Systema Porifera: A Guide to the Classification of Sponges, Edited by John N.A. Hooper and Rob W.M. Van Soest

Family Clionaidae D'Orbigny, 1851

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Clionaidae (Demospongiae, Hadromerida) receives a new definition by accepting *Spheciospongia* and massive species previously assigned to *Spirastrella* (Spirastrellidae). A recently described genus, *Cervicornia* (for *Alcyonium cuspidiferum* Lamarck) is included here and distinguished by its specialized incurrent fistules and endopsammic choanosomal pulp. *Clionaopsis* new name is suggested to replace the preoccupied [*Clionopsis*] Thiele. *Spheciospongia* remains distinct for its pore sieves. All other genera are separated by their spicule complements which include tylostyles (with some oxeote or stylote modifications or additions) as megascleres, and delicate (compared to Spirastrellidae) spirasters, amphiasters, smooth and spiny microxeas, and bent or spiral, smooth or spiny microstrongyles and microrhabds as microscleres. Eight genera are considered to be valid.
Keywords: Porifera; Demospongiae; Hadromerida; Clionaidae; *Cervicornia*; *Cliona*; *Clionaopsis*; *Cliothosa*; *Pione*; *Spheciospongia*; *Thoosa*; *Volzia*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

[Clionidae] d'Orbigny, 1851: 209 (preocc. by Clionidae Rafinesque, 1815 (Gastropoda)). [Clioniadae] Gray, 1867a: 524 (*lapsus*). Spirastrellidae *sensu* Ridley & Dendy, 1886: 490. Thoosidae Rosell & Uriz, 1997: 350. Clionaidae d'Orbigny, 1851 (emended by Bouchet and Rützler, 2002).

Definition

Excavating Hadromerida with tylostyles and a great variety of microscleres; microscleres, including spirasters, amphiasters, microxeas, spiral microstrongyles, and derivatives may be lacking altogether.

Diagnosis

Hadromerida with limestone-excavating capability, having tylostyles as principal megascleres, in some genera accompanied by oxeas or styloid modifications. Microscleres may be absent entirely or in some specimens or populations. If present, they include spirasters, amphiasters, microxeas, microrhabds, or raphides; some spirasters display secondary branching of spines, microrhabds may be smooth or microspined, straight, bent, or spiral.

Scope

Eight genera are here assigned: *Cervicornia, Cliona, Clionaopsis, Cliothosa, Pione, Spheciospongia, Thoosa* and *Volzia*. Two (*Cervicornia, Spheciospongia*) were previously placed in the Spirastrellidae. Several thickly encrusting and massive species formerly assigned to the genera *Anthosigmella* Topsent, 1918, and *Spirastrella sensu lato* (Ridley & Dendy, 1886; 1987), fall to the clionaid genera *Cliona* or *Cliothosa* (Rützler, 1990; Rosell & Uriz, 1997).

History and biology

Historically, the family Clionaidae was applied to sponges with capacity for excavating limestone substrata, despite the fact that many members had spicule complements that were radically different from that of the type genus *Cliona*. For instance, de Laubenfels (1936a: 154) diagnosed the Clionaidae as sponges with spiculation of *Spirastrella* in the family Choanitidae (=Spirastrellidae), with tylostyles as megascleres and spirasters as microscleres, but set off from the latter "on the basis [that they] bore holes in calcareous material and live in the resulting cavities". Yet in discussing the scope of the family, de Laubenfels (1936a: 155) lists genera such as *Aka* (for *Acca* Johnson), which has only oxeas and is now widely considered a haplosclerid (cf. *Aka* and *Siphonodictyon*, Phloeodictyidae) (Rützler & Stone, 1986). Today we know that species of *Aka* (and *Siphonodictyon*) are potent destructors of reef coral (Rützler, 1971), but also that members of other sponge groups that are clearly not related to *Cliona*, for instance, the Poecilosclerida *Paracornulum* and *Zyzzya* (Rützler & Stone, 1986; Schönberg, 2000) are able to efficiently excavate limestone.

Boring into the calcareous substratum results in a three-dimensional network of interconnected chambers or galleries below the substrate surface. The substrate chambers are filled with sponge 'tissue' and spicules without orientation. Papillae are often fortified by contractile cells and specially arranged megascleres (e.g., tylostyles in bouquets or in a palisade), but not by prominent layers of microscleres (as in the Spirastrellidae). In gamma-stage sponges, some megascleres are organized in loose tracts radiating toward the surface; microscleres are dispersed throughout or occur near the surface or along major canals.

Limestone excavation is accomplished by chemical etching compounds that are secreted by pseudopodial processes of special etching cells and help liberate minute (up to about 60 μm) chips (Rützler & Rieger, 1973; Pomponi, 1980). These chips are expelled with the excurrent water, only 2–3% of the calcium carbonate is removed in dissolved form. The remaining cavities or series of chambers (galleries) have characteristically pitted walls and are occupied by the sponge. Communication with the water column is maintained through ostia- and oscula-bearing papillae that protrude slightly from the substrate surface but can fuse to form a continuos sponge crust (beta stage). Systematists may get confused by non-boring sponge species that live cryptically in abandoned clionaid cavities.

Most clionaids have simple ostia and oscula for water exchange but there are some modifications to accommodate special

living habits. Sponges in alpha-stage of excavating (Vosmaer, 1932) develop separate ostial and oscular papillae which puncture the substratum surface, the former bearing many ostia, the latter only one osculum. Sponges in the genus *Spheciospongia*, which excavate rock substrata initially and live on sandy bottoms with high sedimentation rate, are distinguished by pore sieves. These sieves, already apparent in the papillate alpha stage, may help avoid clogging of the actual ostia which are located in the vestibules below. *Cervicornia* was introduced for sponges with an uncommon morphology and life style, also an adaptation to living on sediment bottoms. Large, epibenthic incurrent fistulas serve a pulp-like choanosome that is completely buried in sand or shell and sends root-like exhalant tubes deep into the substrate (Rützler, 1997).

Clionaid sponges typically live in their burrows and connect to the outside world through the papillae. Papillae may fuse and extend to encrusting habit (beta stage). Some species become massive with age or after the original substrate piece has been outgrown (gamma stage). The original incurrent papillae may still show as wart-like structures in gamma-stage sponges although the calcareous substrate is no longer visible.

Remarks

In this treatment, emphasis is put on spicular and structural features and not the excavating capacity alone to assign genera. The presence of tylostyles is the governing character and not the multitude of microscleres. For other genera that excavate limestone, see Alectonidae (e.g., *Alectona*), Phloeodictyidae in the Haplosclerida (*Aka/Siphonodictyon*), and Acarnidae in the Poecilosclerida (*Paracornulum, Zyzzya*).

The distinction between Spirastrellidae, Clionaidae, and Placospongiidae in this revision is further supported by 28Sr RNA-genetic analysis (Chombard, 1998).

KEY TO GENERA

(1) Sponges excavating chambers in limestone substrates, with ostial and oscular papillae remaining at the surface (alpha stage), or forming continuous encrustations (beta stage), or masses (gamma stage) that grow beyond the original substrate piece; without specialized aquiferous structures except, in some species, the original papillae 2
Sponges massive, without endolithic chambering in the adults, with specialized aquiferous morphology 7
(2) Spicules include oxeas 3
Spicules do not include oxeas 5
(3) Oxeas are spiny microxeas, located in the chambers (criss-cross fashion), and are accompanied by straight or sinuous spiny microrhabds ..... ***Pione***
Oxeas are smooth and form a palisade in the papillae 4
(4) Spiculation is restricted to tylostyles and oxeas, no microscleres ..... ***Volzia***
Spiculation includes spirasters in addition to tylostyles and oxeas ..... ***Clionaopsis***
(5) Microscleres are raphides or spirasters, or missing altogether; spirasters may include diplastrose modifications or have lost spines entirely (sinuous microstrongyles) ..... ***Cliona***
Microscleres are amphiasters or euasters 6
(6) Microscleres are two types of amphiasters: stout, smooth, nodulose, and thin-rayed with terminal branching ..... ***Cliothosa***
Microscleres are microspined amphiasters and smooth, thin-rayed oxyasters ..... ***Thoosa***
(7) Sponges irregularly massive, with cribiporal chones and simple but often multiple oscula ..... ***Spheciospongia***
Sponges form large, branched, antler-like inhalant fistules and amorphous endopsammic masses with exhalant stolons ..... ***Cervicornia***

CERVICORNIA RÜTZLER & HOOPER, 2000

Synonymy

Cervicornia Rützler & Hooper, 2000: 342.

Type species

Alcyonium cuspidiferum Lamarck (by original designation).

Definition

Clionaidae with specialized, ectosomal incurrent fistulas, abundant robust tylostyles, and minute uncommon spirasters and derivatives.

Diagnosis

Clionaid sponges with large, smooth, inhalant fistulas protruding from the substratum and buried (endopsammic) choanosomal pulp. Exhalant stolons end underground. No alpha or beta stages are known. With large tylostyles arranged in dense tracts in the fistulas, without orientation in the choanosome. Small and rare spirasters and amphiasters located in ectosome and canal linings.

Previous review

Rützler & Hooper, 2000.

Description of type species

Cervicornia cuspidifera (Lamarck) (Figs 1, 2).

Synonymy. *Alcyonium cuspidiferum* Lamarck, 1815: 168. *Spirastrella cuspidifera*; Topsent, 1933: 41, fig. 4, pl. 2, fig. 4. *Xestospongia tierneyi* (de Laubenfels); Wiedenmayer 1977B: 117, fig. 130, pl. 15, fig. 3, pl. 16, fig. 1. (Not *Prianos tierney* de Laubenfels, 1953a = *Spheciospongia vesparium*). *Spheciospongia cuspidifera*; Pulitzer-Finali, 1986: 94, figs 22, 23; Vicente *et al*., 1991: 217, figs 3d, 4; Rützler, 1997: 1392, figs 1–2. *Cervicornia cuspidifera*; Rützler & Hooper, 2000: 342.

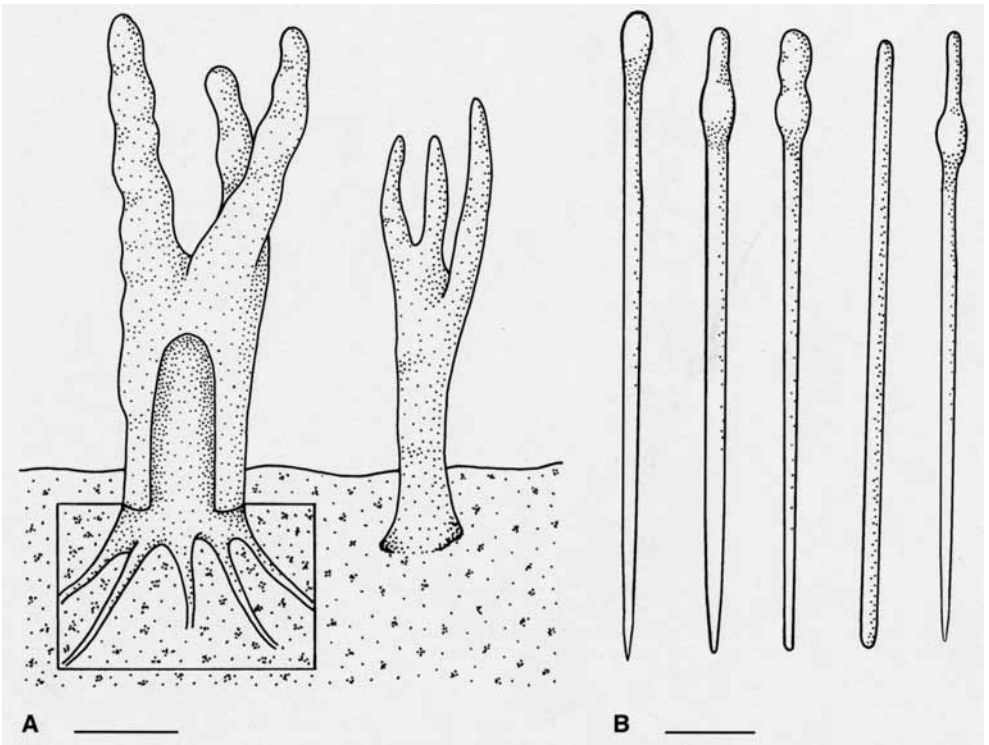

Fig. 1. *Cervicornia cuspidifera,* habitus and anatomy. A, schematic of habitus *in situ* (scale 5 cm). B, tylostyles (scale 50 μm).

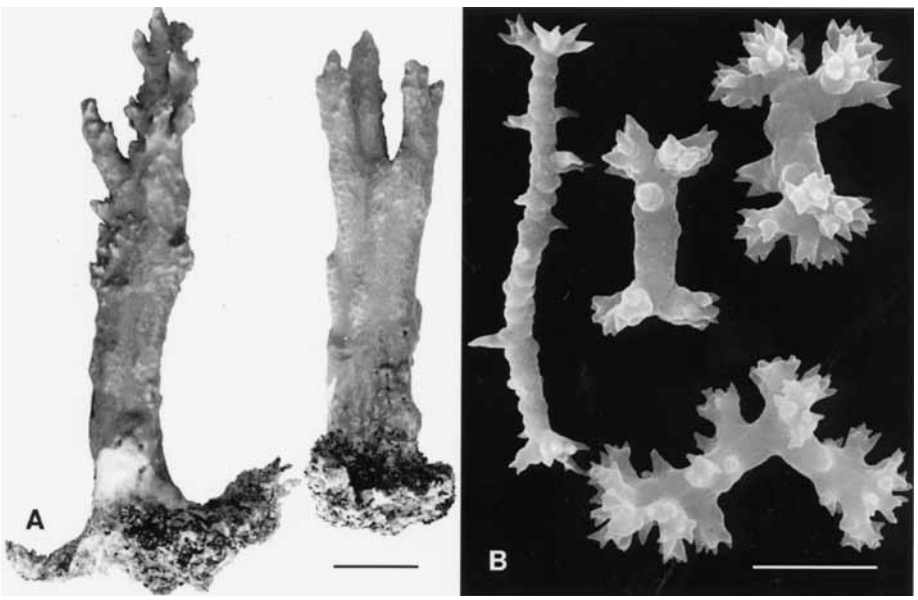

Fig. 2. *Cervicornia cuspidifera*, morphology and microscleres. A, habit of two specimens from Puerto Rico, West Indies (scale 5 cm). B, SEM images of microscleres (scale 5 μm). (From Vicente *et al*., 1991.)

Material examined. Holotype: MNHN LBIM DT 652 – labeled "151. *Alcyonium cuspidiferum* Lmk"; specimens examined by Rützler in Vicente *et al*. (1991: 217).

Description. The dry type at MNHN is a cluster of about 8 slender conical tubes, fused at the bottom, free but blind-ending distally, 44 cm tall, 20–25 mm in diameter at about midway to the top. The original author compared them to a bundle of inverted stalactites. Tylostyles, some modified to tylostrongyles, average 330–400 × 8–11 μm. Spirasters are small (4–13 μm long), many smaller ones (4–6 μm) are modified amphiasters.

The type species was recently described and illustrated in detail (Vicente *et al*., 1991: 217f, figs 3c, d, 4; as *Spheciospongia*). These large, hollow and blind-ending fistulas were considered by previous authors to be the entire sponge until *in situ* observations

and fine-structure study showed their true nature and function (Rützler, 1997). The latter work also showed that the choanosome is burrowing and concealed in unconsolidated calcareous substrate into which exhalant water is discharged.

Remarks. Misidentification of this sponge as *Xestospongia* (Wiedenmayer, 1977B) is explained by the appearance, in some populations, of the tylostyles as strongyles (only few subterminal swelling appear here and there) and the rarity and small size of the spirasters. *Prianos tierney* de Laubenfels, 1953a turns out to be a similar modification of *Spheciospongia vesparium* (Vicente *et al*., 1991).

CLIONA GRANT, 1826

Synonymy

Cliona Grant, 1826a. *Vioa* Nardo, 1833. *Poterion* Schlegel, 1858. *Raphyrus* Bowerbank, 1862b. [*Papillina*] Schmidt, 1862 (preocc. by *Papillina* Conrad, 1855, Mollusca). *Raphiophora* Gray, 1867a. *Taguilla* Boweberbank, 1874: xi (*nom. nov.* for [*Papillina*] Schmidt). *Tapiliata* Bowerbank, 1874: xi (*nom. nov.* for [*Papillina*] Schmidt). *Euryphylla* Duchassaing & Michelotti, 1864. *Euryphylle* Duchassaing & Michelotti, 1864. *Hymeniacidon sensu* Bowerbank, 1866 [not *Hymeniacidon* Bowerbank, 1859]. *Idomon* Gray, 1867a. *Myle* Gray, 1867a. *Pronax* Gray, 1867a. *Sapline* Gray, 1867a. *Osculina* Schmidt, 1868. *Spirastrella sensu* Ridley, 1884a (non Schmidt, 1868). *Papillella* Vosmaer, 1885b. *Papillissa* Lendenfeld, 1888. *Anthosigmella* Topsent, 1918. [*Rhaphiophora*] de Laubenfels, 1936a (*lapsus* for *Raphiophora* Gray). *Delaubenfelsia* Dickinson, 1945. *Bernatia* Rosell & Uriz, 1997 (see also Topsent, 1900; Vosmaer, 1932 (but beware of excessive lumping); de Laubenfels, 1936a).

Type species

Cliona celata Grant, 1826a (by monotypy).

Definition

Excavating, mostly cryptic Clionaidae without elaborate aquiferous morphology; with microscleres composed of raphides or spirasters, including amphiastrose modifications of spirasters or entirely smooth forms (sinuous microrhabds).

Diagnosis

Sponges primarily in alpha growth form (excavating chambers, communicating through papillae), some species developing beta stage by merging of papillae, very few regularly outgrowing their substratum and occurring in gamma stage. Some gamma-stage species attain large, irregular massive or cup shape but do not develop specialized incurrent or excurrent features other than, in some forms, the original pori- and oscula-bearing papillae. Spicules are tylostyles as megascleres, very thin oxeas (raphides) as accessory scleres but never of structural importance, and spiraster-like microscleres. Spirasters are straight, bent, kinked, spiraled, or undulate spiny rhabds, including amphiastrose forms clearly derived from true spirasters; extreme forms may be entirely smooth.

Previous reviews

Topsent (1900); Hartman (1958b); Rosell & Uriz (1997).

Description of type species

Cliona celata Grant, 1826a (Figs 3–7).

Synonymy. *Cliona celata* Grant, 1826a: 78; *Hymeniacidon celata* Bowerbank, 1866: 212; *Vioa celata* Schmidt, 1866a: 40 (see also Topsent, 1900). *Spongia sulfurea* Desor, 1848. *Papillina suberea* Schmidt, 1862: 69.

Material examined. Holotype (not seen): believed to be in the Grant Museum of Zoology and Comparative Anatomy at the University College, London, where R.E. Grant worked (Clare Valentine, personal communication; this information could not be confirmed). Description is based on literature records deemed reliable and specimens at BMNH and USNM. Northeast Atlantic, Celtic Sea – BMNH 1910.1.1.411; Tenby, Wales. Mediterranean – USNM uncatalogued slide: alpha-stage, Tunisia. USNM 31374: Croatia. East coast of the United States (alpha- and gamma-stages) – USNM 5349: off Massachusetts. USNM 7283: Rhode Island. USNM 7492: New York. USNM 22705: Virginia. USNM 23648: North Carolina. USNM 33391: South Carolina. USNM 31065: Georgia. USNM 39608: Florida Gulf Coast.

Distribution. Considered 'worldwide' but that statement would have to be confirmed with improved taxonomic tools, such as molecular techniques. Reliable records indicate occurrence on both sides of the North Atlantic Ocean, in the Mediterranean, and on the Great Barrier Reef, Australia (for instance, Topsent, 1900; Volz, 1939; Hartman, 1958b; Rützler, 1973; Hoeksema, 1983; Wesche *et al*., 1997; Schönberg, 2000). Alpha-stages are particularly common (and obvious) in oyster shells ('oyster pest') between the intertidal and 10 m depth, gamma-stages occur free on sediment bottoms to 40 m depth (New England fishermen call them 'bay pumpkins' and 'porpoise dung').

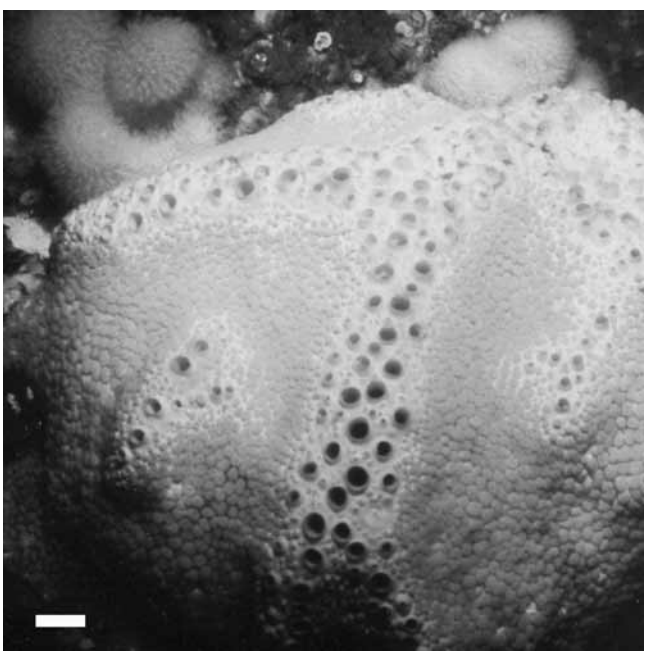

Fig. 3. *Cliona celata*, underwater photograph of gamma stage, eastern North Atlantic, Ireland (ca. 0.5 × natural size) (photo courtesy T. Crabtree).

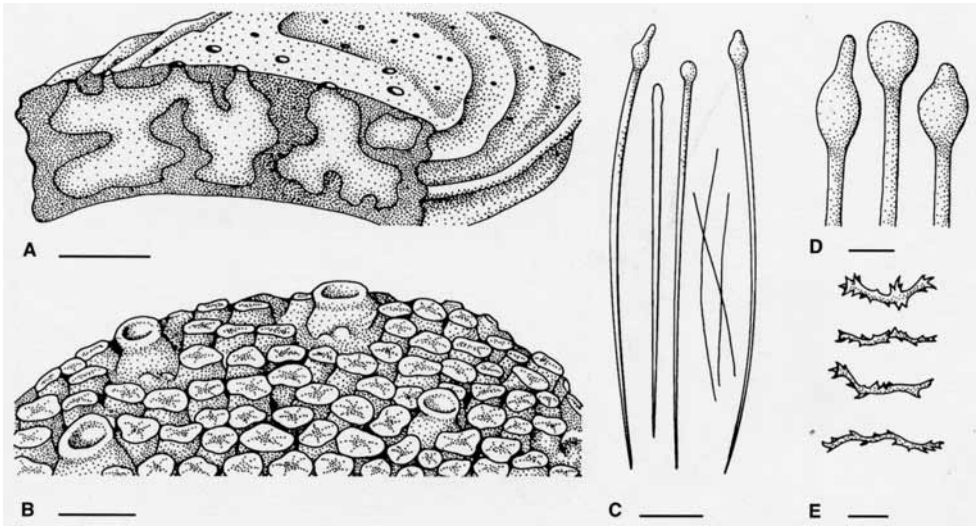

Fig. 4. *Cliona celata*, habitus and spiculation. A, alpha stage in oyster shell, specimen USNM 23360, Tangier Sound, Chesapeake Bay, western Atlantic (scale 5 mm). B, gamma stage, specimen USNM 8514, off Woods Hole Massachusetts, USA (scale 5 mm). C, tylostyles and raphides (from a juvenile), USNM 23360 (scale 50 μm). D, tylostyle heads magnified (scale 5 μm). E, spirasters, reported for some juvenile specimens of the species (Topsent, 1900), but possibly belonging to *C. viridis* (after Vosmaer, 1932) (scale 5 μm).

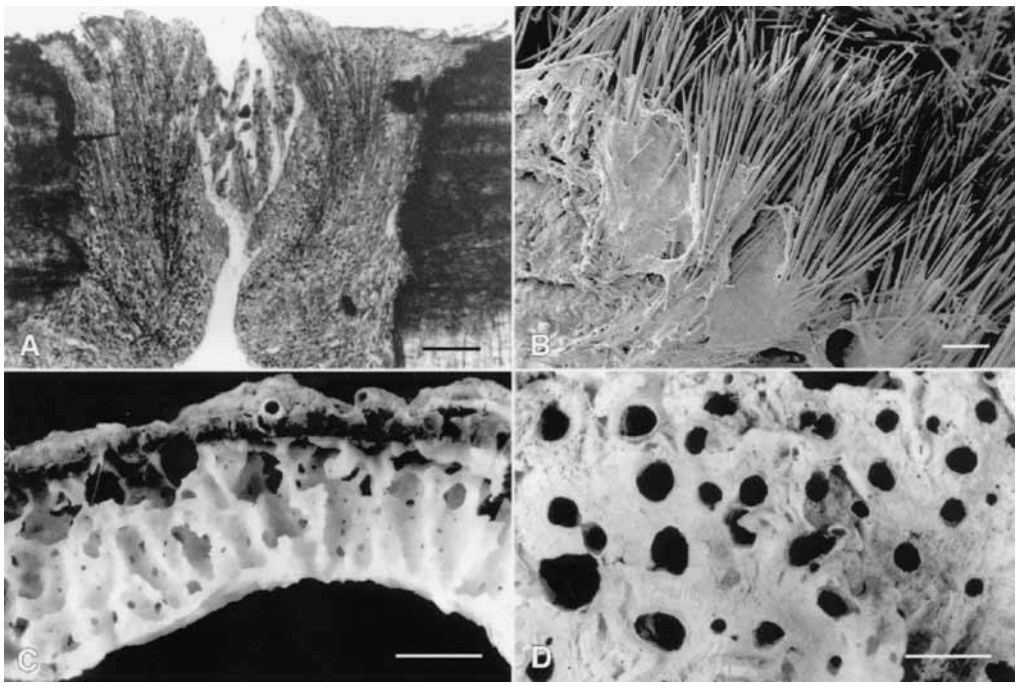

Fig. 5. *Cliona caribbaea* anatomy and excavations. A, longitudinal section through a single papilla (flanked by rock substratum), showing incurrent canals and perpendicular spicule orientation (scale 200 μm). B, SEM view of fractured ectosome with tylostyles in bouquet arrangement (scale 100 μm). C, excavated chambers in (fractured) oyster shell, sponge tissue removed (scale 5 mm). D, excavated papillar openings in oyster shell (viewed from above), sponge tissue removed (scale 5 mm). (A, C, D from Rützler, 1974.)

Description. The color of live specimens is rich yellow to golden and orange yellow. The consistency of the ectosome (including papillae) is rather tough (from spicule reinforcement), the choanosomal chamber tissue is soft. In the alpha-stage, papillae are well separated, 0.5–3.0 mm in diameter. They connect directly to large chambers, 2.5–4.5 mm and more. The walls of the chambers (after sponge material is removed) often appear angular and are connected by numerous small (up to 0.7 mm) circular pores. In older specimens with much of the substratum removed, the sponge ectosome becomes continuous at the surface, between the papillae which retain their structure. After additional growth periods the sponges become massive, hemispherical or irregular, depending on environmental conditions and the nature of the original substratum. Spicules in the papillae are arranged in palisade-fashion, points outward and protruding beyond the ectosome. In the chambers spicules are scattered, particularly in early stages, later become

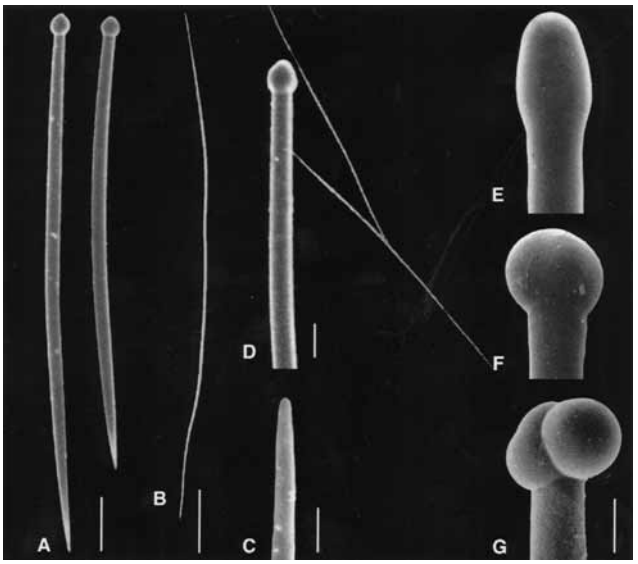

Fig. 6. *Cliona* spiculation. A, tylostyles, *C. amplicavata* (scale 20 μm). B, raphide, *C. amplicavata* (scale 20 μm). C, raphide tip enlarged, *C. amplicavata* (scale 1 μm). D, tylostyle head and raphides, *C. amplicavata* (scale 10 μm). E, tylostyle head, *C. paucispina* (scale 5 μm). F, G, tylostyle heads, *C. caribbaea* (scale 5 μm). (From Rützler, 1974.)

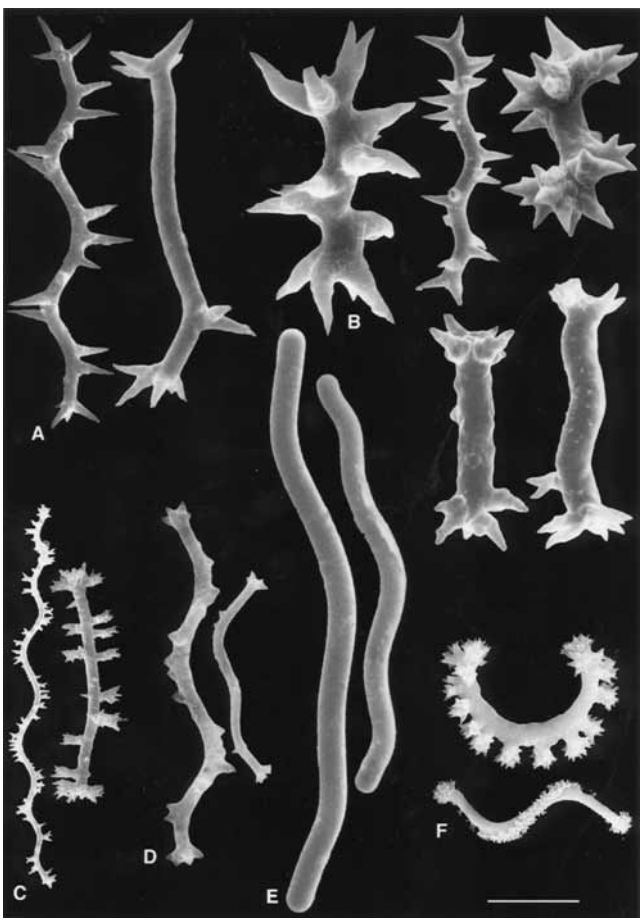

Fig. 7. *Cliona* spiculation, spiraster-type microscleres at the same scale. A, spirasters, *C. flavifodina*. B, spirasters and diplasters, *C. dioryssa*. C, spiraster and diplaster, *C. caribbaea*. D, spirasters, *C. paucispina*. E, sinuous microstrongyles, *C. vermifera*. F, anthosigma and spiraster, *C. varians* (scale 10 μm). (From Rützler, 1974.)

partly organized in tracts. Spicules consist mainly of tylostyles which may be accompanied by raphides as the only microscleres (forming trichodragmas in the chambers). For young specimens, small spirasters have been reported to occur mainly in the papillae (Topsent, 1900). Tylostyles are long and slim and have inconspicuous inflations for heads which are usually subterminal. Their dimensions range with specimen and location from about 200–400 × 3–12 μm, the average is about 300 × 8 μm and tends to be smaller when located in the choanosome. Raphides are 100–150 × <1 μm. Spirasters are reported to be short and stout, 20–25 × 2–3 μm.

Remarks. It has been well established that clionaids may lose one or the other spicule type during the course of one life cycle, for instance, only early stages of *Cliona celata* are with microscleres (Topsent, 1900), making systematic judgement based on museum specimens difficult or impossible. However, cladistical analysis of a large number of species (Rosell & Uriz, 1997) supports the grouping as here defined and the inclusion of the genus *Anthosigmella* Topsent whose characteristic 'anthosigmas' are rare or absent in many specimens but are really derived from typical spirasters. I do, however, disagree with the decision by Rosell & Uriz (1997) to establish a separate genus *Bernatia* (for *Cliona vermifera* Hancock; with smooth, vermiform microstrongyles). The lack of spines on the microscleres of this sponge are considered a minor modification and does not justify generic separation; a transitional form with strongly reduced spines is exemplified by *Cliona paucispina* Rützler (1974). *Delaubenfelsia* Dickinson is massive without known aquiferous specialization (the original material exists only in fragments), and its microscleres are very similar to those of *Anthosigmella*. Two other generic synonyms are included here, following recent rediscoveries of subsequent names to replace [*Papillina*] Schmidt, 1862 (preoccupied by *Papillina* Conrad, 1855, Mollusca): *Taguilla* Boweberbank, 1874, *Tapiliata* Bowerbank, 1874, both curiously introduced in the same work and on the same page. *Raphiophora* Gray, 1867a is an objective synonym of *Poterion* Schlegel, 1858, both having *Spongia patera* Hardwicke, 1822 as their type species.

CLIONAOPSIS NOM NOV.

Synonymy

[*Clionopsis*] Thiele, 1905: 412 (preocc. for *Clionopsis* (*lapsus* pro *Cliopsis*) Bronn, 1862: 645, Mollusca) (according to Neave, 1940).

Type species

Clionopsis platei Thiele, 1905 (by original designation) (Fig. 8).

Definition

Clionaidae with oxeas and spirasters.

Diagnosis

Excavating sponges with tylostyles and oxeas as megascleres and spirasters as microscleres. Only beta- to gamma-stage (thickly encrusting) specimens are known (type material).

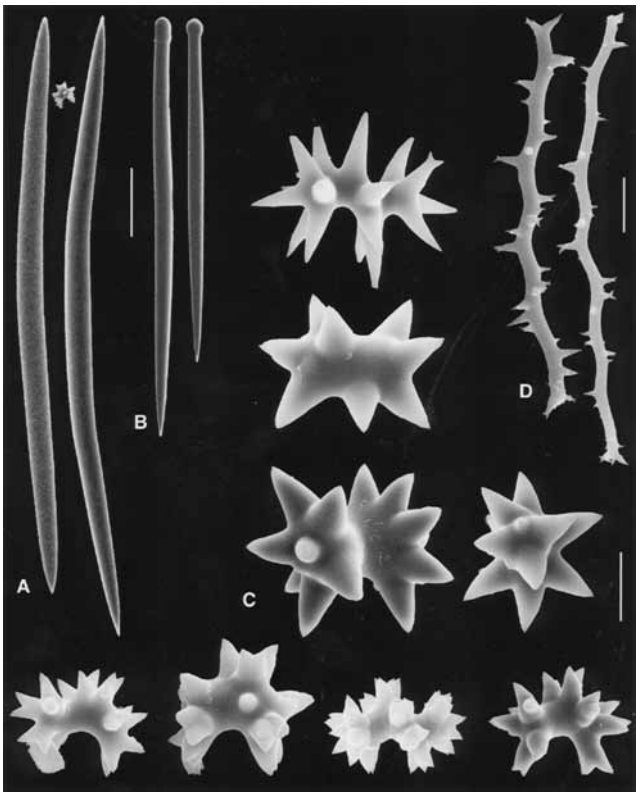

Fig. 8. *Clionaopsis platei*, syntype (ZMB 3270). A, oxeas and spiraster I (scale 50 μm). B, tylostyles (scale 50 μm). C, spirasters I (scale 10 μm). D, spirasters II (scale 10 μm).

Description of type species

Clionaopsis platei (Thiele, 1905) (Fig. 8).

Synonymy. *Clionopsis platei* Thiele, 1905: 412, fig. 37a–d.

Material examined. Syntype: ZMB 3270 – Calbuco, Chile.

Description. The examined type is a flat, 1 cm thick cushion of about 7 cm^2 coverage. According to the original describer (Thiele, 1905: 412), specimens are flat (3–4 cm diameter, 1 cm thick, tapering toward the margin) to cone-shaped (5 cm tall) and incorporate calcareous particles including balanid shells. Colour in alcohol is grayish brown. Inhalant and exhalant areas (2–3 mm papillar regions) are evident on the surface as they are darker than the surrounding surface and slightly depressed. The cortex is generally formed by a dense arrangement of oxeas accompanied by fewer tylostyles and short spirasters. The papillar regions are mainly supported by tylostyles which are oriented perpendicularly to the surface, with points outward, and also joined by short spirasters. The choanosome is packed with oxeas and tylostyles without particular orientation and contains long, thin spirasters. Choanocyte chambers are oval in cross-section, 20 × 30 μm in diameter. Oxeas are smooth, bent in the center, sharply pointed on both ends but in places modified to styloid forms; they measure 440–550 × 17–23 μm. Tylostyles, 300–400 × 11–15 μm, have rounded heads, rarely irregular or subterminal. Microscleres consist of two classes spirasters: short, stout with strong spines (15–35 × 7–23 μm, including spines); and long, slim, sinuous, with delicate spines (53–86 × 5–8 μm, with spines).

Remarks. The specimen described by Desqueyroux (1972) from Montemar (Valparaíso), Chile, is actually *Cliona chilensis* (R. Desqueyroux-Faúndez, pers. comm.).

CLIOTHOSA TOPSENT, 1905

Synonymy

Cliothosa Topsent, 1905a: 95. *Thoosa sensu* Topsent, 1888: 81 (not *Thoosa* Hancock, 1849).

Type species

Thoosa hancocki Topsent, 1888 (misspelled as *T. hancocci*; by original designation).

Definition

Clionaidae with amphiasters as microscleres.

Diagnosis

Excavating sponges of alpha growth form with large tylostyles and generally two types of amphiasters as microscleres: stout, nodulose in the papillae and delicate thin-rayed with terminal branching of the slender rays, in the chambers. The nodulous amphiasters may be absent in some specimens or species (Topsent, 1928b; Rützler, 1973). On the other hand, a third kind, a very small diplaster has been reported to occur in the papillae (Volz, 1939).

Previous review

Topsent (1928b); Rosell & Uriz (1997).

Description of type species

Thoosa hancocki Topsent, 1888 (Figs 9, 10).

Synonymy. *Thoosa hancocki* (as *T. Hancocci*) Topsent, 1888: 81, pl. 7, fig. 12. *Thoosa hancocki*; Topsent, 1928b: 1, fig. 1; Volz, 1939: 25, fig. 8, pl. 4, figs. 2–4; Rützler, 1973: 634, fig. 7; Rosell & Uriz, 1997: 363, fig. 2B. *Vioa ramosa* Lendenfeld, 1897a: 81. *Cliona seurati* Topsent, 1905a: 96.

Material examined. Holotype: MNHN DT 2559 (two slides) – "in *Tridacna gigas*"; no further location given. Specimens from Tunisia (deposited at INSTOP, Salammbô) are described by Rützler (1973). The species is common in the Mediterranean and the Indopacific region; 0.5–10 m depth.

Description. The sponge develops only the alpha-stage. Papillae are bright yellow but may have an orange tinge; they are circular, well separated, 1–6 mm in diameter. Chamber tissue is also yellow, but duller. Chambers may be minute in young specimens (0.3–1.2 mm; Rützler, 1973) but tend to merge and fill larger spaces in advanced stages (5–20 mm; Topsent, 1905a; Schönberg, 2000). The chambers connect to the papillae through a narrow canal of 10 mm length, or more. Spicules consist of large, robust tylostyles, and two types of amphiasters. Tylostyles are straight, with prominent circular or oval head, usually subterminal; in the type they measure 300–410 × 8–12 μm. Ramose amphiasters occur in the choanosome and have long, delicate rays with hooks at their distal ends; they measure 26 × 21 μm, overall. Nodulose amphiasters, if present, are in the papillae; they have bulbous swellings instead of rays; 20 × 15 μm. Amphiasters are rare in preparation MNHN DT 2559(1) but common in MNHN DT 2559(2).

Remarks. The validity of this genus was doubted by Annandale (1915a: 22) on the basis of the fact that the spicule

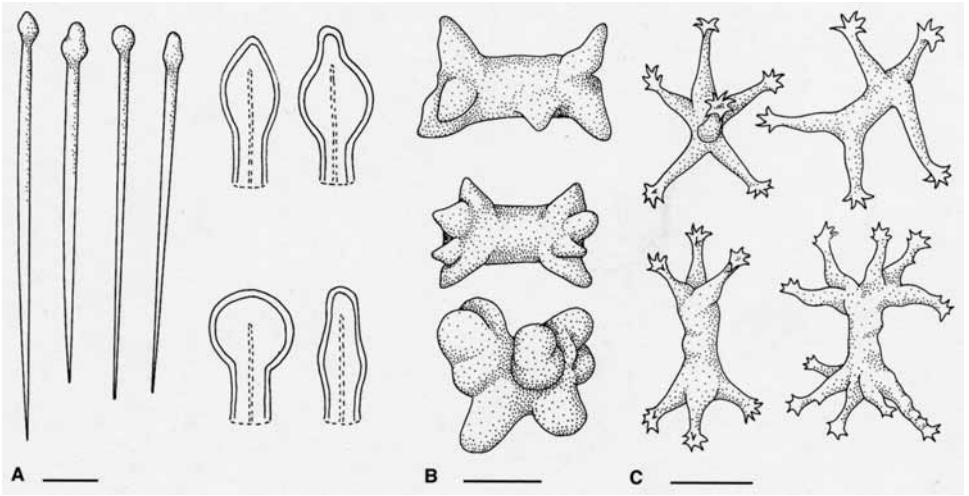

Fig. 9. *Cliothosa hancocki*, spiculation. A, tylostyles and enlarged tylostyle heads (scale 50 μm; 10 μm for heads). B, nodulose amphiasters (scale 10 μm). C, ramose amphiasters (scale 10 μm).

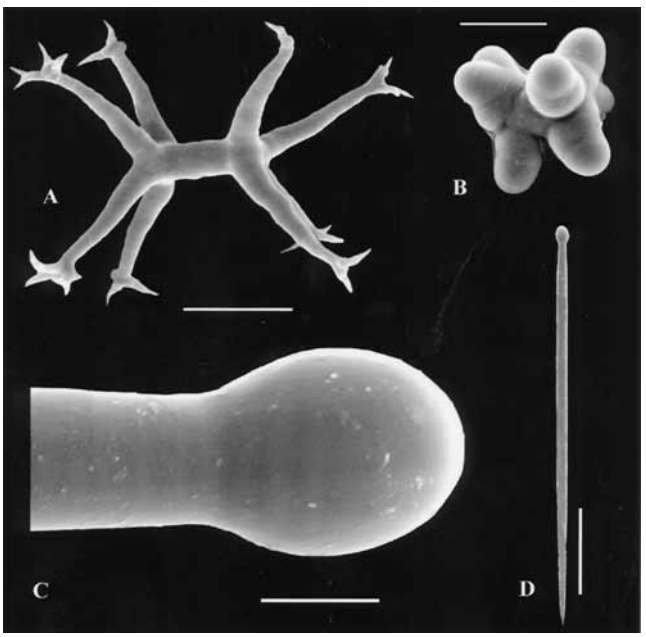

Fig. 10. *Cliothosa hancocki,* SEM views of spicules. A, thin-rayed amphiaster (scale 10 μm). B, nodulose amphiaster (scale 10 μm). C, tylostyle (scale 100 μm). D, tylostyle head (scale 10 μm). (A, C, D, specimen ZMA POR 8661, Indonesia, photo courtesy R.W.M. Van Soest; B, from Schönberg, 2000, photo courtesy C.H.L. Schönberg.)

complement of a species may shift during different growth phases. On the other hand, the possible importance of the presence of two size classes of tylostyles in this genus has been pointed out (Rosell & Uriz, 1979). Two species (in addition to the type) were recently transferred to this genus: *Cliona quadrata* Hancock (by Rützler & Stone, 1986: 666) and *Spirastrella aurivillii* Lindgren (by Rosell & Uriz, 1979: 363).

PIONE GRAY, 1867

Synonymy

Pione Gray, 1867a: 525. *Archaeocliona* Czerniavsky, 1878: 396; 1879: 244, pl. iv, figs 17a–f; 1880: 7. *Gapoda* de Laubenfels, 1936a: 144.

Type species

Cliona northumbrica Hancock, 1849: 336, pl. 14, fig. 5 (=*Cliona vastifica* Hancock, 1849: 342, pl. 15, fig. 2) (by subsequent designation, Rosell & Uriz, 1997).

Definition

Clionaidae with tylostyles and microspined oxeas and microrhabds.

Diagnosis

Sponges in alpha- and beta-forms. Delicate tylostyes as megascleres, accompanied by microspined (rarely smooth) microxea and microspined microrhabds as microscleres. Microrhabds are usually straight or bent but may also be centrotylote and sinuose. Microxeas do not have a particular location or orientation in the tissue.

Previous review

Rosell & Uriz (1997).

Description of type species

Pione vastifica (Hancock) (Figs 11–13).

Synonymy. *Cliona northumbrica* Hancock, 1849: 336, pl. 14, fig. 5; Hancock, 1867: 237, pl. 7, fig. 1; Rützler & Stone, 1986: 665, fig. 5e, f. *Cliona vastifica* Hancock, 1849: 342, pl. 15, fig. 12; Hancock, 1867: 237, pl. 7, fig. 2; Topsent, 1900: 56, pl. 2, figs 3–9; Topsent, 1932c: 558, fig. 3; Topsent, 1934c: 99; Volz, 1939: 8, fig. 2, pl. 1, fig 3, pl. 2, fig. 3, pl. 3, fig. 1; Rützler, 1973:633, fig. 6; Rützler & Stone, 1986: 667, fig. 6c, d. *Cliona lampa* de Laubenfels forma *occulta* Rützler, 1974: 23, fig 17b, d; 20d. *Pione vastifica* (Hancock), Rosell & Uriz, 1997: 362, fig. 3C. (See also Topsent, 1900: 56.)

Material examined. Syntypes (*Cliona northumbrica*): HMN 4.16.15–4.16.17 (3 slides) – northeast coast of England. Syntypes (*Cliona vastifica*): HMN 4.16.36–4.16.39 (4 slides) – Firth of Forth, Scotland. (For further information see Rützler & Stone, 1986: 665, 667.) *Raphyrus hixonii* von Lendenfeld: BMNH 86.8.27.605 – Port Jackson, N.S.W, Australia.

Distribution. The species has been reported from many locations in the boreal and tropical Atlantic, the Mediterranean, and Indopacific; it has tolerance for a wide range of salinity.

Description. Only microscope preparations (cleared tissue squashes and acid-cleaned spicule spreads) are left of the types. Material of *Pione northumbrica* shows tylostyles (330 × 7 μm), microspined oxeas, more or less bent in the center (110 × 5 μm), and microspined microrhabds (14 × 3 μm) that are bent or wavy (2–5 bends); slides of *Pione vastifica* contain tylostyles (300 × 5 μm), microspined oxes, slightly bent in the center (100 × 3 μm), and microspined microrhabds (12 × 3 μm) that range from straight and spindle-shaped to s- and w-shape (Rützler & Stone, 1986: 665, 667; figs 5e, f, 6c, d). The living sponge is usually red to orange-red, in some locations light yellow, with duller-colored interior. Papillae are very small, under 1 mm in diameter. Chambers are equally small and connect directly to the papillae, without canal. As a rule there are three types of spicules, tylostyles, microxeas and microrhabds. Some authors report one or the other category of microscleres missing but thorough search, possibly of several specimens in a population, usually reveals them. The microscleres are covered by minute spines that are easily overlooked by a low-quality compound microscope because their size is at the borderline of light-microscope resolution. Still, some of the microxeas may indeed be smooth. Tylostyles are straight and slender with well pronounced rounded head. Averaging several populations and localities, tylostyles measure about 250–300 × 4–5 μm. Microspined microxeas are fusiform, slightly bent in the center, 60–100 × 2–4 μm. Spiny microstrongyles are straight or bent, or sinuous, depending on the locality; 8–16 × 1–3 μm. The species tolerates fairly low levels of salinity (Old, 1941), and presence of gemmules has been reported (Rützler, 1974).

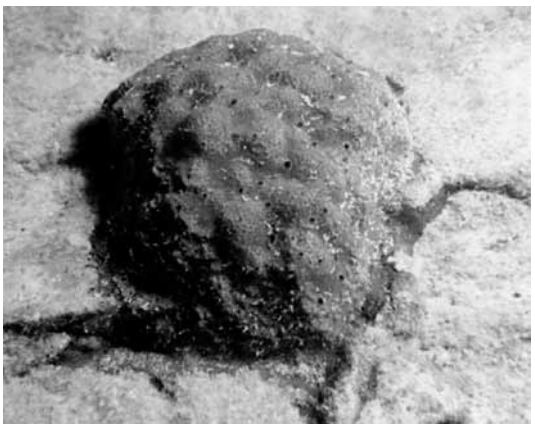

Fig. 11. *Pione lampa*, beta-stage habitus, thinly coating a recently dead coral; from the type locality, Bermuda (0.5×).

Remarks. Rosell & Uriz (1997) resurrected this genus based on their cladistic analysis. These authors also pointed out that Topsent (1888) synonymized the type species of *Pione, Cliona northumbrica* Hancock with *Cliona vastifica* Hancock and favored the latter name although *C. northumbrica* was described several pages before *C. vastifica* (Hancock, 1849: 336, 342). Because the name '*northumbrica*' remained unused for more than 50 years, the type species is correctly called *Pione vastifica* (ICZN Art. 23.9.1.). Rützler (1974) introduced a new papillate 'variety' of *Pione* (as *Cliona*) *lampa*, forma *occulta*, which was considered an alpha-form of the encrusting *P. lampa* (de Laubenfels, 1950a), but subsequently was shown to be a separate species, *P. vastifica* (Rützler, 2002). *Archaeocliona* Czerniavsky is considered to be a brackish-water form of *Pione*, with smooth microxeas and spiny microstrongyles lost or overlooked by the author. *Gapoda* de Laubenfels (established for *Raphyrus hixonii* von Lendenfeld, 1886) has the typical spiculation of *Pione*, but with a third, spiraster-like microsclere added.

SPHECIOSPONGIA MARSHALL, 1892

Synonymy

Spheciospongia Marshall, 1892. *Heterocliona* Verrill, 1907.

Type species

Alcyonium vesparium Lamarck, 1815: 78 (by original designation).

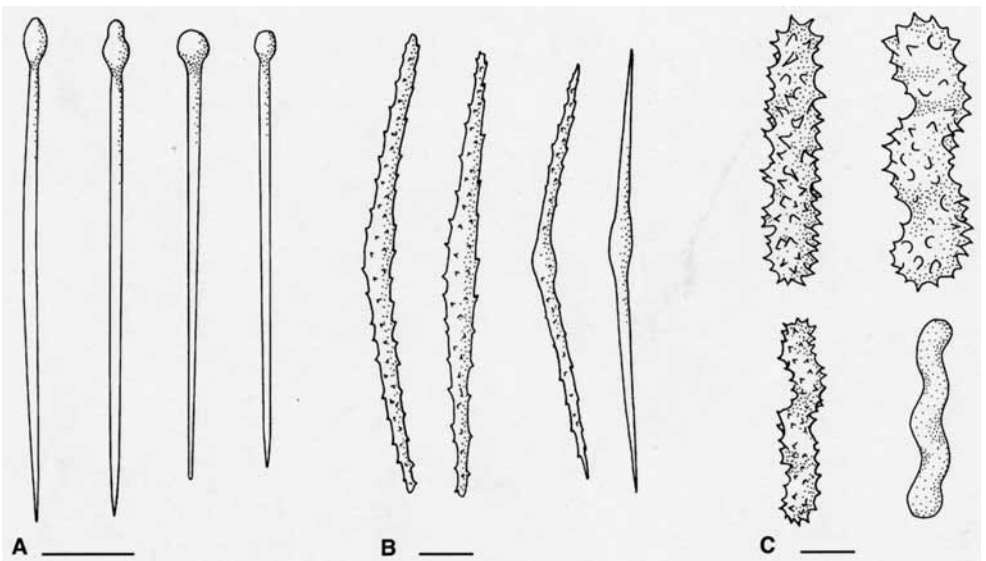

Fig. 12. *Pione vastifica*, spicules. A, tylostyles (scale 50 μm). B, microxeas (scale 10 μm). C, spiny microrhabds (scale 2 μm).

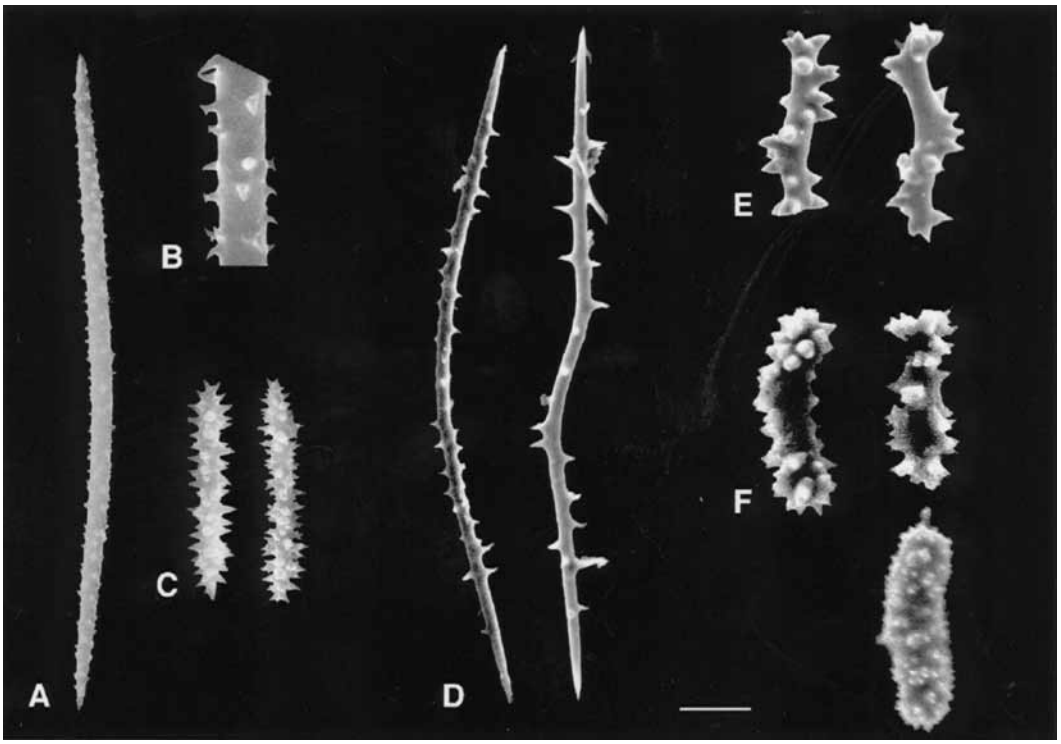

Fig. 13. *Pione*, SEM views of microscleres. A, microspined microxea, *P. lampa*. B, enlarged view of spination on microxea, *P. lampa*. C, spiny microrhabds, *P. lampa*. D, spiny microxeas, *P. hixonii*. E, spirasters, *P. hixonii*. F, spiny microrhabds, *P. hixonii*. (Scales 10 μm for A, D, E; 5 μm for B, C, F.)

Definition

Massive Clionadae with complex, incurrent pore sieves, abundant large tylostyles in the choanosome and rare, minute spirasters and their amphiastrose derivatives in the ectosome.

Diagnosis

Large-growing sponges with cribiporal chones (pore sieves) and simple, multiple, or septate oscula. In the ectosome, numerous robust tylostyles forming a dense tangental network and rare, minute spirasters and spiraster-derived amphiasters; the latter are also located in the canal linings. In the choanosome, tylostyles occur densely scattered and in strands. Tylostyles may be modified to styles, tylostrongyles, and strongyles. Sponges excavate limestone in early growth stage, forming large, tissue-filled cavities, not a series of distinct chambers as do other clionaids.

Previous review

Topsent, 1933; Vicente *et al*., 1991.

Description of type species

Spheciospongia vesparium (Lamarck) (Figs 14, 15).

Synonymy. *Alcyonium vesparium* Lamarck, 1815: 78; *Spheciospongia vesparium* Marshall, 1892: 32. (See also Topsent, 1933; Vicente *et al*., 1991).

Material examined. Holotype: MNHN LBIM DT 3419 – "labelled 142. Alcyonium vesparium Lamarck".

Description. Topsent (1933: 30) states that the Lamarck collection at the Paris Museum contains four specimens, two relatively small ones having a label by Lamarck, and two larger ones, labeled simply "Suberites, Antilles, M. Maugé, 1799". The specimen piece with the label cited above is about 43 cm tall and 30 cm in diameter. has a large oscular cavity with an 11 cm opening on top and several large (5–20 mm) pore sieves along the sides. Pores are 0.5–1.5 mm in diameter and open in a large canal that branches into the interior of the body. Dry specimens are grayish brown to purple, the live animal is nearly black, with a purple tinge, but there is also a yellow variety (forma *pallida*, Vicente *et al*., 1991). The shape may be that of a large cake with many small oscula in a group on top, some resemble volcanoes with just a few large oscula close together. The spicules are large, densely packed tylostyles and minute, rare spirasters and spiraster-derived amphiasters, located mainly in ectosome and canal linings. Tylostyles are curved or double-bent, with small rounded heads and uniform thickness until near the tip where they taper to a point; in the type they are 250–470 × 8–9 μm, population means range 280–410 × 6–9 μm. Spirasters have 1–5 bends and measure 8–26 × 4 μm, including spine clusters; the shorter forms are straight amphiasters.

Remarks. The original author of the genus was not aware of the small spirasters and considered this sponge a simple suberitid (Marshall, 1892: 32). However, Topsent (1933: 32), recognizing the importance of the pore sieves of these sponges, left the genus intact and transferred these sponges to Spirastrellidae. A canal system of substantial extent and bore diameter adds to the unique character of these sponges and supports a large and diverse fauna of endozoic invertebrates (Pearse, 1934; Westinga & Hoetjes, 1981).

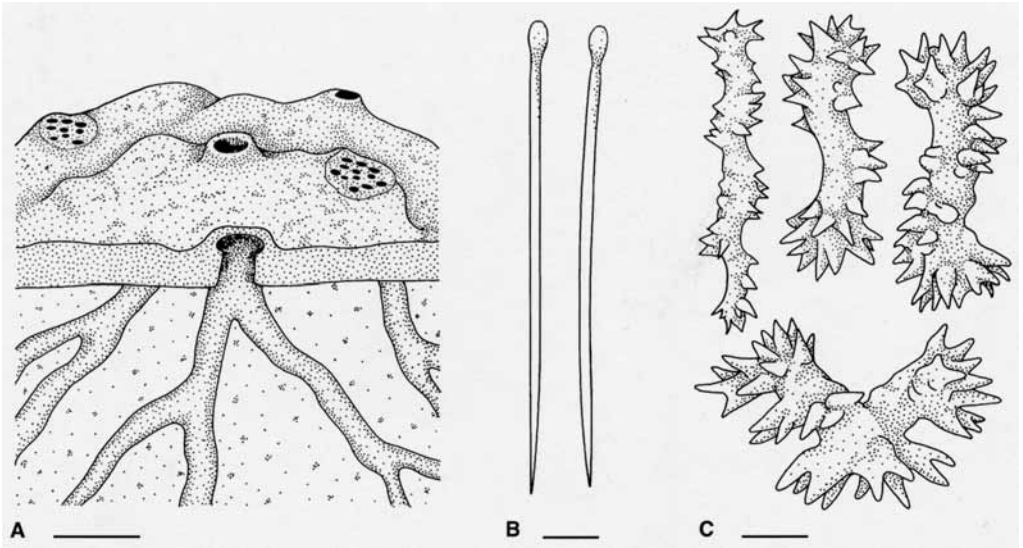

Fig. 14. *Spheciospongia vesparium*, habitus and spiculation. A, early excavating stage, Bermuda (scale 10 mm). B, tylostyles (scale 50 μm). C, spirasters (scale 5 μm).

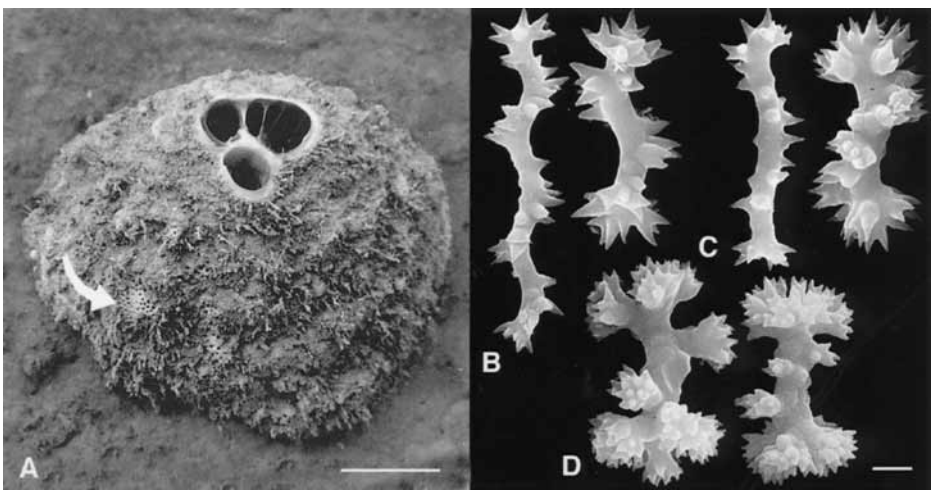

Fig. 15. *Spheciospongia vesparium*, adult habitus and SEM views of spicules. A, specimen from Puerto Rico showing pore sieve (arrow; 0.17×). B, spirasters and amphiastrose derivatives (scale 2 μm). (From Vicente *et al*., 1991.)

THOOSA HANCOCK, 1849

Synonymy

Thoosa Hancock, 1849 (not *Thoosa sensu* Topsent, 1888: 81). [*Annandalea*] Topsent, 1928b: 6. *Annandalena* Topsent, 1932c: 573. *Thooce* de Laubenfels, 1936a.

Type species

Thoosa cactoides Hancock, 1849 (by subsequent designation; de Laubenfels, 1936a: 157).

Definition

Clionaidae with alpha-form morphology and microscleres composed of small, nodular amphiasters with microspined radii and large, thin-rayed euasters.

Diagnosis

Sponges are always papillate. Tylostyles may be missing in some specimens, populations, or species. There are many types and variations of microscleres but most commonly there are amphiasters and oxyasters in the spiculation. Amphiasters are mostly tylote, with microspination on the terminal bulbs but variations in different species include smooth oxeote rays. Oxyasters have a very small center with 1–6 long, slender rays projecting. The common reduction of rays can lead to centrotylote sigmoid or tylostylote forms. Because rays tend to be curved, biradiate forms often appear like birdwings. Accessory microscleres in some species may include microxeas and pseudosterrasters (microspined spheres or rhabds).

Previous review

Rützler & Stone (1986).

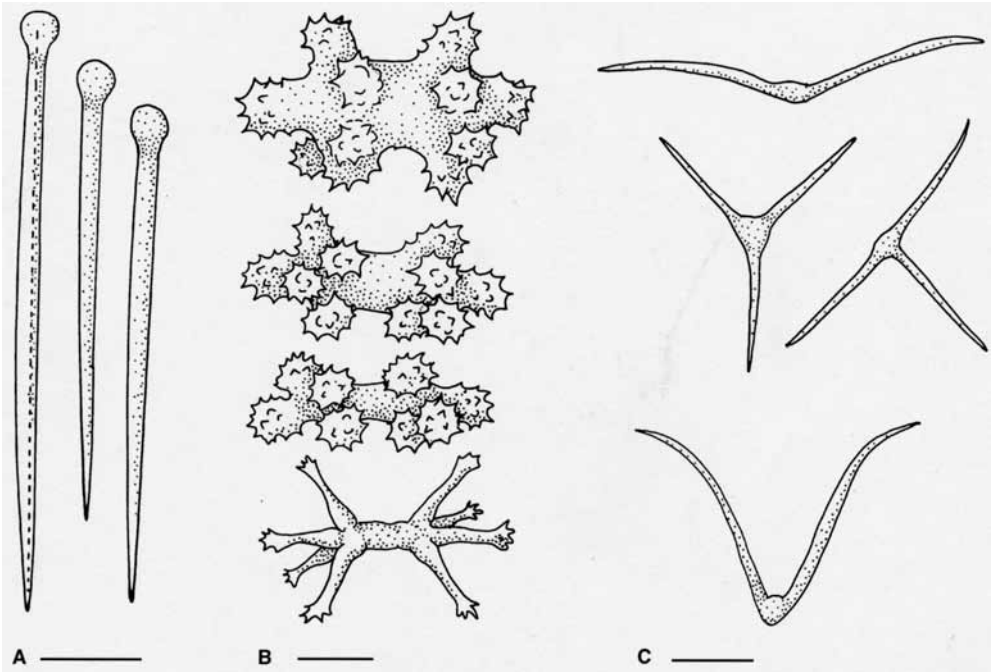

Fig. 16. *Thoosa*, spiculation. A, tylostyles in *T. mollis* Volz (1939) (scale 50 μm). B, amphiasters of *T. cactoides* (scale 5 μm). C, oxyasters (after Topsent, 1905a; Volz, 1939) (scale 20 μm).

Description of type species

Thoosa cactoides Hancock (Figs 16, 17).

Synonymy *Thoosa cactoides* Hancock, 1849: 445, pl. 13, figs 1, 2; Rützler & Stone, 1986: 667, fig. 7b.

Material examined. 'Type': HMN 4.17.05, 4.17.06 – 2 slides (acid-cleaned spicule mounts), no locality stated; substrate: '*Meleagrina margaritifera*', a mollusk shell.

Description. The type slides show only the characteristic nodular amphiasters. They are stout, with tylote rays ornamented by microspination, 23 × 15 μm in average. The original author illustrated the excavation pattern (Hancock, 1849, pl. 13, fig. 1), which extended 15–18 cm through the substrate shell and gave the diameter of the elliptical chambers as 5.1 mm. From better known species (*Thoosa armata*, Topsent, 1904b; *T. mollis*, Volz, 1939) it appears that the papillae are always small (up to 1 mm), at least in comparison to the relatively large chamber, inconspicuous in color (whitish), and contain the nodulose amphiasters (and pseudosterrasters, in *T. armata*). The chamber tissue is supported by tylostyles and the large euasters. Reproduction through gemmulae has been observed. Members of the genus are known from a depth range of 2 m to almost 600 m.

Remarks. The lack of certain spicule types in a population or in some species is not unusual and does not justify establishing a separate genus, as was done in the case of *Thooce* de Laubenfels, 1936a (for *Thoosa socialis* Carter, 1880b: 56). Topsent (1920b) already arrived at that conclusion when he compared species or forms of *Thoosa* missing either tylostyles or oxyasters.

The genus [*Annandalea*] Topsent, 1928b: 6 (preocc. by *Annandalea* Needham, 1909, Neuroptera, Insecta) was erected for type species *Thoosa laeviaster* Annandale, 1915a: 22, fig. 4 (by original designation), a *Thoosa*-like species with angular microxeas of 80 × 3 μm in addition to the usual knobby amphiasters of 40–80 × 6–13 μm and reduced oxyasters of similar size. When Topsent became aware that the name *Annandalea* was already taken, he changed the name in a footnote to *Annandalena* Topsent, 1932c: 573, which is here designated a junior synonym of *Thoosa*.

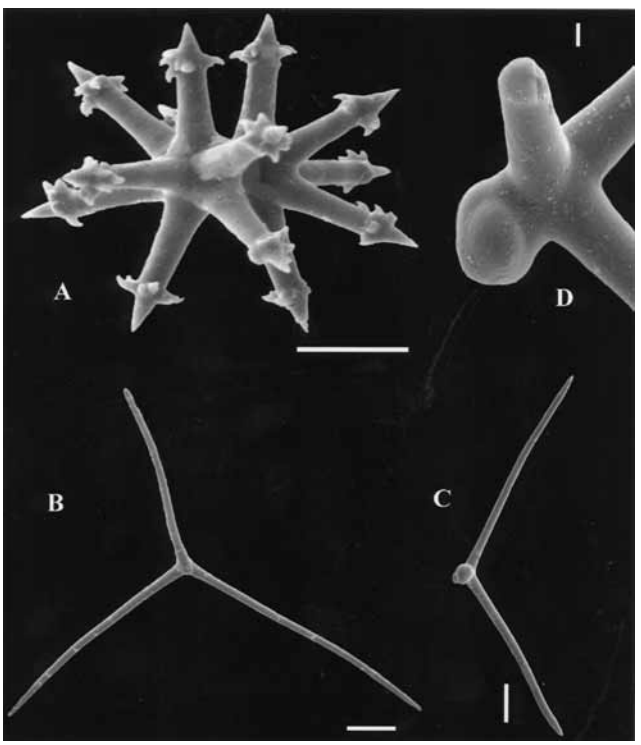

Fig. 17. *Thoosa armata*, SEM views of spicules, specimen ZMA POR 2390, Curaçao, West Indies. A, amphiaster (scale 10 μm). B, C, calthrop-like oxyasters (scale 10 μm). D, enlarged center of oxyaster (scale 1 μm). (Photo courtesy R.W.M. Van Soest).

VOLZIA ROSELL & URIZ, 1997

Synonymy

Volzia Rosell & Uriz, 1997: 363.

Type species

Cliona albicans Volz, 1939 (by original designation).

Definition

Clionaidae with accessory oxeas arranged in the papillae in palisade fashion.

Diagnosis

Sponges display only the papillate (alpha-) growth form. Tylostyles are rare and restricted to the chambers. Oxeas are small but common. Oxeas are mixed-in with tylostyles in the chambers; in the papillae they are arranged in palisade and in peripheral strands. Microscleres absent.

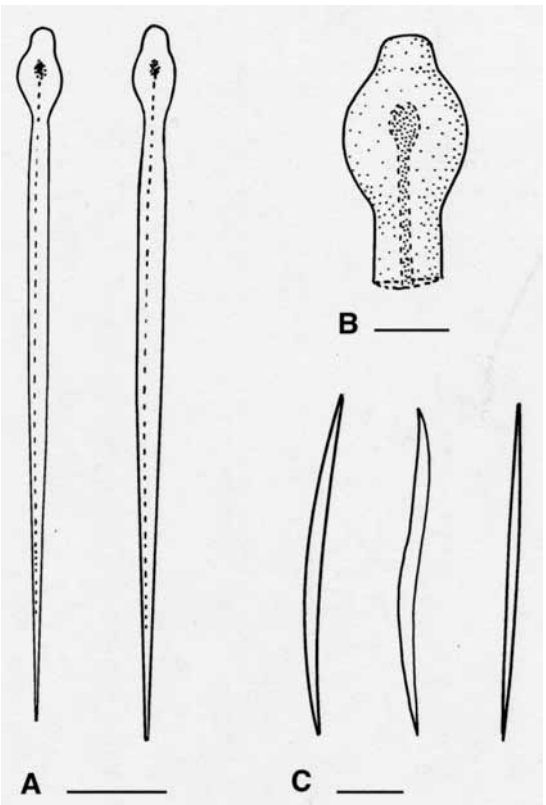

Fig. 18. *Volzia albicans*, spiculation. A, tylostyles (scale 50 μm). B, tylostyle head, enlarged (scale 5 μm). C, oxeas (scale 20 μm). (After Volz, 1939.)

Previous review

Rosell & Uriz (1997).

Description of type species

Cliona albicans Volz, 1939 (Fig. 18).

Synonymy. *Cliona albicans* Volz, 1939: 21, fig. 6, pl. 3 fig. 3; Rützler, 1965: 21; *Volzia albicans*; Rosell & Uriz, 1997: 363.

Material examined. Type material: presumed lost during WW II (but the description by the original author is precise). Other material. A few specimens were found near the type locality off Rovinj, Croatia, 1.2–10 m depth (Rützler, 1965).

Description. Papillae of the live sponge are whitish to brownish and very small (0.5–0.8 mm). The chambers, too, are small (2 mm), spherical, and extend to 20 mm below the substratum surface; they are filled with whitish tissue. Spicules consist of rare tylostyles and an abundance of oxeas. The tylostyles are fairly straight and slender, with gradually narrowing sharp points, 300–360 × 5.00–7.5 μm. Tylostyle heads are barely wider than the shaft and subterminal. The numerous oxeas are slightly bent, shorter when located in the chambers (88–95 μm), longer in the papillae (90–110 μm).

Remarks. Only two species (the type, and *Volzia rovignensis*) from one locality (Rovinj, Croatia) are known. It is significant that the oxeas, although rather small, take the place of tylostyles in forming a palisade in the ectosomal papillae.

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