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

Family Aphrocallistidae Gray, 1867

Henry M. Reiswig

Natural History Section, Royal British Columbia Museum, 675 Belleville Street, Victoria, British Columbia, Canada V8W 9W2 and Biology Department, University of Victoria, P.O. Box 3020 STN CSC, Victoria, British Columbia, Canada V8W 3N5. (hmreiswig@shaw.ca)

Aphrocallistidae Gray (Hexactinellida, Hexactinosida) is distinguished among uncinate- and scopule-bearing dictyonine hexactinosans by possession of diarhyses as skeletal channels. The group has a relatively simple and straightforward history, and presently contains only seven recent species in two genera. Occurrence of members in shallow water directly accessible by SCUBA is responsible for numerous recent studies on their soft tissue organization, biochemistry and genetic sequences. In somewhat deeper shelf waters, members of the family are major constructors of modern bioherms, comparable to fossil hexactinellid reefs.
Keywords: Porifera; Hexactinellida; Hexactinosida; Aphrocallistidae; *Aphrocallistes*; *Heterochone*.

DEFINITION, DIAGNOSIS, SCOPE

Restricted synonymy

Aphrocallistidae Gray, 1867a. Mellitionidae Zittel, 1877. Melittionidae Schulze, 1885. Aphrocallistidae Schulze, 1904.

Definition

Basiphytous Hexactinosa with rigid walls penetrated by cylindrical diarhyses, often closely spaced in a honeycomb pattern.

Diagnosis

Branching-tubular to funnel- or cup-shaped main body with cylindrical or flattened mitten-form radial diverticula; wall 0.6–10 mm thick; dictyonal meshes mainly triangular but occasionally rectangular where broad interdiarhysial septa occur; dermalia usually pinular hexactins but pentactins may predominate; two forms of scopules only dermal or both surfaces; atrialia as pinular hexactins or large spined diactins; large uncinates and probably spined mesohexactins always present; microscleres include regular hexactins, hexasters and hemihexasters or forms elongate in one axis, with disco-, oxy-, and onycho-tips.

Remarks

Gray (1867a) provided no usable diagnosis for the family, but mentioned the round horizontal lateral pores of the walls, reference to structures now recognized as diarhysial channels. Zittel (1877) stressed complete penetration of the wall by the honeycomb arranged skeletal channels in forming his Mellitionidae, but that family, not formed from a name-bearing genus, has no validity. In his preliminary unveiling of the Challenger hexactinellids, Schulze (1885) erected *Melittiaulus ramosus*, perhaps with intent to form a post-hoc name-bearer for Zittel's family, but these ultimately fell to synonymy with Gray's senior genus *Aphrocallistes*, and family Aphrocallistidae. Schulze, and his numerous followers, maintained use of Zittel's family name, with unexplained change in spelling (presumably a correction of form) to Melittionidae, until 1904, when Schulze (1904: 178) independently decided to form a new family, Aphrocallistidae, without reference to Gray's earlier formation. Gray's priority was eventually accepted and has been the family name of use, with few exceptions (e.g., Burton, 1954) since that time. The pattern of aphrocallistid wall channelization, always a major element of the group's diagnoses, was finally give distinction when Ijima (1927) defined and designated them as diarhyses.

Scope

The family contains seven species, two with single named and nominate subspecies, in two valid genera. It is mainly northern and tropical cosmopolitan in distribution, with few reports from the southern hemisphere (Fig. 1). It ranges from 5–2949 m in depth, including the shallowest verified occurrence of any hexactinellid sponge (*A. vastus*). The family is considered closely related to Euretidae (Mehl, 1992), but phylogenetic tie to a genus of that group has not yet been hypothesized or tested.

KEY TO GENERA

(1) With atrialia as large, spined diactins .... ***Aphrocallistes***
With atrialia as pinular hexactins (rarely pentactins) with associated scopules .... ***Heterochone***

APHROCALLISTES GRAY, 1858

Restricted synonymy

Aphrocallistes Gray, 1858b: 114. *Iphiteon* Bowerbank (in part), 1869b: 76. *Melittiaulus* Schulze, 1885: 444, fig. 166.

Type species

Aphrocallistes beatrix Gray, 1858b (by monotypy).

Definition

Aphrocallistidae with diactine atrialia.

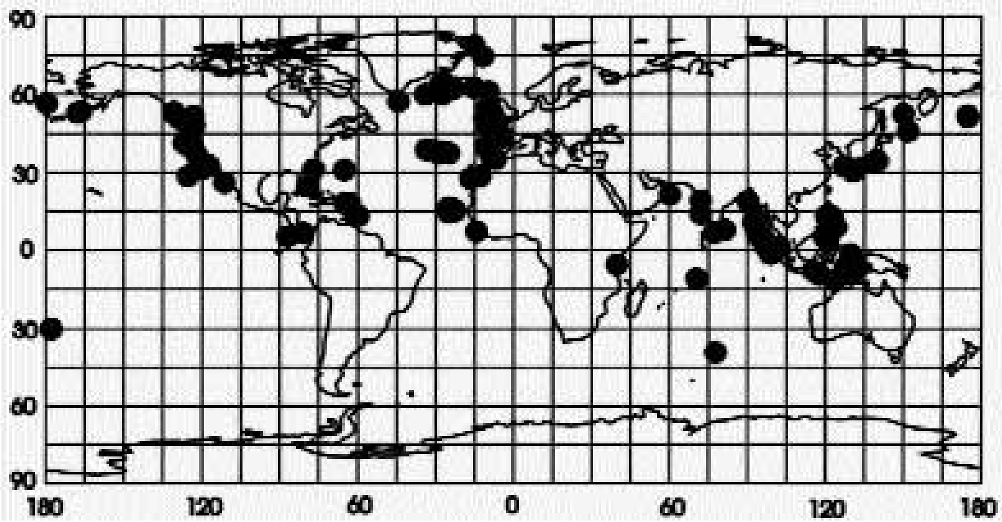

Fig. 1. Distribution of Aphrocallistidae.

Diagnosis

Body form as simple branching tubules to networks of branching and anastomosing tubules to funnel-form, main body bearing radial closed (rarely open) tubules or hollow mitten-form extensions; sieve plates may be formed across main osculum or atrial lumen; rigid wall from 1–10 mm thick; wall structure as very regular, low-density honeycomb resulting from closely packed diarhyses separated by thin, delicate septa, 1–2 dictyonal meshes thick; dermalia generally pinular hexactins but pentactins may occasionally predominate; scopules as accessory dermalia and occasionally atrialia with tine tips varying from strongylote, subtylote, tylote to oxyote, or ending in buttons or toothed discs; typical uncinates present; atrialia as tuberculate diactins with central knobs; microscleres as discohexasters and/or tylohexasters and/or oxyhexasters, often with secondary branching restricted to the two rays of one extended axis (syngrammous).

Remarks

The genus was formed in description of *Aphrocallistes beatrix* by Gray (1858b) for a specimen obtained from Malacca. Ten species and one subspecies have been proposed as members, but few are now considered valid. Schulze (1904) moved *A. bocagei* Wright, 1870, and *A. ramosus* Schulze, 1886, to junior synonyms of *A. beatrix*. He also placed *A. whiteavesianus* Lambe, 1892, as junior synonym of *A. vastus* Schulze, 1886. Koltun (1967) assigned *A. intermedia* Okada, 1932, and *A. yatsui* Okada, 1932, to synonymy with *A. vastus*. He also moved *A. aleutiana* Okada, 1932, to *Chonelasma*, but being unaware of Ijima's (1927) formation of *Heterochone*, that action was erroneous. My restudy of *A. aleutiana* type material has verified its appropriate position as *Heterochone aleutiana*, the transfer made here. Schulze (1904) was unable to decide placement for *A. azoricus* Topsent, 1901c, an inaction misconstrued by Stephens (1915a) and several others. Topsent eventually (1928) decided the form should be moved to Ijima's new *Conorete*, but, as discussed under Euretidae, Topsent's addendum action is rejected and his initial (1928) action is followed, retaining the form as *Pityrete azoricus*. Koltun (1967) erected a new subspecies, *A. beatrix incognitus*, for a few poorly preserved aphrocallistid fragments from the Okhotsk Sea. A new specimen assignable to this form is clearly a member of *Heterochone*, supporting its reassignment as *H. incognitus* Koltun – detailed justification in progress elsewhere. Sim and Kim (1988) made the last addition to the genus, *A. jejuensis*, from Korea. This form falls within the broad range of variation of *A. beatrix* as presently understood. Its lack of oxyhexasters, shared by some specimens of *A. beatrix orientalis* Ijima, 1916, is considered insufficient to maintain its species status; it is here moved to junior synonymy of *A. beatrix*. The genus presently contains only two recognized species, *A. beatrix* with two subspecies, *A. beatrix beatrix* and *A. beatrix orientalis*, and *A. vastus* without subspecies. It is northern-cosmopolitan in distribution with only one report beyond 15°S latitude, and ranges in depth from 5–2949 m. Occurrence of *A. vastus* in shallow water of British Columbia, Canada, easily within SCUBA range, has made possible detailed study of its preserved tissue structure (Reiswig, 1979; Mehl & Reiswig, 1991, Leys, 1999), cytoplasmic streaming in living syncytia (Leys, 1998), biochemistry and genetic sequences as related to phylogeny (Mueller *et al*., 1984). In deeper water, *A. vastus*, with *Heterochone calyx*, has been found to be a major component of modern bioherm construction (Conway *et al*., 1989).

Description of type species

Aphrocallistes beatrix Gray (Fig. 2).

Restricted synonymy. *Aphrocallistes beatrix* Gray, 1858b: 114, pl. 11; Schulze, 1887a: 305, pl. 84, figs 9–10; *Iphiteon beatrix*; Bowerbank, 1869b: 75. *Aphrocallistes bocagei* Wright, 1870: 4, pl. 1. *Aphrocallistes ramosus* Schulze, 1886: 75; Schulze, 1887a: 319, pl. 86, figs 1–11. *Aphrocallistes beatrix orientalis* Ijima, 1916: 173. *Aphrocallistes jejuensis* Sim & Kim, 1988: 29, pls 6–10.

Material examined. Holotype: BMNH 1842.11.30.12 – Malacca.

Description. Body form variable: (1) 'beatrix' form: thin-wall axial funnel to 15 cm long, 8–10 mm diameter at base, 15–24 mm diameter at apex, bearing lateral tubular diverticula 3–8 mm diameter to 3 cm long, closed at ends; (2) 'bocagei' form: similar axial funnel to 24 cm long with close-spaced radial diverticula increasing in length from base to apex; (3) 'ramosus' form: system

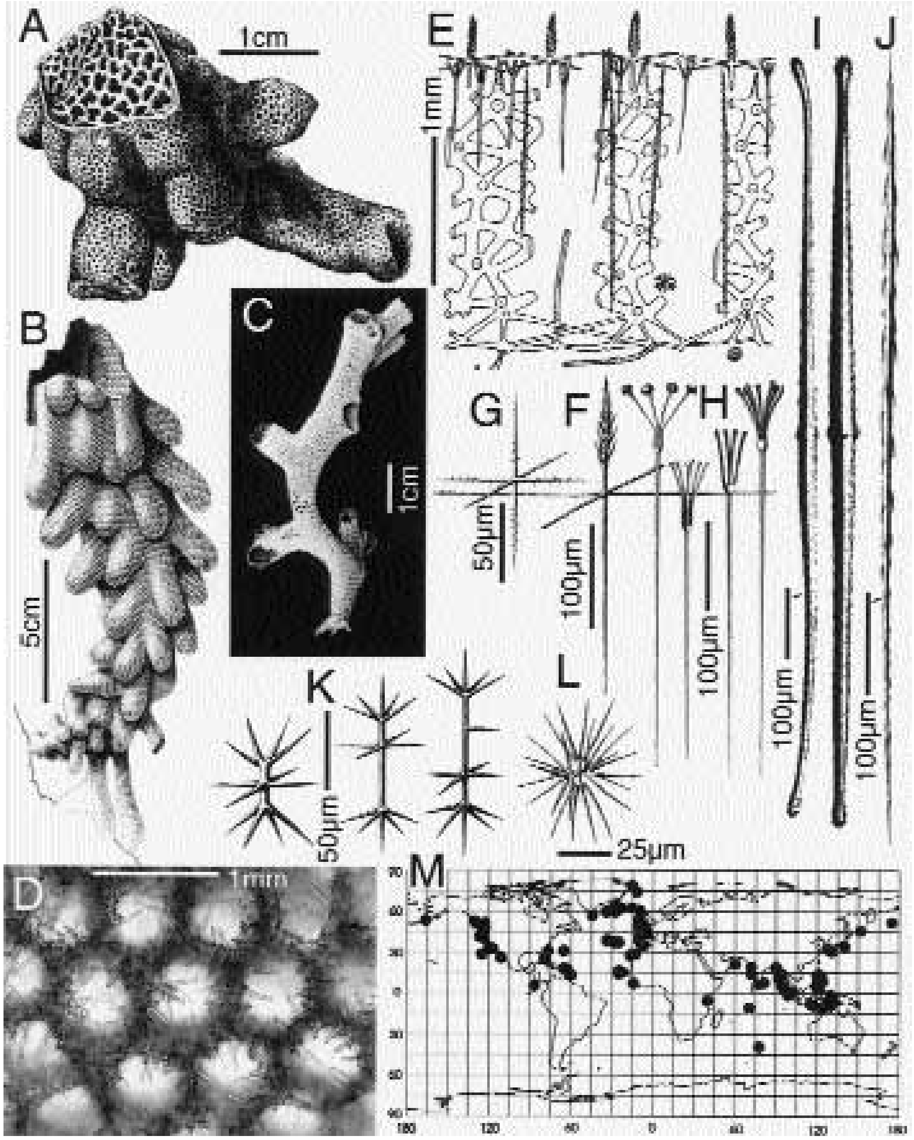

Fig. 2. *Aphrocallistes beatrix* and distribution of *Aphrocallistes*. A, holotype (from Gray, 1858b, pl. 11, fig. 2). B, 'bocagei' form (from Schulze, 1887a, pl. 83, fig. 1). C, 'ramosus' form (from Schulze, 1887a, pl. 86, fig. 1). D, wall surface with diarhyses in honeycomb pattern (holotype). E, transverse section of body wall, 'bocagei' form (redrawn from Schulze, 1887a, pl. 84, fig. 1). F, dermal pinule. G, parenchymal hexactin. H, variety of scopules. I, two atrialia. J, uncinate. K, three syngramme hemioxyhexasters. L, regular oxyhexaster. M, distribution of *Aphrocallistes*. (Spicules: F–I, from 'beatrix' form, Schulze, 1902, pl. 15; J, from 'bocagei' form, Schulze, 1887a, pl. 84, fig. 2.)

of sparsely branching and sometimes anastomosing tubes without axial funnel; thin wall 0.5–3 mm thick; dictyonal framework of closely spaced diarhyses separated by very thin septa, one dictyonal mesh thick, giving a very regular hexagonal honeycomb appearance; rigid transverse sieve plate may cover the main osculum or, when internal, subdivide the atrial lumen; beams tuberculate, 30–80 µm thick; nodes slightly or markedly swollen; dictyonalia of septa with all 6 or 5 rays basally curved to lie in septal plane, with one ray often projecting into channel lumen as spur directed usually dermally or atrially if near atrial surface; secondary dictyonalia occasionally extend over some atrial diarhysial apertures; meshes triangular; dermalia normally pinular hexactins (occasionally pentactins) with narrow, thorned pinulus and distally tuberculate paratangential rays 100–200 µm long, proximal ray longer or shorter; dermal scopules 350–500 µm long, usually in 3 forms but pattern varies: (a) thick scopules with 4–8 nearly parallel tines ending in strongylote or button tips; (b) thin scopule with 4 tines moderately divergent and often geniculate ending in disc or tylote tips; (c) scopule with tines slightly divergent ending in pointed tips; large uncinates of common form; atrialia as diactins 1–2 mm long, entirely tuberculate, bearing 4 central knobs, slightly curved; parenchymal hexactin entirely tuberculate or heavily spined, rays 50–75 µm long; microscleres include hemiasters with secondary branching restricted to one axis (syngramme form) and regular, spherical asters with branching on all primary rays (synstigme form); either form may be oxy-tipped or tylo-tipped; syngramme forms typically 80–150 µm long; synstigme forms typically 25–50 µm diameter; species distribution northern-cosmopolitan, one report from latitude greater than 15°S; depth range 60–2949 m.

Remarks. The species is presently understood to include *A. bocagei* Wright, *A. ramosus* Schulze, and *A. jujuensis* Sim & Kim, as synonyms of the typical subspecies, and *A. beatrix orientalis* Ijima, as a distinct subspecies. Restudy of morphological variation to assess status of these forms and their subtended local populations is warranted but likely to be unrewarding. Use of formal trinomina for bocagei and ramosus forms have no objective supporting evidence and are discouraged. Surprisingly, complete details of spiculation of the type specimen of *A. beatrix* have never been published; a few spicules, notably the distinctive elongate hemioxyhexasters have been figured by several authors. Spiculation description and figures provided here are mainly from specimens obtained near the Andaman Is. (Schulze, 1902).

HETEROCHONE IJIMA, 1927

Restricted synonymy

Chonelasma Schulze (in part), 1886: 76. *Heterochone* Ijima, 1927: 118; Reid, 1963b: 228.

Type species

Chonelasma calyx Schulze, 1886: 77 (by original designation).

Definition

Aphrocallistidae with pinular hexactins as atrialia.

Diagnosis

Funnel- or plate-shaped body with tubular radial extensions of lateral body wall; wall 4–10 mm thick; diarhyses clear in distal regions may be obscured by irregular addition of dictyonalia and beam thickening in older regions; dermalia and atrialia as pinular hexactins; two forms of scopules as accessory spicules on both surfaces; large uncinates of typical form; parenchymalia include spiny mesohexactins and a variety of microhexasters and microhexactine derivatives with disco-, oxy-, tylo- or onycho-ended secondary tips.

Remarks

Ijima (1927: 118) formed *Heterochone* from those species of the euretid genus *Chonelasma* having diarhysial channelization, and selected *C. calyx* as type of his new genus. This origin was confused by Ijima (or the editors of the posthumous work, Y. Okada and M. Weber) later stating *Aphrocallistes* to be the only genus of Aphrocallistidae (ibid: 285). *Heterochone* was never formally diagnosed and was erroneously omitted from the final taxonomic summary list of that work (Reiswig, 1990). In later years it was recognized by some workers (de Laubenfels, 1936a; Reid, 1963b) but ignored and unknown to others (Koltun, 1967; Tuzet, 1973b; Austin, 1985) who retained the relevant species in *Chonelasma*. Presently the genus contains 5 species: *H. calyx* (Schulze, 1886) with two subspecies, *H. calyx calyx* (Schulze, 1886) and *H. calyx schulzei* (Koltun, 1967), *H. tenera* (Schulze, 1899), *H. hamata* (Schulze, 1886), *H. aleutiana* (Okada, 1932) (originally assigned to *Aphrocallistes* and mistakenly moved to *Chonelasma* by Koltun, 1967, but repositioned here), and *H. incognita* (Koltun, 1967; originally *A. beatrix incognitus* Koltun, 1967 but new material proves it to be a member of *Heterochone* (details in preparation elsewhere). Inclusion of Okada's *Aphrocallistes aleutiana* is uneasy since the original description of the severely macerated specimens included both diactins and pinular pentactins as atrialia, a mixture of characters of the two aphrocallistid genera; review of original specimens was not possible since their location remains unknown as of this writing. Disposition of several forms described as *Chonelasma* sp. remains unresolved. Recent distribution of the genus is entirely Pacific, with only one species, *H. hamata*, occurring in the southern hemisphere; depth range is 25–2219 m.

Description of type species

Heterochone calyx (Schulze) (Fig. 3).

Restricted synonymy. *Chonelasma calyx* Schulze, 1886: 77; Schulze, 1887a:326, pl. 89, figs 1–6; Schulze, 1899:78, pl. 19, fig. 5; Koltun, 1967:50, pls 31–32. *Heterochone calyx* Ijima, 1927:118. *Chonelasma calyx schulzei* Koltun, 1967: 53, pls 33–34.

Material examined. None. Lectotype (here) designated: MZUS PO 903. Paralectotype (here designated): MZUS PO 902 – Sagami Bay, Japan.

Description (from the literature). Axial body as cup or funnel to 30 cm tall with large terminal oval osculum and compact stalk attached to hard substrate; lateral walls bearing radial, hollow, finger-shaped diverticula to 15 cm long open at tips by 3–10 mm diameter accessory oscula; lower margins of lower diverticula often extended basally as solid or hollow stolons extending to substrate forming secondary attachments; rigid body wall 4–10 mm thick penetrated by radial or oblique diarhyses opening by apertures externally 1–2 mm and internally 2–3 mm diameter; diarhyses arrayed in regular honeycomb pattern in young tissues; surface lattice of pinular hexactins with accessory scopules cover external diarhysial apertures but extent of internal lattice uncertain; secondary dictyonalia may occlude internal diarhysial channels in older regions; coloration brown to yellow to carrot orange; dictyonal mesh in middle layers regularly rectangular but more irregular with smaller triangular mesh near surfaces; older areas characterized by hypertrophy of longitudinal and transverse beams throughout wall thickness, resulting in occlusion and loss of perceptible regularity of diarhyses; beams partly smooth and partly spined (entirely spined in North American specimens); loose spicules: pinular hexactins as dermalia and atrialia with thorned pinulus 48–115 μm long, tangential rays spined at tips 100–302 μm long, proximal ray 148–1265 μm long; scopules as accessories on both surfaces, 242–550 μm long, bearing 4–6 retro-spined tines with subtylote or strongylote tips; heads in two forms: tines weakly s-form or straight and moderately divergent; parenchymal hexactins entirely spined with rays 80–200 μm long; uncinates numerous, $500–1540 \times 14–54\,\mu$m near and perpendicular to surfaces; microscleres variable: discohexactins and discohexasters 50–100 μm diameter with 2–4 secondaries and terminal discs with 4–6 marginal teeth (interpreted as onychexactins and onychexasters by some); oxyhexactins and oxyhexasters 50–100 μm diameter usually rare but only microsclere form in subspecies *schulzei*; distributed from Japan around N. Pacific margin to Panama at depths of 25–1103 m.

Remarks. Reid (1963b, 1964) questioned the appropriate designation of channelization in *H. calyx* as diarhyses, and suggested study of soft tissues might resolve the issue. The skeletal channels in young regions satisfy the definition of diarhyses (Ijima, 1927) and

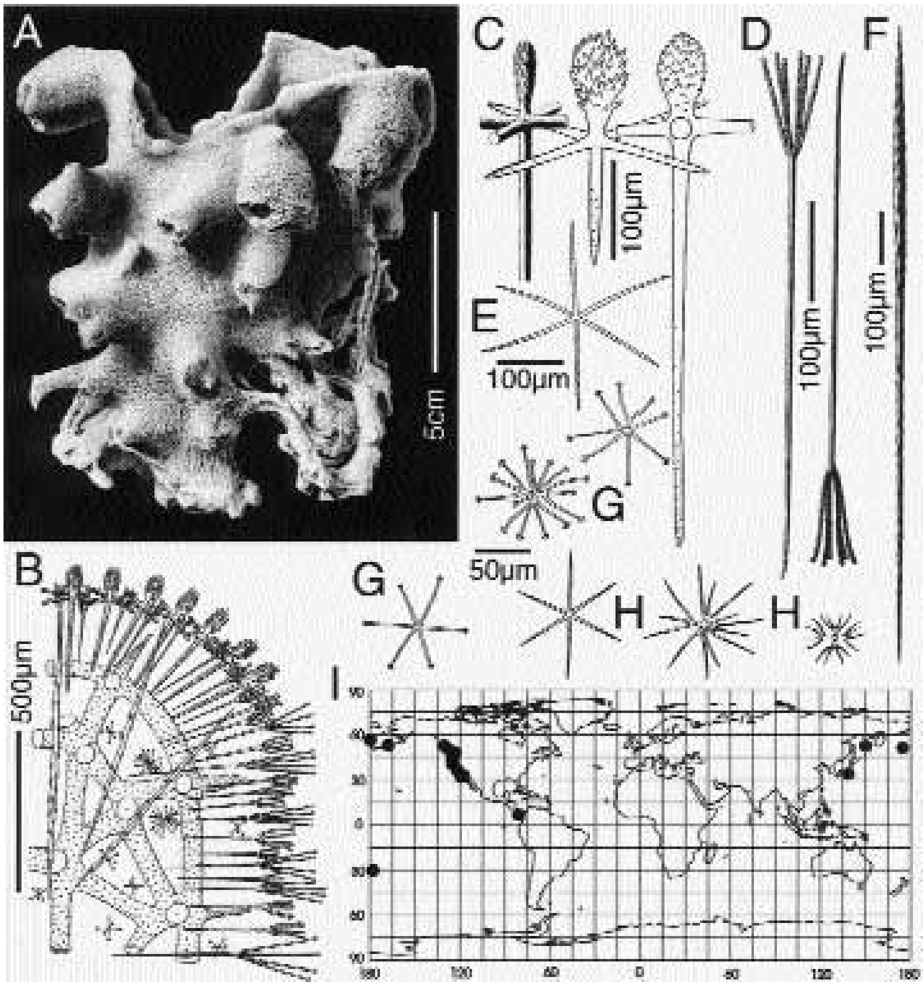

Fig. 3. *Heterochone calyx* and distribution of *Heterochone*. A, body form of lectotype. B, vertical wall section (N. American specimen) showing external surface (top) and diarhysial surface (right). C, pinular hexactins from Japan lectotype (left) and Okhotsk specimen (center and right). D, scopules (lectotype). E, parenchymal hexactin (Okhotsk specimen). F, uncinate (lectotype). G, discohexactin and discohexasters (Okhotsk specimen). H, oxyhexactin and oxyhexasters of *H. calyx schulzei* (Bering Sea). I, distribution of *Heterochone*. A, C (left), D, F, from Schulze, 1887a, pl. 89; B, from Schulze, 1899, pl. 19, fig. 5; C, (center, right), E, G, H, from Koltun, 1967, pls 32 & 34.

there is nothing in that definition to do with living tissues. Schulze (1899) claimed (and figured) scopules were present in channel linings (see Fig. 3B), but he also indicated by the same figure that a dermal lattice did not extend over diarhysial apertures, a very unlikely condition that remains unresolved. While body forms of Japan and North American specimens of *H. calyx* are very similar, there appear to be significant differences in pinulus shape. Schulze (1899), the only worker to have studied specimens from both regions, decided there was no basis for their subdivision. Modern appreciation of gene flow limitations suggests a quantitative survey of samples along the extended species distribution might expose sibling or subspecific populations deserving of taxonomic recognition. Indeed characteristics of the type Japan population is poorly known in spicule data and figures; those provided here are mainly from Okhotsk Sea specimens (Koltun, 1967) since Schulze provided scant dimensions and figures (none of microscleres) for the Japan material. The massive skeletons of the species persist long after death, contributing to bioherm construction of British Columbia, Canada (Conway *et al*., 1989), and providing substrate for settlement of many other sponges (Ijima, 1901, 1904).