

TETILLIDAE (SPIROPHORIDA, PORIFERA) : A TAXONOMIC REEVALUATION

K. RÜTZLER

Department of Invertebrate Zoology
National Museum of Natural History, Smithsonian Institution,
Washington, D.C. 20560, U.S.A.

SYNOPSIS

A large series of tetillid sponges was analysed using museum specimens and live material. The study led to a reevaluation of genera in that family, as well as of characters used to distinguish species. Properties of cortex, porocalices, and unusual accessory spicules are deemed adequate for distinguishing seven genera at the present state of our knowledge : *Tetilla*, *Craniella*, *Cinachyra*, *Paratetilla*, *Amphitethya*, *Cinachyrella*, (elevated from subgeneric status), and *Acanthotetilla*. Only few traditional species characteristics are considered stable enough to allow separating western Atlantic *Cinachyrella*. These apply to five species : *C. alloclada*, *C. kuekenthali*, *C. tarentina*, *C. apion*, and *C. new species* (van Soest & Stentoft, in press). It is recommended to avoid descriptions of new species without representative specimen series and observations of live populations, and to examine additional biological and molecular biological properties of the sponges for possible application in taxonomy.

INTRODUCTION

During the early 1980s a large collection of sponges, among other marine organisms, was made in the course of a continental shelf survey of the United States. The survey was sponsored by the Mineral Management Service (United States Department of Interior) and the collections were turned over to the Smithsonian Institution for deposit. Several hundred diverse looking specimens of the tetillid genus *Cinachyra* (as defined by all contemporary authors) are part of this material and stimulated the present study.

A survey of the literature showed that much thought has been given to

the variability of characters used in genus and species diagnoses but that few workers actually examined large series of specimens, or studied live ones suited for evaluation of taxonomic criteria. The material on hand satisfies both needs because sizeable populations from different habitats and localities can be compared and because living specimens were observed and manipulated in the field.

MATERIAL AND METHODS

Most of my views expressed in this study were formed by examining some 200 specimens of *Cinachyra* (of authors) collected in the subtropical and tropical western Atlantic. Localities include the coasts of South Carolina and Georgia (20-40m depth, non-muddy "live" bottom); Bimini (Bahamas, 3-10m, coral reef); southwestern Florida (Gulf of Mexico, 24-77m, "live" bottom); Puerto Rico and Virginia Islands (8-16m, reef and rock bottoms); Jamaica (30m, reef); Belize (1m, mangrove; 3-30m, reef); and Brazil (off mouth of Amazon River, 60-70m, rock bottom). Experiments with live specimens were conducted at the Carrie Bow Cay field laboratory, Belize, and included observations on current flow, using fluorescein dye, and on morphological changes during handling and fixation. Detailed spicule analyses were made for 64 specimens belonging to four species (Rützler & Smith, in press). Spicule preparations and epoxy resin sections were made the usual way (Rützler, 1978). Spicules were split into two size fractions (light and heavy) and mounted on separate microscope slides to avoid missing large forms and to be able to examine small microscleres under high power. Multiple preparations were made from different parts of a specimen if spicule variety appeared not to be representative.

DIAGNOSTIC CHARACTERS ON THE GENUS LEVEL

The family Tetillidae encompasses tetractinomorph sponges of massive and generally globular shape, with radial skeleton structure, with numerous monaxons and protriaenes as megascleres and spinispire-type microscleres (Dendy, 1922; Lévi, 1973). Ten genera are generally recognized belonging to this family. Criteria for separating them include differentiations of ectosome, aquiferous system, and spicule complement. These characteristics are

certainly useful for establishing taxonomic hierarchies but they have not always been properly employed by a number of authors.

Presence or absence of a cortex, for example, is not easily determined unless special spicules reinforce this structure. Purely organic, fibrous (spongin) ectosomal reinforcements can range from thin layers, detectable only by microscope, to dense, cortex-like structures of 1 mm or more in thickness. Actually, all genera but one are described with some form of a cortex, *Tetilla* being the genus characterized by lacking one.

Characteristics of the aquiferous system concern the incurrent and excurrent openings and may have been subject to misinterpretation. A structure called porocalyx is characteristic of the genus *Cinachyra* Sollas (*sensu stricto*, see definition below) and of the subgenus (*Tetilla*) *Cinachyrella* Wilson. Porocalices are circular, poriferous depressions in the ectosome, interrupting the cortex where present, and appearing as distinctive pits or even flask-shaped structures. At least one genus, *Fangophilina* Schmidt (1880:72), type species *F. submersa* Schmidt, has been defined by having two unlike poriferous pits, one inhalant, the other exhalant (Lendenfeld, 1907 ; Wilson, 1925). I doubt that this diagnosis can be upheld without being physiologically substantiated. Simple, typical oscula have been located in *Cinachyra barbata* Sollas, type species of the genus (Kirkpatrick, 1905 ; Boury-Esnault & Van Beveren, 1982 ; own observations on uncatalogued U.S.N.M. specimens) and in all specimens of four *Cinachyrella* species studied alive by myself, indicating that simple oscula may also occur in *Fangophilina*. Live specimens observed in Belize and then fixed in either absolute ethyl alcohol, 10% formalin-seawater, or by freezing demonstrate that contraction during preservation reduced the oscular openings to solid mounds or wartlike structures, whereas the porocalices remained practically unchanged. This test explains why preserved material usually does not display oscula clearly. Experiments with fluorescent dye administered to live *Cinachyrella* show also that not all porocalices are equally active drawing in water at all times. In a few observations it appeared that flow was reversed, water actually leaving the porocalyx, but closer examination revealed inhabiting polychaetes and amphipods to cause this effect.

Presence of certain spicule types in or below the ectosome, or of unusual (for the family) spicules anywhere in the body appears to be a very useful generic distinction. Absence of microscleres, on the other hand, is hardly a logical reason for establishing a separate genus, particularly since that spicule type (the sigmaspire) is part of the diagnosis of the fa-

mily. With this view, already expressed by Dendy (1924:313), two genera should be dropped : *Tethyopsilla* Lendenfeld (1888:45), type species *T. stewartii* Lendenfeld, and *Craniellopsis* Topsent (1913:14), type species *Tethya zetlandica* Carter. These microscleres are often overlooked by authors, as could be demonstrated by van Soest (1977:2) for *Acanthotetilla* Burton (1959:201), thus placing *Acanthocinachyra* Lévi (1964:306) in synonymy with the former genus. However, single specimens or, possibly, whole populations of a species may indeed lose or not develop microscleres, as I could verify in specimens (USNM 31200, 31415) from the Gulf of Mexico, tentatively identified as *Cinachyra* (sensu stricto), should be assigned to the genus *Cinachyra* (sensu stricto). Others in a similar situation should also be assigned to more appropriate genera.

Another dubious genus is *Chrotella* Sollas (1886:181), type species *C. macellata* Sollas, which is defined by having a "cortex excavated by subdermal cavities and furnished with tangentially disposed spicules" (Sollas, 1888:17). The cavities seem hardly significant and the cortical spicules are neither mentioned in the text describing the type species, nor shown in the accompanying figures (Sollas, 1888 : Pl. IV, Figs 17-18) ; only uncharacteristic, broken spicules seem to occur in a criss-cross fashion. The type species is reported to have toxospores concentrated in the cortex, in addition to the usual sigmaspires of the choanosome, but even this feature is not considered important enough to justify a separate genus. Lendenfeld (1903:21) transferred *C. macellata* to *Tetilla*.

REVISED DIAGNOSES OF TETILLID GENERA

As a result of the above discussion the following seven genera of Tetillidae are now considered valid (see also table 1).

1. *Tetilla* Schmidt (1868:40)

Type species : *T. euplocamos* Schmidt (1868:40)

Diagnosis : Tetillidae without cortex, porocalices, or unusual spicule types.

2. *Craniella* Schmidt (1870:66).

Type species : *C. tethyoides* Schmidt (1870:66)

Diagnosis : Tetillidae with cortex traversed by special spicules, without porocalices or unusual spicule types.

Remarks : cortical oxeas are reported to be in radial orientation (Sollas, 1888:30). However, I have examined a specimen of *C. tethyoides* from Barbados, identified by Schmidt himself (USNM 984), in which the cortical oxeas occur criss-cross in the cortex, as well as, although less densely, in the choanosome.

Table 1 - Valid genera of Tetillidae and principal characteristics used to distinguish them (+ = present ; - = absent).

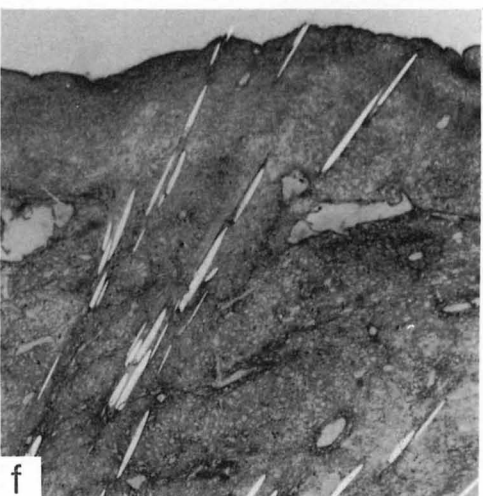
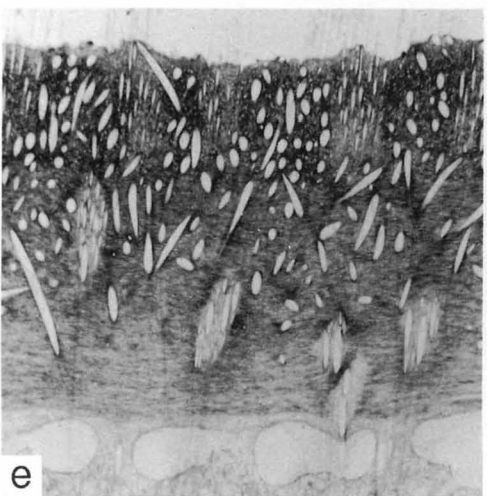
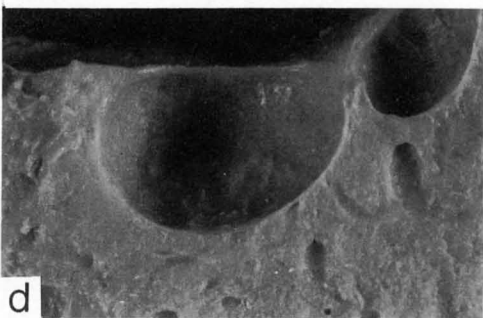
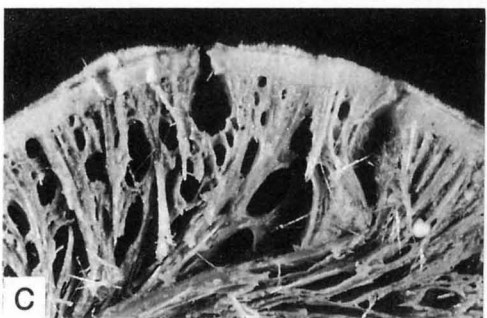
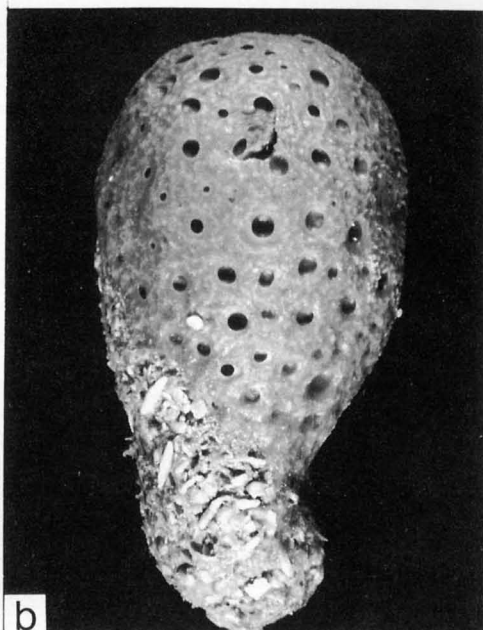
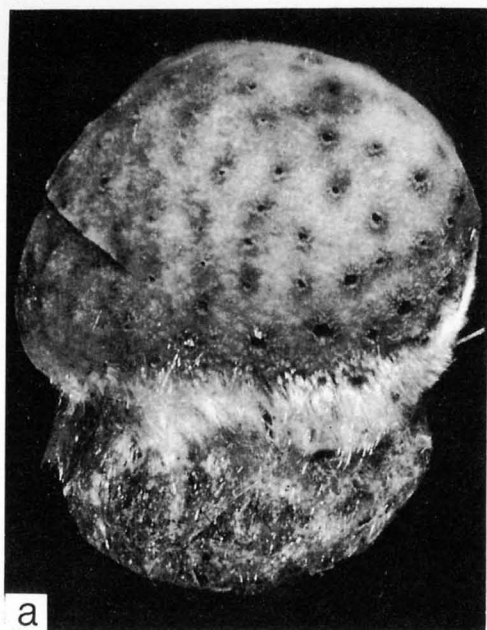
Genus	Cortex	Porocalices	Conspicuous accessory spicules	Nature of accessory spicules
<i>Tetilla</i> Schmidt, 1868	-	-	-	-
<i>Craniella</i> Schmidt, 1870	+	-	-	-
<i>Cinachyra</i> Sollas, 1886	+	+	-	-
<i>Paratetilla</i> Dendy, 1905	-	+	+	calthrop-like
<i>Amphitethya</i> Lendenfeld, 1907	+	-	+	amphiclads
<i>Cinachyrella</i> Wilson, 1925	-	+	-	-
<i>Acanthotetilla</i> Burton, 1959	-	-	+	acanthoxea

3. *Cinachyra* Sollas (1886:183)

Type species : *C. barbata* Sollas (1886:183)

Diagnosis : Tetillidae with pronounced cortex reinforced by special, robust oxeas, with flask-shaped porocalices, without unusual spicule types (Figs 1a, c, e ; 2e).

Remarks : cortical oxeas were originally described to traverse the cortex radiately (Sollas, 1888:23). Boury-Esnault & Van Beveren (1982) found their orientation rather confused except near the porocalices where they become radial. My own observations (uncatalogued specimens in U.S.N.M. collection) confirm this pattern for large specimens, but very small specimens (10-15 mm diameter) have the cortical oxea in almost perfect tangential orientation.



4. *Paratetilla* Dendy (1905:97)

Type species : *P. cineriformis* Dendy (1905:97)

Diagnosis : Tetillidae without cortex, with porocalices, and with a special layer of modified triaenes, resembling calthrops, lying in the ectosome or at the junction between ectosome and choanosome.

Remarks : Wilson (1925:380) reports that species without porocalices occur in this genus. The type species, however, is described as having poriferous "pocket-like depressions" (Dendy, 1905:97).

5. *Amphitethya* Lendenfeld (1907:126)

Type species : *A. microsigma* Lendenfeld (1907:126)

Diagnosis : Tetillidae with cortex, without porocalices, with a layer of cortical amphiclads (amphi-triaenes, -diaenes, -monaenes) and plagiotriaenes.

Remarks : in the type species, at least, the cortex is restricted to the stalk of the sponge (Lendenfeld, 1907:127).

6. *Cinachyrella* Wilson (1925:363)

Type species : *Tetilla hirsuta* Dendy (1889:75)

Diagnosis : Tetillidae without cortex, with poriferous pits (porocalices), without unusual spicule types (Figs 1b, d, f).

Remarks : Dendy (1922:11) already noted that the genus *Cinachyra* has been widely accepted and that many additional species have been assigned to it but that "none of these possesses the radially arranged cortical oxeas so characteristic of the type". With the same observation in mind Wilson (1925) established *Cinachyrella* as a subgenus of *Tetilla* but none of the later authors followed this practice. As a result of a recent study of *Cinachyra barbata* (Boury-Esnault & Van Beveren, 1982), N. Boury-Esnault (in lit., 1986) suggested to raise

Figure 1 - Comparison between *Cinachyra* and *Cinachyrella* : a/ *Cinachyra barbata* Sollas, habit, type species of the genus, Antarctica, x 0.9 ; b/ *Cinachyrella paterifera* Wilson, habit, originally described under *Tetilla* (*Cinachyrella*), Philippines, x 0.9 ; c/ *Cinachyra barbata*, cortex with porocalyx in cross section, x 1.4 ; d/ *Cinachyrella alloclada*, ectosome with porocalyx in cross section, x 1.4 ; e/ *Cinachyra barbata*, spicule reinforced cortex in cross section, x 26 ; f/ *Cinachyrella alloclada*, ectosome and outer choanosome in cross section, x 26.

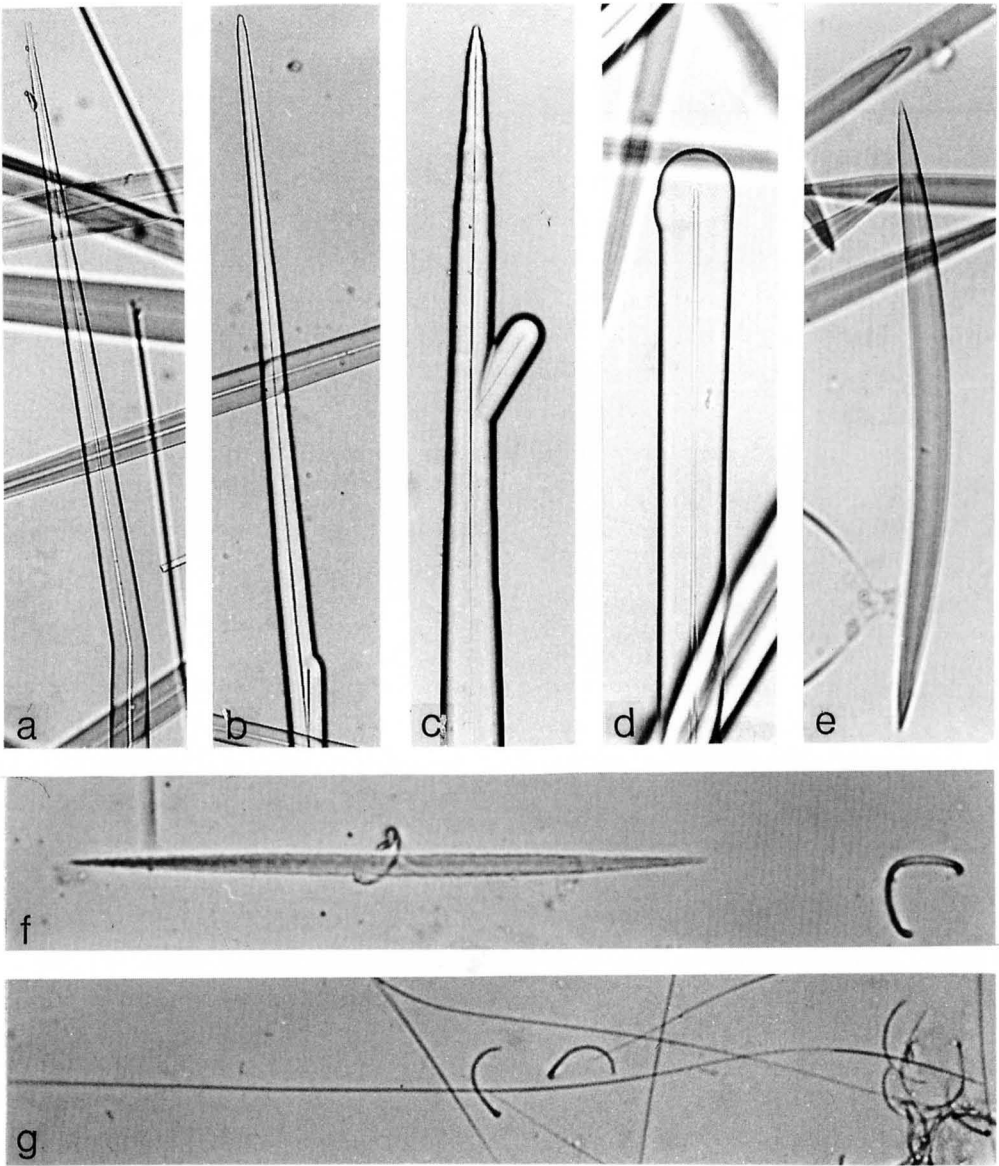


Figure 2 - Type and variability of monaxon spicules in *Cinachyrella* and *Cinachyra* : a/ simple kink near tip of large oxea, *Cinachyrella alloclada*, x 180 ; b/ kink near tip of large oxea showing branched axial canal, *C. alloclada*, x 180 ; c/ stepped tip and branching of large oxea, *C. alloclada*, x 180 ; d/ styloid modification of large oxea in *C. alloclada*, x 180 ; e/ cortical oxea, *Cinachyra barbata*, x 180 ; f/ crenulate accessory oxea and sigmaspires, *Cinachyrella kuekenthali*, x 720 ; g/ raphids and sigmaspires, *C. apion*, x 720.

Cinachyrella to the rank of genus to accomodate the many subtropical and tropical tetillids having poriferous pits but lacking a cortical armature of oxeas.

7. *Acanthotetilla* Burton (1959:201)

Type species : *A. hemisphaerica* Burton (1959:201)

Synonym : *Acanthocinachyra* Lévi (1964:386)

Diagnosis : Tetillidae without cortex, with porocalices, and with conspicuous mid-sized acanthoxeas as accessory megascleres.

Remarks : van Soest (1977:2) demonstrated that Burton (1959) overlooked the sigmaspires in his new sponge. This discovery eliminated the generic differences between *Acanthotetilla* Burton and *Acanthocinachyra* Lévi, placing the latter into synonymy with the former.

DIAGNOSTIC CHARACTERS ON THE SPECIES LEVEL

Based on the detailed analysis of 64 specimens of subtropical and tropical western Atlantic *Cinachyrella*, I tried to form an opinion about the importance and reliability of taxonomic characters used by previous authors to separate species within the family. The specimens were selected from a pool of more than 200 and represented 12 diverse morphological types, 3-10 individuals for each type. The morphological types display combinations of different body shapes (ball, erect pear, horizontal egg, presence of root tufts), size classes, porocalyx properties (diameter, shape, and distribution pattern), and surface conditions (smooth to the touch, bristly). Color, habitat conditions, and depth distribution were also evaluated.

The hypothesis was formed that anatomical details (spicule complement, shape and size, histology) should agree more between individuals whose morphological and environmental characteristics are identical than between those who display very different appearances, or come from different habitats or localities. With this perspective in mind I compared spicules and histological preparations with the following results.

Oxeas (Fig. 2) : they can appear in three distinct size classes ; raphides (some clearly arranged in trichodragmata) can also occur. Care has to be taken not to confuse small foreign oxeas (one of the most common forms in the sediments) with a proper size category. The largest class oxea can be modified to styloid, substyloid, and strongylote forms, a varying number can display stepped tips or a sharp kink close to one tip. The smallest category

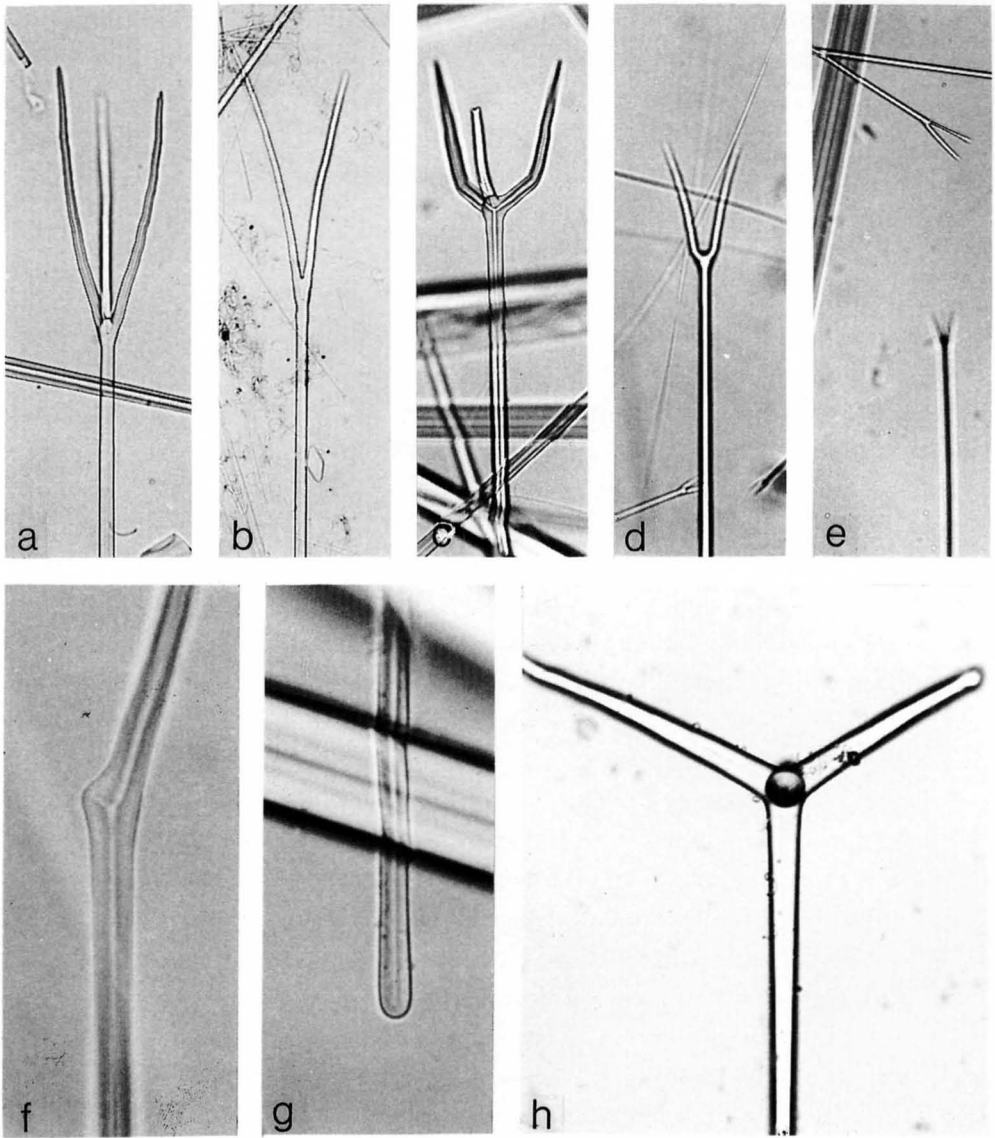


Figure 3 - Types and variability of protriaen-related spicules in *Cinachyrella* : a/ Protriaen, large size class, *C. alloclada*, x 180 ; b/ Prodiaen, *C. apion*, x 180 ; c/ Protriaen, crooked clads, *C. apion*, x 180 ; d/ Prodiaen, shaft diameter increasing toward midlength, *C. apion*, x 180 ; e/ Prodiaenes, small size class, *C. apion*, x 180 ; f/ Promonoaen showing forked central canal, *C. apion*, x 720 ; g/ rounded shaft point of small protriaen, *C. apion*, x 720 ; h/ Plagiotriaen, *C. tarentina*, x 180.

of oxea can be crenulate or roughened, also bent or curved sharply, or s-shaped.

Protriaenes (Figs 3a-g) : these occur in one or two distinct size classes and usually include reduced forms, such as diaenes (common) or monoaenes (rare). Rhabds are usually thickest just below the cladome, but some increase their width toward mid-length. Some rhabds end in sharp points, others in rounded ones. Clads can be long and slender, short and stout, crooked, bifurcate, or reduced to knobs ; some may diverge in angles as much as 120° .

Plagiotriaenes (Fig. 3h) : those observed in this material were common where they occurred and distinctly different from protriaenes because, in addition to the wide (120°) angles between their clads, they have considerably shorter, thicker shafts and longer clads.

Anatriaenes (Fig. 4) : occur only in one size class. Clads can be long, slender, and strongly curved, or short, stubby and almost straight ; some are bifurcate (rare) or reduced to knobs. Anatriaenes can be absent or extremely abundant in specimens that are otherwise undistinguishable and come from the same locality.

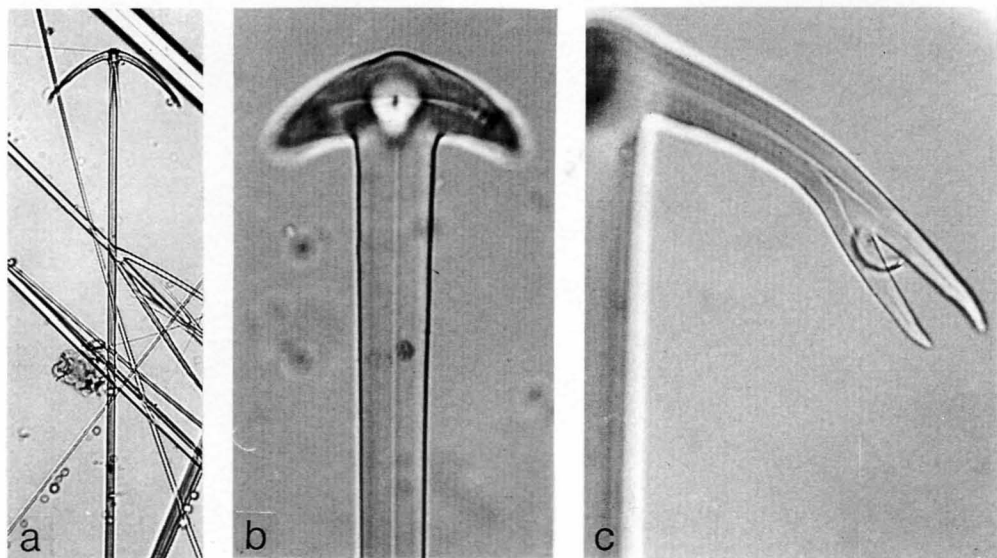


Figure 4 - Types and variability of anatriaenes in *Cinachyrella* : a/ typical anatriaen, *C. apion*, x 180 ; b/ stubby anatriaen, *C. tarentina*, x 720 ; c/ branched clad of anatriaen, *C. apion*, x 720.

Sigmataspires (Figs 2f, g ; 5) : these are c- or s-shaped, twisted to a varying degree, rarely with central swelling (centrotyl), and are beset by fine, thorn-shaped spines which are pointing away from the tips toward the center of the spicule.

Histology : this aspect is difficult to pursue in material, such as most of the present one, fixed for museum purposes. Histological features are not very diverse. The ectosome has a stratified appearance due to layers of spongin, interrupted by the presence of numerous spherulous cells which also occur in the choanosome although they are less dense there. Choanocyte chambers are more or less spherical and measure 25-35 μm in maximum diameter. Symbiotic bacteria have only been noted in one species (*Cinachyrella kueken-thali*). Many incorporated foreign spicules and sediment particles (mostly calcareous, 20 μm and 150-300 μm) are noticeable.

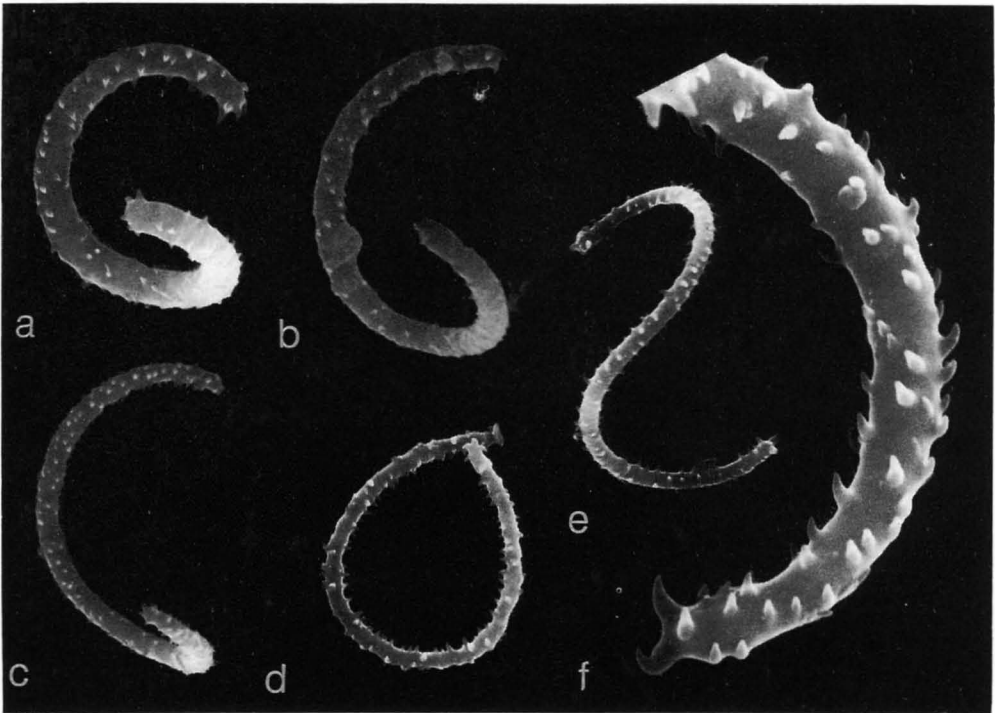


Figure 5 - Sigmaspires viewed by scanning electron microscope : a/ *C. alloclada*, x 3300 ; b/ centrotyl form, *C. alloclada*, x 3300 ; c/ *C. kueken-thali*, x 2100 ; d,e/ *C. apion*, x 3300 ; f/enlarged tip, *C. apion*, x 8200.

Comparing morphologically identical and diverse type groups, and groups from similar and dissimilar habitats, with anatomical characteristics of each specimen I find but few consistencies that allow objective (and, hence, generally applicable) separation of low level taxonomic units (species). Field observations of live material substantiated many theories suggested by study of museum specimens. I have therefore come to the following conclusions.

Specimen shape varies considerably with environment and age. Size is useful only if population averages can be obtained.

Porocalyx size, frequency, and location on the sponge varies much with environmental conditions (water turbulence, sediments) but little with specimen size or method of fixation. Deep (calm) water populations exposed to low sedimentation levels, for instance, develop large (relative to specimen size) porocalices.

Oscula contract easily and fully during fixation ; they are also easily formed new where needed.

Surface properties (bristly or smooth) can be species-characteristic but they are also dependent on environmental conditions (water movement and sediments), growth phase, and circumstances (in museum specimens) of collecting and handling.

Spicule variability is also considerable and only a few properties can be singled out as taxonomically useful. After lumping the 64 specimens of my analysed material into four species (based on at least two stable characters for each) I find that large oxeas with kinks, styloid, stongylate, and subtylostylote forms occur in three (but not all in the same three) species, while two size classes of oxeas occur in two. Protriaenes with rounded rhabd tips are found in all four species, those with rhabds widening at mid-length in three, with crooked and reduced clads in another combination of three. Prodiaenes are always present. Promonaenes (other than the large oxea with kink) were rarely counted because most of them looked distinctly crippled, with one or two knobs in addition to the single clad, or with indication of a forking of the axial canal. Anatriaenes are present in all species, even much more common than protriaenes in some specimens, but rare or absent in many other individuals. Stubby or stout clads occur regularly in two of the species.

A few remaining spicular characters are considered stable and were employed for diagnosing four species of *Cinachyrella* contained in the studied specimen series (Rützler & Smith, in press) : two or more size classes

Table 2 - Described western atlantic species of *Cinachyrella* and proposed taxonomic allocation.

Species named	New allocation	Remarks
<i>Cinachyra rhizophyta</i> Uliczka (1929:38)	<i>Cinachyrella apion</i> (Uliczka)	In agreement with van Soest & Sass (1981). The name <i>C. apion</i> is given preference because the type specimen of this species, presumed lost, is represented by a good quality photographic illustration.
<i>Cinachyra alloclada</i> Uliczka (1929:41)	<i>Cinachyrella alloclada</i> (Uliczka)	
<i>Cinachyra apion</i> Uliczka (1929:43)	<i>Cinachyrella apion</i> (Uliczka)	See comments under <i>C. rhizophyta</i> .
<i>Cinachyra kuekenthali</i> Uliczka (1929:43)	<i>Cinachyrella kuekenthali</i> (Uliczka)	
<i>Cinachyra schistospiculosa</i> Uliczka (1929:45)	<i>Cinachyrella kuekenthali</i> (Uliczka)	In agreement with van Soest & Sass (1981)
<i>Trachygellius cinachyra</i> Laubenfels (1936:158)	<i>Cinachyrella alloclada</i> (Uliczka)	A new spicule preparation from the holotype (U.S.N.M. 22433) revealed protriaenes, prodiaenes and anatriaenes which were obviously missed by the original describer.
<i>Cinachyra subterranea</i> van Soest & Sass (1981:337)	<i>Cinachyrella alloclada</i> (Uliczka)	After examination of a microscope preparation from the holotype (U.S.N.M. 32231, courtesy R.W.M. van Soest) I consider this an immature or stressed specimen of <i>C. alloclada</i> .
<i>Cinachyra</i> n. sp. van Soest & Stentoft (in press)	<i>Cinachyrella</i> n. sp. van Soest & Stentoft	Possesses raphides, but megascleres are different from <i>C. apion</i> (1 size class only).
<i>Cinachyra tarentina</i> Pulitzer-Finali (1983:477)	<i>Cinachyrella tarentina</i> (Pulitzer-Finali)	Possesses plagiotriaenes. This listing is the first record of the species for the western Atlantic.

of oxeas (*C. alloclada*, *C. kuekenthali*) ; smallest oxeas rough or crenulated (*C. kuekenthali*) ; presence of plagiotriaenes (*C. tarentina*) ; presence of two size classes protriaenes and of raphides (*C. apion*).

VALID SPECIES OF WESTERN ATLANTIC *CINACHYRELLA*

The four species emerging from our analysis, and a fifth species still unpublished (van Soest & Stentoff, in press), appear to be the only ones described for the western Atlantic region. Carrying further the evaluation presented by van Soest & Sass (1981:338, table 2) I am proposing the allocations summarized in table 2.

CONCLUSIONS AND RECOMMENDATIONS

One lesson learned by this study was already well expressed by Wilson (1925:356) who wrote that "*Tetilla* and its relatives offer excellent illustrations of the fact that sponge genera become more and more difficult to distinguish as the number of known species increases". The same seems to hold true for species and specimens. Chances are that the taxonomic criteria accepted here may turn out just as invalid as the ones rejected.

Perhaps a more biological approach than most museum collections allow could help to better classify families of so few and so variable characters as the tetillids. Until advanced molecular systematical methods have been tested it seems well advised to undertake careful regional studies with live material and to describe and illustrate morphological and anatomical characteristics before they become distorted by preservation, handling, and shipping. Without such data it will be impossible to ever attempt objective ecological or zoogeographical analyses.

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