

Didiscus verdensis spec. nov. (Porifera: Halichondrida) from the Cape Verde Islands, with a revision and phylogenetic classification of the genus *Didiscus* *

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Key words: Porifera, Halichondrida, *Didiscus*, Cape Verde Islands.

A new species of the circumtropical/subtropical genus *Didiscus* Dendy, 1922 is described from the Cape Verde Islands. Based on a phylogenetic analysis of all known species of the genus, using morphological and microscopical (including SEM) characters, it was demonstrated that the new species is closest to the eastern Mediterranean *D. styliferus* Tsurumai, 1968.

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Introduction

The genus *Didiscus* Dendy, 1922, was erected for *D. placospongioides* Dendy, 1922, characterized by the microscleres referred to as discorhabds, simple micro-oxeotes with one central disc and one, usually smaller disc between the centre and one of the apices. Prior to that date several authors already described sponges possessing similar spicules, and invariably they assigned them to the Hadromerid genus *Latrunculia*, viz.: *Latrunculia acerata* Ridley & Dendy, 1886, *Latrunculia clavigera* Kirkpatrick, 1900, and the fossil species *Latrunculia obtusa* Hinde & Holmes, 1891. Careful examination of *Latrunculia* microscleres (popularly known as "chessmann spicules"), however, made it clear that these are derived from spirasters, and not from microxea. Other details of *Latrunculia*, such as the skeletal architecture and the megasclere complement, show little similarity to "*Latrunculia*" *acerata/clavigera*, nor to *Didiscus placospongioides*. Recently, it was discovered that several *Didiscus* species show a high similarity in habit and skeletal architecture with the Halichondrid genus *Myrmekioderma* (Diaz *et al.*, in press), and consequently the genus is now firmly established as a member of that group (see for further details Van Soest *et al.*, in prep.).

Didiscus species have been reported from the tropical western Atlantic, the eastern Mediterranean, and the Indian Ocean; there is a dubious record from the Great Barrier Reef of a few stray discorhabds in a preparation of another sponge. In the material recently collected in the Cape Verde Islands (NNM's CANCAP-VII Expedition, 1986) a species of *Didiscus* was found, that appears to be undescribed. The purpose of the present paper is to describe it and compare it to its congeners. This comparison takes the form of a world revision and a cladistic analysis of the genus.

* CANCAP-project contribution no. 95.

Material

Didiscus verdensis spec. nov. : ZMA POR. 6935 (CV/D01A/11), CANCAP-VII Expedition, Ciudad Velha, São Tiago, Cabo Verde, 10 m. ZMA POR. 6953 (CV/D03/14), CANCAP-VII Expedition, Ilheus Rombos, Cabo Verde, 15 m. ZMA POR. 6987 (CV/D05A/04), CANCAP-VII Expedition, off Maio, Cabo Verde, 6 m.

Didiscus placospongioides: BMNH 21:11:7:112, Cargados Carajos, Indian Ocean (Dendy's holotype).

Didiscus aceratus: BMNH 87:5:2:79, Challenger Expedition, no locality (Ridley & Dendy's holotype). ZMA (013/IV/13), Snellius-II Expedition, Pulau Pulau Maisel, Banda Sea, eastern Indonesia, 10-15 m. ZMA (016/II/31), Snellius-II Expedition, Kaledupa Reef, Banda Sea, eastern Indonesia, 1-4 m. ZMA (016/II/32), Snellius-II Expedition, Kaledupa Reef, Banda Sea, eastern Indonesia, 1-4 m. ZMA (044/II/01), Snellius-II Expedition, Binongko, Banda Sea, eastern Indonesia, 1-4 m.

Didiscus anisodiscus: ZMA (152/III/20), Snellius-II Expedition, Guang, near Saleyar, Flores Sea, Indonesia, 4-10 m.

Didiscus styliferus: Hebrew University, Myk. 188, off N Coast Israel, 0-7 m (Tsunami's holotype). Mus. Giacomo Doria, Genova, ZZ.32, Zinzulusa Bay, southern Italy, Adriatic, 25 m.

Didiscus oxea: YPM 8968, Bahia, Brasil, 60 m (Hechtel's holotype). IDO Ac.405, Cuba (USNM fragment of Alcolado's holotype of *D. habanensis*). ZMA POR. 4889, Curaçao, 33m (Van Soest's holotype of *D. flavus*). ZMA POR. 4890, Curaçao, 10-15 m (paratype of *D. flavus*). ZMA POR. 4891, Curaçao, 10-15 m (paratype of *D. flavus*). ZMA POR. 4892, Curaçao, 12-16 m (paratype of *D. flavus*).

Methods

Sponges were examined microscopically by making tangential and perpendicular hand sections; spicule mounts were made by soaking in luke-warm sodium hypochloride (10% solution). SEM spicule preparations were made similarly, but with the added treatment with 20% nitric acid (see for further methodology: Buizer & van Soest, 1977). SEM skeletal preparations were obtained using a slightly modified form of the "thick hand section method of Wilkinson" (see Hooper et al., 1990): sections were gently placed in plastic pill-boxes with 10% sodium hypochloride for about two hours at room-temperature, after which time the chemical was removed by pipet and replaced by distilled water. Next, the section was exposed for a similar period to 30% hydrogen peroxide, after which this was replaced by 100% alcohol. This was evaporated immediately prior to coating. The recommended drying of sections between microscopic slides in a stove (Hooper et al., 1990) tended to flatten the sections and rendered them useless for our purpose.

Cladistic techniques are used according to Wiley (1981). The taxon-character matrix was improved time and again by using the computer-programs *PHYLIP* (Felsenstein, 1986) and *Tree-Tools* (Ellis, 1986).

Systematic descriptions

Class Demospongiae Sollas, 1888
 Subclass Ceractinomorpha Lévi, 1955
 Order Halichondrida Vosmaer, 1887

Emended pro: Halichondrida and Axinellidae partim sensu Lévi, 1973; see Díaz et al., in press.

Definition.— Demospongiae with plumoreticulate skeletons built of interchangeable styles, oxea and intermediate spicules.

Family Halichondriidae Vosmaer, 1887

Emended (pro: Halichondriidae and Hymeniacionidae partim sensu Lévi, 1973); see Díaz et al., in press.

Definition.— Halichondrida with a high spicular density, vague choanosomal spicule tracts, and many spicules in confusion.

Genus *Didiscus* Dendy, 1922

Definition.— Halichondriidae with discorhabds.

Remarks.— *Didiscus* is very closely related to *Myrmekioderma* Ehlers, 1870. Many species of the two genera show characteristic surface grooves bearing pores and oscules; they often follow a meandering or angular course. The skeletal architecture of both is also similar: a surface palissade or paratangential mass of smaller spicules (discorhabds and smaller oxea in *Didiscus*, smaller oxea only in *Myrmekioderma*) carried by a thin basal layer of tangential spicules. The crust is carried by irregular radiating tracts of larger megascleres, often quite confused depending of the amount of spongin, which may be considerable. The mesohyl of both is highly collagenous. Where *Didiscus* has discorabds as a distinguishing character, *Myrmekioderma* has one or more categories of (often sinuous) trichodragmata, and several species have spined smaller oxea. *Didiscus oxea* contains a characteristic and unusual biochemical compound called curcuphenol; it is not yet known whether other species of the genus exhibit similar compounds.

Didiscus verdensis spec. nov.

(figs. 1, 2e, pl. 1: figs. 1-4)

Material. — Holotype: ZMA POR.6935 (CV/D01A/11), CANCAP-7 Expedition, Ciudad Velha, São Tiago, Cabo Verde, 10 m. Paratypes: ZMA POR. 6935 bis, same data as the holotype; ZMA POR. 6953 (CV/D03/14), Ilheus Rombos, Cabo Verde, 15 m. ZMA POR. 6987 (CV/D05A/04), off Maio, Cabo Verde, 6 m.

Description.— Shape, size and consistency: Thinly (1-2 mm) incrusting. Surface irregular, but without obvious meandering grooves. Lateral expansion indefinite. Consistency soft.

Colour: yellow in live, beige in alcohol.

Ectosome: ill-developed, barely differentiated from the choanosome; spicules are predominantly tangential, confused, without any distinct arrangement.

Choanosome: relatively low spicular density; arrangement of the skeleton utterly confused with little or no visible spongin; spicules remarkably slender.

Spicules: basically there are the usual two sizes of megascleres and discorhabds;

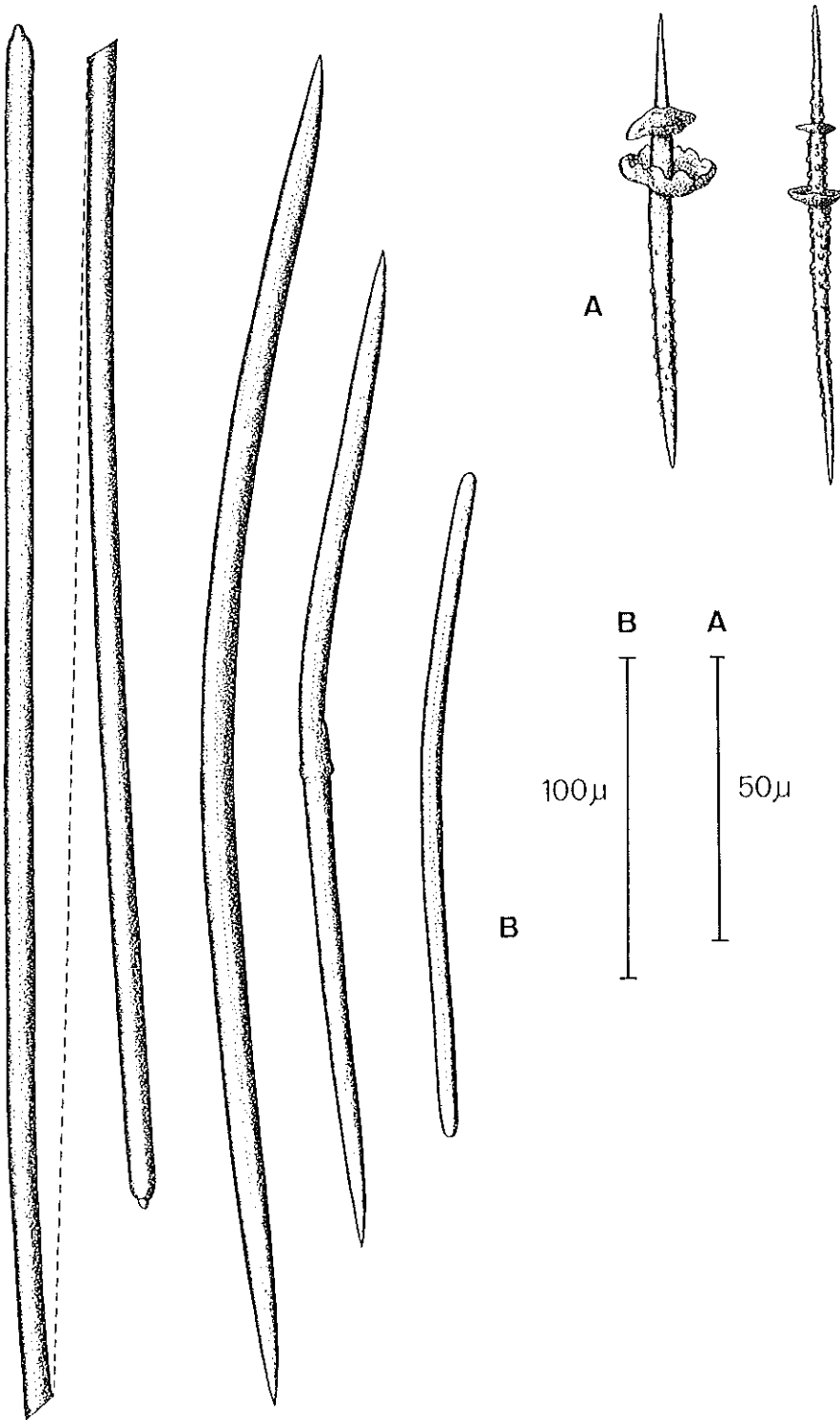


Fig. 1. Spicules of *Didiscus verdensis* spec. nov.

like in *D. styliferus* and *D. aceratus* the megascleres are extremely variable as to their apices, varying from bluntly rounded through stair-stepped to sharply pointed, but basically they are oxeotes.

Oxeotes of the large category: mostly oxea and styles, occasionally also strongyles: 430-1300/5-13 μm .

Oxeotes of the smaller category: often centrotylote, very frequently strongyles: 190-336/2-4 μm .

Discorhabds: long and slim, always sharply pointed, acanthose over most of their length except the apices, disc-rims often very irregular and ragged: 65-90/2- 2.5 μm , discs average 12 and 8 μm in diameter and they are typically curved inwards.

Ecology.— Incrusting coralline knolls at 6-15 m depth.

Etymology.— Name refers to the type locality.

Discussion.— The other species of *Didiscus* are briefly diagnosed and keyed out below. The new species shares the thinly incrusting habit, the variability of megasclere shape, and the incurved discs of the discorhabds with *D. styliferus* from the eastern Mediterranean. The two differ in the overall shape of the discorhabds (long, slim and sharp-pointed against short, relatively thick and blunt-ending), and in the thickness of the megascleres. *D. styliferus*, although thinly incrusting, bears distinct surface grooves and is a lot more elaborate in skeletal architecture. From Indian Ocean *D. aceratus* the new species differs in habit (thinly incrusting against massive), the proportion of strongylote megascleres (rare against very abundant), and the development of spongin (virtually absent against considerably developed). The discorhabds of *D. aceratus* are more heavily spined (also at the blunt apices) and short; their discs are not incurved. From western Atlantic *D. oxeata* the new species differs in habit (incrusting versus clump-like masses), the greater variability of the megascleres (against almost uniform oxea), and the pointed against the blunt nature of the fully-grown discorhabds. The other species of *Didiscus* show similar or even greater differences with the new species.

Didiscus placospongioides Dendy, 1922
(pl. 2: fig. 6)

Didiscus placospongioides Dendy, 1922: 135, pl.7 fig. 10, pl.18, figs. 3a-c; Vacelet & Vasseur, 1971: 107, fig. 64.

Description.— Massively incrusting. Colour in life unknown; in alcohol whitish. Surface strongly and angularly grooved, showing a polygonal pattern. Ectosome a thick tough crust, which breaks rather than tears. Choanosomal skeleton shows confused radial tracts carrying the ectosomal crust. Spongin moderately developed. Oxea variable, in two size categories, largest up to 1400/20 μm ; smallest about 400/11 μm , some centrotylote. The smaller oxea often malformed into "tylostyles". Discorhabds sharply pointed, acanthose in two "bands" near, but not on the apices, 90/5 μm . Discs 12 and 18 μm in diameter, ragged rims, more or less in one plane.

Distribution.— Only known from the Indian Ocean: Cargados Carajos (type locality) and Madagascar (Vacelet & Vasseur, 1971) (although the latter record is doubtful because of small spicule sizes quoted in the description).

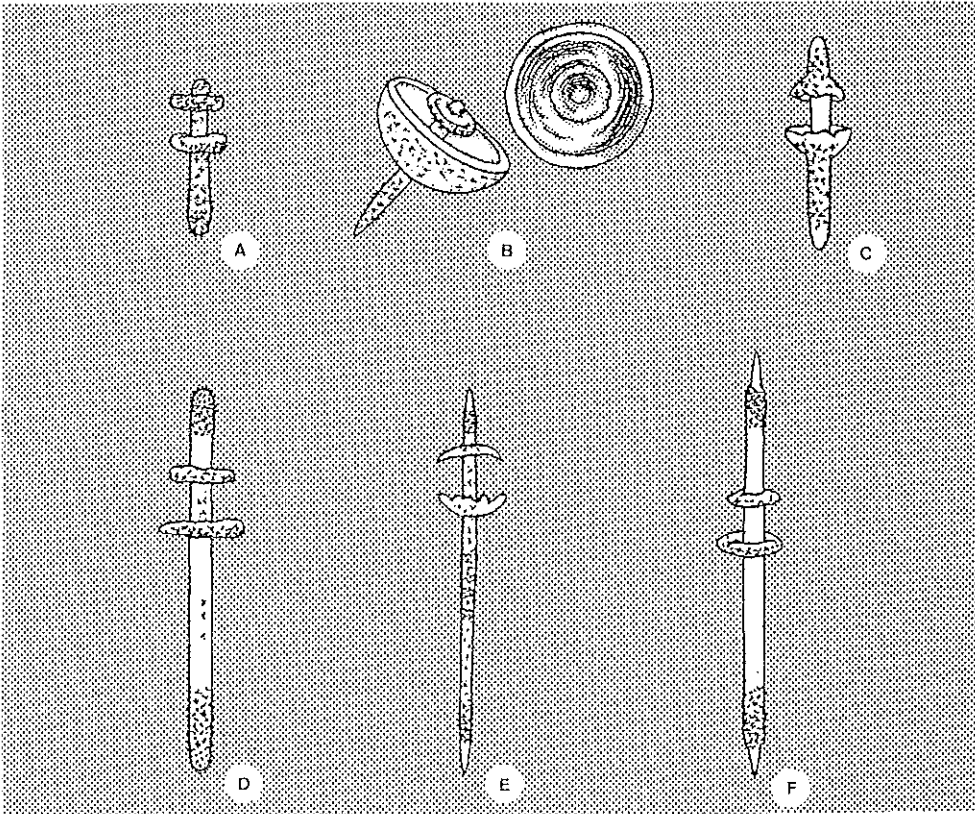


Fig. 2. Sketch drawings of discorhabds of *Didiscus* spp.: a, *D. aceratus*; b, *D. anisodicus*; c, *D. styliferus*; d, *D. oxedata*; e, *D. verdensis* spec. nov.; f, *D. placospongioides*.

***Didiscus aceratus* (Ridley & Dendy, 1886)**
(pl. 2: fig. 4)

Latrunculia acerata Ridley & Dendy, 1886: 492; 1887: 239, pl. 29 fig. 3.

Latrunculia clavigera Kirkpatrick, 1900: 354, pl. 14 fig. 2.

Didiscus styliferus; Vacelet & Vasseur, 1971: 107, fig. 65 (not of Tournamal, 1968).

Didiscus clavigerus; Vacelet & Vasseur, 1971: 106, fig. 63.

Unnamed discorhabd; Carter, 1879: pl. 29 fig. 20.

Description.— Massively incrusting to lump-shaped. Colour ochreous. Surface with thin grooves surrounding round hillocks. Ectosomal crust relatively thin, tough. Choanosomal skeleton with a lot of spongin binding spicule tracts into an irregular reticulation. Megascleres almost exclusively strongyles with a low proportion of styles: 850-1295/9-15 and 275-450/7-10 μm ; some "tylostyles" may be found. Discorhabds short, relatively robust, blunt ending, heavily spined including the apices: 25-54/2-6 μm , discs 8 and 12 μm , relatively regular rim, both in one plane.

Distribution.— Indian Ocean (Seychelles, Funafuti, Madagascar, Indonesia). The

type specimen is of unknown origin, but unlikely to be Atlantic as Dendy (1922) contended.

***Didiscus anisodiscus* Vacelet & Vasseur, 1971**
(pl. 2: figs. 1-3)

Didiscus anisodiscus Vacelet & Vasseur, 1971: 108, fig. 66.

Description.— Massively incrusting to lump-shaped. Colour white. Surface grooves deep, surrounding papilla-like hillocks. Ectosome leathery-tough. Choanosomal skeleton with thick radiating spicule bundles; little spongin. Megascleres oxea with a few stylote modifications: largest up to 1200/15, most smaller are 500-600/10, but there is a possible third category of 200-350/7 μm which was overlooked by Vacelet & Vasseur, 1971. Discorhabds small, almost entirely acanthose, including the blunt apices, 45/4 with extremely developed central disc of up to 30 μm in diameter, and tiny, almost apical smaller disc, 10 μm in diameter. The discs are finely granulated and have a regular rim.

Distribution.— Europa Island, western Indian Ocean; Indonesia.

***Didiscus styliferus* Tsurumal, 1969**
(pl. 1: figs. 5-6)

Didiscus placospongioides; Burton, 1936: 23 (not of Dendy, 1922).

Didiscus styliferus Tsurumal, 1969: 343, fig. 1; Pulitzer-Finali, 1983: 512.

Didiscus spec. Pulitzer-Finali, 1978: 51; 1982: 93.

Description.— Thinly incrusting. Colour yellow. Surface bears narrow angular grooves dividing the surface into polygonal areas. Ectosomal crust thin. Choanosomal structure confused. Larger megascleres predominantly styles, 500-1320/4-13 μm , smaller oxea and strongyles, with centrotylotes common and also some "tylostyles", 90-310/2-11 μm . Discorhabds short, blunt-ended, apices smooth, averaging 40-65/2-5 μm (according to Tsurumal up to 86 μm , but this cannot be confirmed), discs 10-12 and 5-9 μm .

Distribution.— Eastern Mediterranean: Israel, Egypt, Crete, Aegean Sea (pers. comm. Dr Eleni-Voultsiadou), Adriatic, Tyrrhenian Sea; so far not known from the well-investigated western Mediterranean. Examination of Pulitzer-Finali's (1982) slide from the Great Barrier Reef containing a few discorhabds has led to the assumption that it was contaminated by the Mediterranean species, because the discorhabds are closely similar. So far no actual specimens of Australian *Didiscus* have been reported.

***Didiscus oxcata* Hechtel, 1983**
(pl. 2: fig. 5)

Didiscus oxcata Hechtel, 1983:76, figs. 20-21.

Didiscus flavus van Soest, 1984:146, pl. 11 figs. 1-4, text-fig. 57.

Description.— Irregular knolls or lumps. Colour yellow. Surface smooth, with distinct meandering grooves which contract in alcohol. Ectosomal crust rather thin. Choanosome: pulpy-crumbly; architecture confused, with few distinct tracts, and little spongin. Megascleres predominantly oxea, 570-1370/8-20 μm and 220-400/3-4.5 μm ; some "tylostyles" may be present. Discorhabds large and thick, with blunt acanthose apices and largely smooth shafts, 55-80/4-6 μm ; discs 15-20 and 6-12 μm , more or less in one plane, with crenulated edges.

Distribution.— Tropical western Atlantic (Brasil, West Indies).

Didiscus obtusus (Hinde & Holmes, 1891)

Latrunculia obtusa Hinde & Holmes, 1891: 220, pl. 11 fig. 22.

Didiscus obtusus; Hinde & Holmes, 1891: 220.

Description.— This concerns a single discorhabd found in a fossil spicule mass dating from the Eocene/Oligocene of the South Island of New Zealand. Other than providing evidence of the long existence of the genus, it cannot be compared to the other species for lack of characters. The discorhabds seem not unlike large *D. aceratus* discorhabds.

Key to the living species of *Didiscus*

1. Megascleres predominantly oxea or stylotes 2
 - Megascleres predominantly strongyles; discorhabds short, stocky and heavily spined (fig. 2a) *D. aceratus*
2. Discs of the discorhabds of highly unequal diameter, bowl-shaped (fig. 2b); discorhabds < 50 μm in length *D. anisodiscus*
 - Disc diameters less different (usually within the range 6-20 μm) 3
3. Megascleres predominantly styles; discorhabds small (not over 60 μm), blunt-ended, discs incurved (fig. 2c) *D. styliferus*
 - Discorhabds over 60 μm in length 4
4. Full-grown discorhabds blunt-ended (fig. 2d) *D. oxea*
 - Discorhabds always sharply pointed 5
5. Megascleres unusually slender, with all intermediates between true oxea and true styles and strongyles; discorhabds thin, with disc edges frayed or malformed (fig. 2e) *D. verdensis*
 - Megascleres predominantly stout oxea; discorhabds likewise stout (fig. 2f) *D. placospongioides*

Cladistic analysis

Outgroups.— As argued above, the nearest outgroup is the genus *Myrmekio-*

derma Ehlers, 1870; for comparison several species of this genus have been studied (notably *M. styx* De Laubenfels, 1953 and *M. granulata* (Lamarck, 1814), but also *M. rea* (De Laubenfels, 1934) and *M. dendyi* (Burton, 1959) are well represented in the collections of ZMA). As a second outgroup *Spongosorites* Topsent, 1896 was studied as it is the nearest to *Myrmekioderma* and *Didiscus*; this is based on a phylogenetic analysis of the family Halichondriidae by van Soest et al. (in prep.). Several *Spongosorites* species were studied (e.g., *S. ruetzleri* (Van Soest & Stentoft, 1988) and *S. siliquariae* (Van Soest & Stentoft, 1988)).

Table 1. Taxon/character matrix for the phylogenetic analysis of *Didiscus* species.

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Taxa																
<i>Spongosorites</i>	0	0	?	0	?	?	?	0	?	1	0	0	?	0	?	0
<i>Myrmekioderma</i>	0	0	?	1	?	0	?	0	?	0	0	0	?	0	?	0
<i>placospongioides</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>D. oxcata</i>	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>D. verdensis</i>	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
<i>D. styliiferus</i>	1	0	1	0	1	1	1	1	1	0	0	1	0	0	0	0
<i>D. aceratus</i>	1	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0
<i>D. anisodiscus</i>	1	0	1	0	1	1	0	0	0	0	0	0	1	0	1	0

Characters (see table 1).— 1. Presence of discorhabds: although these are a synapomorphy for the genus, they are considered homologous with small oxea found in both *Spongosorites* and *Myrmekioderma*. Based on this assumption the ancestral condition of the discorhabd is: relatively long, pointed apices, spines on the shaft in zones leaving the apices smooth.

2. Megasclere size: the smaller category of megascleres in the outgroups dwindles down to less than 100 μm (condition 0); in *D. placospongioides* they do not become smaller than 400 μm (condition 1).

3. Apices of the discorhabds: as argued above, these are assumed pointed in the ancestral condition (0); blunt apices (1) occur in most species except *D. placospongioides* and *D. verdensis*; in the latter species that condition is regarded a reversal.

4. Smaller megascleres centrotylote (0) is found in *Spongosorites* and in most *Didiscus* species, except for *oxcata*; its absence (1) is considered an autapomorphy for that species.

5. Discorhabd size: in several species these are 60-100 μm (0), in *D. styliiferus*, *D. aceratus* and *D. anisodiscus* they are less than 50 μm (1); in *D. verdensis* there is an assumed reversal to larger size.

6. Zonal arrangement of spines on the shaft of the discorhabd: spines near the apices, but absent inbetween: this condition is found in *Myrmekioderma* and in *D. placospongioides*, and *D. oxcata*; the loss of it is considered a synapomorphy (1) for the remaining species.

7. Direction of disc curvature: most species have more or less parallel discs (0), or discs turned upwards; in *verdensis* and *styliiferus* discs are curved towards each other (1) (and sometimes even meet), which seems a distinct synapomorphy for the two.

8. Growth form: although notoriously variable and considered of little phylo-

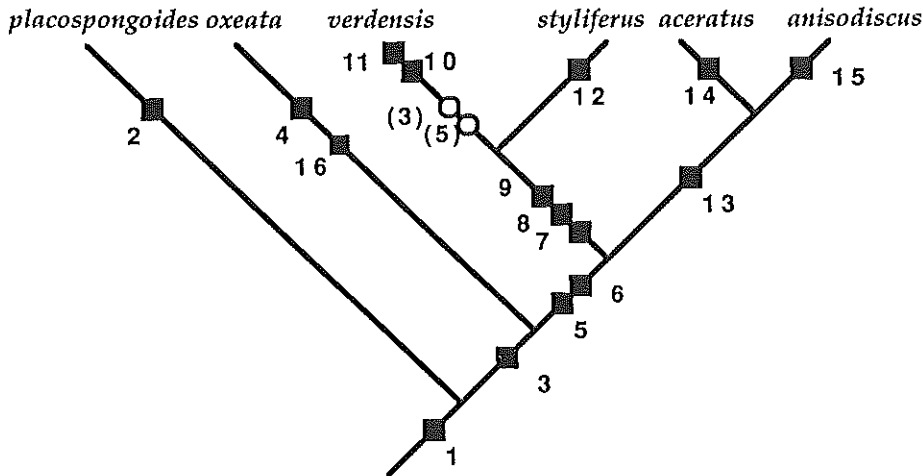


Fig. 3. Cladogram depicting the phylogenetic relationships of species of *Didiscus*; numbers refer to characters listed in table 1, and discussed in the text; black boxes are presumed apomorphies, open circles reversals.

genetic significance, Halichondriidae in general, and many species of *Didiscus* in particular exhibit massive, lumpy forms (0). Both *D. verdensis* and *D. styliferus* are thinly incrusting (1), and this is considered a synapomorphy of the two.

9. The discs of the discorhabds of most species tend to be somewhat ragged (0), but the malformed, frayed condition (1) usually found in discorhabds of *D. verdensis* and *D. styliferus* is considered a synapomorphy of those species.

10. Species of *Myrmekioderma* and most species of *Didiscus* show a system of surface grooves with pores and oscules (0); such grooves seem to be absent in *D. verdensis* (1).

11. Species of *Myrmekioderma* and most species of *Didiscus* have larger megascleres of up to 20-35 μm in diameter, and smaller megascleres 4-10 μm in diameter; *D. verdensis* has unusually thin megascleres of on the average 7 and 2.5 μm in diameter (1).

12. Although megascleres tend to have variable apices in many Halichondrids in general, in *Spongisorites*, *Myrmekioderma* and most species of *Didiscus* in particular, a predominance of true styles (1) such as found in *styliferus* is considered an autapomorphy of that species.

13. Most species have discorhabds with smooth parts (0); in *D. anisodiscus* and *aceratus* the discorhabds are entirely uniformly spined including the apices (1).

14. Megascleres may be oxete, stylote and strongylote in many Halichondrids, *Myrmekioderma* and *Didiscus*, but a predominance of strongyles (1) as found in *D. aceratus* is considered an autapomorphy of that species.

15. Disc sizes are variable in the different species, but the extreme expansion of the lower disc (1) in *D. anisodiscus* is considered an autapomorphy of that species.

16. *D. oxeata* has been shown to produce a unique biochemical compound called curcuphenol/curcudiol, but since the other *Didiscus* species have not been investigated it is an uncertain autapomorphy of that species.

The most parsimonious cladogram of the species is presented in fig. 3.

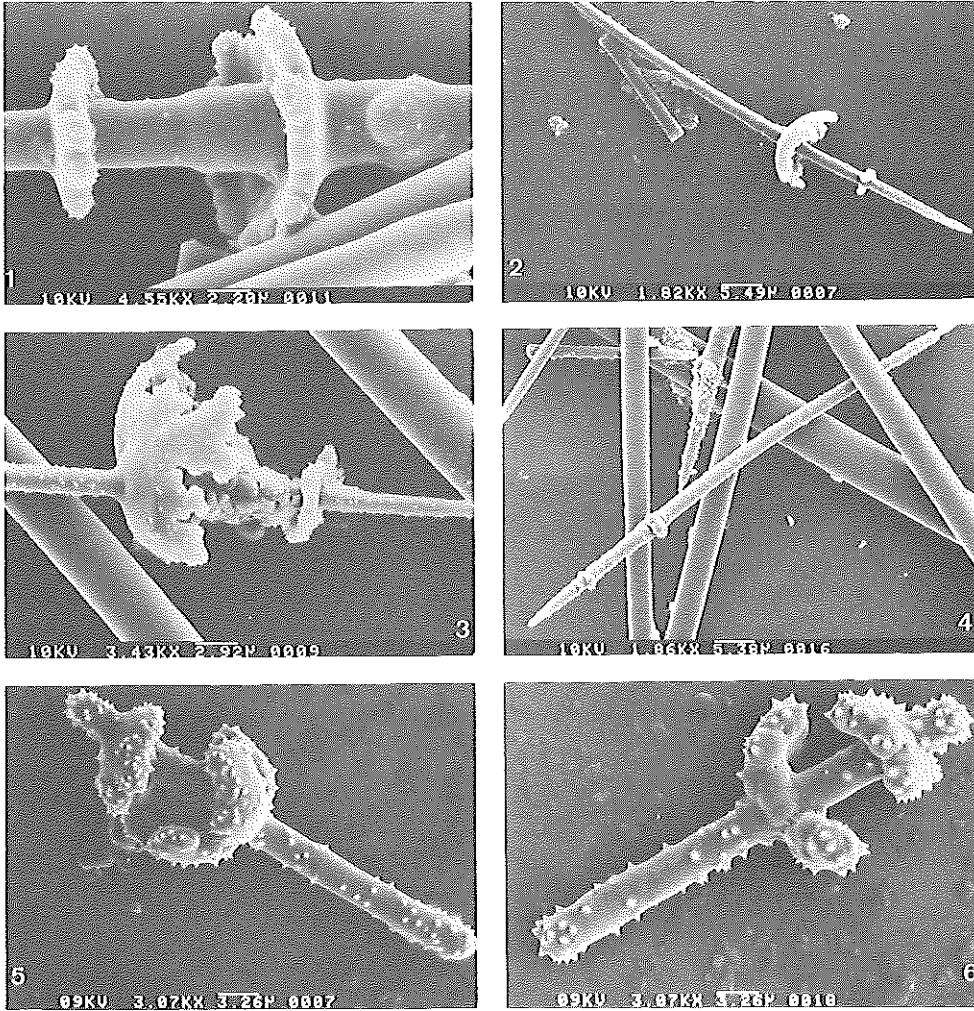


Plate 1, SEM photos of *Didiscus* discorhabds. 1-4, Discorhabds of *Didiscus verdensis* spec. nov.; 5-6, *D. styliferus* (taken from holotype).

Discussion

The new species shows many reduced properties: the thinly incrusting habit, the absence of a system of surface grooves, the absence of the usual ectosomal crust and more or less elaborate choanosomal architecture, the thinness of the spicules and the many malformations in the discorhabds; as a consequence the impression might be formed that the specimens could be reduced recruits of one of the other closely related species. However, the Western Atlantic species *D. oxeata* shows important differences in non-metric characters, and clearly cannot be considered closely related. The genus *Didiscus* is not known from the Mediterranean west of Naples, and not from the Atlantic coasts of West Africa (other than the Cape Verde Islands), although it is

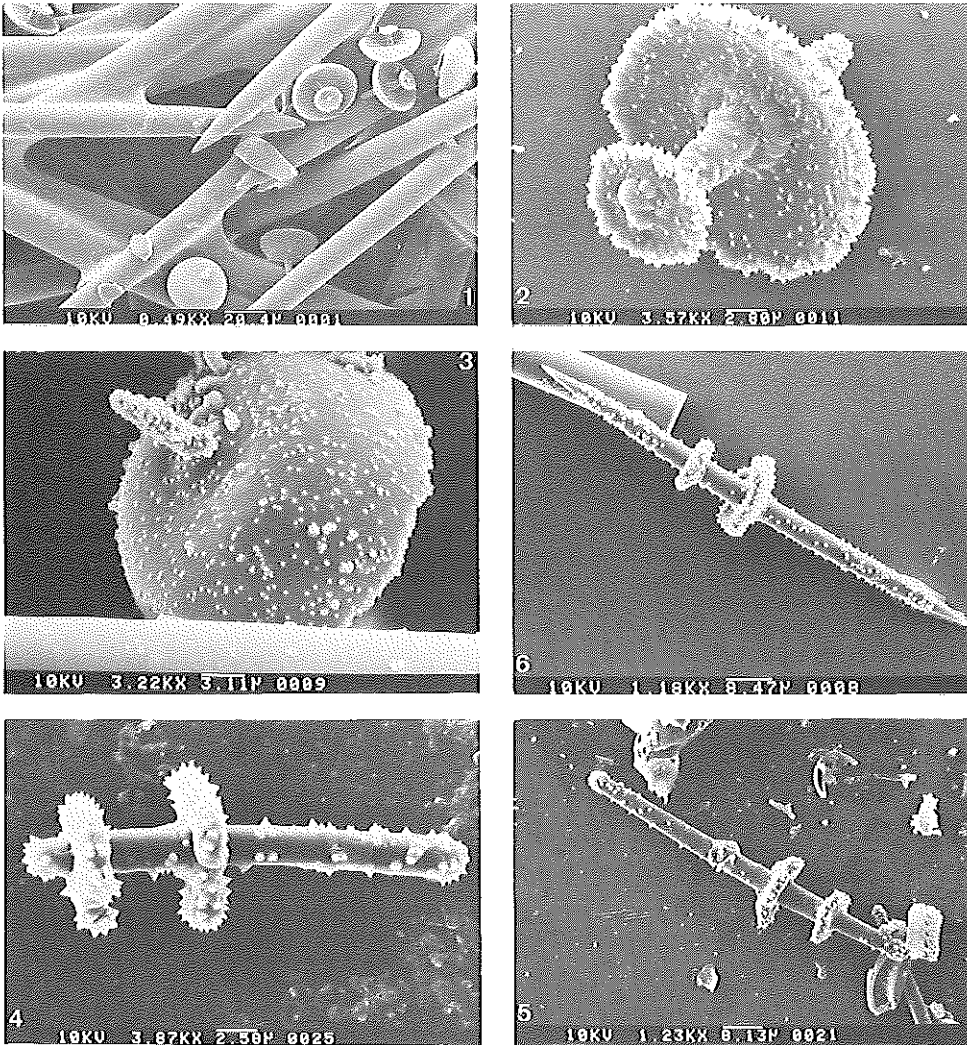


Plate 2, SEM photos of *Didiscus* discorhabds: 1-3, *D. anisodiscus*; 4, *D. aceratus*; 5, *D. oxeata*; 6, *D. placospongioides* (taken from holotype).

likely to occur there. Thus a clear zone devoid of *Didiscus* exists between the the distributions of the Cape Verdean species and its closest sister taxon, *D. styliferus*; both differ especially in the shape of the discorhabds, so conspecificity is not obvious. It is most likely that both are descendants from a Miocene-Pliocene ancestor, which diverged into two daughter taxa after the occurrence was restricted to West African and eastern Mediterranean refugia by the Pleistocene cooling.

The genus *Didiscus* is known at least from the upper Oligocene of southern New Zealand, demonstrating that the genus existed outside the Tethys area. The cladogram shows that there must have been species of *Didiscus* before the Tethys broke up, because *D. oxeata*, *D. verdensis*, *D. styliferus*, *D. aceratus* and *D. anisodiscus* show a pattern which is in accordance with the historical sequence of events of the break-up

(Harland et al., 1982), whereas the pattern of *D. placospongioides* is clearly different and must stem from the Tethys period or before.

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Dr M.C. Díaz (Univ. South California) kindly put a fragment of the holotype of *D. oxata* at our disposal; Dr N. Ben-Eliahu (Hebrew University) sent the holotype of *D. styliferus* on loan; Dr K. Rützler (United States National Museum) donated a fragment of *D. habanensis*; Miss S.M. Stone (The Natural History Museum) allowed the study of the holotypes of *D. placospongioides* and *D. aceratus*; Dr G. Pulitzer-Finali (Genoa) allowed the study of Mediterranean species of *Didiscus*.

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