Family Dactylocalycidae Gray, 1867

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Dactylocalycidae Gray (Hexactinellida, Hexactinosida) is returned from Lychniscosida to Hexactinosida due to lack of convincing evidence for interpretation of its dictyonal nodes as lychniscid. It is distinguished among Hexactinosida by lack of side-to-side fusion of dictyonal rays in its primary framework, and thus its members bear beams with single axial filaments. Three Recent genera, including five species, are assigned to the family: the type genus *Dactylocalyx, Auloplax*, and *Iphiteon*, the latter here recognized as the senior synonym of Schmidt's *Margaritella* and *Joannella*. *Diplacodium* Schmidt is transferred to junior synonymy of *Dactylocalyx*. All forms are thick-walled bodies constructed of branching and anastomosing tube systems, sometimes including cavaedial systems within body profile, but in the type genus, a single continuous labyrinthic complex without an associated cavaedial system is present. Channelization of the thin tubule walls is absent or barely marked in one genus as hemispherical depressions on both dermal and atrial tube surfaces. Spiculation includes pentactins, commonly with hexactins, as dermalia and atrialia, where they occur. Microscleres include discohexasters or discohexactins, with or without tylohexasters, onychexasters or oxyhexasters. Small uncinates without barbs occur in one genus but sceptrules are lacking (with one possible exception). The family is entirely Atlantic in distribution, roughly between 30°N and S latitudes, and has been recovered from depths of 88–2500 m.

Keywords: Porifera; Hexactinellida; Hexactinosida; Dactylocalycidae; Auloplax; Dactylocalyx; Iphiteon.

DEFINITION, DIAGNOSIS, SCOPE

Restricted synonymy

?Lithospongiae Duchassaing & Michelotti, 1864. Dactylocalycidae Gray, 1867a; Schulze, 1885; Ijima, 1903; Reid, 1957b. Aphrocallistidae (in part), Sollas, 1877b. Maeandrospongidae (in part) Zittel, 1877; Schulze, 1886. Auloplacidae Schrammen, 1912. Euretidae (in part); Ijima, 1927.

Definition

Basiphytous Hexactinosida with rigid walls composed of branching systems of tubes or tubules whose primary framework (tube/tubule walls) not euretoid in construction; dictyonal polyradial nodes result from tip-to-node and tip-to-tip fusion of dictyonalia; tube/tubule walls not channelized but may bear shallow hemispheric depressions on both surfaces.

Diagnosis

Body form as funnel, cup or curved plate; body wall composed of branching and anastomosing tubes or tubules 1–7 mm diameter opening terminally and on outer body surface but not in all cases opening to central body cavity; walls of tubes/tubules unchannelized but may be evenly pocked by shallow hemispheric depressions; body dermalia as rough pentactins, with or without hexactins, with club or pointed ray tips; sceptrules absent or questionably present in one genus which also has small barbless uncinates; microscleres include only discohexactins or combinations of discohexasters, tylohexasters, hemioxyhexasters to oxyhexactins, onychexasters; large broken 'monaxons' in one genus probably proximal rays of very large pentactins or hexactins.

Remarks

In original formation of the family, Gray (1867a) assigned to it the genera Dactylocalyx, Myliusia (now in Euretidae), MacAndrewia (a lithistid demosponge) and Farrea (now in Farreidae) but provided no useful definition for the group. Schulze (1885) briefly used the family name without definition, including only Dactylocalyx, Scleroplegma (a lychniscosan) and Margaritella (now junior synonym of Iphiteon, this work). Schulze (1886) abandoned the family in favor of Zittel's (1877) Maeandrospongidae as a receptacle for Dactylocalyx, and his decision was followed by most workers for many years. Ijima (1903) ressurected Dactylocalycidae, again without definition or diagnosis, assigning to it Dactylocalyx, Margaritella, Myliusia, Aulocalyx (now Aulocalycidae), Euryplegma (now Aulocalycidae), and all lychniscid sponges, Recent and fossil. Schulze (1904) finally provided the first family diagnosis, stressing the tubular construction of the cup or funnel bodies and presence of a cavaedial system between tubes. He excluded the lychniscid members, but his constituent genera were otherwise identical to Ijima's. After Ijima (1927) had again abandoned the family in favor of moving Dactylocalyx to Euretidae, Reid (1957b) once more resurrected Dactylocalycidae, including only Dactylocalyx and several fossil genera. He focused his family diagnosis upon interpretation of dictyonal nodes of Dactylocalyx as suppressed (hypersilicified) lychniscs and recognition that the tubules constituted a single intercommunicating labyrinth system open to both dermal and atrial body surfaces. Reiswig (1991), Mehl (1992) and Pisera (1997) have rejected Reid's claim of the lychnisc character of Dactylocalyx nodes due to absence of convincing supporting evidence. Dactylocalyx and Dactylocalycidae are thus returned here to Recent Hexactinosida. The diagnosis of the family as formulated above accepts and includes

Scope

Reid's assessment of the labyrinthic tubule system common to three genera, all of which lack euretoid formation of their primary dictyonal frameworks – the walls of the tubes/ tubules. Present assessment of the importance of this dictyonal fusion pattern should be considered preliminary and requiring reassessment, both within the newly defined family and in other hexactinosans where primary framework construction is poorly known.

KEY TO GENERA

AULOPLAX SCHULZE, 1904

Synonymy

Auloplax Schulze, 1904, 47; Schrammen, 1912:229; Ijima, 1927: 219; de Laubenfels, 1936a:185; Reiswig, 1990: 742. Not *Hexactinella* Carter 1885 (in part), Reid, 1963b: 228.

Type species

Auloplax auricularis Schulze, 1904: 47 (by monotypy).

Diagnosis

Dactylocalycidae constructed as a fan of laterally fused, thinwall tubes; with large dermal pentactins and thin uncinates with poorly developed brackets but without barbs; scopules may be present; only discohexactins as microscleres.

Definition

Monospecific (see type species description).

Remarks

The genus does not enjoy a stable relationship to other genera, reflected in its family assignments: Dactylocalycidae, Auloplacidae,

Tretodictyidae. Ijima (1927) justified his transfer of the genus to the Tretodictyidae by considering the fine uncinates as similar (homologous) to those of several tretodictyids and the doubtful strongylose scopules as proper. His interpretation of the tubule/ aperture system as schizorhyses is unacceptable. They are, in any interpretation, unlike the tortuous narrow-gauge schizorhyses characteristic of proper Tretodictyidae. They are not channels in a dictyonal framework, but they are tubules, and as such, are the dictyonal framework. Thus the basis for Ijima's (1927) and Reid's (1963b) suggestions that Auloplax might be a synonym of Hexactinella, and the latter's move of Auloplax to a subgenus of Hexactinella, are baffling and unsupportable. Search for more natural relatives will depend upon detailed analysis of dictyonal construction, not possible with presently available material. The genus contains only one other species, Hexactinella filholi Topsent, 1904a, which has never been figured. Topsent's description of that species from NW Spain (1900 m depth) differs in minor details (beam ornamentation, uncinate size and position) from Schulze's description of A. auricularis; H. filholi will very likely prove to be a synonym of A. auricularis.

Description of type species

Auloplax auricularis Schulze (Fig. 2).

Synonymy. Auloplax auricularis Schulze, 1904: 47, pl. 10, figs 1–15; Ijima, 1927: 219.

Material examined. Lectotype (not seen): ZMB 5389 (here designated). Paralectotype: ZMB 5390 (here designated) – SW



The family contains a total of five species in three genera, *Auloplax* Schulze, 1904. *Dactylocalyx* Stutchbury, 1841. *Iphiteon* Bowerbank, 1869c, but these all may prove monospecific when variability within the three type species is better known. It is restricted to the Atlantic Ocean between latitudes 31°S and 30°N (Fig. 1), and occurs at depths of 88–2500 m.



Fig. 2. *Auloplax auricularis* and distribution of *Auloplax*. A, body form with soft parts intact (from Schulze 1904, pl. 10, fig. 3). B, macerated skeleton of lectotype ZMB 5389 from both sides (from Schulze 1904, pl. 10, figs 4, 5). C, spicules: dermal pentactin, two uncinates, a dislodged young dictyonal hexactin and two discohexactins (from Schulze 1904, pl. 10, figs 10–15). D, dictyonal wall frame viewed from surface (from Schulze 1904, pl. 10, fig. 8). E, spicule lattice covering lateral tube apertures and a small part of the intervening grooves (from Schulze 1904, pl. 10, fig. 6). F, transverse section through surface layers (from Schulze 1904, pl. 10, fig. 7). G, distribution of *Auloplax*.

of Cape Bojador, NW Africa. Paralectotype: BMNH 1908.9.24.41 – same location, from ZMB by exchange.

Description. Flat or weakly curved plate (ear-form), to 8.5 cm tall, 8–12 mm thick, attached directly to hard substrate by narrow end (no stalk); composed of thin-walled (1 mm), nearly parallel tubes 3–4 mm wide, laterally fused and sharing inner walls; tubes branch at acute angles, forming a fan; tube lumina (atrial cavities?) are confluent through gaps in shared walls and open exteriorly by round to oval, 3–5 mm diameter, terminal and lateral gaps on both body faces; margins (walls) of lateral gaps often project out slightly from body surface plane; lateral apertures covered

by coarse, square-meshed spicule lattice; external grooves between tubes (cavaedia or intercanalar spaces) covered by finer-mesh (inhalant?) spicule lattice and communicate by small 1 mm wall apertures into tube lumina; texture stony but fragile; framework of fused dictyonalia forming rectangular meshes in inner layer but, due to irregular addition of supplementary macrohexactins (not microhexactins), meshes of superficial layer and older regions mainly triangular-irregularly polygonal; wall only 2 meshes thick; beams mainly smooth, some bearing profuse, sharp conic spines; peripheral spurs long, profusely spined and terminally swollen; nodes not thickened; megascleres: (1) rough dermal oxypentactins, $600 \,\mu\text{m}$ tangential ray length; (2) nearly smooth uncinates, $400-600 \times 2-4 \,\mu\text{m}$, with fine brackets but without barbs, tangential in dermis; club-tipped hexactins occur as detached (broken) dictyonalia; atrialia absent; microscleres as only rough discohexactins, $60 \,\mu\text{m}$ diameter, terminal disc $6 \,\mu\text{m}$ -wide with 5–7 teeth.

Remarks. The species remains known only from the mostly macerated original type collection from NW Africa (2500 m). Neither its spiculation nor its basic dictyonal framework construction are adequately known. Rare strongyle-tipped scopules were originally considered of possible foreign origin and never figured.

DACTYLOCALYX STUTCHBURY, 1841

Restricted synonymy

Dactylocalyx Stutchbury, 1841:87. *Diplacodium* Schmidt, 1880b: 57.

Type species

Dactylocalyx pumiceus Stutchbury, 1841:87 (by monotypy).

Definition

Dactylocalycidae with thick walls composed of dense network of irregularly branching and anastomosing tubules of small calibre, 1 mm diameter, completely penetrating body wall and opening on both surfaces; body wall incompletely penetrated by deep round or oval holes or longitudinally oriented grooves 2–10 mm wide.

Diagnosis

Body form as basal funnel, expanded distally as either a flat plate, bowl or uniform-diameter cup; tubule walls 1–3 dictyonalia in thickness; dictyonal meshes irregular, mostly triangular or polygonal; nodes polyradial; spined beams are single dictyonal rays; dermalia and atrialia as thin hexactins and pentactins with clubbed ray tips; large "monaxons" projecting from both surfaces probably proximal rays of very extended pentactins or hexactins with head broken off; microscleres predominately spherical discohexasters, but onychexasters may occur; sceptrules and uncinates are absent.

Remarks

The genus has been assigned to several families in its long history: to Dactylocalycidae by Gray (1867a), Aphrocallistidae by Sollas (1877b), Maeandrospongidae by Zittel (1877), Dactylocalycidae by Schulze (1885), back to Maeandrospongidae by Schulze (1886), back to Dactylocalycidae by Ijima (1903) and Schulze (1904), Euretidae by Ijima (1927) and most recently back to Dactylocalycidae by Reid, 1957b, its present position. Reid's (1957b) argument for removing *Dactylocalyx* from the Euretidae included interpretation of its dictyonal nodes as suppressed (hypersilicified) lychniscs and recognition that the tubules comprising the entire skeletal framework form a single, interconnected labyrinthic system. Reid's claim of lychnisc nature of nodes was rejected by Reiswig (1991) since convincing evidence of symmetrical octahedral formation has not been shown and has not been found when

searched for. Return of the genus and family from Lychniscosida to Hexactinosida proposed here, is supported by Mehl (1992) and Pisera (1997). Reid's claim of a single confluent tubule labyrinth, without distinction of dermal and atrial sides, is accepted. Channelization nomenclature developed for other hexactinosans are inappropriate for this structural pattern. A basic structural feature noted by Sollas (1877a) has not been mentioned by recent workers - that dictyonalia do not form euretoid junctions by sideto-side ray fusion, but instead fuse either ray tip-to-node or ray tipto-tip. This un-euretoid form of dictyonal soldering, resulting in polyradiate nodes as in the irregular secondary layers of some hexactinosans, further separates the genus from the Euretidae. Most of the species names assigned to this genus have been either reassigned to lithistid Demospongiae (Schulze, 1887a), relegated to synonymy with the type species, D. pumiceus, or are indeterminate or Hexactinosida incertae sedis, e.g., D. crispus Schmidt, 1870, D. patella Schulze, 1886, D. potatorum Schmidt, 1880b, and Lithospongia torva Duchassaing & Michelotti, 1864. The genus presently contains only two accepted species, D. pumiceus from tropical and subtropical western Atlantic and D. subglobosus Gray from the same region. The original location, Malacca, claimed for the latter is incorrect; the coral attached to the specimen base is definitely Madracis mirabilis, a shallow-water West Indian form (S. Cairns, pers. comm. 22/2/90). Similarity in body form of the two species supports argument that D. subglobosus might be a synonym of D. pumiceus, but the respective type specimens differ in microscleres - two classes of discohexasters in D. subglobosus and one in D. pumiceus. Since precise origin of D. subglobosus is unknown, distribution of the genus is that of the type species, D. pumiceus: western Atlantic from southern Brazil, through the Greater and Lesser Antilles and the Bahamas, from depths of 91-1966 m.

Description of type species

Dactylocalyx pumiceus Stutchbury (Fig. 3).

Restricted synonymy. Dactylocalyx pumiceus Stutchbury, 1841: 87; Gray, 1867a: 506, pl. 27, fig. 2; Carter, 1873c: 357; Sollas, 1879c: 123, pls 7–8; Schulze, 1887a: 348; Reid, 1957b: 821; Mothes de Moraes, 1977: 42, figs 1–3. *D. ingalli* Bowerbank, 1869b: 78. *D. pumiceus stutchburyi* Sollas, 1879c: 131, pls 5–6. *D. subglobosus*, Schmidt (not Gray, 1867a), 1880b: 53, pl. 4, fig. 8; Schulze, 1887a: 349, pl. 99, figs 1–6. *Diplacodium mixtum* Schmidt, 1880b: 57, pl. III (1879), fig. 16, pl. IV, fig. 7.

Material examined. Holotype: BMNH 1867.2.19.1 (dry) & BMAG D.p.#1 (slides) – Barbados, West Indies. Other material. *D. pumiceus stutchburyi*, holotype (slides): BMAG D.p.#2 – origin unknown. Specimens: CMN 1987-0227A & B – Barbados, West Indies; RMM I-4851 – Barbados; RMM I-6473 – Grand Bahama Is., Bahamas; RMM I-6527 – Lee Stocking Is., Bahamas; MCN Nos 195, 381, 382, 384 – all southern Brazil. Lectotype of *Diplacodium mixtum* (here designated): MCZ 8214 – N. of Cuba. Paralectotypes (here designated): MCZ 8212 & 8213 – Havana and N. of Cuba.

Description (measurements from holotype). Body basally as a thick-walled funnel attached to hard substrate by restricted disc, extending distally as either an expanded plate or an isodiametric tube or form between those extremes; body wall 20–30 mm thick, penetrated on both outer and inner surfaces by deep circular pits or longitudinally-oriented meandering grooves 2–10 mm wide, occasionally branching; outer body surfaces between pits/grooves inflated and smoothly continuous with pit/groove margins; atrial



Fig. 3. *Dactylocalyx pumiceus* and distribution of *Dactylocalyx*. A–B, body form of holotype. C, atrial and D, dermal surfaces of holotype. E, closer view of atrial surface tubule openings. F, relationship between dermal spicule lattice and framework surface (no scale available). G, broken proximal ray of large broken pentactin or hexactin (?). H, two hexactins. I, two pentactins. J, discohexaster with magnified terminal disc. K, onychexaster with magnified terminal claws. L, distribution of *Dactylocalyx*. (A–D, from Reiswig, 1991; F, from Sollas, 1879c.)

surfaces flatter with sharp edges at pit/groove margins; all framework surfaces completely porous, consisting of openings of small calibre tubules of 0.5-0.8-1.5 mm lumen diameter and 0.13-0.29-0.53 mm wall thickness; tubules extend throughout body wall, branching and anastomosing as single labyrinthic system, tortuously connecting dermal and atrial surfaces; all external body wall surfaces covered by delicate irregular loose spicule lattice, extending into pits/grooves but not spanning across large apertures; large single rays interpreted as proximal rays of distally broken pentactins or hexactins project in sparse numbers from framework surface through the dermal and atrial lattices; entire framework consists of tubule walls 1-3 dictyonalia thick forming irregular triangular to polygonal meshes; dictyonal rays fuse tip-tonodes or tips-to-tip, not side-by-side, so beams have single axial filaments and framework nodes are polyradial; beams coarsely spined or tuberculate, 24-47-95 µm thick, mesh sides 200-600 µm long; meshes rounded by silica deposition in corners and often reduced in size by synapticulation and beam thickening in

older areas, by intercalation of nets of small point-fused pentactins and hexactins in near surface areas; free megascleres: straight single rays of large pentactins or hexactins with head broken off 12-22-29 µm thick to 12.5 mm long, smooth except rough proximal end; sword hexactins, entirely microspined, with short distal rays as body dermalia and atrialia, occur in regular and irregular forms with thin cylindric rays 2.1-4.2-7.2 µm thick; regular form with club-end tangential rays 28-109-273 µm long, club-end distal ray 25-86-174 µm long, acute proximal ray 243-425-746 µm long; irregular forms with one or two entirely aborted or very elongate, sinuous, tangential rays; similar pentactins common as body dermalia and atrialia with tangential rays 33-135-432 µm long and proximal rays 80-266-598 µm long (includes short forms); tangential ray branching and fusion may occur; microscleres: spherical discohexasters (always abundant) with short primary rays bearing 3–5 straight, rough secondary rays 23–44–55 µm diameter; onychexasters (may be absent) with short primary rays bearing 2-4 straight, rough secondary rays 45-56-64 µm diameter; very rare oxyhexasters (may be absent) of similar form $55-58 \mu m$ diameter; distributed along western coast of Atlantic Ocean between 30° N and S, at depths of 91-1966 m.

Remarks. Sollas' (1879c) claim that Stutchbury used not one, but two, Bristol Museum specimens in formulation of his original species description, remains unsubstantiated. Both D. pumiceus specimens at the Bristol Museum described in detail by Sollas (1879c) were destroyed in WWII bombing, but survive as extensive sets of slides. The 3 type specimens of Diplacodium mixtum Schmidt bear spicules indistinguishable from typical Dactylocalyx pumiceus; that taxon is here designated a junior synonym of D. pumiceus. The two common West Indian species, Iphiteon panicea (often reported as its junior synonyms Margaritella or Joanella) and D. pumiceus have often been confused in literature due to their similar body form and spiculation. They are easily distinguished on the basis of the uniform smallcalibre tubules that make up the wall of *D. pumiceus* and the much larger calibre tubes and covered intercanal spaces in Iphiteon. They are nearly impossible to distinguish in photographic or video surveys. Although hundreds of D. pumiceus exist in zoological collections world-wide, providing material suitable for assessment of local genetic and geographic variation within the species, few have been examined in detail. The few reports in the literature have been either uncritical in methodology or incomplete in data reported. In the material Reid (1957b) surveyed, he noted that most surface megascleres were pentactins instead of the hexactins reported for the holotype, and microscleres consisted only of discohexasters (no onychexasters), but he did not provide details of specimen origin and disposition. Mothes de Moraes (1977) reported absence of pentactine megascleres and presence of oxyhexasters in specimens from southern Brazil; review of those specimens show oxyhexasters are absent and pentactine megascleres are common. A valid assessment of the variation in spicules of D. pumiceus across its broad geographic range is needed in order to establish the status of D. subglobosus as either a distinct species (present status) or a variant of D. pumiceus. Interpretation of the large spicules projecting from the surfaces of both species as pentactins is consistent with the lack of a central cross in the remaining parts and similar occurrences in other Hexactinosida. In terms of living tissue organization, D. pumiceus remains unique among the few surveyed Hexactinellida in the combined absence of both the secondary trabecular reticulum and the porous plugs joining differentiated parts of the syncytium (Reiswig, 1991). These points of tissue organization and the unique arrangement of dictyonal framework set D. pumiceus apart from the few other Hexactinellida for which tissue structure has been investigated to date.

IPHITEON BOWERBANK, 1869

Synonymy

[*Iphiteon*] Bowerbank, 1858: 310 (*nomen nudum*). *Iphiteon* Bowerbank, 1869b: 76; Ijima, 1927: 166. *Margaritella* Schmidt, 1880b: 54 (type by monotypy, *M. coeloptychioides* Schmidt); Schulze, 1887a: 351; Ijima 1927: 165. *Joannella* Schmidt, 1880b: 55 (type by monotypy, *J. compressa* Schmidt); Schulze, 1887a: 424.

Type species

Iphiteon panicea Bowerbank, 1869b: 76 (by monotypy).

Definition

Erect funnel-shaped basal cone flaring to trumpet-shape distally in large specimens; external surface with large apertures or longitudinal grooves, bordered by rounded ridges bearing numerous smaller apertures; internal surface of funnel constructed of strikingly flattened, longitudinal ridges joined by lateral bridges outlining longitudinal or spiral series of irregular apertures or slits with acute, sharp edges; basic whole-specimen wall constructed of longitudinally oriented, anastomosing tubes, sometimes flattened, interspersed with meandering system of inter-canals (intercavaedia); tubule walls not channelized but pocked by hemispherical depressions on both surfaces; dictyonal framework with triangular meshes arranged in spoke-like rotulate pattern and lacking dictyonal strands; main loose spicules as spined pentactins with some hexactins of regular and semi-pinulate form; tangential rays of megascleres with distinct club tips; microscleres as irregular oxyhexactins to oxyhemihexasters, tylohexasters and discohexasters; sceptrules and uncinates absent.

Diagnosis

Monospecific (see type species description).

Remarks

See under type species.

Description of type species

Iphiteon panicea Bowerbank (Fig. 4).

Synonymy. Iphiteon panicea Bowerbank, 1869b: 76; Bowerbank, 1869b: 323, pl. 21, fig. 1, pl. 22, fig. 1; Ijima, 1927: 166; Van Soest & Stentoft, 1988: 11. *Margaritella coeloptychioides* Schmidt, 1880b: 54, (1879) pl. 7, fig. 7; Schulze, 1887a: 351, pl. 101, figs 3–8; Wilson, 1902: 382; Ijima, 1927: 165; Van Soest & Stentoft, 1988: 11. *Joannella compressa* Schmidt, 1880b: 55, (1879) pl. 4, fig. 11. *Auloplax compressa*; Van Soest & Stentoft, 1988: 11.

Material examined. Holotype: MNHN LBIM. No. H.x.6 – Puerto Rico. Other material. YPM 9340 – Cuba; HBOI 003:00925 – Grand Turk Island, S. of Bahamas. Holotype of *M. coeloptychioides* (here designated): MCZ 6342 – Cuba , latitude of Havana. Other material: MCZ 6341 – locality unknown; USNM 23321 – locality unknown; USNM 23391 – Puerto Rico; UWIJ EST 352 & 530 – south of Jamaica; HBOI 002:00020 – Long Is., Bahamas. Specimens of *Joannella compressa* (type series not yet established): MCZ 6181ni & 6515 – off Santiago, Cuba; MCZ 6516 – Gulf of Mexico; MCZ 6824 – sw coast of Cuba; USNM 22337 – w of Puerto Rico; BMNH 1939.2.10.32 – Gulf of Mexico; YPM 519 – Cuba; ZMUB 26 – off Santiago, Cuba.

Description (measurements: mean \pm st. dev.). Basic funnel shape body, (holotype 18 cm tall by 18 cm distal diameter), with opening flared to trumpet shape in larger specimens; color light yellow when alive and golden-yellow when dried; sponge wall thickness 1.5–2.5 cm; wall composed of network of branching and anastomosing tubules 3–7 mm internal diameter, mainly circular in section but parts of the system flattened to various degrees perpendicular to the wall plane; tubule system arises from a basal ring at the inner wall surface, extends distally giving rise to curving radial branches terminating on the outer body surface as large exhalant



Fig. 4. *Iphiteon panicea* Bowerbank. A, dictyonal framework of the holotype with rotule arrangement (from Bowerbank 1869c). B–C, holotype MNHN LBIM No. H.x.6. D, outer surface of MCZ 6181ni (*Joannella compressa*). E, outer surface of lower body of YPM 9340. F, pentactins with club-tipped tangential rays. G, regular hexactin with club tips. H, two semi-pinulate hexactins. I, regular hexactin with sharp tips. J, diactin. K, oxyhemihexasters. L. discohexaster with magnified ray tip. N, distribution of *Iphiteon* (scale 100 µm for all megascleres; 30 µm for all microscleres).

apertures 3–7 mm in diameter or, when flattened, as deep grooves of same width; externally tubule walls, 0.8-1.6 mm thick, extend laterally to join with those of adjacent tubules forming distinctive, rounded, external ridges which serve as thin-walled perforated cover of extensive inter-canal system (intercavaedia) of same width as the tubule system; inhalant perforations 0.6-1.2 mm diameter on ridges open directly into inter-canal spaces; inner surface of funnel bears sharp-edged inhalant apertures between exceptionally flattened ridges as irregular slits or longitudinal or spiral series of ragged holes communicating directly with inter-canal spaces; no exhalant apertures open into the internal funnel cavity; tubule walls unchannelized, but uneven and undulating in section due to alternating 0.5-0.8 mm hemispherical depressions in both external and internal surfaces; dictyonal framework meshes mainly triangular with $80-140 \,\mu$ m sides arranged in spoke-like rotules; dictyonal strands and alignment of successive beams absent; external framework with smaller, more irregular mesh; internal nodes unswollen and microspined but external nodes slightly swollen and ornamented with few rough warts; spurs on external surface short and digitate; beams usually 30 μ m thick, lightly and evenly microspined; lower body portion hardened and increased in skeletal density by thickening of dictyonal beams to 90 μ m and addition of dictyonalia, narrowing all external apertures and solidifying external ridge surfaces; free spicules mainly spined pentactins with straight or slightly bowed club-tip tangential rays 135±29 μ m long, proximal ray highly variable in length 217±67 μ m with acute or rounded tip, distal ray as vestigial knob; all other megascleres less abundant including regular hexactins with rays 101±28 μ m long with club tips; semi-pinule hexactins with club-tip tangential rays 107±25 μ m long, proximal ray 151±90 μ m long, slightly inflated distal ray $76\pm19 \,\mu$ m long; smaller hexactins with acute-tip rays $92\pm20 \,\mu$ m long; club-tip diactins $291\pm97 \,\mu$ m long; occasional triactins and tetractins occur; microscleres include most abundant irregular oxyhemihexasters ranging to oxyhexactins $42\pm7 \,\mu$ m diameter; tylohexasters $68\pm11 \,\mu$ m diameter with solid centrum enclosing and obscuring primary rays and 20–50 rough secondary rays varying in length; discohexasters of highly variable size (perhaps 2 size classes) $43\pm11 \,\mu$ m diameter with short primary rays bearing 3–5 rough secondary rays; known distribution limited to northern Caribbean Sea at 88–1957 m depth.

Remarks. Bowerbank used the names '*Iphiteon*' and '*I. panicea* Valenciennes', in several publications prior to 1869 (Bowerbank, 1858: 310, 1862a: 817, 1862b: 1096, 1864: 203, 1866: 11) but in all cases he referred to specimen labels and expressed no intention to erect a new taxon. His ultimate description of the new form (1869b) was so poorly illustrated that other workers, e.g., Schmidt, were unable to recognize it when encountered. Schmidt (1880b) likewise failed to adequately illustrate and describe his new

species J. compressa and M. coeloptychioides, and it is only fortuitous that he provided Schulze with a fragment of the latter for Schulze's (1887a) adequate description of its framework and spicules. M. coeloptychioides, made recognizable by Schulze's description, became widely accepted and the similar (identical), but then distinct species, I. panicea and J. compressa, were essentially forgotten or considered unrecognizable forms. Ijima (1927) resurrected Iphiteon as a valid genus of Euretidae, but added nothing to clarification of its features and had no suspicion of its identity with Margaritella, a genus he also accepted as valid within Euretidae, nor with the unrecognizable Joannella. Inspection of the holotypes of I. panicea, M. coeloptychioides, and several specimens identified as J. compressa by Oscar Schmidt in his own handwriting, have shown all of these to be parts of specimens of the same species. The lack of mention of any of these genera by Reid (1963b) in his reorganization of the Hexactinosida is very surprising. The species has recently been used in a molecular study attempting to resolve relationships between the classes of Porifera (McInerny et al., 1999).