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The freshwater medusae of the world – a taxonomic and systematic literature study with some remarks on other inland water jellyfish

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Abstract

Several medusa species have been described from inland waters in Australia, Eurasia, Africa and America. The chief objective of this study is to summarize all species described from freshwater and from saline lakes, because the knowledge about this group is sparse and scattered in the literature. I summarize all accessible literature to deduct how many species of freshwater medusae exist and to show their distribution, relation and their phylogenetic origin.

All medusae described from freshwater except *Halmomises* are Olindiidae (Limnomedusae). More than 20 Olindiidae species (in 6 genera) have been recorded from freshwater. However, about half of them may not be valid species or have been described insufficiently or improperly. Within the genera *Craspedacusta* only 3 (or 5) species are certain (*C. sowerbii*, *C. iseanum*, *C. sinensis* (and maybe *C. sichuanensis* and *C. ziguiensis*)). The genera *Limnocnida* may consist of 6 species, three from Africa (*L. tanganjicae*, *L. victoriae*, *L. congoensis*) and 3 from India (*L. indica*, *L. biharensis*, *L. nepalensis*). The status of *Astrohydra* (from Japan), *Mansariella* and *Keralika* (both from India) is uncertain. Additionally, the present study suggests that *Craspedacusta* and at least one type of *Calpasoma* hydrants are identical and *Astrohydra* may be closely related to *Craspedacusta* and/or *Calpasoma*.

A comparison of the freshwater medusae with species described from saline lakes and brackish sites (*Australomedusae* from Australia and *Moerisia* from Egypt, Black Sea, Caspian Sea and Ganges Estuary) shows that these two groups are not closely related.

Introduction

Several species of inland water medusae have been described from localities all over the world. On the Indian subcontinent (including Nepal), six species (in three genera) of freshwater medusae and one in the Ganges estuary are recorded, and from East Asia (China, Japan, Sakhalin, Taiwan) several *Craspedacusta* species or variations are described (summarized by Dumont, 1994; Bouillon & Boero, 2000b). From Africa several species of inland water medusae (mostly *Limnocnida*) are known, while from Europe and the North and South American continent (excluding Trinidad, see below) only *Craspedacusta sowerbii* is reported. It is obvious that *Craspedacusta* and *Limnocnida* have different distribution centres with dufferent regional distributions of each single species while *Craspedacusta sowerbii* is the only freshwater medusa with a cosmopolitan distribution. Although freshwater medusae have been known for more than 100 years (Lankester, 1880) and much literature is available, our knowledge (systematic, ecology) about these animals is unsatisfactory (Dumont, 1994). Many ecological observations remain unexplained, the number of existing freshwater medusae is unclear and only speculations exist concerning their phylogenetic origin (Dumont, 1994). Recently, some reports were published about the predatory impact of *Craspedacusta sowerbii* on pelagic systems (Dodson et al., 1983; Spadinger et al., 1999; Jankowski, 2000; Jankowski

& Ratte, in press). Some older studies dealt with the irregularity of mass occurrences and the factors which induce medusae budding (Reisinger, 1957; McClary, 1959, 1961; Lytle, 1959, 1961; Acker, 1976). It is likely that freshwater medusae are a geologically young and polyphyletic group (Hadzi, 1928), though it is unknown yet when and where the medusae moved into freshwaters. Two hypotheses exist on the origin of freshwater medusae. *Craspedacusta* may be related to *Gonionemus* (a marine member of the same family) and have originated in Eastern Asia. Alternatively, medusae may have colonized the freshwater twice during Tethys: *Craspedacusta* the Northern and *Limnocnida* the Southern continents (Stadel, 1961). However, new *Craspedacusta* species (*C. vovasi*, from a marine site) and new genera (*Keralica*, *Mansariella*, *Astrohydra*, all from freshwater) described, revive the question of the phylogenetic origin of the inland water medusae. Potentially closely related species can be medusae from saline lakes and brackish sites. The genera *Moerisia* is known from saline inland waters (Caspian Sea, Lake Qurun) and an estuary (Ganges), and *Australomedusa* is known from an Australian salt lake. Are these species the origin of the freshwater medusae? How closely related are these species from saline sites to the freshwater ones?

It is important from an ecological, evolutionary and physiological point of view at which time and where the medusae were able to colonize lacustrine systems. However, current knowledge about freshwater medusae is scarce, and further detailed phylogenetic investigations are only possible if both the number and status of the species are clear. Therefore, this review collects all information available on inland water (mostly freshwater, some brackish and saltwater) medusae. I focus on a comparison of morphological traits, discuss their usefulness to distinguish species and summarize this information to point out which of the described species may be in fact identical. Morphological as well as geographical information are used to compare different hypotheses on the origin of freshwater medusae.

Some remarks on systematics

The high-rank systematics of the Hydrozoa are complicated and confused (for a discussion see Bouillon & Boero, 2000a). Here, I follow the systematic and terminology of Bouillon & Boero (2000a,b) who presented a system based on embryological, developmental and morphological features of each Hydrozoan sub-group.

All species described from inland waters (fresh, brackish and saline) belong to the superclass Hydrozoa. In contrast to older systematics (Mayer, 1910; Russell, 1953; Kramp, 1961) modern systematics (Bouillon, 1985; Hartwich et al., 1993; Westheide et al., 1996; Bouillon & Boero, 2000a,b) are based not only on embryological, developmental and morphological features but also on nematocyst structure. Currently (Bouillon & Boero, 2000a,b), inland water jellyfish are distinguished into two sub-classes within the class Hydroidomedusa: Athecata/Anthomedusa with the orders Filifera (*Australomedusa*) and Capitata (*Moerisia*, *Halmomises*), and Limnomedusae (e.g. *Craspedacusta*, *Limnocnida*). It is remarkable that the nematocyst composition (Table 1 and Fig. 1) among other characters of several species (*Keralica*, *Astrohydra*, *Mansariella*) of freshwater medusae is unknown as indicated in Table 1. Therefore, their systematic position is unclear

Species described from fresh waters, brackish waters and saline lakes

In the following descriptions of species from inland waters are presented. In many cases, original citations are used for the most objective and most simple determination possible. The order of listed species follows the systematics of Bouillon & Boero (2000a,b).

Limnomedusae: Olindiidae

Genus Craspedacusta *Lankester, 1880*

Genus diagnosis, medusa (Kramp, 1959; Kramp, 1961; Bouillon & Boero, 2000b): “Olindiidae with four simple radial canals; without centripetal canals; with pendent pouch-like gonads on radial canals; with evenly distributed marginal tentacles all of the same kind, without organs of adhesion; with closed ecto-endodermal statocysts situated in the velum”.

Genus diagnosis, hydroid (Bouillon & Boero, 2000b): “Solitary or forming small reptant colonies of 2–4, rarely 7 polyps; hydranths without tentacles, cylindrical, with apical mouth (hypostome) surrounded by cnidocysts forming a spherical capitulum under which the polyp is slightly tapering, forming a distinct neck; basal portion of hydranths with periderm covering, attaching colonies to substrate; medusa buds lateral, on the middle or lower part of the body-

Table 1. Nematocysts-type, habitat-type and records of species described from inland waters, grouped after Bouillon (1985); sl=salt lake, b=brackish, m=marine; lg=lagoon, l=lake/reservoir, p=pond/pool, r=river, a=acidic water, h=hard water, te=temperate, h=humic, st=subtropical, ms=monsoon, tr=tropical, cos=cosmopolitan; BMNH=British Museum of Natural History (London). [1]= according to Holstein, 1995

	Desmonemes	Atriches	Basitriches	Anisorhizes	Microbasic euryteles	Stenoteles	Habitat	Date of first record	Locality of first record	Deposition of holotype
Sub-class Athecata/Anthomedusa										
Order Filifera, Fam. Australomedusidae										
Australomedusae baylii Russell, 1970	x				x		sl st–te	Dec., 1969	salt lake, near Lake Eliza, SW Australia	BMNH
Order Capitata, Fam. Moerisiidae										
Halmomises lacustris Kennel, 1891							tr lg	March	Lagoon, East coast of Trinidad	
Moerisia gangetica Kramp, 1955							b h–tr	May, 1926	Ganges Estuar, Calcutta, India	
Moerisia horii	x		x			x				
Moerisia (=*Ostroumovia*) *inkermanica* Platschikowa-Ostroumovia, 1925	x	(x)		(x)		x	m te–st		Black Sea	
Moerisia lyonsi Boulenger, 1908	x	x				x	sl st		Lake Qurun, Egypt	
Moerisia pallasi Derzhavin, 1912	x	(x)				x	m		Caspian Sea	
Sub-class Limnohydrina, Fam. Olindiasidae										
Astrohydra japonica Hashimoto, 1981							l st p	1974	pond, Nomorinoike, Shizuoka, Japan	
Calpasoma dactyloptera Fuhrmann, 1939					x[1]		l p r te–st cos		Aquarium	
Craspedacusta sowerbii Lankester, 1880					x		l p r te–st–tr cos	1880	Victoria regia basin, London	
C. iseanum Oka & Hara, 1922							st	Sep., 1921	old well, Tsu, Ide, central Japan	
C. sinensis Gaw et Kung, 1939							p h–st	1939	pool around Kiating, Szechuen, China	US. Nat Mus; Wuhan Univ

Continued on p. 94

Table 1. Continued

	Desmonemes	Atriches	Basitriches	Anisorhizes	Microbasic euryteles	Stenoteles	Habitat	Date of first record	Locality of first record	Deposition of holotype
C. vovasi Naumov & Stepaniants, 1971							m		saline lagoon, South Sakhalin, Russia	
C. marginata Modeer, 1791 (Hummelinck, 1938)							b	1762	small oligohaline river, Harlem, Netherlands	
C. kuoi Shieh & Wang, 1959							p tr	Nov. + Dec., 1959	artifical waterlily pond, Taipei, Taiwan	
C. chuxiongensis He et al., 2000							p	June 1995	pond, Chuxiong City, Yunnan, China	Henan Normal Univ.
C. sichuanensis He & Kou, 1984							p	Aug. 1953	pond, Mt. Qingcheng, Sichuan, China	Univ. of Sichuan
C. ziguiensis He & Xu, 1985							p	1982–1984	pool, Guizhou town, Hubei, China	Henan Normal Univ.
Keralica idukkensis Khatri, 1984							1a tr	March, 1983	Idukki Reservoir, Kerala, SE-India	
Limnocnida tanganjicae Böhm (Günther, 1893)					x		l h–tr	1883	Lake Tanganyika, Africa	
L. victoriae Günther, 1907 (Bouillon, 1957)							l h–tr	Aug., 1903	Lake Victoria, Africa	
L. congoensis Bouillon, 1957							p (r) h–tr		Stanley-Pool, Brazzaville, Kongo	Mus Roy du Congo Belge
L. indica Annandale, 1911					x		l p r h–tr		deep pools, Koyna and Yenna River, Western Ghats, W-India	
L. biharensis Ahmad et al., 1987							?	Aug., 1981	Aquarium, Ranchi, India	BMNH
L. nepalensis Dumont, 1976							p cool–te	May, 1973	large pond (Tau Daha), Kathmandu, Nepal	Zool. Inst. Univ. Gent, B
Mansariella lacustris Malhorta et al., 1976							l st ms	Sep. + Okt.	Mansar Lake, Jammu, N-India	Mus Dep. Biosci Univ. of Jammu

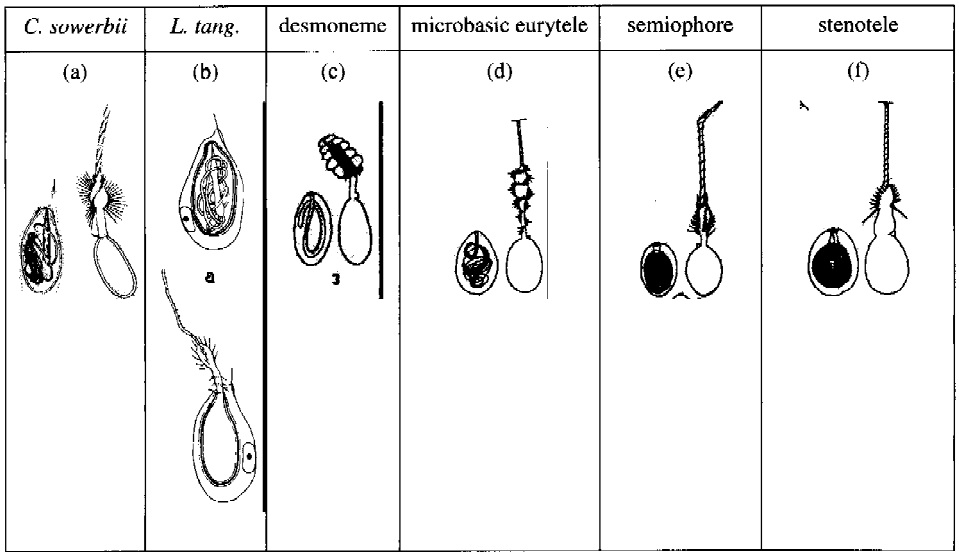

Figure 1. Different types of nematocysts [from (a) Dejdar (1934), (b) Bouillon (1957) and (c–f) Hartwich et al. (1992)].

column, often becoming terminal by hydranth reduction; asexual reproduction by frustules, transversal division and resting stages".

I have found 11 different *Craspedacusta* species described in the literature. However, two of them were annulled by the authors, 3–6 seems to be similar with *C. sowerbii*, or are variations of *C. sowerbii*, and one is perhaps a young (or pathological form of) *C. sowerbii*. For detailed tabular comparison of the *Craspedacusta* 'species' see Table 3.

Craspedacusta sowerbii *Lankester, 1880 (Figs 2, 3 and 4)*
(= *Microhydra ryderi* = *Microhydra germanica* = *Limnocodium victoria* = *Limnocodium sowerbii* = *Limnocodium kawaii* = *Limnocodium sowerbii var. kawaii* = *Craspedacusta ryderi* = *Craspedacusta germanica* according to Dejdar, 1934)

Medusa diagnosis (Dejdar, 1934): Nematocysts (15.8 – 19 × 6.6 – 8.3 μm) in groups (2–10) on papillae; statocyst/tentacles ratio around 0.5; statocysts regulary distributed on the velar and each is produced into a long centrifugal canal, passing through the thickness of the velum and ending blindly near its margin; diameter up to 25 mm; number of tentacles ranges between 200 and 400 (for a diameter from 8.5 to 20 mm). The prominent size of the four perradial tentacles is evidently a constant feature in *C. sowerbii* from all parts of the world (Kramp, 1951).

Polyp diagnosis (*Microhydra*-type, Fig. 6): described first as *Microhydra ryderi* (Potts, 1885); "cylindrical; 0.5–2.0 mm high; without tentacles; with apical mouth surrounded by nematocysts forming a capitulum; basal portion with thin periderm covering; solitary or in small colonies of two or four, rarely seven polyps" (Russell, 1953). For a more detailed description see Payne (1924) and Dejdar (1934) (see also *Calpasoma* and *Astrohydra*).

C. s. *var* kiatingi *Gaw & Kung 1939 (Figs 2, 3 and 4)*
Found in great abundance in a pool around Kiating (1939) and Peh-pei (1946), both in Szechuen, China (Kramp, 1951).

Medusa diagnosis (Kramp, 1951): Size ranges from 13 to 18 mm and number of tentacles from 297 to 336. "The nematocysts of the tentacles are collected in roundish warts almost hemisphaerical in shape, each wart usually containing 10–14 nematocysts when fully developed. The arrangement of the nettle warts is very characteristic. In the small tentacles [...] and in the distal portion of the larger ones, the warts are distinctly placed in transverse belts, forming complete rings encircling the tentacle. The spaces between the rings are smooth and completely destitute of nematocysts; the length of the smooth spaces depends on the state of contraction of the tentacle. In the large tentacles, however, the rings of nettle warts are not equally developed all round the tentacle, but the warts, which are large and densely set on the abaxial side, are gradually diminishing in size towards both sides [...], and in the middle and proximal proportions of the tentacle the ring are not complete, but grasp around only part of

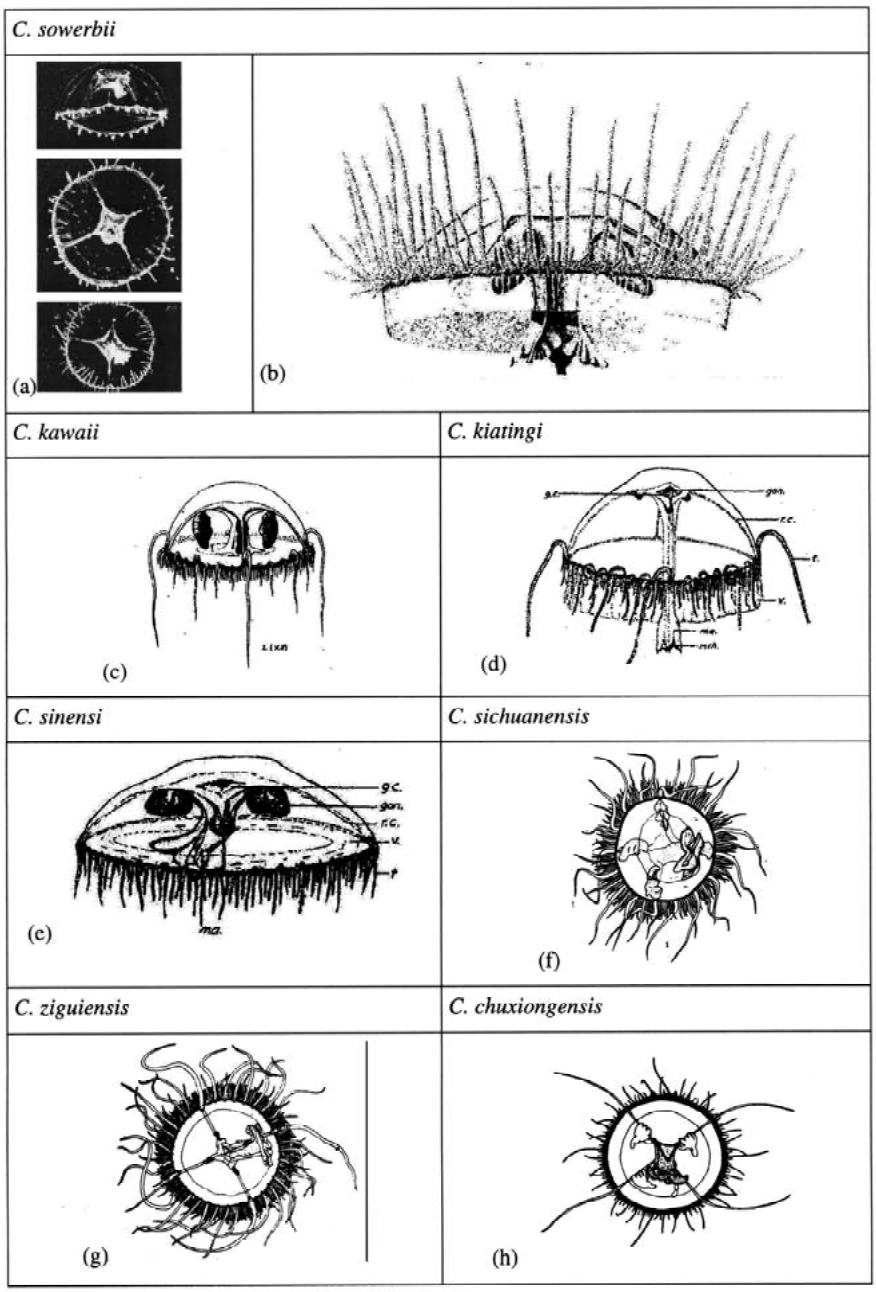

Figure 2. Habitus of different *Craspedacusta* species [from (a) Reisinger (1972), (b) Dejdar (1934), (c) Oka (1906), (d–e) Kramp (1951), (f) He & Kou (1984), (g) He & Xu (1985), (h) He et al. (2000)].

the circumference like a clasp, leaving the adaxial side free of nematocysts, the clasps being gradually shorter towards the proximal part of the tentacle. This arrangement of the nettle warts is particularly distinct in the large perradial tentacles, but is also seen in those of the second and third series. The basal part of the tentacles is completely destitute of nematocysts."

Kramp (1951) points out the great similarity with *C. s.* var *kawaii* Oka, 1906 (Figs 2–4). But both differ substantially in the arrangement of nematocysts.

*"*C. s. *var* kawaii *Oka 1906" (Figs 2–4)*

Found on April, 1906 in Yangtzekiang close to Yichang, province Hupeh, Central China. Oka (1906)

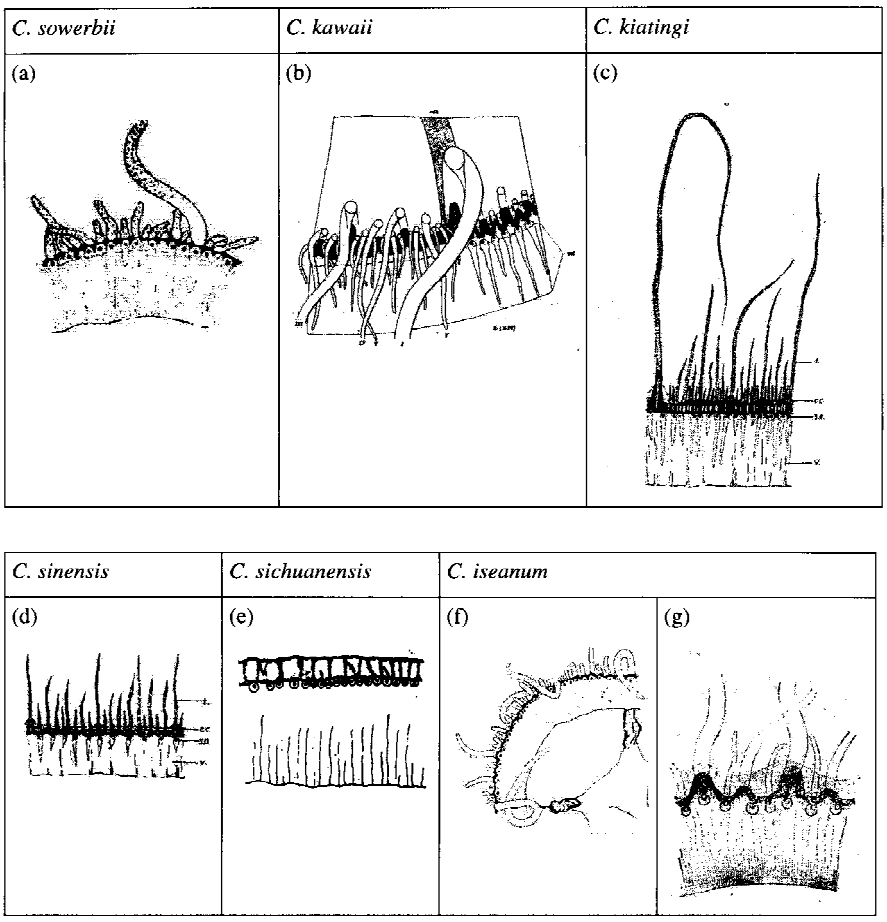

Figure 3. Umbrella margin with statocysts and velar canals of different *Craspedacusta* species [from (a) Uchida (1951), (b) Oka (1906), (c–d) Kramp (1951), (e) He & Kou (1984), (f) Uchida (1955), (g) Oka & Hara (1922)].

separates *C. kawaii* from *C. sowerbii* by the different number of tentacle orders, first as a new species and later as *C. s.* var. *kawaii* (Oka & Hara, 1922). But Dejdar (1934) points out that all these characteristics, like different size and number of tentacle as well as the different number of tentacle orders are not different from *Craspedacusta sowerbii* 'type' (see also Kramp, 1951).

C. iseanum *Oka et al., 1922 (Figs 2–4)*

Found on September, 22 1921 in an old well in the town Tsu, Province Ide, central Japan. Medusa diagnosis (Uchida, 1951, 1955) like *C. sowerbii*, but differs in distribution of nematocysts and statocysts; "In the tips of young tentacles, however, the nematocysts are thickly set, somewhat as in the tips of the tentacles of *C. sowerbyi*, but not clustered in groups as in the latter. The frequency and distribution of the nematocysts are quite different from those of *Craspedacusta sowerbyi*. The statocysts are nearly equal in number to the tentacles and each round or oval in shape as in *Gonionema*. All statocysts lack centripetal velar canals; investigated fullgrown medusae had a diameter up to 5.5 mm".

Dejdar (1934) states that this arrangement of nematocysts was an artifact due to the fixation method. Additionally, he found globular statocysts typical of young *C. sowerbii* medusae and argues at lacking a centripetal canal can be a pathological feature, though there are differences in the arrangement of statocysts. Dejdar (1934) points out the unclear status of this species, whereas other authors (Uchida, 1955; Kramp, 1961; Bouillon & Boero, 2000a) separated *C. iseanum* as a distinct species. For a detailed separation from *C. sowerbii* see Table 2. To my knowledge, up to now only five individuals of this species have been found (Oka & Hara, 1922; Uchida, 1955).

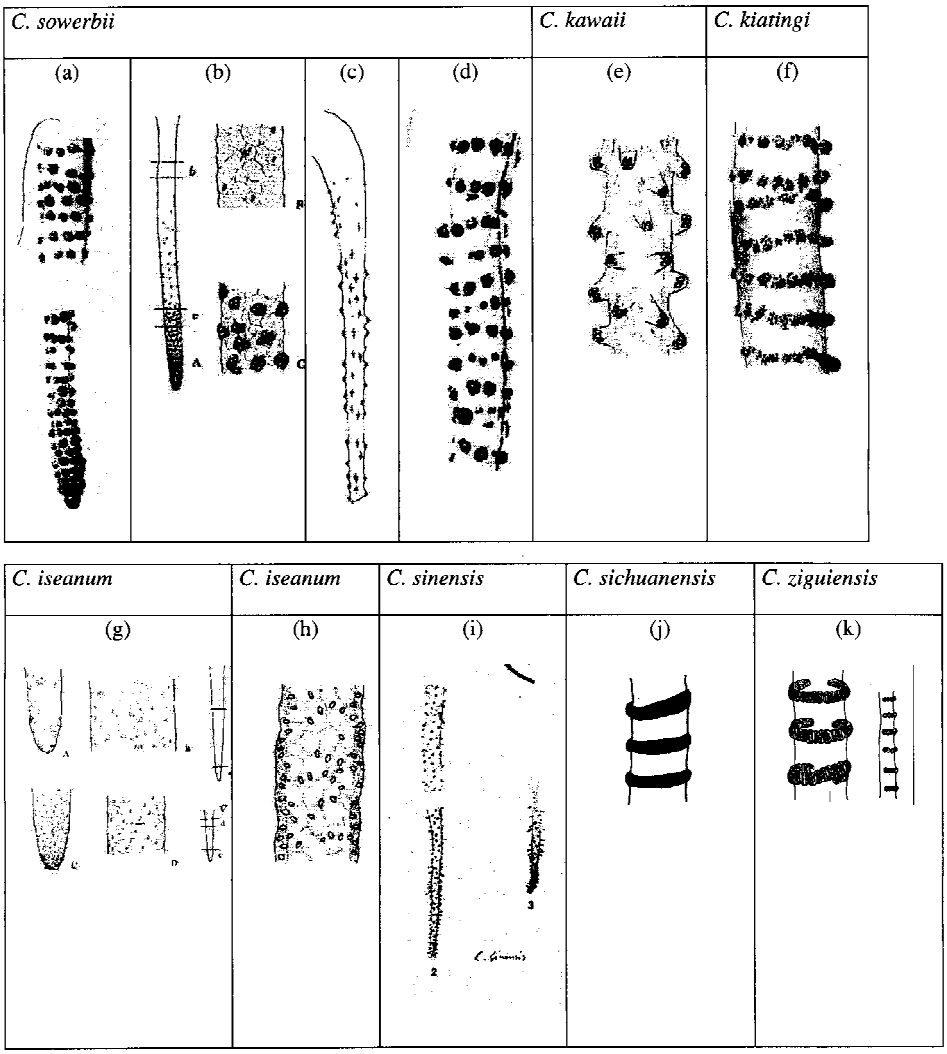

Figure 4. Tentacles and arrangement of nematocysts of different *Craspedacusta* species [from (a, d, f, i) Kramp (1951), (b) Uchida (1951), (c) Dejdar (1934), (e, h) Oka & Hara (1922), (g) Uchida (1955), (j) He & Kou (1984), He & Xu (1985)].

C. sinensis *Gaw & Kung 1939 (Figs 2–4)*
Found in great abundance in a pool around Kiating (1939) and Peh-pei (1946) in Szechuen, China (Kramp, 1951).

Medusa diagnosis (Gaw & Kung, 1939; according to Kramp, 1951): "The size of the animal varies considerably. The diameter of the umbrella measures from 0.48 to 1.8 cm during diastole. At systole, during active swimming, the change of diameter and height of the umbrella is very characteristic. The manubrium is relatively shorter, and the ratio to the umbrella during diastole is about 1–2. The number of tentacles varies from 136 to 217. They are of four kinds with respect to size, arranged in a very irregular fashion. The number of sense organs varies from 78 to 178. The four gonads, when sexually matured, appear to be brownish yellow in color. They are situated at the junction of the gastrovascular cavity and the four radial canals".

Preserved specimens are kept in the Smithonian Institution, U.S. National Museum, Washington DC, U.S.A. and the Department of Biology (Invertebrate Collection), National Wuhan University, Kiating, Szachuen, China.

Medusae diagnosis (Kramp, 1951): "Most of the features emphasized by Gaw and Kung as characters distinguishing this species from *C. sowerbyi* var. *kiatingi* are relative and subject to individual variation or more or less dependent on state of contraction and cannot, therefore, be designated as reliable specific characters. [...] Besides the relative characters there

Table 2. Differences between *Craspedacusta sowerbii* and *C. iseanum* (adapted from Uchida, 1955)

C. sowerbii	*C. iseanum*
The statocysts are tubular, and extend within the tissue of the velum nearly to the margin	The statocysts are globular
The nematocysts on the tentacles are crowded on papilla-like processes	The nematocysts on the tentacles are scattered
Tentakles in fullgrown specimens are 300–400	Tentacles in fullgrown specimens are 128

are, however, three structural features by which *C. sinensis* is decidedly distinct from *C. sowerbyi* with its varieties".

1. The displacement towards the exumbrella of the points of issue of the tentacles is only very slightly indicated in *C. sinensis*. In accordance herewith, the nematocyst ring of the umbrella margin is only very slightly wavy.
2. There are no large perradial tentacles.
3. The nematocysts of the tentacles are placed on elongated papillae which are not arranged in transverse belts.

Detailed separation from *C. sowerbii* (Kramp, 1951): "As a matter of fact, in no case are the tentacles in the intervening off or near the radial canals any larger than several of the tentacles at all outside a radial canal [...], or the perradial position is occupied by one of the small tentacles. This seems to be a very important distinctive mark separating this species from *C. sowerbyi*, leaving no doubt of the specific difference between the two forms. [...] The structure and arrangement of the nettle warts are likewise a very characteristic feature of *C. sinensis*. Though the shape of the nettle warts in *C. sowerbyi* may be somewhat dependent on the state of contraction (as pointed out by Dejdar, 1934, p. 623), they never attain an appearance like that seen in *C. sinensis*. In this species, the nemotocysts are placed in the distal end of elongated, cylindrical or somewhat club-shaped papillae which give the whole tentacle a hairy appearance. [...] There are usually about 6–8 nematocysts in each of the larger papillae".

For a detailed discussion of the nematocyst arrangement, see Kramp (1951) and Dejdar (1934).

C. sichuanensis *He & Kou, 1984 (Figs 2–4)*

Found in August 1953 in a pond on Mt. Qingcheng, Guanxian County, Sichuan Province, China.

Medusa diagnosis (He & Kou, 1984): "Umbrella higher than a hemisphere, 11–14 mm in diameter, flat in apical portion. Velum wide, about 1/4 of the umbrella. Tentacles arranged very regularly in four orders of 4, 12, 16 and 75–117, giving a total number of 107–149. Perradial tentacles four, not longer than other tentacles. Stomach large, with a conical distal portion and a broad square base. Manubrium large, with four large lips, extending beyond umbrella margin. Nematocysts in tentacle collected into ring warts, regularly arranged and with an obvious interval between every two ring warts as bamboo joints. Marginal nematocysts ring brownish in color. Statocysts spherical, situated at the basal region of tentacles or between two tentacles, 91–122 in number".

Type specimens are kept in the Department of Biology at the University of Sichuan, China.

This species seems to be different from the other known *Craspedacusta* species by the non-prominent size of the four perradial tentacles (like *C. sinensis*) and the globular statocysts (like *C. iseanum*, but with centripetal velar canal).

*?*C. ziguiensis *He & Xu, 1985 (Figs 2 and 3)*

In 1982, 1983 and 1984 hundreds of medusae were found in a pool around Chixi river in Guizhou town (31° N, 110° 40′ E), Zigui Count, Hubei Province, China.

Medusa diagnosis (He & Xu, 1985): "Umbrella bell-shaped, 17–24 mm in diameter. Velum narrow, about 1/7 of the diameter of umbrella. Marginal tentacles varying from 314 to 423 in number and arranged regularly in four orders of 4, 28, 32 and 250–359, respectively. Stomach square, the manubrium a tetragonal prism, with four large lips, extending beyond the umbrella margin. [...] Nematocyst warts on the tentacles arranged in a horseshoe pattern, occupy-

ing about 2/3 of the circumference of tentacles. The nematocysts at the basal regions of tentacles [are] not collected into clusters. Statocysts tubular, 126–156 in number".

Type specimens are kept in the Department of Biology, Henan Normal University, Xinxiang, China.

Although this horseshoe like arrangement of nematocysts papillae were never observed in other *Craspedacusta* species, Bouillon & Boero (2000b) suggest that it is probably identical with *C. sowerbii*.

C. chuxiongensis *He, Xu & Nie, 2000 (Fig. 2)*

On June 1995, hundreds of freshwater medusae were collected from a pond of Chu-xiong National Normal School (25° N, 101.30° E) in Chuxiong City, Yunnan Province, South-Central China.

Medusa diagnosis (He et al., 2000): "The umbrella is a flat hemispere 9–13 mm in diameter with most specimens larger than 10 mm. Velum narrow, about 1/6 of the diameter of umbrella. Marginal tentacles varying from 256 to 273 in number and arranged in five orders of 4, 4, 32–40, 40–60 and 74–88, respectively. Those of the first order, situated in the perradii, are nearly 2/3 of diameter of umbrella. Stomach large, square in shape, the manubrium long with four lips expending beyond the umbrella margin. Four gonads flatted pocket-like twisted with a fingered projection beneath gonads, slightly yellowish green in color. The nematocyst warts are lower conical in shape, arranged irregularly, each wart containing 7–10 nematocysts. Statocysts tubular, 152–162 in number. Shape and color of gonads of new species are different from all known species".

Preserved specimens are kept in the Department of Biology, Henan Normal University Xinxiang, Nenan Province, China.

Because of the few distinguishing characters, this is probably a synonym of *C. sowerbii* (Bouillon & Boero, 2000b).

*"*C. kuoi *Shieh & Wang, 1959"*

The medusae were "found in an artifical waterlily pond in the campus of Taiwan Normal University, Taipei, Taiwan" in November and December 1959.

Shieh & Wang (1959) separate *C. kuoi* together with *C. kawaii* from *C. sowerbii* on basis of the different number of tentacle orders and from *C. kawaii* on basis of the "longer manubrium, extending beyond the velar opening". Additionally, they point out the different arrangement of nematocyst: "especially the distribution and the type of nematocyst being different from others".

The described differences, like number of tentacle order, size of manubium as well as the arrangement of nemocysts, seems to be (compared with the observations of Dejdar, 1934) not is sufficient to separate *C. kuoi* from *C. sowerbii*. For example, Shieh & Wang (1959) pointed out the large manubrium of *C. kuoi*, but Figures 16 and 23 of Dejdar (1934) show that *C. sowerbii* has a large manubrium too, extending beyond the velar. Therefore, Kramp (1961) and Bouillon & Boero (2000b) included this species *C. sowerbii*.

"C. vovasi Naumov & Stepanjants, 1971" (Original in russian) (Fig. 5)

Original summary: "16 specimens of jellyfish from the genus *Craspedacusta* were found in the saline Bousset Lagoon (South Sakhalin) at a depth of 4–7 m. All known species of the genus are freshwater. The specimens in question are included in a new species *C. vovasi* Naumov et Stepanjants sp. n".

Stepanjants (1988, pers. com.) annuled this species, because the described individuals were found to be *Eperetmus typus* Biglow 1915, and pointed out that it could be a new variation: *E. typus* var. *vovasi*.

Eperetmus is a marine arctic Olindiadid, only found in the Northern Pacific (Kramp, 1961).

*"*C. marginata *Modeer 1791 (Hummelinck, 1938)" (Fig. 5)*

The name *C. marginata* was established by Hummelinck 1938 for a medusa found in 1762 by M.W. Schwenke in the Spaarne, a small eutrophic, oligohaline river next to Haarlem (Netherlands). Hummelinck (1941) annulled this species because this medusa seems to be *Maeotias marginata* Modeer 1791, not *Craspedacusta*.

Calpasoma dactyloptera *Fuhrmann, 1939 (Fig. 6)*

This hydranth-type was described first as a new species. Buchert (1960) found both *Craspedacusta*- (= *Microhydra* = Type A) and *Calpasoma* (Type B) in Hungary and stated that these were different forms of the same species. Matthews (1966) and Rahat et al. (1974) carried out isolated cultures of atentacular ('*Microhydra'*) and tentacular ('*Calpasoma'*) polyps but could not observe interconversion between the two forms. Additionally, in all other studies where *Craspedacusta* polyps were cultured this conversion was never observed (e.g. Kuhl, 1947; Reisinger, 1957; Lytle, 1959; McClary, 1961). Nevertheless, in some

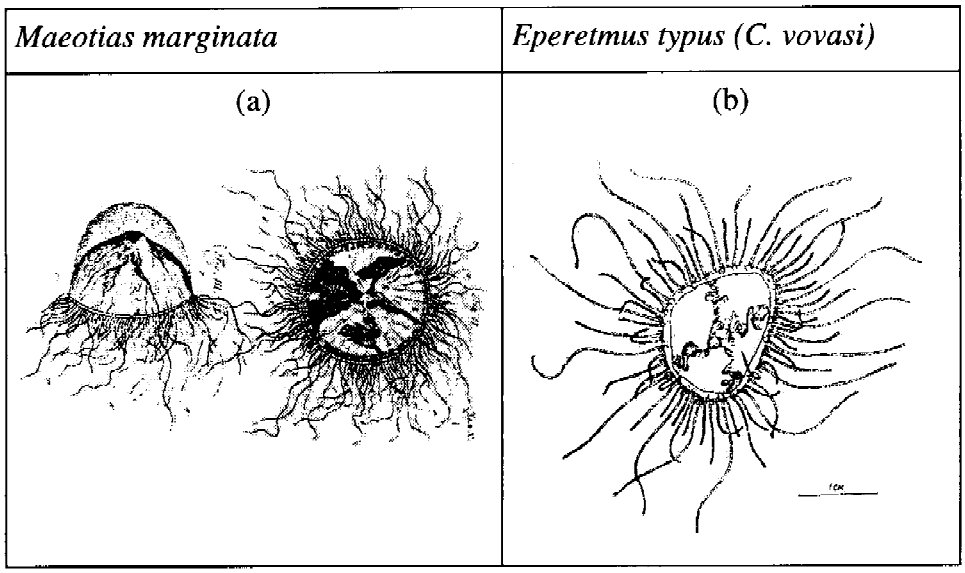

Figure 5. Habitus of different Olindiasidae [from (a) Hummelinck (1938) and (b) Naumov & Stepaniants (1971)].

reviews, the *Calpasoma*-polyp is described as a special form of *Craspedacusta* (Reisinger, 1972). Recently, Emschermann (reported in Holstein, 1995, pers. comm.) observed the transformation from a *Craspedacusta*-polyp to a *Calpasoma* form, but not in the opposite direction. Both polyps possess only heterotrichous microbasic euryteles. This suggests that the *Calpasoma*-type is an additional polyp form of *Craspedacusta* (see also *Astrohydra japonica*).

Polyp diagnosis (Buchert, 1960; Rahat & Campbell, 1974): 0.1–0.4 mm long; transparent to whitish; 8–32 (to 54) tentacles, 68–234 μm long and 8–15 μm wide; each tentacle contains 5–20 non grouped nematocyts (0.14 μm). Note that there are differences between the drawings of Holstein (Fig. 6b; polyp according to Fuhrmann) and Matthews (Fig. 6c; polyp according to Buchert). But for both, a similarity with *Craspedacusta* was pointed out (Buchert, 1960; Holstein, 1995).

Astrohydra japonica *Hashimoto, 1981 (Figs 6 and 7)*

The polyps were first found in a freshwater pond, Nomorinoike, Shizuoka Prefecture, Japan, in 1974.

Medusa diagnosis (Hashimoto, 1984, Hashimoto, 1985): "The newly released medusa is only 0.5 mm in diameter and its umbrella is a normal bell-shape with four long and four short tentacles. The tentacles of this medusa bear many bristle-like papillae with one to two nematocysts on apices. A papilla consists of only a vacuolate single cell and sometimes reduces to a short process particularly when tentacle is retracted. This structure of tentacle is symbolical of the medusa of *Astrohydra*. The radial canals are mostly four in number and the manubrium forms a quadrangular prism, of which the basal half functions as a stomach. The statocysts of this medusa are devoid of velar centripetal canals. One medusa grew to a diameter of 1.35 mm with about 15 statocysts and 29 tentacles, but died of disease. The gonads were not found".

Polyp diagnosis (Hashimoto, 1981): "Body size varies from 0.1 to 0.3 mm long in natural condition. Body color of living polyp whitish and rather transparent. The polyp is quite variable in shape, mostly barrel form or often bottle shape. [...] Each tentacle is fine, long and almost straight. Sometimes the tentacles are branched off particularly at the distal portion. The number of tentacles varies from about 10 to 30. The nematocysts are only single sort, penetrant, more or less arched in shape and not grouped to form any knob or ring but freely scattered over tentacles. Size of the stinging capsule 4.5×2.0 μm".

The polyp stages of *Astrohydra* and the *Calpasoma*-type B seem to be very similar. They have approximately the same length, color, number of tentacles, arrangement of nematocysts and general appearance. This suggests that *Astrohydra*, *Calpasoma* and *Craspedacusta* may all be identical. If this is true the *Astrohydra* medusa is probably only another (may be pathological) medusa stage of *Craspedacusta*.

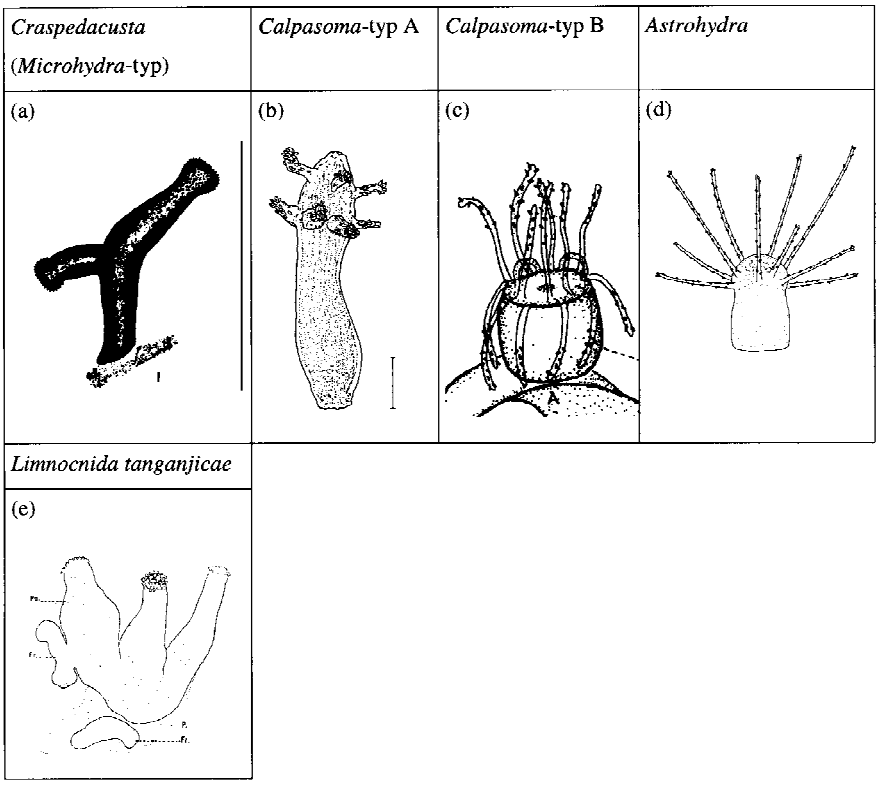

Figure 6. Hydranths of (a) *Craspedacusta* (Payne, 1924), (b) *Calpasoma* (Holstein, 1995, according to Fuhrmann, 1939), (c) *Calpasoma* (Matthews, 1966, according to Buchert, 1960, (d) *Astrohydra* (Hashimoto, 1981) and (e) *Limnocnida tanganjicae* (Bouillon, 1957).

Genus Limnocnida *Günther, 1893*

Genus diagnosis, medusa (Kramp, 1961; Bouillon & Boero, 2000b): "Olindiidae with circular flat manubrium, with large, simple circular mouth, with four simple radial canals; with gonads on manubrium only, with enclosed marginal statocysts; with marginal, folded band of nematocysts; with numerous marginal tentacles and statocysts; the proximal portion of the tentacles is adherent for some distance to the exumbrella".

Genus diagnosis, hydroid (Bouillon & Boero, 2000b): similar to *Craspedacusta*. I have found eight *Limnocnida* species described in the literature. Two of them are identical with *L. victoriae*. From the remaining three are described from India and three from Africa. For detailed tabular comparison of the *Limnocnida* species, see Table 4.

Limnocnida tanganjicae *Böhm, 1883 (Günther, 1893) (Figs 6, 8 and 9)*

(= *L. tanganyicae*, *L. tanganicae*). The medusae were first found in Lake Tanganyika, Africa, in 1883.

Medusa diagnosis (Kramp, 1961): "Up to 25 mm wide; disk-shaped; with usually four, but sometimes 5–7 radial canals; with 300–400 tentacles of different sizes, irregularly distributed; with a large and variable number of statocysts, irregularly distributed; medusae may be produced by budding on the stomach wall".

Limnocnida victoriae *Günther, 1907 (Boullion, 1957) (Fig. 8)*

(=*L. tanganyicae* ssp*victoriae* Günther, 1907, = *L. rhodesia* Boulenger, 1912, *L. cymodoce* Jordan, 1934 according to Bouillon, 1959). The medusae were first found in Lake Victoria (Nyanza), Kisumu, Africa, in August 1903.

Medusa diagnosis (Günther, 1907): "[...] the proximal ends of the older tentacles are more deeply sunk in the jelly of the exumbrella than in *Limnocnida tanganicae* and the jelly-mass is more deeply grooved in consequence [...] About one third of the length of the older tentacles is smooth and free from nematocyst warts, which are confined to the distal two-thirds. The proximal ends of the tentacles which are adherent to the exumbrella are specially supported by the devel-

Table 3. Comparison of *Craspedacusta* species according to different authors (Dejdar, 1934; Kramp, 1951; 1961; Uchida, 1955; Shieh & Wang, 1959; Dumont, 1994; He et al. 2000)

Species	Arrangement of numatocysts	Arrangement of papillae	Statocysts/ tentacles	Max. diameter [mm]	Centripetal velar canal	No. of tentacles	Statocysts	4 large perradial tentacles	Distribution
C. chuxiongensis	groups (7–10) on lower conical papillae	scattered	~0.5	9–13		256–273	tubular	present	China
C. iseanum	scattered	(no papillae)	~1	5.5	absent	128	globular	present	Japan
C. kiatingi	round papillae (10–14)	in rings		13–18					China
C. kuoi	in circles		0.6–0.8	10	present	~160	oval shaped	present	Taiwan
C. sichuanensis	in rings	in rings	~0.8	11–14	present	107–149	spherical	absent	China
C. sinensis	groups (6–8) on elongated, cylindrical papillae	scattered	0.6–0.8	18	present	136–217	spherical	absent	China
C. sowerbii	groups (2–10) on	scattered / rings	~0.5	< 25	present	up to 400	tubular	present	cosmopolitan
C. ziguiensis	spherical papillae	horseshoe	~0.4	17–24		314–423	tubular	present	China

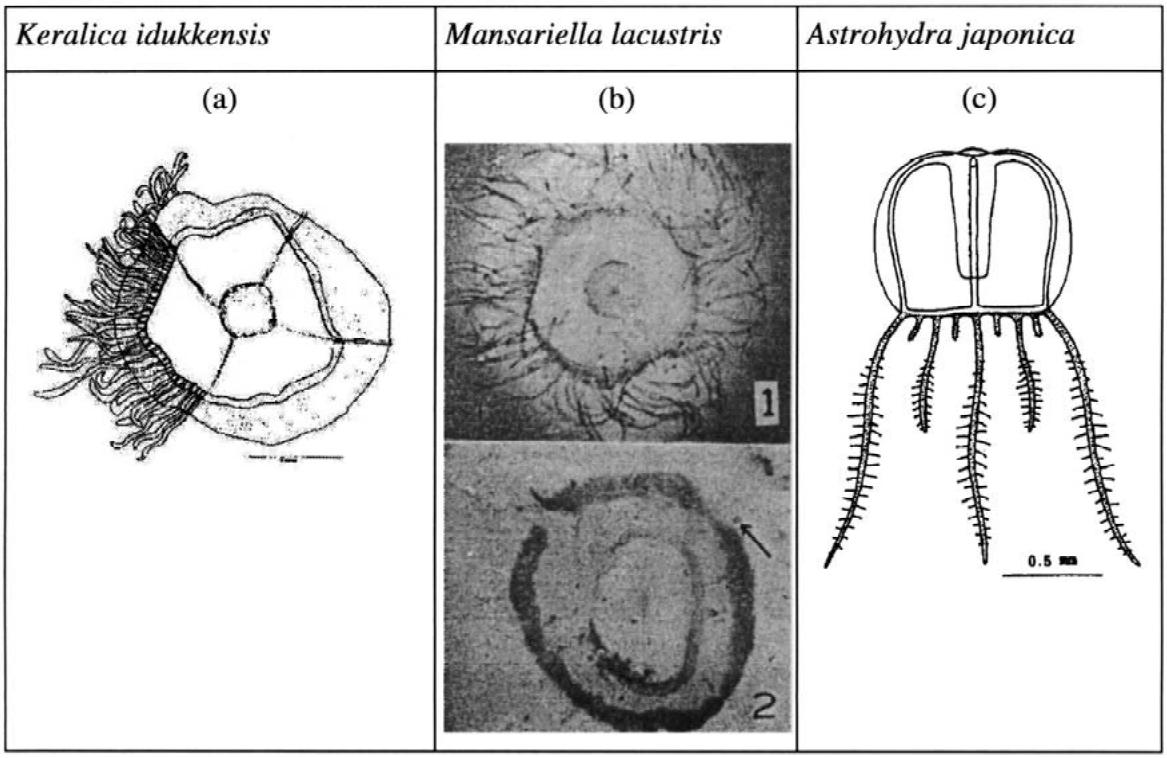

Figure 7. Habitus of *Mansariella lacustris*, *Keralica idukkensis* and *Astrohydra japonica* [from (a) Khatri (1984), (b) Malhorta et al. (1976), and (c) Hasimoto (1985)].

opment of the grooved lumps or ridges of the jelly in which they lie. I have never seen these so strongly developed in any *Limnocnida* from Lake Tanganyika. The sense-organs were numerous, and very prominent on the margin of the umbrella. The specimens examined were all females of about the same age, with mature ova on the manubrium, and with tentacles of the VIIth order". The investigated specimens were approximately 13 mm in diameter, with a manubrium of about 7.5–8 mm in diameter. All had 4×30 sense organs and 4 radial canals.

Bouillon & Boero (2000b) listed not *L. victoriae*, but *L. rhodesia* and suggested it could be *L. tanganjicae*.

L. congoensis *Bouillon, 1957 (Fig. 8)*

The medusae were isolated from Stanley-Pool near Brazzaville, Africa.

Medusa diagnosis (Bouillon, 1957): "Anneau urticant: L'extrémité marginale de l'exombrelle de *Limnocnida congonensis* est ourlée d'un anneau urticant particulièrement développé. D'aspect brunatre, il est lisse ur du matériel vivant, fixé il est plus ou moins fetonné suivant le degré de contraction des muscles du velum. L'anneau urticant s'étale chez *Limnocnida congonensis* sur la basedes tentacules: cé caractère est propre à l'espèce, la base des tentacules de *Limnocnida tanganyicae*, *victoriae* et *indica* étant complètement dégragée de l'anneau urticant [...]. Les tentacules sont très nombreux. Chez les plus grands individus leur nombre excède 800 (650 à 850, 30 comptages) [...]. Les nématocystes de *Limnocnida congonensis* appartiennent au type eurytèle microbasique hétérotriche [...]. Les statocysts sot moins nombreux que les tentacules (300 à 400 environ), le rapport moen du nombre des premiers au nombre des secons est de 0.48 [...]. Le plus grand développement de l'anneau nerveux externe pourrait étre lié au nombre de tentacules: *Limnocnida congonensis* possède nous l'avons vu un nombre de tentacules au moins deux fois plus élevé que les autres espèces".

Holotype specimens are kept in the 'Musée Royal du Congo Belge'.

L. indica *Annandale, 1911*

The medusae were collected first in deep pools of the Koyna and Yenna rivers (Western Ghats, India)

Table 4. Comparison of *Limnocnida* species according to different authors (Günther, 1907; Bouillon, 1957, 1959; Dumont, 1976; Ferro, 1979; Ahmad et al., 1987)

No. of tentacles	Max. length of tentacles [mm]	Statocysts/ tentacles ratio	Max. diameter [mm]	Scale-like membrance	Distribution	Species
Secondary tentacles organized in irregular groups						
Medusae viviparous						
300	20	0.8	22.0		E-Africa	*L. tanganjicae*
Medusae not viviparous						
< 400	16	0.93	13.5		E-Africa	*L. victoriae*
800	12	0.48	25.0		W-Africa	*L. congonensis*
Secondary tentacles organized in regular groups						
384		0.33	15.0	absent	India	*L. indica*
240	0.99	0.50	4.3	absent	India	*L. biharensis*
34–83		0.11–0.20	7.8	present	Nepal	*L. nepalensis*

and occur regularly in these rivers every dry season (Annandale, 1911).

"In structure of manubrium and digestive system, the position of the gonads, the structure of the tentacles, and the form of the umbrella these medusae agree precisely with *Limnocnida tanganyicae*". (Annandale, 1911).

Medusa diagnosis (Kramp, 1961): "15 mm wide, almost three times as wide as high; with four radial canals; with two distinct series of marginal tentacles; up to 64 long primary tentacles, tapering in thickness from base outwards, and five times as many small secondary tentacles of almost equal width throughout; two statocysts between successive primary tentacles".

L. nepalensis *Dumont, 1976 (Figs 8 and 9)*

The medusae were first found in a large pond (Tau Daha) in the neighborhood of the City of Kathmandu, Nepal, in May 1973.

Medusa diagnosis (Dumont, 1976): "Diameter: of whole animal (flattened): 5 mm; of manubrium: 2 mm; of stomach: 2 mm [...]. The gonad lies twisted in and around the wall of the manubrium. The velum is relatively narrow. The exumbrella appears as a festoon, upon which are implanted the statocysts and the tentacles [...]. An enlarged view of the margin of the exumbrella [...] shows a fairly regular pattern in the tentacular apparatus. They [tentacles] are differentiated in primary ones, with a deeper implant, and secondary ones, implanted on a bud tissue with granular aspect and opaque margins. The secondary tentacles, slightly thinner than the primary ones, stand behind a scale-shaped membrane, alternating with the primary tentacles. The secondary tentacles are grouped in sets of four. In the paratype female, rarely sets of three were observed and also one set of five, the fifth tentacle being very small and short. There are 53 primary tentacles in the holotype. The statocysts are fairly large, and there is only one per set of tentacles. They are thus 53 in number. Their position relative to the membrane is variable, being either central or excentric. In the paratype female, there is one short sector on the exumbrella where six statocysts lie closely together, thus disturbing locally regular pattern described above".

Differential diagnosis and comparison with *L. indica* (Dumont, 1976): "Both species are so closely related that some might doubt the specific status of *L. nepalensis*. Our final decision to regard it as a good species has been influenced by geographical, climatical and historical reasons, as a supplement to the following morphological ones.

1. The number and arrangement of the statocysts: two per set of tentacles in *L. indica*; only one in *L. nepalensis*.
2. The number of secondary tentacles per set: five in *L. indica*, four in *L. nepalensis*.
3. The difference in shape and structure of primary and secondary tentacles: distinctly less pronounced in *L. nepalensis* than in *L. indica*.
4. The statocyst/tentacle index [...]: from all the species of the genus, this is lowest in *L. indica*: 0.33; in *L. nepalensis*, it is still distinctly lower: 0.20.

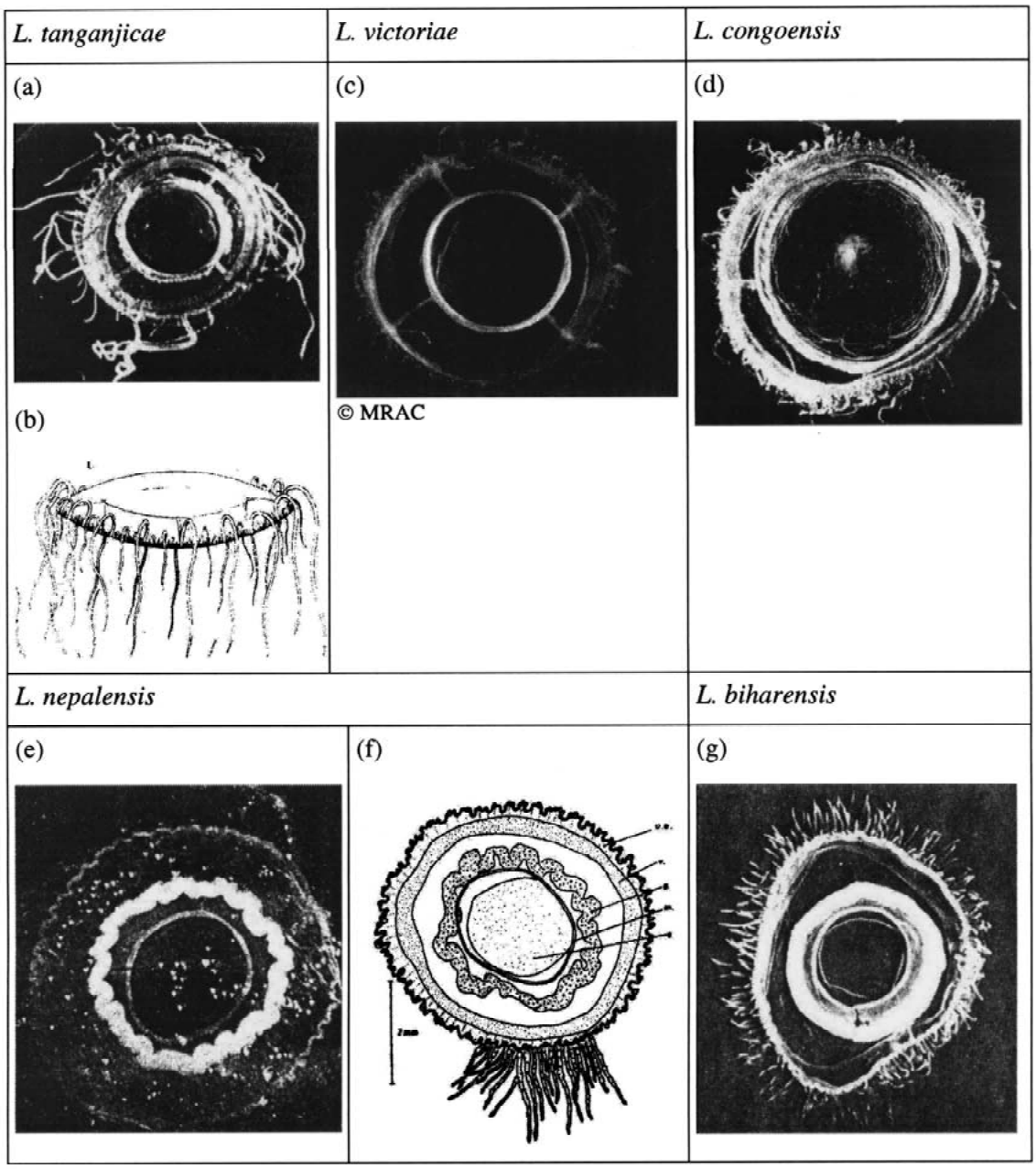

Figure 8. Habitus of different *Limnocnida* species [from (a,d) Bouillon (1957), (b) Günther (1893), (c) Bouillon (1959), (e,f) Dumont (1976), (g) Ahmad et al. (1987)].

5. The scale-like membrane on the exumbrella: present in *L. nepalensis*, not reported from *L. indica*".

Type specimens are kept in the Zoological Institute (Systematic and Morphology) at the University of Ghent, Belgium.

L. biharensis *Ahmad et al., 1987 (Fig. 8)*

Found in a laboratory aquarium in the Department of Zoology, Ranchi University, Ranchi (22° 55′ N, 85° 10′ E), India, in August 1981.

Medusa diagnosis (Ahmad et al., 1987): "The umbrella (bell) is shallow with a flat surface on the exumbrellar side in the adult [...]. The diameter ranged

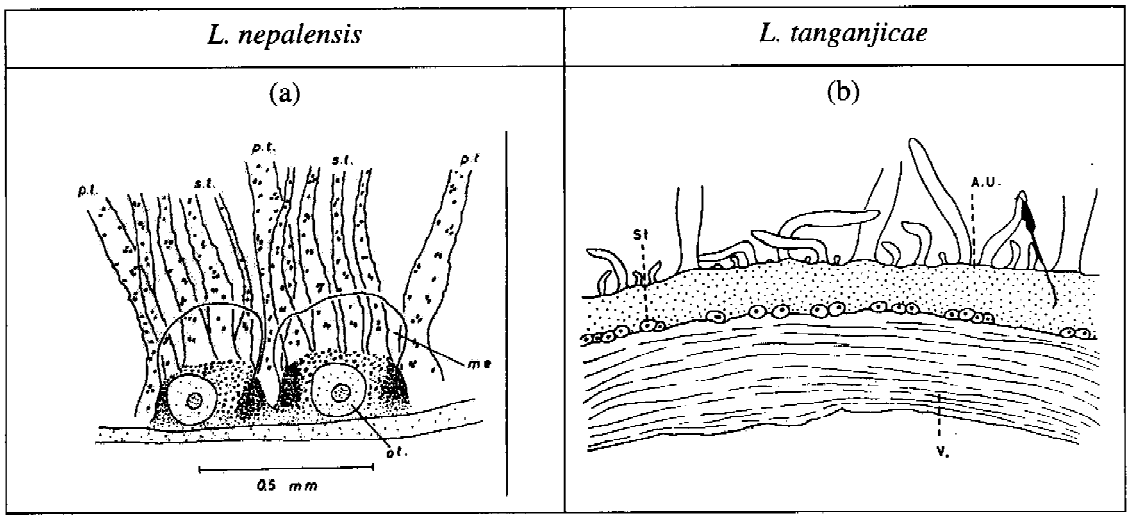

Figure 9. Scale-like membrane of *L. nepalensis*. [from Dumont (1976) p.t. = primary tentacle, s.t. = secondary tentacle, me = scale-like membrane, ot = statocyst] and (b) umbrella margin of *L. tanganjicae*. [from Bouillon (1957)].

from 3.2–4.3 mm. An indiscernible manubrium is represented by a shallow ring [...]. The mouth opens directly into the stomach, and is completely closed when contracted, leaving a distinct star-shaped aperture. The tentacles can be differentiated into a primary and a secondary set of tentacles; the former measures an average of 0.99 mm and the latter 0.50 mm. The secondary tentacles are located in between every two primary tentacles, but this pattern was inconsistent. There are about 60 primary tentacles and 180 secondary ones. Radial tentacles are not differentiated from primary ones. The otocysts, though arranged in regular order, are inconspicuous. Every set of three tentacles has two otocysts at its base; the total number of otocysts never exceeded 120. Numerous nematocysts without cnidocil are located around the bell margin and tentacular base. The nematocysts possessing cnidocils are arranged only along the bell margin. The sexes are separate. The gonads are opaque masses located around the stomach. In females, the gonadial ring is notched while in males it is continuous".

Type specimens are kept in the British Museum of Natural History, London (accession number 1982.8. 2a and 2b) and in the Department of Zoology, Ranchi University, India.

Mansariella lacustris *Malhorta et al., 1976 (Fig. 7)*

Found in "large numbers during September and October in Mansar Lake, Jammu, India. It is a subtropical, isolated freshwater lake...". Medusa diagnosis (Malhorta et al., 1976): "The medusae [...] are umbrella-shaped, each attaining a maximum diameter of 15 mm at its sub-umbrella margin. The margin is best with highly extensile tentacles (reaching over 20 mm in maximum stretched condition), numbering nearly 160 in total (around 40 in each quadrant). The tentacles are arranged in a single row and do not show any terminal sucker or adhesive pad. In the living condition the bases of tentacles are swollen, with each swelling containing a statocyst. The mouth is circular 5 mm dia, when open manubrium is short and opens into a circular gastric cavity from where, emerge 4 radial canals at right angles to another. No gonads, however, were seen in any specimen examined. Young medusoid forms appeared to bud off [...] from the gastric region of the bigger forms. Each young medusa bears a circlet of 16 closely set tentacular buds all along the rim of the umbrella. But for size, number and simplicity in its tentacles, each young medusa shows all identifiable structures of the adults. Indian peninsular forms (*Limnocnida*, *Limnocodium* and *Microhydra*) differ markedly from the present form in number and arrangement of the tentacles and the comparatively higher mouth–umbrella diameter ratio".

Holotype deposited in the museum, Department of Bioscience, University of Jammu, India. Bouillon & Boero (2000b) suppose it might be an immature specimen of a *Limnocnida* species.

Keralica idukkensis *Khatri, 1984 (Fig. 7)*

Found in Idukki Reservoir, Kerala, India. They occurred "in masses during March 1983 [...]. It prefers

acidic waters while the basic nature of the habitat was found to restrict its distribution".

Medusa diagnosis (Khatri, 1984): "The medusae are umbrella-shaped. The diameter of umbrella ranged from 4 to 5 mm. The manubrium size varied from 2.7 to 3 mm. In height, the umbrella measured up to 4 mm in some specimens. The margin of umbrella is beset with 128 tentacles (32 between two radial canals [...]). All tentacles are uniform in length measuring up to 2 mm and are arranged in a single row. Tentacles are solid, originating from circular canal forming a beaded structure at the base due to the presence of a balancing organ, the statocyst. They do not have any terminal sucker or an adhesive pad. Mouth is circular 1 mm in diameter when open, lips are radially arranged forming six-lobed structure [...]. Manubrium is large and bell-shaped opening into a circular gastric cavity. The radial canals originate from mouth and join the marginal circular canal. Gonads are slightly visible as a small thickening on radial canals in young forms. A few forms have eggs masses loaded in the manubrium [...]. The earlier forms made their appearance suddenly for a short period while the present form was observed throughout the year leaving one or two monthly samplings ... . The present form differs markedly from the peninsular forms e.g. *Limnocnida*, *Limnocodium* and *Microhydra* in the number and arrangement of the tentacles and mouth–umbrella ratio".

Bouillon & Boero (2000b) consider this an insufficient diagnosis, that needs confirmation. They judge the systematic position as doubtful.

Athecata/Anthomedusa: Filifera: Australomedusidae

Australomedusa baylii *Russell, 1970 (Fig. 10)*

Six medusae were first collected by Bayly from a small unnamed inland salt lake near Lake Eliza (Southwest Australia) on 29th of December 1969 (salinity was 34.4%, up to 60%; Temp: 21 °C)

Genus diagnostic, medusa (Russell, 1970): "Stomach cylindrical with simple mouth. Four unbranched radial canals. Gonads surrounding stomach and on radial canals. Four per-radial tentacular marginal bulbs, each with numerous solid tentacles".

Medusa diagnosis (Russell, 1970): "Umbrella hemispherical, about as high as wide, with fairly thick jelly especially in apical region. Velum narrow. Stomach short with simple mouth. Four unbranched radial canals and ring canal narrow. Male gonads surrounding stomach and on four radial canals; each radial canal gonad bean-shaped, situated on distal half of canal and connected by thin strand of gonadial tissue with gonad on stomach. Four per-radial tentacular marginal bulbs, pear-shaped, each with one central ocellus on its distal extremity [... the number of tentacles on a marginal bulb might vary from six to nine (Russell, 1971)]. Four inter-radial short spur-like non-tentacular marginal bulbs each with a single ocellus. Without marginal vesicles. Height 2.0 mm".

Russell (1971) found only two kinds of nematocysts: desmonemes (5 × 3.5 μm) and microbasic euryteles (8–9 × 4–4.5 μm). "The occurence of only two types of nematocyst indicates that the medusa should be placed in a new family, Australomedusidae, fam. nov. since Moerisiidae apparently may also have stenoteles in addition". The combination of only desmonemes and microbasic euryteles classifies this species as Athecata, which may be placed within the Filifera.

Type specimens are kept in the British Museum of Natural History, London (accession number males: 1970.10.19.1 and females 1970.10.19)

Athecata/Anthomedusa: Capitata: Moerisiidae

Halmomises lacustris *von Kennel, 1891*

Collected in large numbers in a freshwater lagoon at the East coast of Trinidad, south of Mayaro Point in a Cocos plantage (in March).

Medusa diagosis (von Kennel, 1891): "Ohne Randkolben, Cirrhen und Randbläschen. Umbrella halbkugelig, 16–18 (24?) Tentakel, mit leicht kolbig verdickter Basis, auf deren Aussenseite je ein Ocellum (einfacher Pigmentring), Velum dünn, aber breit, Mundstiel kräftig, mit breiter Basis, stumpf vierkantig, Mund ohne Lappen, kreuzförmig, die 4 Spalten in der Richtung der Kanten. Magen klein, aber distinkt. 4 Radiärkanäle, in den zentralen Dreivierteln stark erweitert, gegen die Subumbrella vorspringend; hier mit krausenartigen Gonaden besetzt, durch deren Entwicklung geschlängelt verlaufend. Letztes, peripheres Drittel der Radiärkanäle eng, gerade verlaufend. Groesse 2–2.5 mm Scheibendurchmesser, Farbe glashell, schwach gelblich, Gonaden gelblichbraun".

Genus Halmomises *(Kramp, 1961)*

"Moerisiidae with radial lobes of stomach, with twisted and folded gonads; tentacles with rings of nematocysts. Polyp unknown".

Medusa diagnosis (Kramp, 1961): "2–2.5 mm wide, slightly higher than hemisphere; stomach

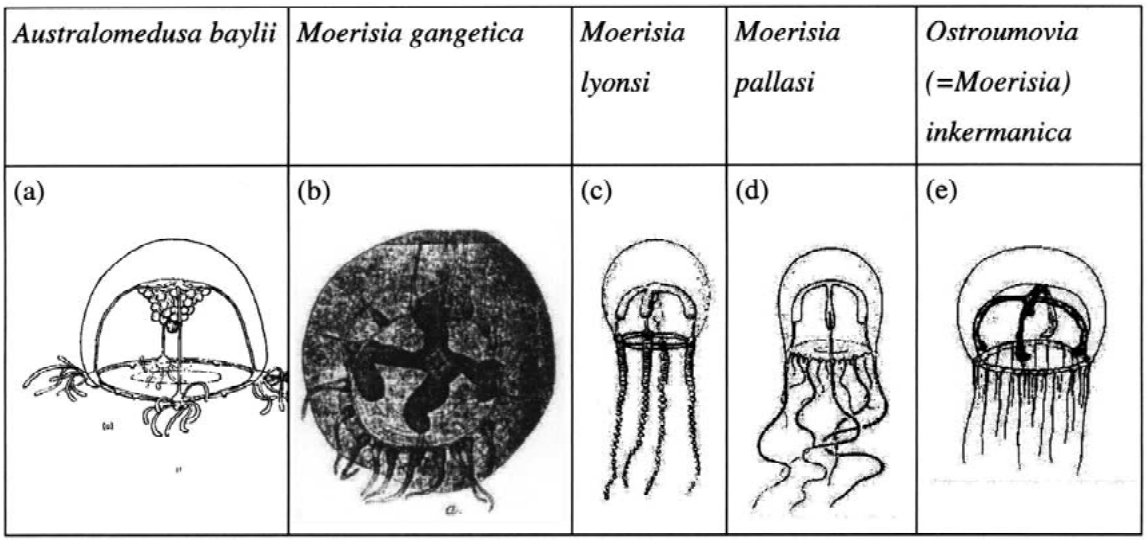

Figure 10. Habitus of (a) *Australomedusae baylii* [from Russell (1971)] and (b–e) of different Moerisiidae [from Kramp (9155, 1959)].

powerful, cross-shaped in section; no oral lips; radial lobes with twisted and folded gonad extending along proximal 3/4 of the length of radial canals; 16–18 very long and fine tentacles, with rings of nematocysts throughout their length".

Additional translated description after von Kennel: high vaulted to hemispherical; Velum horizontal, very wide (∼ 1/3 of diameter); nematocyst in closely packed twirls; gonads yellow-brown; length of tentacles from 6 to 10 mm (no declaration of number of orders); ocellum on the exumbrella of each tentacle base; no other sensory organs.

Halmomises were sorted into the Moerisiidae because of the "manubrium forming radial lobes", which is typical for this family (Bouillon & Boero, 2000b). To my knowledge, *H. lacustris* was only found once by von Kennel in a lagoon at the Eastern coast of Trinidad. It is doubtful if this was in fact a freshwater lagoon. It seems that this lagoon was an (oligo-) haline habitat, or this species is marine and was introduced to this lagoon.

Moerisia *Boulenger 1908*

Genus diagnosis (Kramp; 1961; Bouillon & Boero, 2000b): "Moerisiidae with 4, 16–32 moniliform marginal tentacles with rings of nematocysts throughout their length; bulbs globular, not clasping exumbrellar margin; stomach cruciform, without a peduncle; mouth without distinct lips, gonads on interradial walls of manubrium; without centripetal canals. Polyp with filiform tentacles in one more or less distinct whorl; with a thin perisarc".

Moerisia gangetica *Kramp, 1955 (Fig. 10)*
Only one specimen found in the Ganges Estuary near Calcutta, May 1926, brackish water.

Medusa diagnosis (Kramp, 1959; 1961): "3 mm wide, 2 mm high, globular, very thick; manubrium very small, mouth opening cross-shaped, no lips; radial lobes extending nearly to ring canal, distal parts sac-like, pendent; 19 tentacles of equal size, with semiglobular basal bulbs".

Moerisia pallasi *Derzhavin, 1912 (Fig. 10)*
Described from the Caspian Sea. Salinity in the Caspian Sea ranges between 11 and >14 % (Dumont, 1998).

Medusa diagnosis (Kramp, 1959; 1961): "3 mm wide, 3.5 mm high, dome-shaped, jelly thick; manubrium short, cruciform, mouth with four slightly indicated lips; radial lobes about two-thirds the length of the radial canals; up to 32 tentacles of different length in regular succession according to age".

Moerisia lyonsi *Boulenger, 1908 (Fig. 10)*
Described from Lake Qurun, an inland salt lake in Egypt.

Medusa diagnosis (Kramp, 1959; 1961): "4.5 mm wide, 4 mm high, globular, very thick; manubrium cylindrical, mouth round, without lips; radial lobes about two-thirds the length of the radial canals; tentacles

usually four, sometimes 16, rarely up to 22, long, with prominent rings of nematocysts".

Conclusions

All species described from freshwaters are placed into the family Olindiidae (according to Bouillon, 1985; Bouillon & Boero, 2000b; except *Halmomises*, see below). However, of several species (*Astrohydra*, *Keralika*, *Mansariella*) neither the nematocyst composition nor other important morphological features are known and consequently their classification is unclear.

All *Craspedacusta* species are freshwater species. *C. vovasi* Naumov & Stepaniants, 1971 (from marine sites) and *C. marginata* Modeer, 1791 (Hummelinck, 1938) (from brackish water) have been annulled. Numerous species of *Craspedacusta* have been described from China (*C. chuxiogensis*, *C. kawaii*, *C. kiatingi*, *C. kuoi*, *C. sichuanensis*, *C. sinensis*, *C. ziguiensis*) but *C. kuoi* Shieh & Wang, 1959 is identical to *C. sowerbii* Lankester, 1880. Neither the tentacle nor the nematocyst arrangement are different from *C. sowerbii*. The same is true for *C. kawaii* Oka, 1906. *C. kiatingi* Gaw & Kung 1939 seems to be a variation of *C. sowerbii* Lankester, 1880 (Kramp, 1961). Bouillon & Boero (2000b) pointed out that the Chinese 'species' (without *C. sinensis*) probably represent only variations of *C. sowerbii*. The only three species of *Craspedacusta* seem to be *C. sowerbii* Lankester, 1880, *C. iseanum* Oka & Hara, 1922 and *C. sinensis* Gaw & Kung 1939, but the state of *C. sichuanensis* and *C. ziguiensis* remains unclear.

Observations (Buchert, 1960; Holstein, 1995) of the hydrants suggest that *Calpasoma* is similar to *Craspedacusta*. Additionally, the drawings of *Astrohydra* (Hashimoto, 1981) and *Calpasoma* (Buchert, 1960; Matthews, 1966) suggest that these are identical. Perhaps all *Craspedacusta*, *Calpasoma* and *Astrohydra* are all one and the same species. Alternatively, *Microhydra*-type and *Calpasoma* type A maybe the same species and *Calpasoma* type B and *Astrohydra* are closely related.

In *Limnocnida* there are probably six distinct species within the genus, three from Africa (*L. tanganjica*, *L. victoriae*, *L. congoensis*) and 3 from the Indian subcontinent and Nepal (*L. indica*, *L. napalensis*, *L. biharensis*). But Bouillon & Boero (2000b) point out that *L. nepalensis* and *L. biharensis* may be identical with *L. indica*. Some authors separate this genus into the family Limnocnididae (Kramp, 1961; Hartwich et al., 1993).

Mansariella, *Keralica* and *Astrohydra* are genera and species described from freshwaters too. Their systematic position is unclear, although Bouillon (1985) and Bouillon & Boero (2000b) place them into the family Olindiidae. There are some differences between these species and e.g. *Craspedacusta* or *Limnocnida*, but their nematocyst structure and developmental characters are not known.

Some remarks on the distribution and habitat of the freshwater medusae: *C. sowerbii* is the only cosmopolitan species. All other species of the genus *Craspedacusta* are restricted to East Asia (China and Japan). *Astrohydra* too is restricted to Japan. The habitats of these species range from small artificial pools to ponds, lakes and rivers. It seems that they prefer eutrophic ponds over oligotrophic large lakes. In contrast, *Limnocnida*, *Mansariella* and *Keralica* are found primarily in large lakes and reservoirs. However, *Limnocnida nepalensis* and *L. congoensis* were up to now only found in ponds. Whereas *Mansariella* and *Keralica* are restricted to India, *Limnocnida* is present with three species in Africa and three on the Indian subcontinent.

Halmomises, the only Anthomedusae (Fam. Moerisiida) described from freshwater, was found only once. It is unclear whether it is a freshwater species. However, the name means 'hating salt' and so the describer was apparently aware of its being found in freshwater (Dumont, pers. com.). Its systematic position seems doubtful. Maybe the medusae were introduced from a marine site.

The species within the genera *Moerisia* and *Australomedusa* are from marine/brackish sites and saline lakes. *Australomedusa* is restricted to Australia (SW-Australia and Victoria), whereas *Moerisia* has a distribution from Egypt to the Caspian Sea and the Ganges Estuary. This distribution seem to be the consequence of the settlement during Tethys times. Some authors (discussed by Stadel, 1961 and Reisinger, 1972) suggest that the divided distribution of *Craspedacusta* in the North and *Limnocnida* in the South can be a consequence of colonization during Tethys times, too. And the Moerisiidae may be the origin of the freshwater medusae. This was supported by Kramp (1951) who supposes "that the Olindiidae are closely related to the Moerisiidae". However, their (modern) systematic position within the Athecata/Anthomedusae suggests that the origin of the Moerisiidae is inde-

pendent of the true freshwater species. Thus the inland water medusae may have a polyphyletic origin.

Another hypothesis states that *Craspedacusta* are closely related to *Gonionemus* (Oka, 1906; Dumont, 1994). This is supported by their systematic position resulting from their nematocyst composition (Bouillon, 1985) and their distribution in the North Pacific (Russel, 1953) and the brackish littoral zone of the Mediterranean Sea (Reisinger, 1972). The origin of freshwater medusae is not clear yet, especially due to the newly described species' (*Mansariella*, *Keralika*, *Astrohydra*) but unknown systematic position.

This review end with many open questions. Neither the number nor the origin of the freshwater medusae are known. For further research on inland water medusae, it seems essential to focus on the nematocyst-type of the (newly described) species and employ molecular genetic methods to clarify the systematic and phylogeny of the freshwater medusae.

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