

## OCEANAPIA SAGITTARIA FROM THE GULF OF THAILAND

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*Oceanapia sagittaria* (Sollas) is redescribed from shallow water, soft benthic communities surrounding the limestone islands of Ko Samui, southwest Gulf of Thailand, with additional new records from southern Papua New Guinea. Morphological redescription is based on live material, highlighting in particular a unique, tentacle-like, dendritic series of exhalant canals with its complex of oscules on the apex of the primary (open) fistule. Evidence is presented to suggest that this capitate structure serves as both a complex series of exhalant pores and canals, and an asexual dispersal propagule. Scanning electron microscope studies also detected an additional morphology of toxa microscleres, not previously recorded for the species, and studies of skeletal structure indicate that the species is more appropriately included in the family Oceanapiidae (Porifera, Demospongiae, Haplosclerida), being the sixth member of the 'biminia' group of *Oceanapia* species. The distribution and comparative morphology of this species group are discussed. □ *Oceanapia sagittaria*, Porifera, Demospongiae, Haplosclerida, Oceanapiidae, Gulf of Thailand, oscular structure, asexual propagule, taxonomy.

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Species of *Oceanapia* are common, with more than 50 nominal species recorded for the Indo-west Pacific region alone, relatively abundant in both soft and hard substrates, and widely distributed (known throughout the world's oceans: Antarctic, ampho-Atlantic, Mediterranean, Red Sea, western and eastern Indian Ocean, Indo-Malay archipelago, Indo-west Pacific, Japan, New Zealand and eastern Pacific Ocean). However, many of these species are poorly known: most *Oceanapia* species have been described only from preserved material; in many cases they have been described only once; in several instances species descriptions are based solely on incomplete individuals (e.g. fistules); and in some cases species were created on the basis of only minor differences in spicule morphometrics from their siblings. These problems are common to many groups of sponges, but possibly they are most apparent in the relatively morphologically depauperate Haplosclerida, including *Oceanapia*. Whilst reexamination of the type material for many of these species is usually necessary (the original descriptions being very brief and/or very poor), generally this process does no more than confirm or refute those characters already described for the species. Consequently, *Oceanapia*

appears to contain many species differing from each other only slightly in any of their major characters (growth form, spicule morphology, spicule size, skeletal structure), whereas in situ observations of live populations are much more informative in discriminating sibling species. In this present paper we redescribe *Oceanapia sagittaria* (Sollas) from live populations in the Gulf of Thailand, including in situ observations of intact capitate, oscular structures peculiar to this species, whereas the species had previously been described only from preserved material (Sollas, 1902; Burton, 1934; Bergquist, 1965), virtually all fragmented. We also describe some observations of populations from southern Papua New Guinea.

### METHODS

Preparation of material for light microscopy and scanning electron microscopy (SEM) is described elsewhere (Hooper, 1991). The descriptive language system DELTA was used to prepare the taxonomic description (Dalwitz & Paine, 1986). Abbreviations used in the text are as follows: BMNH, Natural History Museum, London; NCI Q66C-, US National Cancer Institute shal-

low water collection program (Australian Institute of Marine Science, Townsville, contract) – primary material now in Smithsonian Institution, NTM and QM; NMV, Museum of Victoria, Melbourne; NTM, Northern Territory Museum, Darwin; PMBC, Phuket Marine Biology Center, Phuket, Thailand; QM, Queensland Museum, Brisbane; ZMA, Zoological Museum, Amsterdam.

## SYSTEMATICS

### Family OCEANAPIIDAE van Soest

#### *Oceanapia* Norman, 1869

*Oceanapia* Norman, 1869 [type species: *Desmacidon jeffreysii* Bowerbank, 1866 (= *D. robusta* Bowerbank, 1866 (Carter, 1882))].

*Rhizochalina* Schmidt, 1870 [type species: *Rhizochalina oleracea* Schmidt, 1870].

*Phloeodictyon* Carter, 1882 [type species: *Phloeodictyon isodictyiforme* Carter, 1882].

*Biminia* Wiedenmayer, 1977 [type species: *Oceanapia toxophila* Dendy, 1922].

### DIAGNOSIS

Haplosclerida, predominantly fistulose, with a unispicular, tangential, subisotropic ectosomal skeleton, often detachable, and an irregular, longitudinal and/or transverse system of multispicular tracts with a subisotropic reticulation of single spicules dispersed between forming the choanosomal skeleton; microscleres may include sigmas and toxas (modified from de Weerd, 1985).

### REMARKS

The genus, its contents, generic synonymy and relationships with other oceanapiids have been discussed at length by several contemporary authors (Bergquist & Warne, 1980; van Soest, 1980; de Weerd, 1985; Wiedenmayer, 1989; Fromont, 1991). The synonymy cited above is now generally accepted, although de Weerd and van Soest (1986) also note that *Rhizochalina* and *Oceanapia* s.s. could be considered two 'convenient' subgenera, differentiated by their consistency and development of their spongin fibre skeletons; the first having strongly developed spongin fibres and the second with a pulpy choanosomal skeleton. However, these apparent differences are not clear-cut for all species (i.e. several species in both nominal genera have intermediate character states), and formal recognition of these 'convenient' subgenera may not be fully justified. In fact, there is equal justification

for recognising alternative 'convenient' subgenera within *Oceanapia*, based on microsclere diversity for example (e.g. *Biminia* with toxas and sigmas, *Oceanapia* (s.s.) with only sigmas, and *Phloeodictyon* (s.s.) without microscleres), but this system also lacks a sound phylogenetic basis (de Weerd and van Soest, 1986).

#### *Oceanapia sagittaria* (Sollas)

(Figs 1-20)

*Gellius sagittarius* Sollas, 1902: 212, pl.15, fig.7.

*Adocia sagittaria*: Burton, 1934: 538.

*Orina sagittaria*: Bergquist, 1965: 155-157, figs 18a-c.

### MATERIAL EXAMINED

NTM Z3679, QM G301346, QM G300640, PMBC 9210: E side of northern island, Ko Wao Yai Group Marine National Park, NW of Ko Samui, S Gulf of Thailand, 9°47.0'N, 99°41.0'E, 6 June 1990, 12.5m depth, coll. M. Riddle, S. Sorokin, J.N.A. Hooper, SCUBA (stn JH-90-016). Unregistered material: Motupore I., southern Papua New Guinea, various dates 1987, coll. M. Kelly-Borges.

### DISTRIBUTION, SUBSTRATE AND DEPTH RANGE

This species is only recorded from Kepulauan Bidang, north of Penang, Andaman Sea (Sollas, 1902), Ko Samui, southern Gulf of Thailand and Motupore Island, southern Papua New Guinea (present study), Koror I., Palau Islands, central western Pacific (Bergquist, 1965), and the Low Isles, Great Barrier Reef (Burton, 1934). It is probably a widely distributed Indo-Malay species, but because of its small, relatively cryptic, burrowing habit the extent of its distribution is still not fully known. The recorded depth distribution is from shallow subtidal waters to approximately 14m. The Thailand collection site – located 50m from shore, at 12m depth on sand and coral rubble slope, rising to coral dominated slope and *Porites* heads, at base of limestone cliffs rising to greater than 70m altitude – contained a population of this species with many specimens, although the species was not seen in any other sites in this region. In southern Papua New Guinea the species is also relatively abundant, found in muddy silt substrates.

### DESCRIPTION

*Shape*. Sponge burrowing into soft sediments; slightly enlarged basal root submerged completely below substrate, with one or more fistules protruding above surface (Fig. 1). Basal root (or 'body' of sponge) expanded, bulbous, subspheri-



FIG. 1. *Oceanapia sagittaria* (specimen NTM Z3679) in situ (photo M.Riddle).

cal, more-or-less solid, attached to detritus in soft sediments (Fig. 6). All collected specimens consisted only of single primary fistules, with or without smaller, vestigial, secondary (blind) fistules, erect on single basal roots; primary fistule cylindrical, tubular, hollow, with cavernous central lumen, widest at base, tapering to constriction below apex; fistules simple-flagelliform, flexible, fleshy, mucous-covered in life, although more fragile, thin-walled when preserved. Apex

of primary fistule with unusual capitate structure (= capitum), which in life is extremely fragile, sub-spherical, membranous on its exterior surface, completely translucent, clearly showing dendritic fibre and canal system within (Fig. 1); membranous capitum collapses upon collection, leaving only dendritic fibres and spicule tracts, tapering at their ends (Figs 7,8). Dimensions: basal root 11-23mm diameter; primary (open) fistule 33-54mm long, 2-4.5mm external diameter, 1.5-4.0mm internal diameter; secondary (blind) fistules 8-18mm long, up to 2.5mm external diameter; capitum (in life, when intact) approximately 20mm diameter, when preserved (i.e. dendritic fibres situated on apex of fistule) 7-11mm long, 4-10mm wide. Growth form consistent for all known specimens.

*Colour.* Live colouration of basal root dark brown or black; fistules dark red-brown (Munsell 5R 4/10); fibre bundles inside translucent capitum pale red in life (2.5R 6/10) (Fig. 1). Live colouration relatively consistent. Colour of specimens in ethanol grey-brown.

*Oscules.* Oscules confined to distinct areas on membranous capitum at apex of sponge; terminal, situated at the ends of dendritic fibre bundles (which probably surround/support exhalant canals), protruding from apex of sponge (Fig. 6); primary fibre bundles thickest at centre of capitum, bifurcating only once or twice within membranous capitum, with each exhalant canal slightly swollen at apex, and each bearing a single oscule; oscules more-or-less evenly distributed

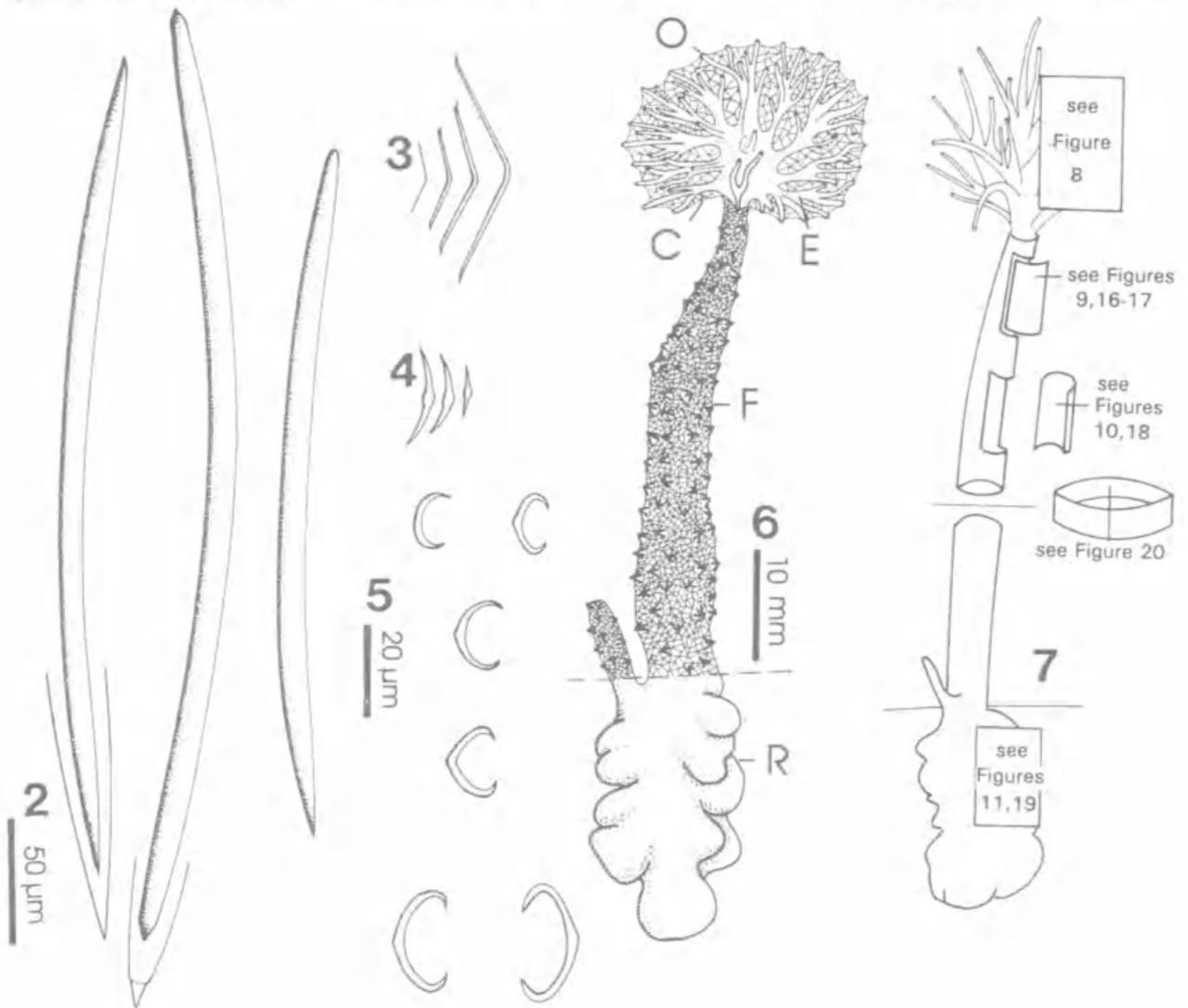
over entire capitum, minute, 0.2-0.5mm diameter, but not observable in preserved material (i.e. capitum collapses). Inhalant pores not seen.

*Texture.* Fistule soft, elastic, flexible, fragile, easily torn both in life and when preserved; basal root solid, woody, inflexible, easily crumbled.

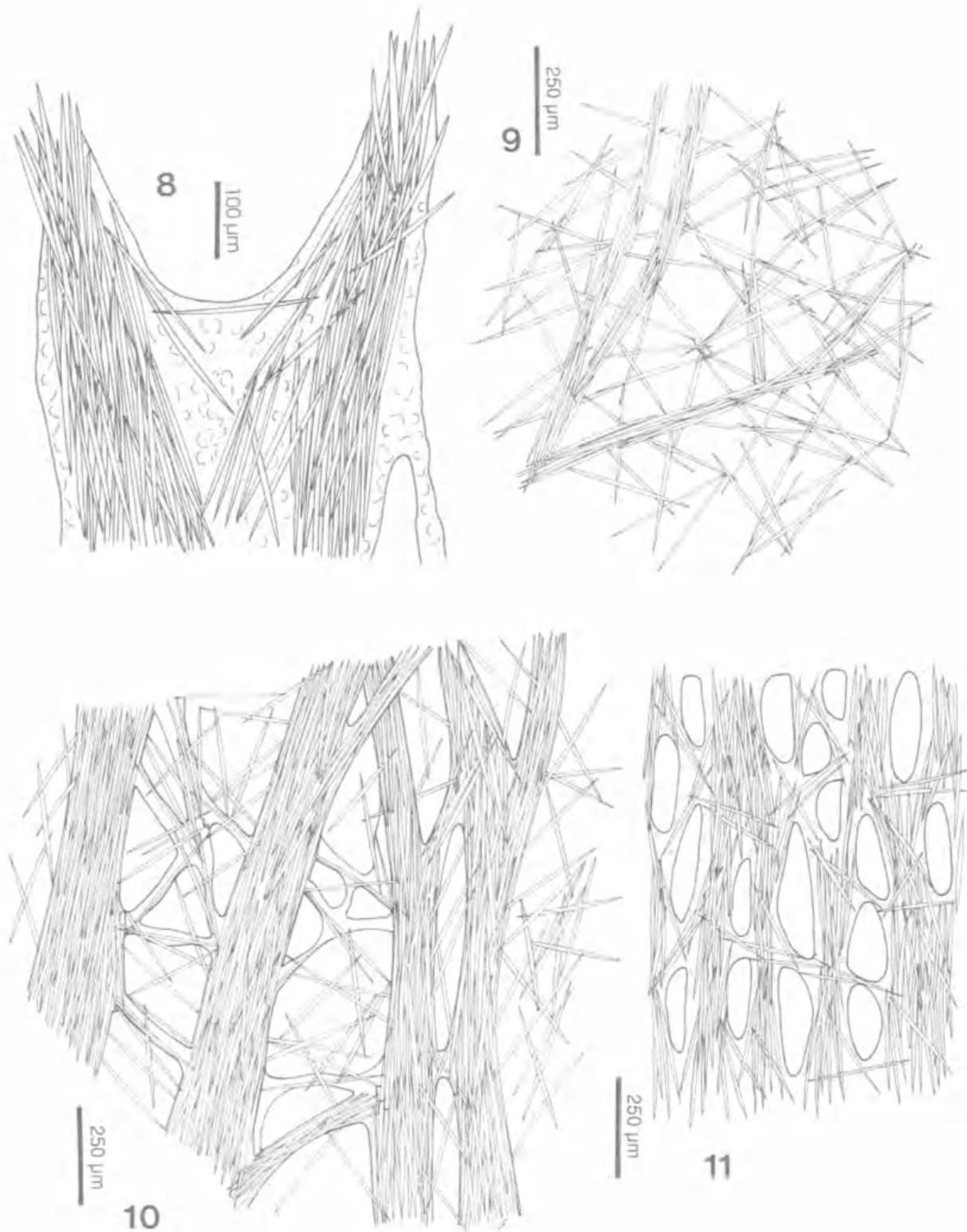
*Surface characteristics.* Fistule fleshy, collagenous, pigmented, microconulose, prominently sculptured in life (Fig. 6), with prominent tangential spicule skeleton forming a microscopic, triangular, cobweb-like network (Figs 9,16-17), although appearing more shaggy when preserved. Membraneous capitum skin-like,

glabrous in life, with faint, fragile, irregularly isodictyal, tangential spicule skeleton; capitum is translucent in life and choanosomal fibres clearly visible through membraneous surface. Basal root dense, spiculose, heavily pigmented, with smooth surface, and loose, irregular, tangential spicule skeleton, although the latter is not a prominent feature.

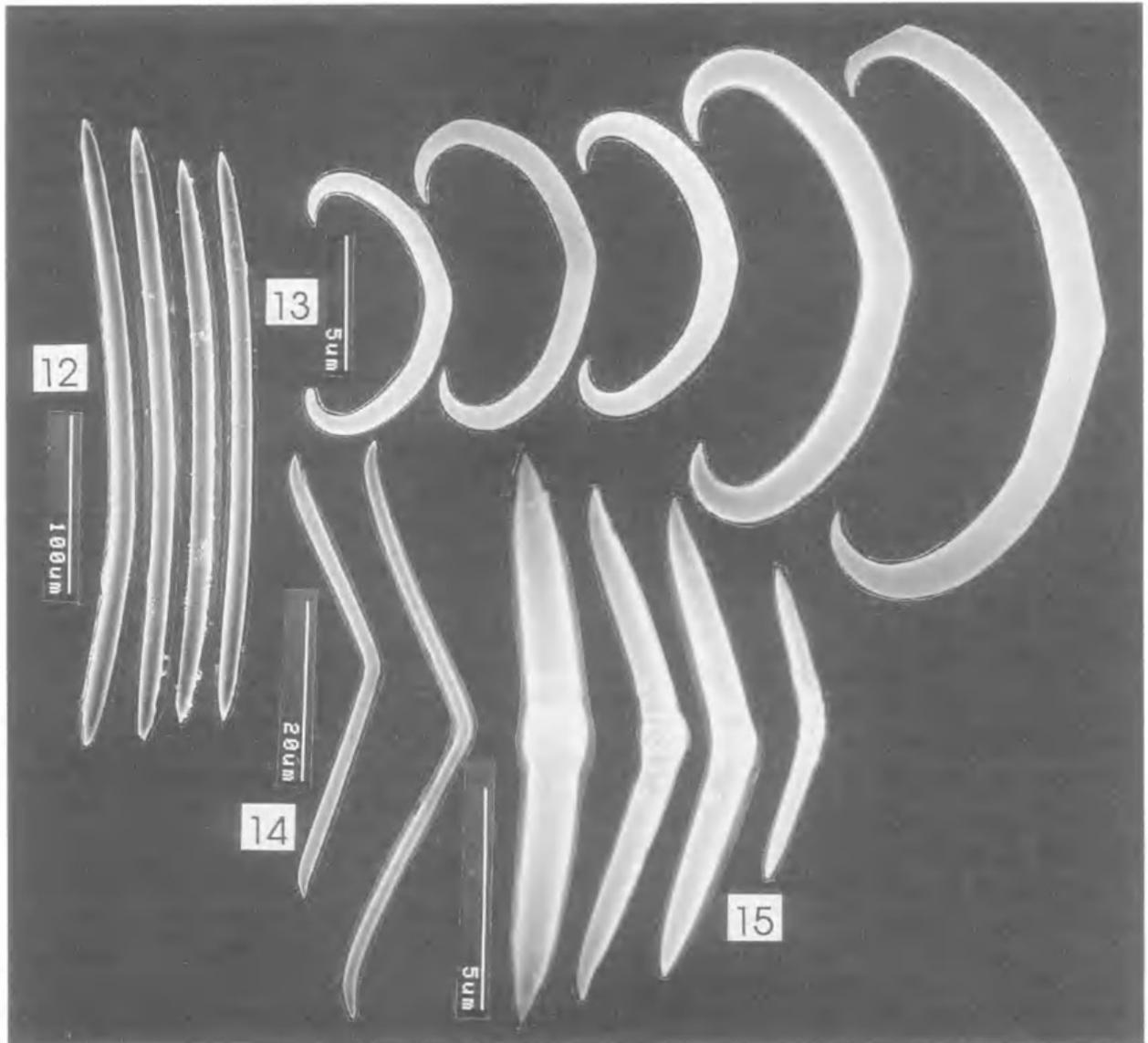
*Ectosome and subectosome.* Ectosomal skeleton with both unispicular and paucispicular tangential tracts of oxeads (Figs 9,17). Capitum, when intact, with unispicular, subisodictyal, tangential ectosomal tracts, without any support underlying



FIGS 2-7. *Oceanapia sagittaria*, spiculation and morphology. 2, oxeas (and rare anisoxeas). 3, long toxas. 4, robust, centrangulate toxas. 5, centrangulate sigmas. 6-7, interpretation of live, whole specimen (from Fig. 1), with stippled basal region indicated below substrate. 7, guide to location of sections depicted in figures 8-20. F=tubular fistule, C=membraneous capitum, R=basal root, with woody exterior and pulpy interior, O=oscule, E=exhalant canal.



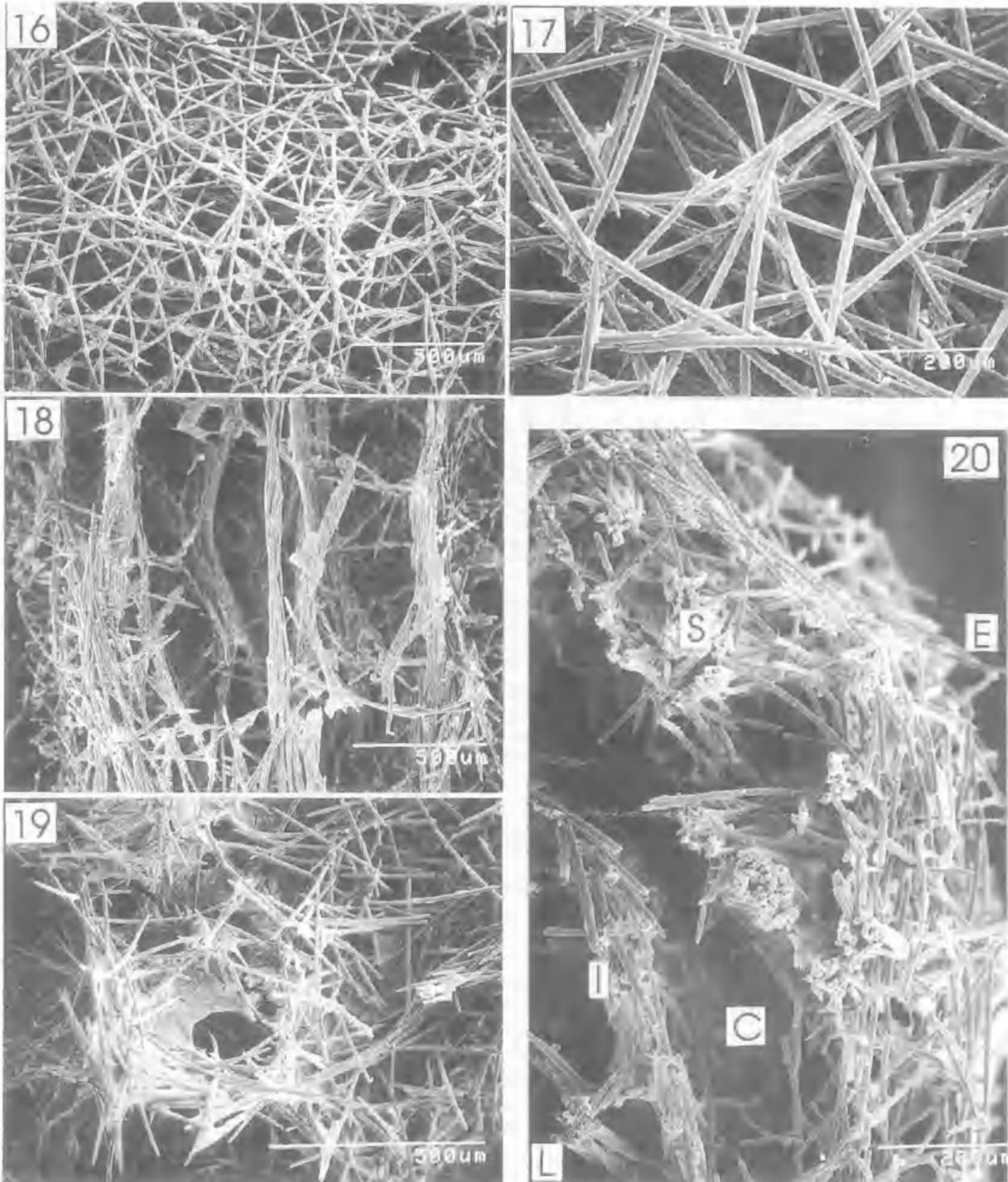
FIGS 8-11. *Oceanapia sagittaria*, interpretation of regional skeletal structures. 8, tip of capitulum in preserved condition, showing ascending spicule bundles supporting individual exhalant canals (oscles collapsed). 9, external wall of fistule, showing unispicular, isotropic overlying skeleton and multispicular supporting tracts of subectosome. 10, internal wall of fistule, showing multispicular choanosomal tracts, interspersed with unispicular, isotropic spicules. 11, section through basal root (or 'body' of sponge, burrowing into substrate), with reticulate, pulpy architecture.



FIGS 12-15. *Oceanapia sagittaria*, scanning electron micrographs of spicules. 12, oxeas. 13, centrangulate sigmas. 14, long toxas. 15, robust, centrangulate toxas.

ectosomal skeleton (unlike most other parts of the skeleton). Fistule with both uni- and paucispicular tracts of oxeas tangential to surface, with multispicular tracts visible just below surface (Fig. 9), and a prominent cavernous area between ectosomal (unispicular and paucispicular) and choanosomal (multispicular) regions (Fig. 20). Basal root with dense, disorganised, unispicular, tangential tracts and dense, multispicular, tracts below the ectosome (Fig. 19), both close to surface. Extra-fibre spicules (i.e. those not associated with the tangential unispicular ectosomal or multispicular subectosomal skeletons) lie in sparse, single or paucispicular subsodiectyl tracts throughout the skeleton (Fig. 10).

*Choanosome.* Choanosomal skeletal structure reticulate, composed of relatively homogenous, dense spicule tracts differentiated into primary (longitudinal) and secondary (transverse) skeletal lines. Primary tracts long, multispicular, 70-160 $\mu\text{m}$  diameter, joined by shorter pauci- or multispicular secondary tracts, 30-50 $\mu\text{m}$  diameter, together forming irregular elongate or elliptical meshes, 450-1500 $\mu\text{m}$  long, 120-250 $\mu\text{m}$  wide. Extra-fibre spicules scattered between choanosomal meshes, in unispicular, subsodiectyl tracts. Basal root ('body' of sponge), pulpy, occupying most of 'body' diameter, with central lumen of fistules extending several millimetres into 'body', and with large, cavernous meshes pro-



FIGS 16-20. *Oceanapia sagittaria*, scanning electron micrographs of skeletal structure (see Fig. 7 for location of sections). 16, tangential, unispicular, isotropic reticulation of ectosome, exterior wall of fistule. 17, close-up of same. 18, multispicular, mostly longitudinal reticulation of interior wall of fistule. 19, cavernous, pulpy choanosomal skeleton of basal root ('body' of sponge). 20, cross-section through fistule wall, showing exterior unispicular tracts (E), with subectosomal support (S), a cavernous region in between (C), interior multispicular tracts of choanosome (I) lining lumen of fistule (L).

duced by reticulation of longitudinal and transverse skeletal tracts, up to 0.5mm diameter (Figs 11,19). Fistules with greatly compressed choanosomal skeleton, attached directly to the interior of fistule walls (Figs 10,18). Spongin fibre skeleton greatly reduced; spongin fibres typically very light (Figs 10,11), whereas spicules between major tracts (i.e. forming the subsodiectyl skeleton) usually bound together by sparse, granular, lightly pigmented collagen. Collagen in mesohyl abundant, darkly pigmented, dispersed evenly throughout, slightly granular, packed with microscleres. Choanocyte chambers minute, ovoid, 12-26 $\mu$ m diameter, lined by sigma and toxo microscleres.

*Megascleres.* Relatively long, thin, smooth oxeas (Figs 2,12), slightly curved, with fusiform points or occasionally slightly constricted near apex and bearing a sharp, mucronate, abrupt point; very homogenous in size throughout skeleton (length 329-363.4-393 $\mu$ m; width 9-10.8-12 $\mu$ m).

*Microscleres.* Two categories of microscleres present, both very abundant. C-sigmata (Figs 5,13), of a single size class, varying only slightly in size, usually very small, thin, typically centranulate, never s-shaped or contort, completely smooth (length 8-12.6-22 $\mu$ m, width 0.5-1.2-2 $\mu$ m).

Toxas include two morphs, the larger more common: (i) long, thin, v-shaped toxas (Figs 3,14), with wide angular central curvature, and reflexed points (at extremities only) (length 28-41.9-68 $\mu$ m; width 0.5-1.2-2.5 $\mu$ m); (ii) short, thin, robust toxas (Figs 4,15), with only slight angular central curvature and slightly swollen (centranulate) at centre, and with straight (unreflexed) points (length 8-13.7-23 $\mu$ m; width 0.5-0.9-1.5 $\mu$ m).

*In situ observations.* Field and laboratory observations were made over a period of several weeks in 1987 (M.K.B.). In the field, the capitum is easily dislodged from the apex of the fistule with only moderate movement of the water column above the specimen. Several dislodged capitata structures were observed lying on sand, in coral reef interstices and seagrass beds in the vicinity of Motupore Island. Laboratory observations on several intact specimens suggest that the capitum may have an asexual reproductive function. Several observations were made: 1, several capitata structures were carefully detached from transplanted aquarium specimens, through gentle movement of the water column directly above specimens. After detachment, capitata structures

rolled over the aquarium floor until they became wedged in substrate; 2, after 24 hours of resting on the substrate the dendritic exhalant canal tubes, easily visible within the capitum (Fig. 1), extended towards and became attached to the substrate, forming a plate-like, basal, anchoring structure; 3, 36-48 hours after detachment these spherical capitata structures deflated, slightly flattened at the apex, and spread laterally into a thickened plate with single apical oscule.

Field observations in the Gulf of Thailand (J.N.A.H. and M.R.) also noted that these capitata structures are elaborate exhalant devices. Small particles of silt and other detritus were observed to be periodically expelled from the small oscules scattered over the capitum. Ostia (inhalant pores) were not seen.

#### REMARKS

*Oceanapia sagittaria* is unique amongst all oceanapiids (in fact, as far as known, amongst all sponges), in having the peculiar capitata structure on the apex of its primary fistule. Bergquist (1965: 155) first hypothesised that these 'terminal caps', apparently observed free floating in the Palau Islands, might be asexual dispersal mechanisms. We confirm this idea in the present study, and suggest that this structure is the first documented case of a specialised asexual propagule recorded for the Haplosclerida, although many cases of 'unspecialised' surface and basal buds are known for several Hadromerida (e.g. *Polymastia* (Battershill & Bergquist, 1990), *Tethya* (Bergquist & Kelly-Borges, 1991), *Aaptos* (Bergquist, 1968)).

The holotype of *O. sagittaria* was apparently originally deposited in the Zoological Museum at Cambridge University, but this material has not been mentioned since Sollas's (1902) publication and it is unknown if it still survives. A spicule preparation of the holotype is also apparently located in the Natural History Museum, London (BMNH 1938.8.7.3), but this preparation contains no details of skeletal structure (F. Wiedenmayer, pers.comm.). Although *O. sagittaria* has now been described from three separate collections, only the description of Bergquist (1965), based on preserved material, is adequate by modern standards. Sollas (1902) provided an extremely brief description, essentially only describing spicule shape and size, without any useful information on skeletal structure. Oxeas were cited as 300-350 $\times$ 10-13 $\mu$ m, sigmas 12-16 $\mu$ m long, and toxas were 49 $\mu$ m long. Burton (1934) did not provide any details of the Great

Barrier Reef material, but merely compared his and Sollas's fragments. Bergquist's (1965) more detailed description of Palau Islands specimens gave spicule measurements as: oxeas (325-375 × 5.5-10 μm), centrangulate sigmas (10.5-20.5 μm long), and toxas (36-50 μm long). These dimensions, compared to those seen in the Gulf of Thailand specimens, indicate that the species is relatively homogeneous across its range, although live colouration differs slightly: Burton (1934) reported that Great Barrier Reef material was magenta and ultramarine, whereas both the present specimens and those described by Bergquist (1965) were simply red-brown or bright red, respectively.

*Oceanapia sagittaria* has been previously included with the family Chalinidae Gray (or its synonym Adocidae de Laubenfels), whereas it is clearly a member of the Oceanapiidae and consequently defined in this family in the present study. The Chalinidae have a more-or-less regular, unilayered, unispicular, isotropic, tangential ectosomal skeleton, with three-sided spicule meshes. In *Oceanapia* this peripheral skeleton may also be regular, isodictyal, with vaguely triangular meshes, but the tangential layer of spicules is substantially more dense and the nodal spongin, prominent in many species of Chalinidae, is usually absent (Fig. 16). Similarly, choanosomal structure in the Chalinidae is ladder-like, with uni-, pauci- or multispicular tracts, whereas in *Oceanapia* primary ascending fibres are multispicular, supporting the dense tangential ectosomal skeleton, and supplemented by a secondary (isotropic) reticulation of single spicules lying between the main fibres (Figs 10, 11, 18) (de Weerd, 1985).

In the strict sense, the present species belongs to the nominal genus *Biminia*, in having both centrangulate sigmas and toxa microscleres in a fistulose, reinforced oceanapiid skeleton. However, de Weerd (1985) and de Weerd & van Soest (1986) argue that these microscleres may represent the retention of a primitive character and hence not valid at the generic level. They suggest that the genus should be dropped into synonymy with *Oceanapia* as the two nominal genera are virtually identical in all other respects. Several other haplosclerids have both sigma and toxa microscleres, including species of Chalinidae (e.g. *Orina*) and Callyspongiidae (e.g. *Callyspongia*). *Orina* lacks the distinctive pulpy, reinforced, multispicular choanosomal skeleton of *Oceanapia*, having instead a unispicular, isotropic choanosome, and *Callyspongia* has a dis-

tinctive network of tangential primary, secondary, and occasionally tertiary fibres in the ectosomal skeleton, and typically regularly reticulate, wide-meshed, choanosomal fibres cored by single or few spicules. Both Burton (1934) and Wiedenmayer (1977) discuss examples of this convergence between *Oceanapia* (as *Biminia*), *Orina* and *Callyspongia* further.

An alternative point of view, offered by de Weerd & van Soest (1986), is that the distribution of 'biminias' may reflect a possible Tethyan distribution of their common ancestor, although they are sceptical about whether this combination of characters is an apomorphy for *Oceanapia* [as inferred by Wiedenmayer (1977) and Hooper (1984)], or whether it is a synplesiomorphy and thus contains no phylogenetic information [as proposed by van Soest (1980)]. Further analysis of this possibly ancestral, possibly Tethyan distribution should be made by comparing the distributions of both the 'biminia' and non-biminid groups of *Oceanapia*, and the comparative distributions of the *Orina* and *Reniera* groups of Chalinidae. However, much of the type material relevant to this analysis, presently unavailable, firstly requires re-examination.

In addition to *O. sagittaria* there are five other species of *Oceanapia* that fit in the 'biminia' group: *Oceanapia toxophila* Dendy, 1922:45 from Providence I., Seychelles Is, western Indian Ocean (holotype BMNH 1921.11.7.37 re-examined); *O. stalagminis* (Wiedenmayer, 1977:124) from the Bahamas; *O. voita* (Hoshino, 1981:122) from Japan; *O. macrotoxa* (Hooper, 1984:55) from the Timor and Arafura Seas, northwest Australia (holotype NMV F51373); and *O. cancap* de Weerd & van Soest, 1986:39 from the Madiera region, West Africa, southeast North Atlantic. In addition to these taxa, re-examination of Ridley's (1884:424) material of '*Gellius fibulatus*' from Torres Strait, Qld (BMNH 1822.2.23.281) found that it is neither a chalinid nor conspecific with *Reniera fibulata* Schmidt, 1862, but belongs to Oceanapiidae and furthermore appears to be identical to *O. macrotoxa*. The identity of an Indonesian specimen collected by the Siboga expedition (ZMA POR 1709), cited as *O. toxophila* by de Weerd (1985:81), is not certain, but it too is possibly conspecific with *O. macrotoxa*. An alternative point of view is that these three nominal Indo-west Pacific 'biminia' species, *O. toxophila*, *O. macrotoxa* and *O. voita*, may be geographic variants of a single, widely distributed species, extending from the Seychelles Islands to Japan, Indonesia, northwest and northeast Australia,

Apart from the peculiar capitum seen in *O. sagittaria*, there are few major differences between any of the 'biminia' species in external morphology, skeletal structure, spicule geometry or spicule size (as noted by Hooper, 1984: table 1). Thus, it would be equally justifiable to synonymise all six known 'biminia' species as it would be to combine the three Indo-west Pacific species on the basis of these conventional morphometric characters. For the present we maintain all these species in the 'biminia' group, but recognise that only more comprehensive collections of *Oceanapia* throughout the Indo-Pacific may discover material with intermediate characteristics, resolving present doubts.

Apart from the peculiar capitum, *O. sagittaria* is most similar to *O. toxophila*. However, oxeas are sharply pointed, fusiform, or occasionally mucronate in the present species, whereas in *O. toxophila* they are hastate or rounded; oxea size is relatively homogeneous within both species but substantially larger in *O. sagittaria*; microscelere dimensions are similar in both species (see dimensions below for *O. toxophila*), although *O. toxophila* has both c-shaped and contort sigmas, and *O. sagittaria* was discovered to have a morphologically distinct, smaller category of centrangulate, robust toxas, not previously described for the species. Although these differences in spicule size and geometry could be construed as being relatively trivial, they are certainly as substantial as any of the differences between all other 'biminia' species.

Morphological characteristics of other 'biminia' species are as follows. *Oceanapia toxophila* Dendy has a tubular, burrowing, globular, simple base, with very thin, single fistules on each end of the body (the larger, open fistule is apical, the smaller, blind fistule is a basal rootlet); fistules up to 50mm long, 5mm diameter; ectosomal skeleton is a detachable, thin, unispicular, subisodictyal crust; choanosomal skeleton contains both reticulate, multispicular bands and a dense feltwork of subisodictyal spicules; oxeas hastate or rounded, mostly blunt (265-315×5-12µm); microscelers are only moderately common; sigmas very small, c-shaped or contort (12-26×0.5-1.5µm); toxas sharply angular at centre, straight arms, slightly reflexed points (12-55×0.5-2.5µm) (redescribed from the holotype BMNH 1921.11.7.37 (RN XX.2) and Dendy (1922) in part).

*Oceanapia stalagmitis* (Wiedenmayer) has a semi-incrusting, burrowing, massive base, with multiple, short, open and blind fistules on upper surface, rhizome-like blind fistules on under sur-

face; fistules up to 17mm long, 10mm diameter; ectosomal skeleton a dense, subisodictyal, unispicular layer over a denser detachable crust; choanosomal skeleton an irregular reticulation of both stout and thin fibres, with unispicular subisodictyal spicules dispersed between; oxeas usually sharply pointed, fusiform (100-155×3.5-5µm); microscelers abundant; sigmas centrangulate, c-shaped (11-32×0.5-1µm); toxas small, slight central curvature, straight arms, very slightly reflexed points (10-32×0.5-1µm) (Wiedenmayer, 1977).

*Oceanapia ooita* (Hoshino) has a massive, subspherical, burrowing base, with numerous, open, wide fistules on upper surface, and rhizome-like, blind fistules on under surface; fistules up to 40mm long, 8mm diameter; ectosomal skeleton dense, unispicular, subisodictyal; choanosomal skeleton with densely packed, longitudinal spicule tracts, interdispersed with subisodictyal single spicules; oxeas homogenous, abruptly pointed, hastate (180-218×7-9µm); microscelers abundant; sigmas c-shaped, centrangulate (14-35µm up to 1µm); toxas slightly curved at centre, straight arms, straight points (up to 45µm, thin) (Hoshino, 1981).

*Oceanapia macrotaxa* (Hooper) has a burrowing, massive, subspherical base with many long, thin, open and blind fistules on the upper surface, and smaller, thinner, rhizome-like blind fistules (rootlets) on the under surface; fistules are up to 60mm long, 8mm diameter; ectosomal skeleton is a thick, detachable, unispicular, subisodictyal crust; choanosomal skeleton with multispicular tracts, some ascending as well as uni- or paucispicular, subisodictyal tracts dispersed between; oxeas are divided into two indistinct size classes, fusiform to subhastate, mostly sharply pointed (94-260×1.5-7µm, 171-279×6-11µm); microscelers abundant; sigmas are small, centrangulate, c-shaped (9-35×0.5-2.0µm); toxas have angular central curves, straight arms and reflexed points (8-82×0.4-3.5µm) (Hooper, 1984).

*Oceanapia cancap* de Weerd and van Soest is burrowing, fistulose, although the base is unknown; fistules are open, single or bifurcate, up to 80mm long, (?) 50mm diameter; ectosomal skeleton unispicular, tangential, subisodictyal; choanosomal skeleton (only known for fistule walls) is longitudinal, branching and anastomosing, multispicular tracts with interdispersed subisodictyal single spicules; oxeas fusiform, sharply pointed (up to 320×8µm); sigmas c-

shaped, centrangulate (20µm, thin); toxas with slight central curvature, straight arms, slightly reflexed points (50-75µm, thin) (de Weerd and van Soest, 1986).

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