on an unweighted analysis of the available skeletal information.

INTRODUCTION

Discorhabdella Dendy, 1924 and *Crambe* Vosmaer, 1880 are two poecilosclerid genera characterized by bearing pseudoastrose acanthostyles and sphaeroclone desmas, respectively. These are two spicule types really rare in living poecilosclerids, but relatively frequent in fossil material. In general, *Discorhabdella* and *Crambe* have traditionally been considered to be unrelated, except for the shared presence of ancho-

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rate isochelae (Hajdu et al., 1994). However, there is an incomplete puzzle of information surrounding both genera, which makes a reexamination and reinterpretation of the skeletal features obligatory. The lack of information to support any suprageneric assignment is clearly reflected in the erratic taxonomical history of these taxa, which comprises a list of conflicting proposals. The genus *Crambe* has successively been placed in various poecilosclerid families, such as Desmacidonidae (Vosmaer, 1880; Topsent, 1928), Myxillidae (Burton, 1929), Crambidae (Lévi, 1963; Boury-Esnault, 1971; Maldonado & Benito, 1991), Esperlopsidae (Lévi, 1973). It has even been assigned to other orders or sub-orders different from Poecilosclerida, such as Lithistida (Lendenfeld, 1903), Hadromerida (Schmidt, 1879), and Halichondrida (Laubenfels, 1936). The relationships of the genus *Discorhabdella* remain similarly controversial. The first known species of this genus was assigned to Hymedesmiidae, under the name of *Hymeraphya tuberosocapitata* Topsent, 1892. The genus *Discorhabdella* was later erected by Dendy (1924) to harbor the species *Discorhabdella incrustans*. The genus was initially placed in the Hadromerida (family Spirastrellidae, sub-family Spirastrellinae) by presuming an astrose nature for its acanthostyles. Subsequently, the genus was moved into the family Euryponidae by Topsent (1928), who assumed homology between the pseudoastrose acanthostyles and the acanthostyles of *Eurypon*. Recently, the genus *Discorhabdella* has been relocated within the family Hymedesmiidae by Boury-Esnault et al. (1992), who described a third species, *Discorhabdella hindei* Boury-Esnault, Pansini & Uriz, 1992.

Observations on the spicule ontogeny of the genera *Crambe* and *Discorhabdella* have revealed a polyaxonid origin of both the sphaeroclones of *Crambe* and the pseudoastrose acanthostyles of *Discorhabdella* (Maldonado, 1993; Uriz & Maldonado, 1995). Nevertheless, the shape difference between sphaeroclones and pseudoastrose acanthostyles also indicates that an unknown amount of evolutionary divergence has taken place between the two genera. This paper investigates the way in which this evolutionary process is reflected by the remaining skeletal characters. The goal is to gain a better knowledge of the phylogenetic relationships between these controversial poecilosclerids as well as of the evolutionary pathways connecting different spicule forms.

MATERIAL AND METHODS

The following holotypes were reexamined for skeletal characterization: *Discorhabdella tuberosocapitata* (Monaco Museum, MN-040323); *Discorhabdella incrustans* (British Museum of Natural History, BMNH: 1923.10.1.157); *Discorhabdella hindei* (Muséum National d'Histoire Naturelle de Paris, MNHN-LBIM, D-NBE-1991-1); *Crambe tuberosa* (Centro de Estudios Avanzados de Blanes, CEAB-ALB-44-C); *Crambe erecta* (Museo Civico de Storia Naturale, MCSN-RN KEN 57C.E. 48311). Other studied material was as follows: specimens of *Crambe acuata* from Namibia (Benguela-VI and VII cruises, 1984; see Uriz, 1988); specimens of *Crambe tailliezi* from the Catalan coasts of Spain (Eco-pharm-I cruise, see Uriz et al., 1992) and from the Alboran Island (Fauna-I cruise, see Maldonado, 1993; Templado et al., 1993); specimens of *Crambe crambe* from the Northeast coast of Spain and the Balearic Islands (CEAB collection), as well as numerous slides stored in the collection of the Station Marine d'Endoume (material collected by Topsent, Vacelet & Boury-Esnault).

Spicule micrographs were taken through a Hitachi SEM, after cleaning, dehydration

and coating with gold-palladium according to the standard method (e.g. Boury-Esnault et al., 1992).

SKELETAL CHARACTERIZATION

Genus *Crambe* Vosmaer

This genus contains five living species. In addition, a fossil species from New Zealand originally described under the name of *Vetulina oamaruensi* Hinde & Holmes, 1882 has recently been claimed as belonging to the genus *Crambe* (Uriz & Maldonado, 1995). The characterization of the living species is as follows:

Crambe tuberosa Maldonado & Benito, 1991

Species only known by a unique, small encrusting specimen collected from the coralligenous facies of Alboran Island. The spicule set consists of tuberoso choanosomal acanthostyles (Fig. 1A), ectosomal subtylostyles, sphaeroclone desmas (Fig. 3A, B), and five-toothed isoanchorae (Fig. 5A-C), occasionally with three teeth only. Desmas have a crown of short spine-like actines on the centrum and between four and seven, long, downwards-curved actines named "arms". A flat expansion with an irregular outline occurs at the tip of the arms, usually named "zygomatic plate".

Three skeletal features, unnoticed in the original description, have been revealed by the present study: (1) Occurrence of a profuse microspination at the pointed end of the ectosomal subtylostyles (Fig. 2A); (2) Partial fusion of the lateral teeth of chelae (Fig. 5B) and occasional reduction of the central tooth (Fig. 5A); (3) Spicules with acanthostyles, originally described as tylostyles-II (Maldonado & Benito, 1991), have been confirmed to be ontogenetic stages of the tuberoso tylostyles (see Uriz & Maldonado, 1995).

Crambe tailliezi Vacelet & Boury-Esnault, 1982

Species formerly discovered off the Mediterranean coasts of France and subsequently found in other Western Mediterranean locations (Bibiloni, 1990; Uriz et al., 1992; Maldonado, 1993).

The main monactines are tylostyles with a slightly inflated tyle that was weakly tuberoso in some specimens from the Cabrera (Fig. 1B) and Alboran Island (Fig. 1C). The ectosomal megascleres are subtylostyles exhibiting a microspiny point, whose ornamentation can be slightly or intensely spiny, depending on the specimens (Fig. 2B, C). Desmas are always present in all specimens, although sometimes they are rare. Their appearance ranges from an astroclonal shape to a sphaeroclonal shape (sensu Reid, 1970), depending on the specimens. The former shows radiating arms with weakly developed, or even absent, zygomatic plates (Fig. 3E, F), whereas the latter has all arms addressed to the same direction and large complicated zygomatic plates (Fig. 4D). The microscleres are three-toothed isoanchorae (Fig. 5D), sometimes with reduced teeth, along with slightly fusiform, microspiny microxeas (Fig. 6D).

Crambe acuata Lévi, 1958

Species known from the Atlantic and East coasts of Africa, the coasts of Madagascar, and the Red Sea. We have noted that the whole amount of specimens assigned to this species exhibits a great skeletal variation. However, this variation can basically be

organized into two skeletal groups (henceforth referred to as *C. acuata*-I and *C. acuata*-II). These groups show disjunct biogeographical distributions, in the South Atlantic and in the Indian Ocean–Red Sea, respectively.

C. acuata-I is characterized by choanosomal tylostyles with globose tytes (Fig. 1D), ectosomal subtylostyles, scarce asteroid desmas, three-toothed isochelae in one or two size categories, and spiny microxeas (Fig. 6A, B). Desmas are absent in specimens described from Madagascar and Aldabra (Lévi, 1958; Vacelet et al., 1976). Microxeas are also absent in some specimens (Lévi, 1958, 1961).

C. acuata-II, i.e. South Atlantic specimens described by Lévi (1960, 1963) and Uriz (1988), is characterized by the occurrence of abundant desmas with large zygomatic plates (Figs 3C, 4C), the occurrence of only one category of isochelae (Fig. 5E), and the presence of sigmoid elements (Fig. 5G). The ectosomal subtylostyles of these specimens show a weak microspination identical to that illustrated in *C. tailliezi* in Figure 2C.

Crambe crambe (Schmidt, 1868)

It is one of the most abundant sponges in the infralittoral Mediterranean assemblages. Its geographical distribution covers the whole Western Mediterranean, even reaching Atlantic zones, such as the Canary Islands and the Saint Vincent Cape (Portugal). Specimens display thin or thick encrusting growth habits. The spicule set usually consists of styles-subtylostyles in two categories of thickness, corresponding to choanosomal and ectosomal locations (Fig. 1F). These spicules have an irregular point, usually telescopic (Fig. 2E). The microspinosity noticed in other species is here reduced to a rugose appearance (Fig. 2F). These spicules may also be transformed into a kind of anisostrongyles or asymmetrical styles, especially in oligotrophic environments (Bibiloni, 1990). Other spicule types, such as three-toothed anchorate isochelae and asteroid desmas (Fig. 3G), have only been reported in a few specimens (e.g. Topsent, 1925; Boury-Esnault, 1971). These spicules usually have aberrant morphologies, such as underdeveloped teeth in chelae and reduced arms in desmas. Only those desmas observed in Topsent's slides (specimens from Banyuls) were reasonably well formed, displaying a shape similar to that shown by some desmas of *C. erecta* (Fig. 3D).

Crambe erecta Pulitzer-Finali, 1992

Species known from only one specimen collected from North Kenya Banks (East African coasts). Unlike the remaining species of this genus, the holotype is an erect, compressed, massive specimen. The spicule set consists of choanosomal subtylostyles with a slightly marked tyle (Fig. 1E), ectosomal subtylostyles, asteroid desmas (Fig. 3D), and anchorate isochelae in two size categories, but without any morphological differentiation (Fig. 5F). The point of ectosomal subtylostyles is slightly microspiny, displaying an ornamentation intermediate between that of *C. crambe* and those of species *Discorhabdella* (Fig. 2D). The third category of rudimentary isochelae mentioned by Pulitzer-Finali (and suggested as uncertainly proper) was not found in the present holotype reexamination. Desmas are astroclons displaying a morphology transitional between those of *C. acuata* and *C. crambe*. Most of them have long arms whose zygomatic plates are reduced or even absent (Fig. 4D).

Skeletal arrangement in *Crambe*

In all five species of the genus *Crambe*, the choanosomal spicule skeleton is settled on a thin, basal layer of spongin. However, the arrangement of the spicules shows some differences depending on the species and even on the specimens, as follows:

(1) In *C. tuberosa* and in Atlantic specimens of *C. acuata*-II, desmas are joined by articulate zygoes to make a basal multilayered skeleton (Fig. 4A, C), which is just monolayered in some specimens of *C. tailliezi* (Fig. 4D). In some specimens of *C. tailliezi*, *C. erecta*, *C. acuata*-II, and *C. crambe*, desmas occur as scattered elements that are not joined one to another by zygoes (Topsent, 1925; Lévi, 1958, 1961; Boury-Esnault, 1971; Vacelet et al., 1976). They can even be absent in most specimens of the last two species.

The general structure of fossil desma-skeletons of Sphaerocladina, as described by Moret (1925: 134), was identical to that hereby illustrated from *Crambe tuberosa*, even in the minor details of the zygoes. The zygomatic plates of a desma are settled on the centrum and branches of adjacent and subjacent desmas, closely surrounding one or several spine-like structures (Fig. 4B, D).

(2) Main monactines are in a hymedesmioid pattern, traversing the desma layer in *C. tuberosa* and *C. tailliezi*. They are in a plumose fashion in *C. erecta* and *C. crambe*. Both arrangements can occur in *C. acuata* (Fig. 4C), depending on the specimens (see Lévi, 1958, 1960, 1963; Vacelet et al., 1976; Uriz, 1988). The amount of spongin in the spiculate bundles becomes important in *C. erecta* and *C. crambe*.

(3) Ectosomal subtylostyles are tangential to the sponge surface in *C. tuberosa*, whereas they are placed obliquely, forming bundles in *C. crambe* and *C. erecta*. Both arrangements occur in *C. acuata* and *C. tailliezi*, depending on the specimens.

(4) Isochelae and microrhabds, if present, are especially abundant in the ectosome, although they can also be scattered throughout the choanosome.

Genus *Discorhabdella* Dendy

The genus *Discorhabdella* has three living species. However, a fossil species from New Zealand, originally described in the genus *Latrunculia* by Hinde & Holmes, 1892, was recently reinterpreted as belonging to the genus *Discorhabdella* by Boury-Esnault et al. (1992). In general, the scarcity of records does not allow a comprehensive interpretation of either the actual biogeographical or bathymetric distribution. The few available data suggest that this genus has epibathyal depth distribution in temperate and subtropical latitudes. The characterization of the living species is as follows:

Discorhabdella incrustans Dendy, 1924

Indo-Pacific species that is only known from one specimen. The spicule set consists of tuberoso tylostyles (Fig. 7D), ectosomal subtylostyles with slightly microspiny points (Fig. 8C), short pseudoastrose acanthostyles without distal point (Fig. 9C), five-toothed isoanchorae usually with divided teeth (Fig. 10F, G), and microxeas ("oxydiscorhabds" sensu Dendy, 1924) with the spines mostly concentrated in two whorls (Fig. 6D, E).

Discorhabdella hindei Boury-Esnault, Pansini & Uriz, 1992

Species known from four specimens collected on the Mediterranean side of the Straits of Gibraltar. The spicule set consists of irregularly tuberoso tylostyles (Fig. 7A),

ectosomal subtylostyles with microspiny points (Fig. 8B), astrose acanthostyles with or without a short distal point (Fig. 9B), anchorate isochelae with seven or eight teeth, sometimes dico- or trichotomically divided (Fig. 10D, E), and sigmoid spicules.

Discorhabdella tuberosocapitata Topsent, 1892.

Species known from a single specimen from the Azores. Its spicule set consists of tuberose tylostyles (Fig. 7B, C), ectosomal subtylostyles with microspiny points (Fig. 8A), basal acanthostyles with "regular" (non-astrose) appearance (Fig. 9A), and anchorate isochelae with seven, occasionally eight, teeth (Fig. 10A-C).

Skeletal arrangement in *Discorhabdella*

The skeletal arrangement is common to all three living species of the genus. It consists of a thin, basal layer of spongin on which pseudoastrose acanthostyles (or typical acanthostyles in the case of *D. tuberosocapitata*) are densely settled in vertical orientation, forming a monostriated layer. Isolated tuberose tylostyles are sparsely scattered among the pseudoastrose acanthostyles. Subtylostyles are grouped in thin bundles, predominantly placed in oblique fashion to the ectosome. Anchorate isochelae, spiny microrhabds and sigmoids are widespread in the ectosome, and maybe in the choanosome too, although we were unable to corroborate this fact.

REMARKABLE FEATURES

Some morphological features deserve special consideration because they are either new findings or features shared by both genera, which can help us to understand their phylogenetic relationships:

(1) Tuberose tyles are present in all species belonging to *Discorhabdella* (Fig. 7). In the genus *Crambe*, this character was evident in *C. tuberosa* and some spicules of some specimens of *C. tailliezi* (Fig. 1A-C). In spicules of *C. acuata* and *C. erecta*, there are only slight swellings; these, however, can be interpreted as remains denoting the ancestral presence of a tuberose tyle (Fig. 1D, E). This evolutionary reduction process of the tyle would culminate in its loss in *C. crambe* (Fig. 1F).

The shaft of these main megascleres is apparently smooth, but some scarce and very tiny spines were revealed around the proximal zone under SEM magnification.

(2) According to the recent confirmation of a polyaxonid origin for sphaeroclones and pseudoastrose acanthostyles (Uriz & Maldonado, 1995), it can be said that *Discorhabdella* and *Crambe* share the presence of a basal skeletal layer made of polyaxonid spicules.

These basal elements can be densely arranged, sometimes even joined by zygoes in the case of desmas. In these articulate zygoes, the perfect fitting of the zygomatous plates around the spine-like structures of adjacent desmas suggests that growth of the spine-like structures has to be finished before the zygomatous plates contact with them. From morphological observations, it has been postulated that the silicification process in desmas has two phases (Lévi, 1991; Uriz & Maldonado, 1995). The first phase, where silicification is guided by the axial filament, would yield crepis of very constant shape. After this phase, a subsequent silicification characterized by little control on the silica deposition has been thought to take place, since the final shape of desmas is certainly pleomorphic. However, it must be conceded that to get a perfect fitting between

zygomatic plates and spine-like structures, an accurate control of the silica deposition is needed. This assumption is also reinforced by other invariant features in the morphology of desmas, such as the presence of spines on the arms following a regular pattern (Fig. 4A) and the occurrence of smooth surfaces at the inferior side of desmas (Fig. 3B).

Desmas show a gradual morphological simplification across the set of species of *Crambe*. The change in shape, which ranges from sphaeroclone to astroclone morphologies (Fig. 3), is associated to a rarefaction in the number of desmas. This process seems to be culminated in *C. crambe*, where desmas are absent in most specimens.

As for the astrose acanthostyles, the most remarkable fact is the apparent evolutionary transfiguration from a pseudoastrose morphology, present in *D. hindei*, *D. incrustans* and fossil spicules, to a typical acanthostilic morphology, such as that occurring in *D. tuberosocapitata* (Fig. 9). Acanthostyles of *D. tuberosocapitata* have the "proximal spines" more developed than the remaining spines on the shaft (Fig. 9). This is also known in many other poecilosclerid groups. However, it has been demonstrated that the proximal spines, at least in *Discorhabdella*, are different from the remaining spines on the shaft because they are actually reduced actines containing an axial canal (see Uriz & Maldonado, 1995).

(3) Straight ectosomal subtylostyles were present in all species of both taxa. Choanosomal and ectosomal styles have not usually been described separately in *C. crambe*, but we have observed that they are of two kinds that can be distinguished by their skeletal arrangement and by their thickness.

There is a peculiar microspination surrounding the point of these ectosomal subtylostyles. This ornamentation, recently reported for the first time in *Crambe tuberosa* (Maldonado, 1993), has also been found in all species of *Crambe* and *Discorhabdella*. The intensity of the ornamentation displays a variation, especially in *Crambe*, where it ranges from a strong microspinosity to a rugose outline (Fig. 2). The spiny character of the point is moderate in all three species of *Discorhabdella* (Fig. 8). This pattern of ornamentation, characterized by spines around the point, clearly differs from that observed in species of *Myxilla*, where spines are located at the top of the points and sometimes even splitting the point of the spicule.

(4) Both genera share the presence of anchorate isochelae whose number of teeth ranges from three to eight across the species. Morphological evidence suggests that the number of teeth in chelae is currently subjected to a process of evolution. However, it is not clear whether the process involves an increase or a decrease in number of teeth. The three-toothed isoanchorae of *C. crambe*, *C. tailliezi*, *C. acuata* and *C. erecta* show interesting peculiarities. In *Crambe acuata*, the three-teeth isoanchorae have one or two additional small teeth (either vestigial or new formation?) located at the base of the lateral or central teeth (Fig. 5E). The isoanchorae of *C. erecta* sometimes show a small fissure on the alae (Fig. 5F) which could mean either remains of the fusion of a lateral tooth or the beginning of neogenesis of a lateral tooth. Isochelae of some specimens of *C. crambe* sometimes show all three teeth reduced to unguiferous structures; most frequently isochelae are absent in this species. It is noteworthy that, in the specimen of *C. tailliezi* from Alboran, some chelae are three-toothed at one end but five-toothed at the other end (Fig. 5D).

In general, in species having chelae with five or more teeth, the central tooth of these chelae was more clearly individualized than the remaining ones, which were fused in

combinations of two or three at their bases (Figs 5B, C, 10A, C). Isoanchorae with seven teeth usually occurred in *C. tuberosa*, *Discorhabdella tuberosocapitata* and *D. hindei*. In such chelae, the central tooth remained isolated, whereas the lateral teeth were also diversely fused in groups of two or three (Fig. 10A, D). The central tooth was only found to be dichotomous in some eight-toothed isoanchorae of *Discorhabdella hindei*.

Types with three, five and seven teeth exhibited a symmetrical arrangement of teeth and were notably more abundant in the species than types with four, six or eight teeth. Isoanchorae with four and six teeth seemed to be occasional irregularities derived from the three- and five-toothed major models. Types with five and seven teeth also seem to arise from or converge to the three-toothed model, since lateral teeth are always fused with each other at their bases (Figs 5B, 10C). This three-toothed morphology, in turn, may be related with the sigmoid spicules occurring in some species, at least in the case of *Crambe*. In this genus, the central tooth, unlike the lateral ones, is a real prolongation of the central shaft of the chela (Fig. 5B). Thus, any underdevelopment of teeth would most likely originate sigmoid elements. However, sigmoid elements are also present in some species of *Discorhabdella* even though the central tooth does not appear to be a real prolongation of the central shaft of the chelae (Fig. 10C). In general, sigmoid spicules of both genera look somewhat different from the usual, typical poecilosclerid sigmata because of their blunt ends and the rugose outline of the shaft.

As a curiosity, note the presence of a spine on the shaft of a chelae of *D. hindei* in Figure 10E.

(5) Microxeas, either with spines arranged in two distal whorls or scattered throughout the shaft, occur in several species of both genera (Fig. 6). At first sight, oxydisco-rhabds might be considered as streptastrose spicules (Fig. 6D). However, after a SEM study of the spination in several ontogenetic stages no axial canal was observed. Thus, both types of microrhabds are assumed to be monaxonid microscleres, but having different patterns of ornamentation (Uriz & Maldonado, 1995).

DISCUSSION

The main aim of this study was to find new morphological information to solve the controversial relationships surrounding the genera *Crambe* and *Discorhabdella*. However, although a detailed skeletal description of both genera has been accomplished, the taxonomic interpretation of these skeletal features must be tackled cautiously. There is a high skeletal variability affecting most of the spicule types of *Crambe*, especially in *C. crambe* and *C. acuata*. We have noticed that there is almost no skeletal difference between, for instance, some specimens of *C. crambe* and some other assigned to *C. acuata*: both lacking isoanchorae and desmas. Similar levels of skeletal closeness occur between specimens of the latter species and *C. tailliezi*. An additional complication is that the variability in *C. tuberosa* and *C. erecta* can not be assessed since there is only one specimen known from each of these two species.

On the other hand, most of the skeletal variability found in *C. acuata* occurs in the group of Indian specimens (*C. acuata-I*). Specimens from the West coasts of Africa (*C. acuata-II*) have relatively stable skeletal features. It is interesting to remember that the current concept of *Crambe acuata* is based on a taxonomic fusion between two previous species: *Crambe acuata* Lévi, 1958 and *Crambe chelastra* Lévi, 1960. Although this

second species was claimed to be a junior synonymy of *C. acuata* (Lévi, 1963; Vacelet & Boury-Esnault, 1982), we find from the present study that a reconsideration of such a synonymy would be advisable.

The intraspecific skeletal variability in *Crambe*, except for the above mentioned case of *C. acuata*, seems to be a result of genetic polymorphisms, since the same characters appear and disappear at interspecific levels, as typically done by rampant parallelisms. This variability, traditionally considered to be taxonomically useless, can be a potential source of information to clarify the phylogenetic relationships (e.g. Saether, 1979, 1983; Sluys, 1989). However, from a phenetic analysis it is not possible to distinguish between parallelism and convergence in a reliable way. Consequently, we can not objectively decide a priori which subset of skeletal features is the best to infer the phylogeny in *Crambe*.

The taxonomical meaning of some skeletal features (i.e. the morphological gradation in chelae, the presence-absence of sigmoids and microxeas, and the sphaeroclone-acanthostyle relationship) is also too controversial to infer the relationships at the suprageneric level. For example, note that although we have illustrated a gradual variation in the morphology of the isochelae, this evidence is not enough to demonstrate whether the evolutionary trend is a reduction or an increase in number of teeth. The polarized sequence "palmate → arcuate → anchorate" has recently been suggested by Hajdu et al. (1994) in a revision of this character at the ordinal level. However, our present findings at the generic level rather support the ordination "palmate–anchorate–arcuate", whereby the direction remains unclear.

Sigmoid elements occur in some species of both genera. The low frequencies of these elements in the specimens along with some peculiarities in their shape give rise to doubt the homology between these "sigmoids" and the typical sigmata of other poecilosclerid sponges such as, for instance, *Myxilla* or *Pronax*. Besides, there is the fact that these sigmoid elements have sometimes been interpreted as reduced states of isoanchorae (e.g. Vacelet & Boury-Esnault, 1982; Van Soest, pers. comm.). This interpretation agrees with our observations on isoanchorae of *Crambe*, but it is not supported by observations on isoanchorae of *Discorhabdella*. Thus, the interpretation of this information also remains controversial.

As for the monaxonid microscleres, they only occur in some species of the two genera, and their presence is known to be affected by a high intraspecific variability (e.g. Vacelet et al., 1976). These spicules cannot be directly used to establish the taxonomy because it is unknown whether this character reflects the pattern of intrageneric speciation; or whether it is rather a rampant parallelism indicating that *Crambe* and *Discorhabdella* are sister groups, or just a morphological convergence in the shape of the microscleres.

The taxonomic level at which *Crambe* and *Discorhabdella* are related remains unclear, even taking into account the homology between sphaeroclones and pseudo-astrose acanthostyles. It is obvious that these spicules have primitive morphologies. This agrees with the results of some recent studies suggesting some species of both genera to be very ancient, probably Tethyan Mediterranean relicts (Boury-Esnault et al., 1992; Maldonado & Uriz, 1995). According to the fossil record, sphaeroclones and pseudo-astrose acanthostyles already showed their current shape in the Lower Tertiary (Hinde & Holmes, 1892). The amount of morphological divergence between sphaeroclones, pseu-

doastrose acanthostyles, and typical acanthostyles (present in *D. tuberosocapitata*) cannot be clearly translated into taxonomy. The question remains whether the amount of change between sphaeroclones and astrose acanthostyles is more important than the whole set of shared morphological features in determining the phylogenetic-taxonomic relationships between both genera. There are several conflicting suggestions for the suprageneric taxonomic location of these taxa, depending on the different taxonomic value that different authors concede to every particular skeletal feature. So, for instance, by paying special attention to the sphaeroclone skeleton, a tentative relationship of the genus *Crambe* with some fossil genera was suggested by Maldonado & Benito (1991). This proposal also leads us to the problem of the relationships between *Crambe* and the enigmatic genus *Vetulina* Schmidt, 1879. Such relationships are extremely difficult to be corroborated since only desma skeletons are conserved from fossil material. Furthermore, there are two controversial reports about the probable presence of ectosomal strongyles in living specimens of *Vetulina stalactites* (Laubenfels, 1955; Soest & Stentoft, 1988), which need to be reexamined. As for the genus *Discorhabdella*, it has recently moved into the family Hymedesmiidae (Boury-Esnault et al., 1992) by considering mostly the skeletal arrangement. In contrast, Hajdu et al. (1994) suggest a close relationship among *Crambe*, *Monanchora*, *Discorhabdella*, and *Myxilla* because of the shared occurrence of anchorate isochelae. From the present study, some morphological features suggest a relationship between *Crambe* and *Discorhabdella*, but any assessment of their relationships with the genera *Monanchora* and *Myxilla* is beyond the scope of this study.

It is obvious that to advance in the inference of the taxonomic relationships it is necessary to falsify some of these competing taxonomic hypotheses using a method different from the traditional phenetic weighted inspection. This aim is intended in a separate paper that will investigate the congruence level among different subsets of skeletal features as well as the stability of the different taxonomic classifications derived from them (authors, current research).

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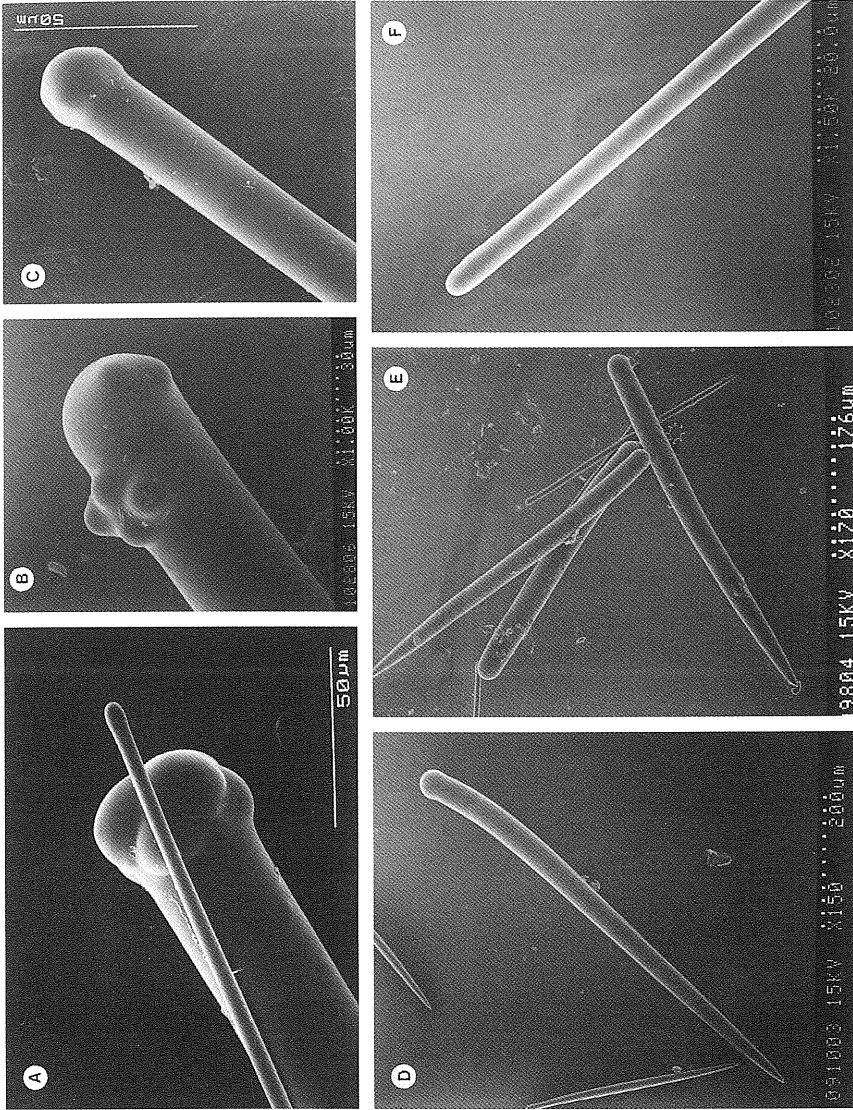


Fig. 1. Main choanosomal monactines of *Crambe*. A: *C. tuberosa*. Note the comparative size between choanosomal and ectosomal monactines. B: *C. tailliezi*, specimen from the Cabrera Island (from Uriz & Maldonado, 1995 by courtesy of Biol. J. Linn. Soc.). C: *C. tailliezi*, specimen from the Alboran Island. D: *C. acuta*. E: *C. erecta*. F: *C. crambe*

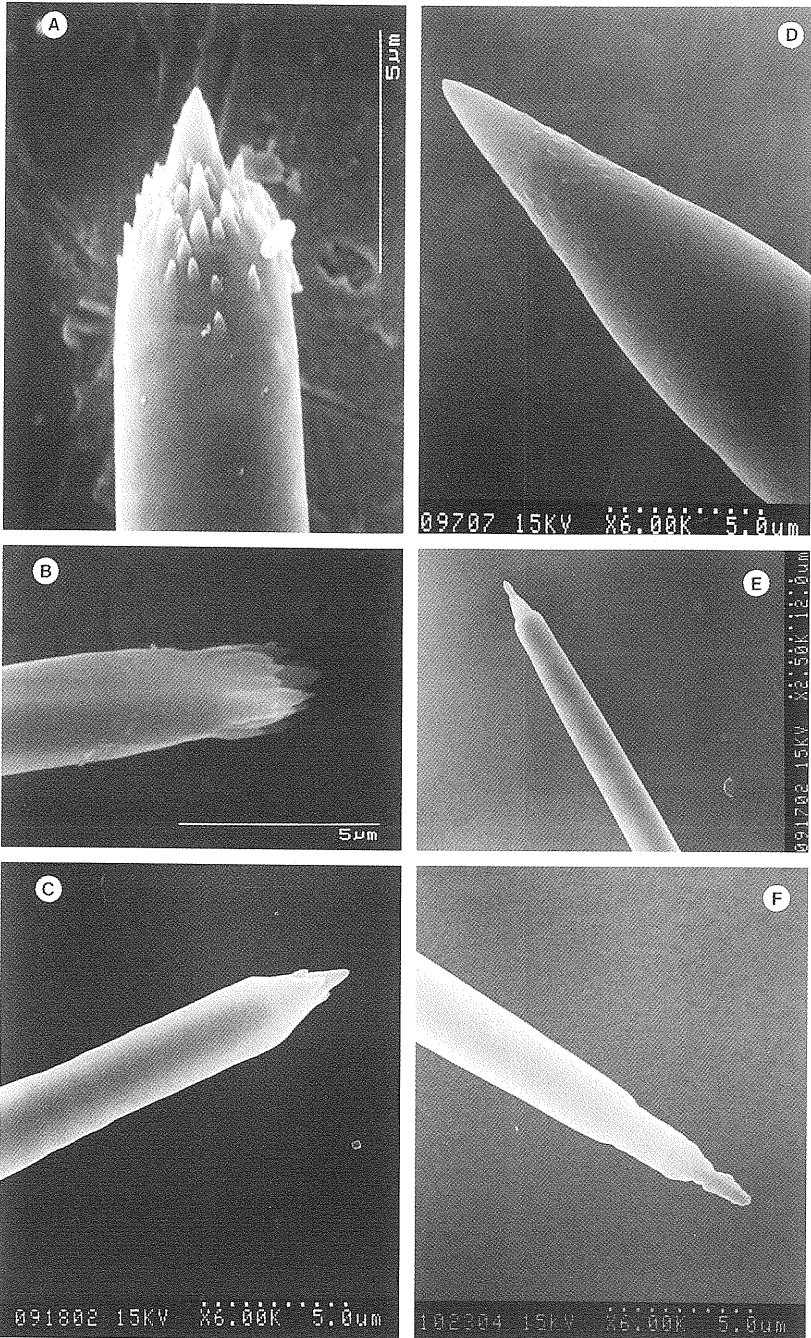


Fig. 2. Points of ectosomal monactine of *Crambe*. A: *C. tuberosa*. B: *C. tailliezi*, specimen from the Alboran Island. C: *C. tailliezi*, specimen from the Cabrera Island. D: *C. erecta*. E, F: *C. crambe*, Mediterranean specimens from the Northeastern coast of Spain

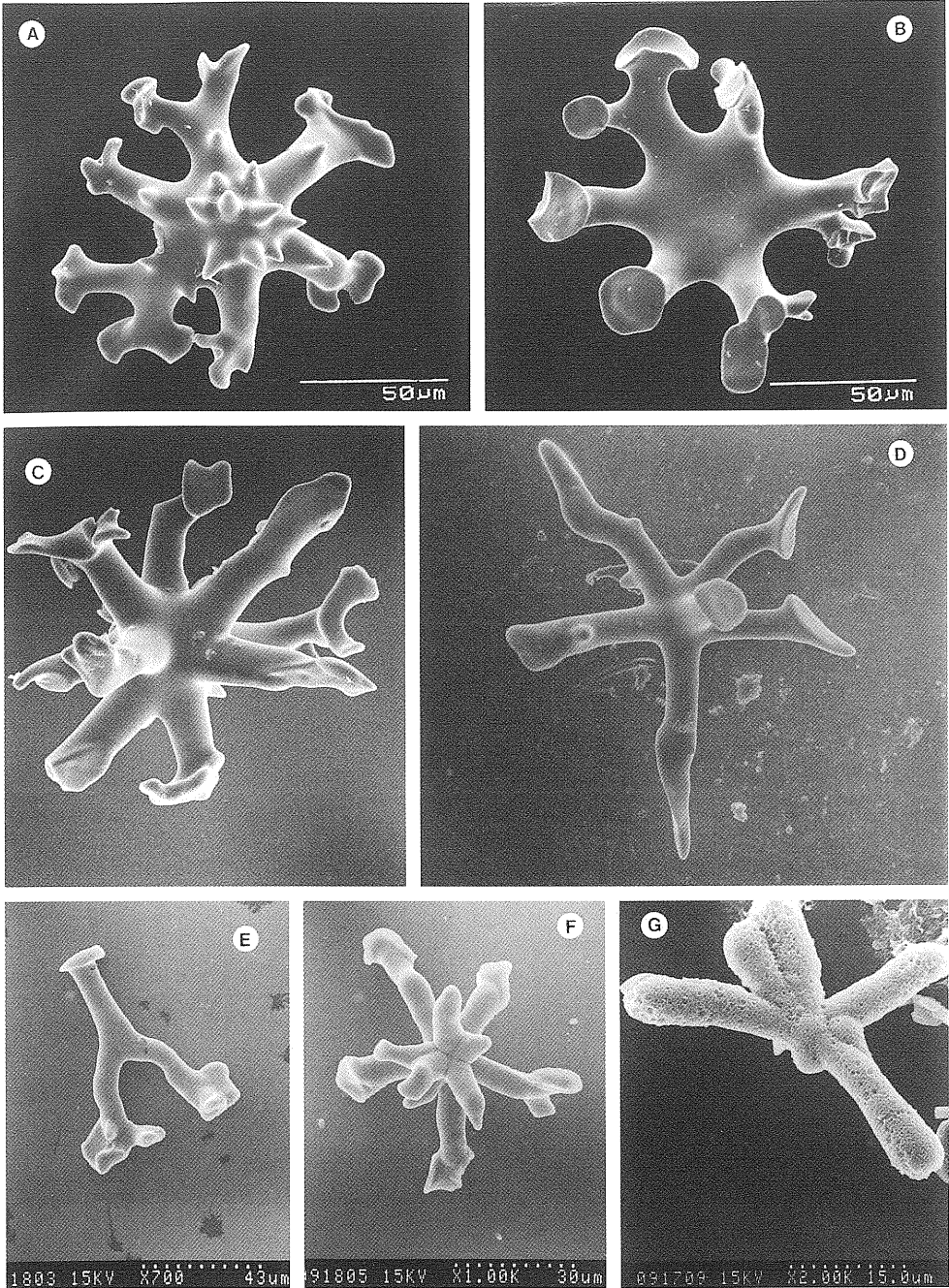


Fig. 3. Astrose desmas of *Crambe*. A, B: *C. tuberosa*, superior and inferior views of a desma. C: *C. acuta*, specimen from Namibia. D: *C. erecta*. E, F: *C. tailliezi*, specimens from the Northeastern coast of Spain. G: *C. crambe*, specimen from the Northeastern coast of Spain. Figures A and F taken from Uriz & Maldonado, 1995 by courtesy of Biol. J. Linn. Soc.

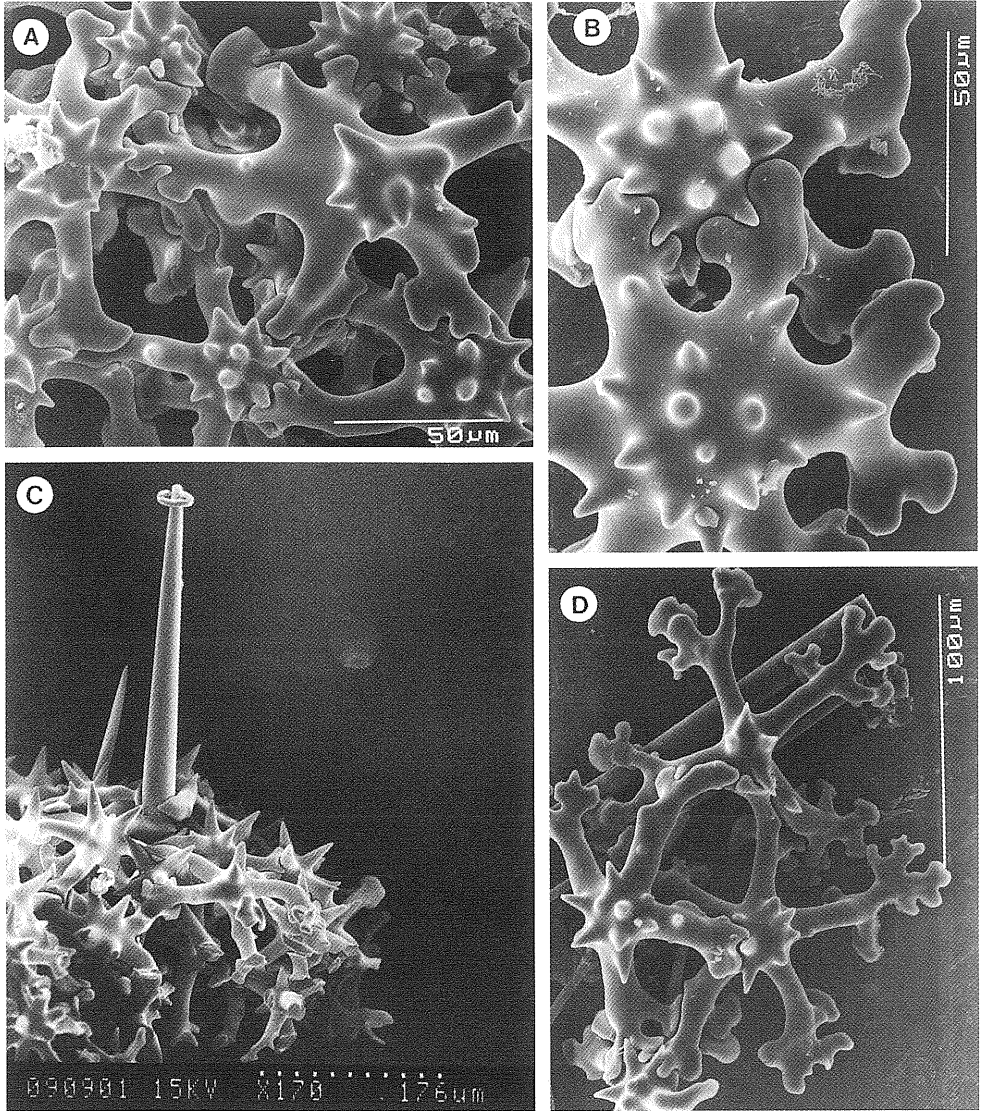


Fig. 4. Desma skeletons of *Crambe*. A, B: *C. tuberosa*. C: *C. acuata*, specimen from Namibia. D: *C. tailliezi*, specimen from the Alboran Island (from Uriz & Maldonado, 1995 by courtesy of Biol. J. Linn. Soc.)

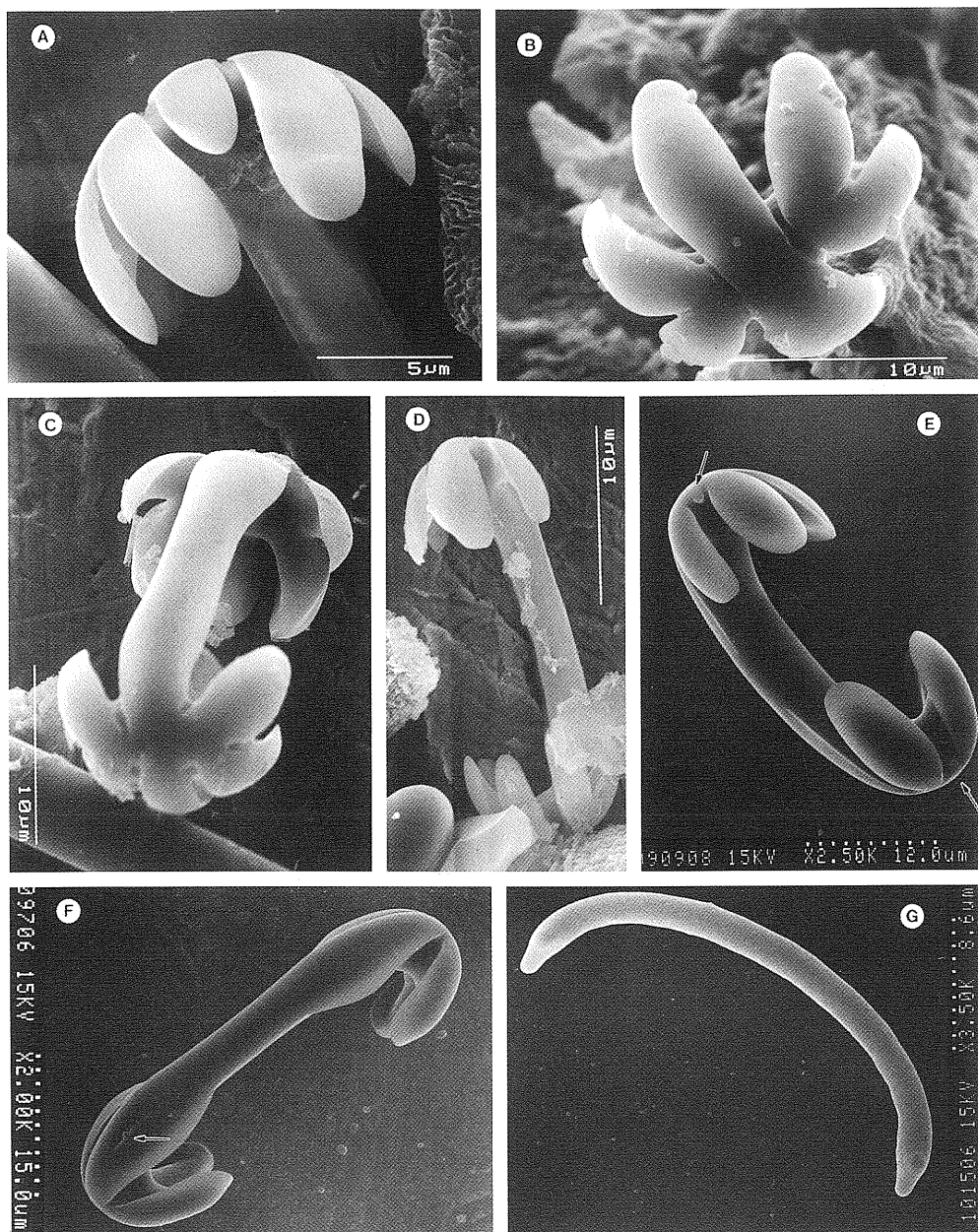


Fig. 5. Anchorate isochelae of the genus *Crambe*. A, B, C: *C. tuberosa*. D: *C. tailliezi*, specimens from Alboran Island. E: *C. acuta*, specimen from Namibia. Arrows indicate small teeth. F: *C. erecta*. Arrow indicates a fissure on the alae. G: Sigmoid element of *C. acuta* from Namibia

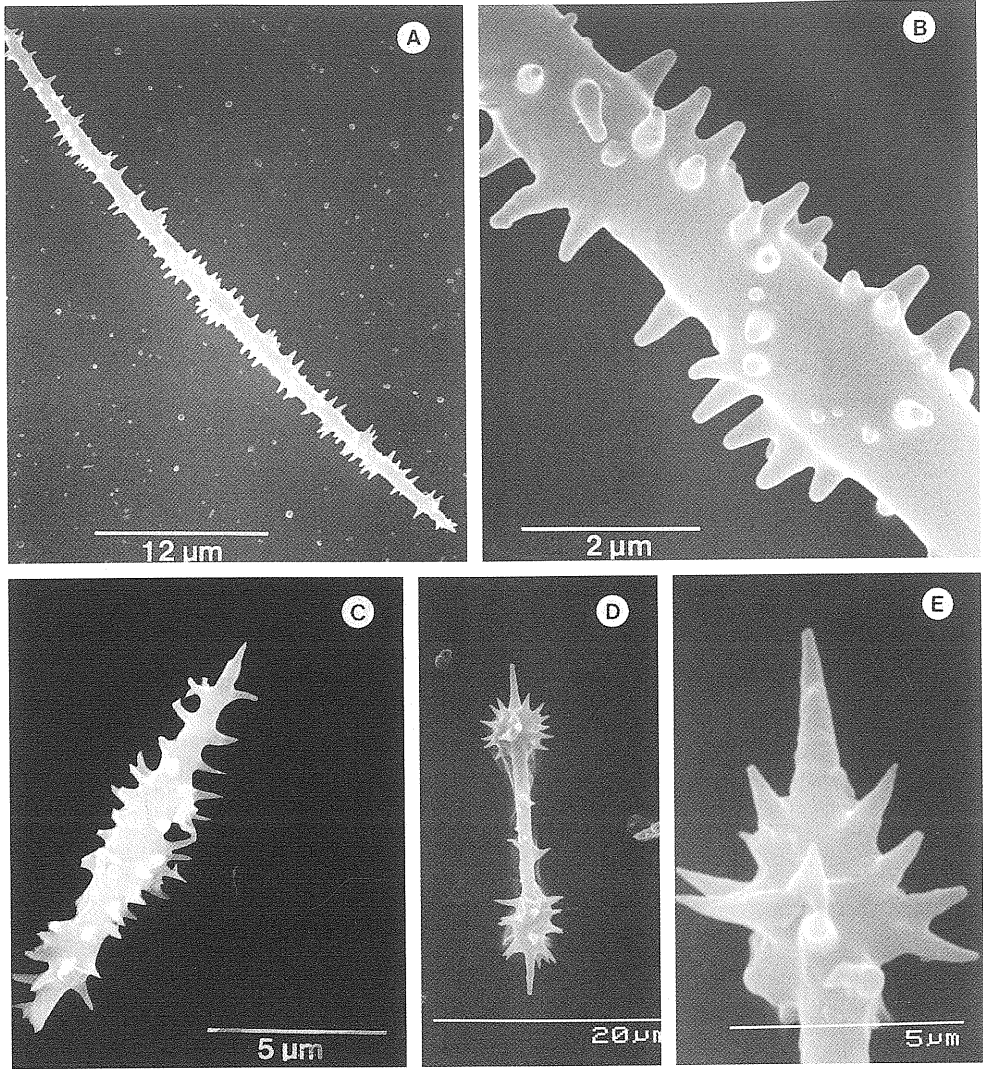


Fig. 6. Diactinal microscleres. A, B: *Crambe acuata* from Namibia. C: *C. tailliezi* from Alboran Island. D, E: *Discorhabdella incrustans* (oxydiscorhabd)

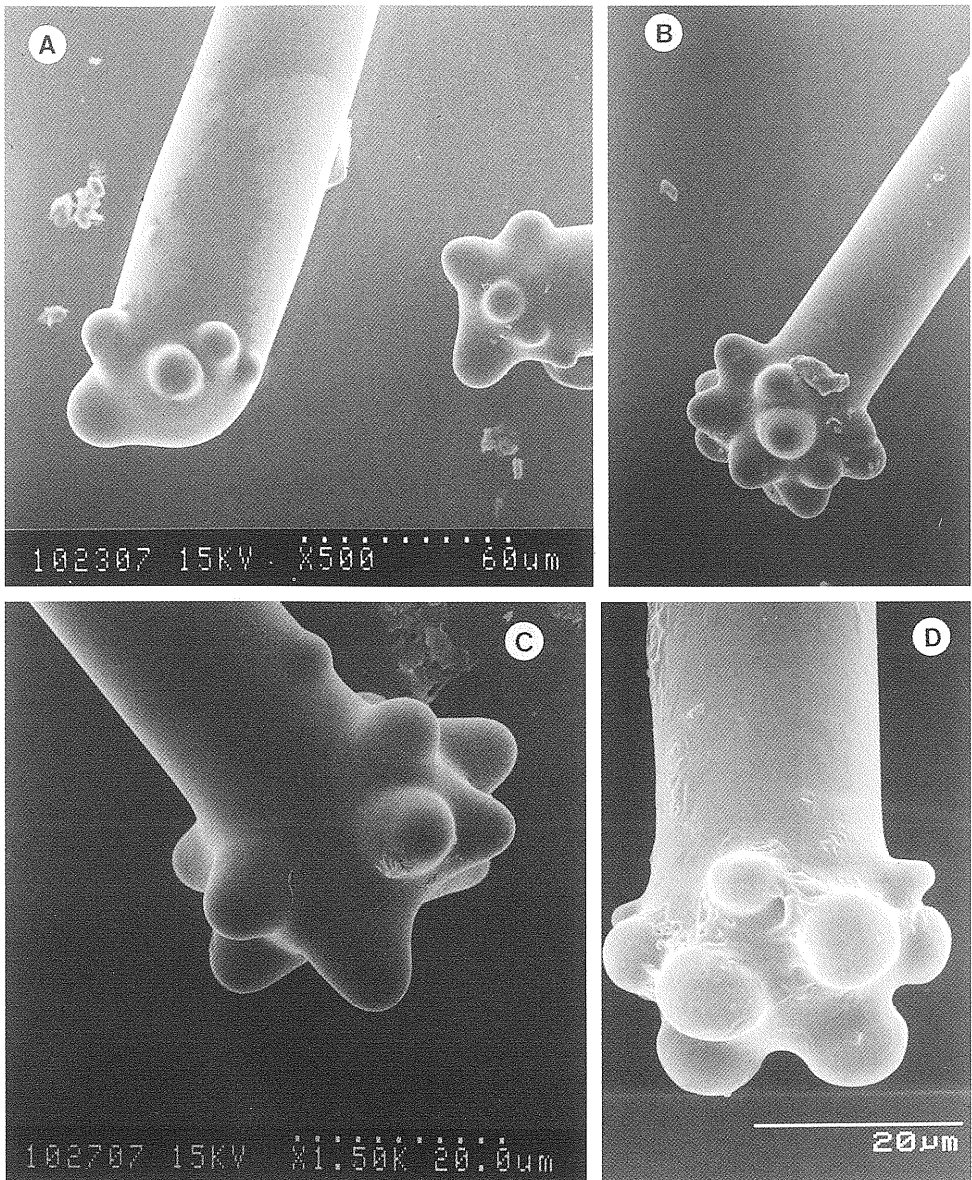


Fig. 7. Main choanosomal monactines of *Discorhabdella*. A: *D. hindei*. B, C: *D. tuberosocapitata*. D: *D. incrustans* (from Uriz & Maldonado, 1995 by courtesy of Biol. J. Linn. Soc.)

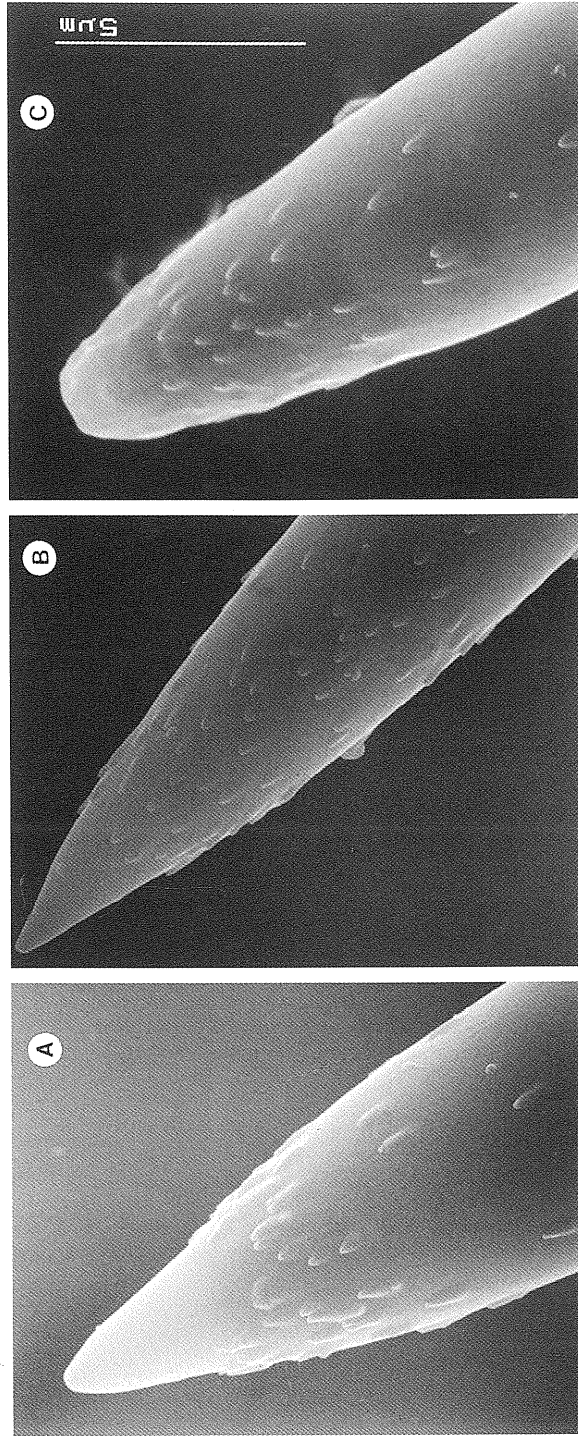


Fig. 8. Points of ectosomal megascleres of *Discorhabdella*. A: *D. tuberosocapitata*. B: *D. hindei*. C: *D. incrustans*

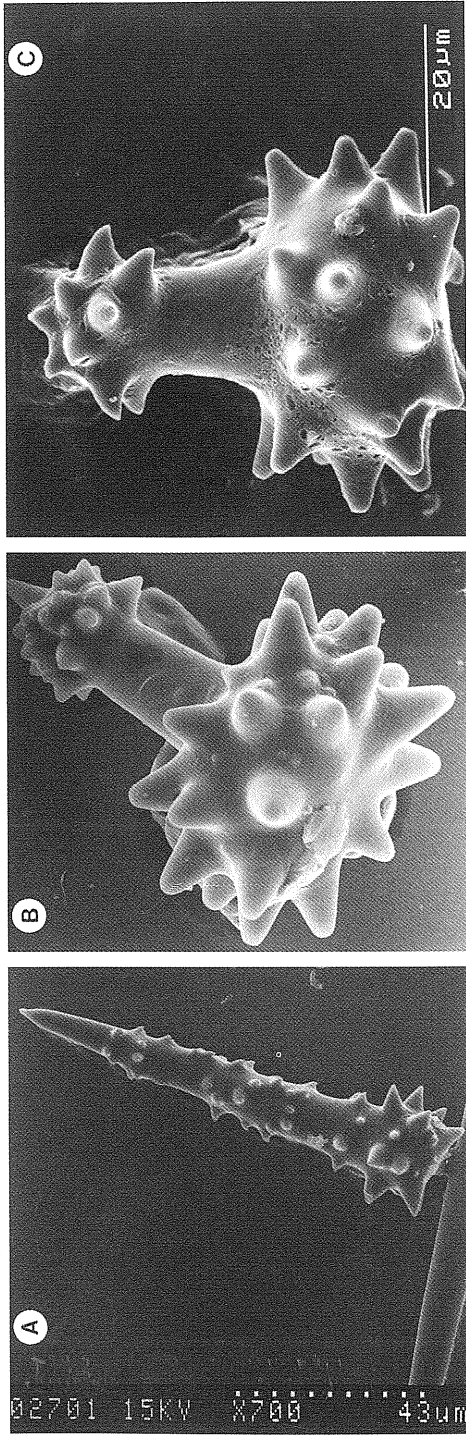


Fig. 9. Pseudostroste acanthostyles of *Discorhabdella*. A: *D. tuberosocapitata*. B: *D. hindei*. C: *D. incrustans*

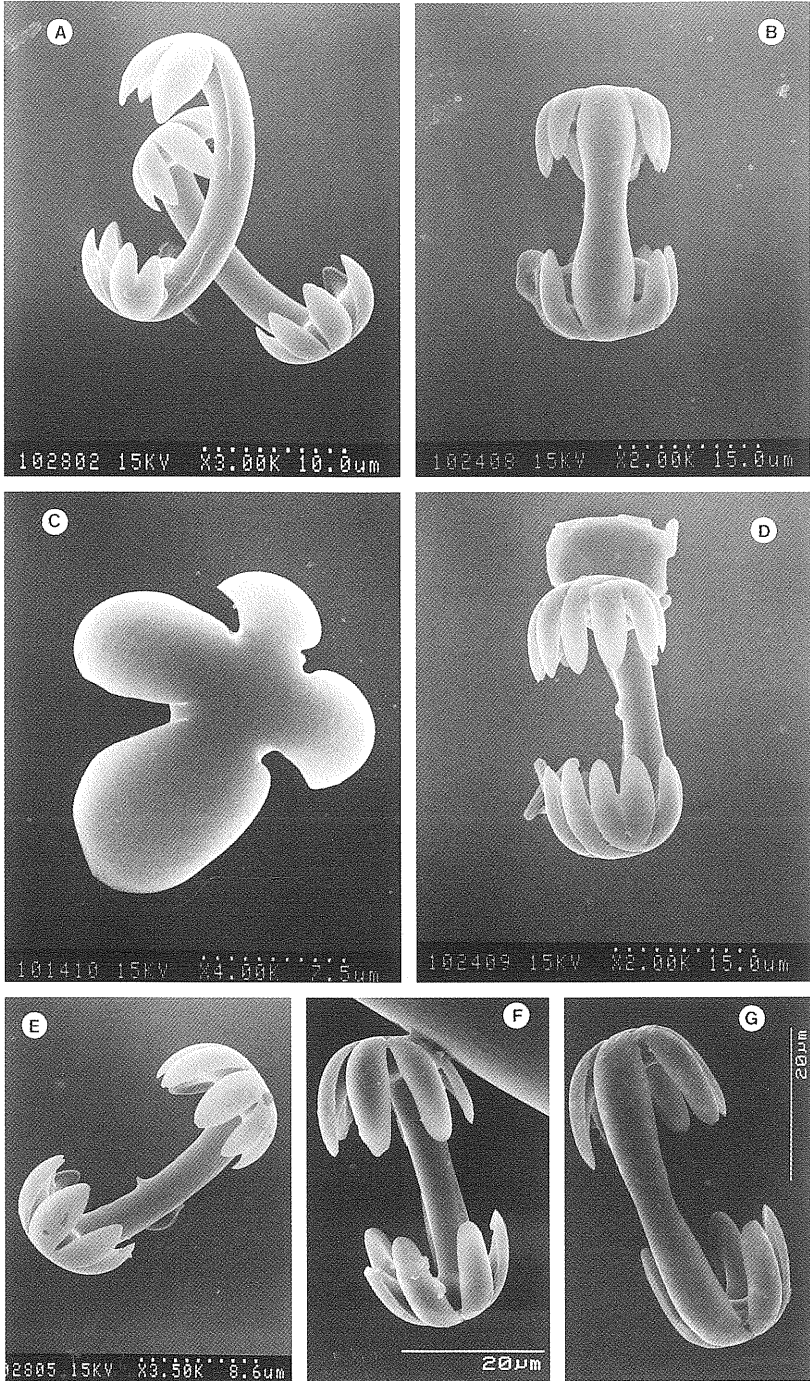


Fig. 10. Anchorate isochelae of *Discorhabdella*. A, B, C: *D. tuberosocapitata*. D, E: *D. hindei*. F, G: *D. incrustans*