Hydrobiologia **272**: 1–12, 1994.
H. J. Dumont, J. Green & H. Masundire (eds), Studies on the Ecology of Tropical Zooplankton.

The distribution and ecology of the fresh- and brackish-water medusae of the world

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Key words: Cnidaria, *Craspedacusta*, *Limnocnida*, *Halmomises*, *Moerisia*, *Aurelia*, inland waters, biogeography, predation, egg-predation, osmoregulation, passive dispersal

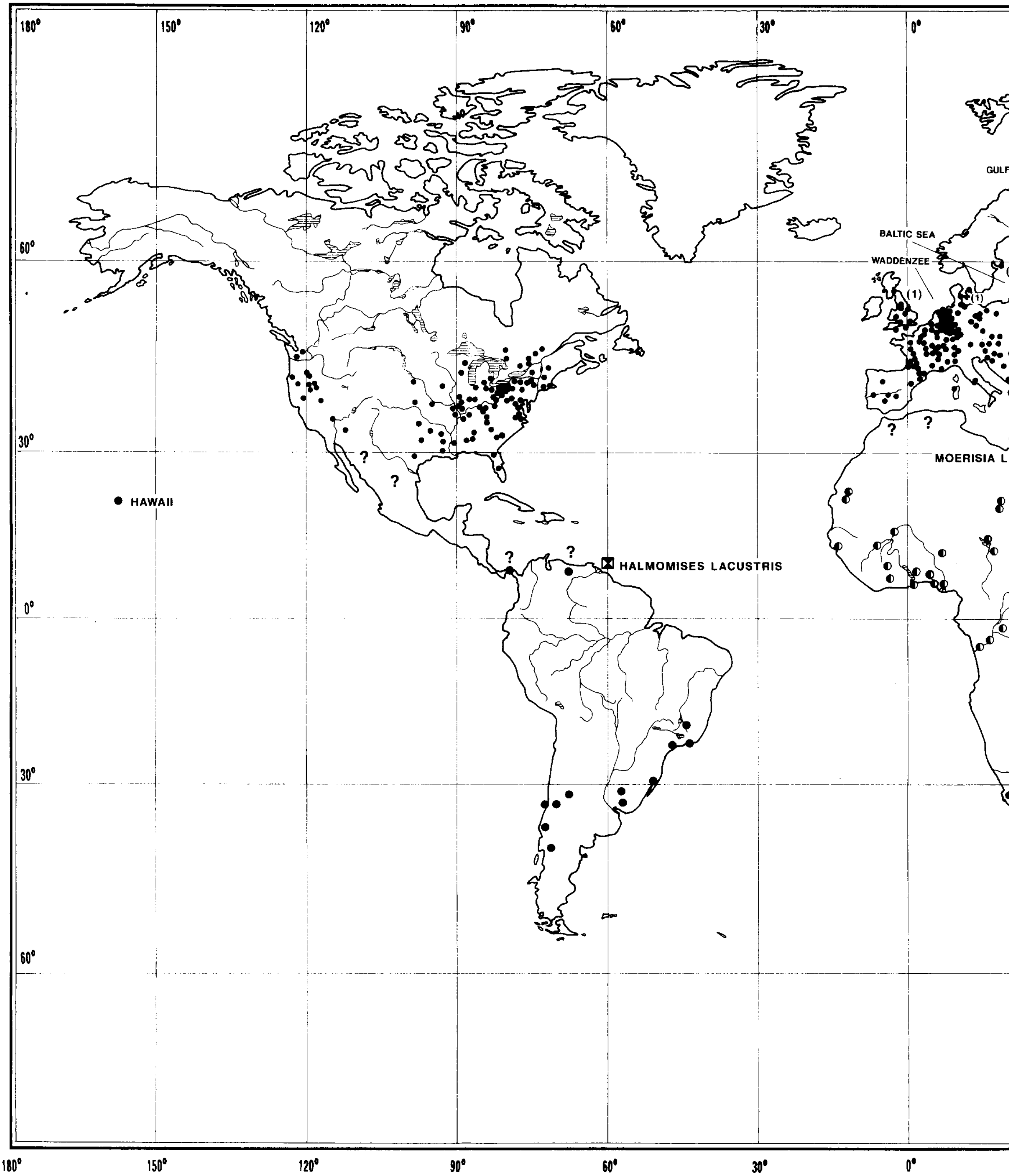
Abstract

Limnocnida and *Craspedacusta* are the two main genera of Cnidaria from continental waters which have a free-swimming medusa in their life cycle. Both originated in tropical-subtropical Asia, but *Limnocnida* is also found in *Africa*, with one species (*L. tanganjicae*) perhaps endemic to lake Tanganyika. *Halmomises* from Trinidad, and two genera (*Mansariella*, *Keralica*) from India have limited ranges. No freshwater medusae evolved in Europe and the Americas (aside from Trinidad), but *Craspedacusta sowerbii*, by virtue of its drought resistant stages, has managed to colonise all continents, except Antarctica, in the course of the twentieth century. In all, there are about 10–14 freshwater species of medusae. An additional 4–5 species of *Moerisia*, *Australomedusa*, and *Craspedacusta* are sequestered in continental salt-lakes, while a few genera occur in brackish-water seas and estuaries (e.g. *Moerisia*, *Odessia*, *Ostroumovia*). This reduced diversity is probably due to (1) a rarity of drought resistant stages, adjusted to upstream dispersal, in the life cycle, and (2) difficulties to adapt the osmoregulatory system to a hypotonic environment.

The feeding ecology of the freshwater medusae is also examined. Like all Cnidaria, they are opportunistic predators. However, fish egg predation might be their major means of subsistence, other types of food being taken only occasionally, or when fish eggs and larvae are scarce. Their impact on the true zooplankton might therefore be limited to short pulses of planktivory. Whether they are themselves limited by predation remains to be studied; many fish in the invasive part of their range avoid them, but some macrocrustaceans readily consume them. It is hypothesized that this might explain their success in Lake Tanganyika, and their absence from lake Baical. Finally, the absence of endemic species from South America could relate to the great diversity of small-sized predatory aquatic reptiles on this subcontinent.

Introduction

Limnic medusae have been inadequately studied. To begin with, nobody has attempted to find an answer to the obvious question why there are so few genera and species of Cnidaria (and no Ctenophora) in inland waters. Being and old and primitive group, the Cnidaria have had plenty of time to adapt to freshwater conditions. Yet, this has only occurred to a limited degree, in contrast to the ever more primitive Porifera, which have undergone adaptive radiation in ancient lakes like Baikal, Tanganyika, and Malawi, and in South America.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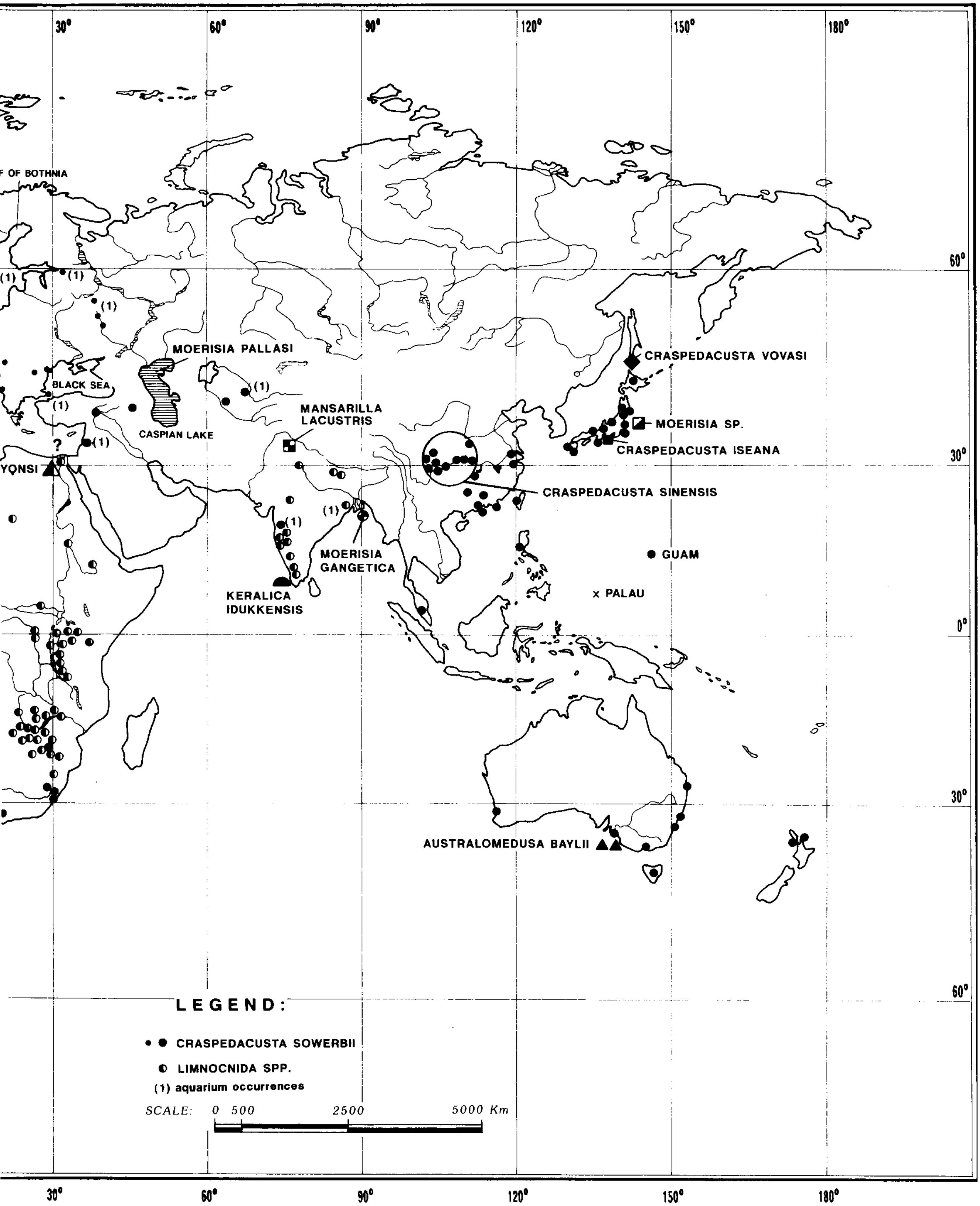

Fig. 1. World distribution of the freshwater and brackish-water Medusae.

Secondly, while the developmental cycle of the two main genera, *Craspedacusta* and *Limnocnida*, has been well studied (Dejdar, 1934; Reisinger, 1957; Bouillon, 1957), and hundreds of notes and several reviews discuss occurrences of limnic medusae all over the world (Arnold, 1968; Bruneau de Miré *et al.*, 1960; De Vries, 1992; Dumont, 1971; Dumont & Verheye, 1984; Fish, 1971; Goy, 1977; Kramp, 1951, 1961; Lytle, 1960, 1962; Parent, 1981, 1982; Pitman, 1965; Rayner & Appleton, 1989; Schmitt, 1939; Stadel, 1961), their role in aquatic foodwebs remains obscure.

The present paper (1) reviews global distribution patterns of fresh, inland saline, and brackish-water medusae, and (2) discusses questions about the feeding and some other aspects of the ecology of the genera *Limnocnida* and *Craspedacusta*, with the aim of stimulating future research. Sessile, non-medusae forming Cnidaria like *Hydra* and related genera, including the colonial fresh- and brackish-water *Cordylophora*, will not be considered in this article. However, the statement that they are poorly diversified in inland waterbodies, applies to them with equal strength as to the inland Limnomedusae.

The distribution of the limnetic limnomedusae: an overview

Strictly, freshwater medusae belong to three genera: *Halmomises*, *Craspedacusta*, and *Limnocnida*. The validity of a further two Indian genera, *Keralica* and *Mansariella*, both monotypic and both known from a single locality only (Malhotra *et al.*, 1976; Khatri, 1984) is in need of confirmation. Even the number of species within each genus is controversial. There emerges a consensus (Parent, 1982) that *Craspedacusta* comprises four species, all in East Asia (Fig. 1). In *Limnocnida*, the situation is more confused, and ranges between extreme lumping, by Leloup (1951), Kramp (1954), and Goy (1977), who recognize only a single, or perhaps two, species across the whole Afro-Indian range of the group, and extreme splitting, with 4–5 species in Africa, and up to 5 species on the Indian subcontinent. However, this taxonomic aspect is of only minor importance to the present account, and will not be discussed any further.

The worldwide pattern of occurrence, shown in Fig. 1, is quite eloquent: medusae are widespread in most tropical–subtropical areas. They also occur in temperate areas, but only in summer. There are no subarctic–arctic or antarctic occurrences.

Limnocnida is a tropical genus, that penetrates the subtropics, but is limited to Africa and the Indian subcontinent. It occurs in rivers in inconspicuous numbers but builds up large populations in lakes, reservoirs and backwaters. It has not yet been found in Madagascar and Sri Lanka. A few relict populations occur in the southern Sahara (Mauretanian Adrar mountains: guelta Molomhar; some lakelets in the Tibesti mountains, Chad). No records exist from the Arabian subcontinent, including the well-studied Levant (Por, 1989) suggesting that the disjunction with India is not due to a lack of data. No records from Iran and Pakistan exist either, the genus appearing only east of the Indus River. Remarkably, there are no records from tropical Bangladesh, the valley of the Brahmaputra included, the only east Indian record (Firoz Ahmad *et al.*, 1987) being an aquarium occurrence. To the north, *Limnocnida* penetrates the Himalayas up to an altitude of c. 1400 m (Dumont, 1971; Ferro, 1979; Malhotra *et al.*, 1976; Tilak *et al.*, 1976). A disjunction between the Indian *Limnocnida* and the presumed centre of origin of *Craspedacusta*, the Yangtze (Chang) River, occurs across the valleys of the Brahmaputra, Irrawaddy, Salween, and Mekhong rivers. That freshwater medusae originated from marine ancestry, probably (but not necessarily) before the closing of the Tethys sea, seems logical. If *Limnocnida* is really absent from Madagascar, this might suggest a comparatively recent origin. On the other hand, the aridification of Arabia and South West Asia may have eliminated intermediate populations. Such populations may still exist, but have not yet been discovered because of a lack of research. However, the fact that African and Indian Limnocnida are separated by at least one character (Secondary tentacles organized in regular groups in India, in irregular groups in Africa), indicates a long isolation between the two areas.

The reason for placing the origin of *Craspedacusta sowerbii* and *sinensis* in the Yangtze valley has been well explained by Kramp (1951) and by Parent (1981): yearly recurrent occurrence of both sexes in the river and its floodplain lakes, in contrast to the populations elsewhere, which may strongly fluctuate in density between years, and are almost invariably 100% male *or* female, not both. This unisexuality is believed to result from the small size (possible one resting stage) of introduced propagules. The presence of two more species in Japan and Sachalin (one of which is living in a saline Lake) (Uchida, 1951; Naumov & Stepaniants, 1971) further indicates that the genus *Craspedacusta* (and probably *Limnocnida* as well – see further) are derived from a (common) marine ancestor, which lived in the West Pacific Ocean.

Australia, a continent with a long history of aridity (Williams, 1980), has an endemic genus, *Australomedusa*, which occurs in coastal saline lakes (Fig. 1) (Russell, 1970, 1971; Bayly, 1971). It probably could not bridge the intervening arid areas to colonise the numerous (but often intermittent) lakes of the arid interior of the continent.

More puzzling is the case of the Americas. Neither in North, Central nor South America have endemic freshwater medusae evolved, except for one truly freshwater species, *Halmomises lacustris*, which lives on the island of Trinidad (Von Kennel, 1891) (Fig. 1). In the entire amazonian basin, no medusa has been recorded. H. Sioli (pers. comm.), who intensively collected all types of aquatic biota across the whole basin for more than twenty years, positively asserts that no such animals exist there. South and north of the american tropics, the dispersalist *Craspedacusta sowerbii* became widespread in the course of the 20th century only (see further). The identity of (not properly identified) medusae in a freshwater lake in Panama (Smith, 1925) and in a reservoir in Venezuela (Infante, pers. comm.) is suggestive of *Halmomises*, but may also have been *Craspedacusta*.

It has been brought to my attention by J. Mertens that the absence of freshwater medusae from tropical south and central America might be the consequence of predatory exclusion (see further).

Craspedacusta sowerbii (Lankester, 1880): a case of successful passive dispersal

C. sowerbii is the most abundant and widespread freshwater Cnidarian. Except for the Antarctic it occurs on all continents and subcontinents, including many major and minor islands. Although we do not know the life cycle of *C. sinensis* (Gaw & Kung, 1939), of the now extinct *C. iseana* (Oka & Hara, 1920), and of *C. vovasi* (Naumov & Stepaniants, 1971), it seems clear that its success is intimately linked to the unique occurrence, in its complex reproductive cycle, of two or three resting stages. Two of these are drought-resistant (podocysts and spherical frustules) (Reisinger, 1957). Co-transportation with aquatic plants, fish, and man is thus more than a mere possibility. It has been noted (Uchida, 1955), that *C. sowerbii* started spreading across Japan shortly after American troops entered the country after World War II. Similarly, Williams (1980) asserts that the species first appeared in Australia around 1950, but quickly expanded across the Southern fringe of the continent thereafter.

Because of longstanding commercial contacts with China, the invasion of Europe and North America had probably started as early as the mid 19th Century (claims that *C. sowerbii* occurred in the Dutch Waddenzee in the 17th Century having been dismissed as erroneous by Kramp (1961) and by Parent (1981)). Likewise, the absence of records from Mexico may be more apparent than real, as well as that from the Maghreb countries of North Africa. An aquarium record from Israel is again suggestive of a man-made introduction (Rahat, 1961). South American records begin in 1930, with an aquarium observation (Gliesch, 1930), quickly followed by sightings in Chile, Brazil, Argentina, and Uruguay (Fig. 1 – see also Parent, 1982). As stated above, the true tropics of

South America have hardly been colonised. Records from Malaysia (Berry & Dhaliwal, 1962) and from the island of Guam (Belk & Hotaling, 1971), accompanied by good figures, are trustworthy, however.

Aerial dispersal (perhaps ornithochory), or other means of upstream and inter-valley dispersal must occur, and are certainly significant. In Belgium (*ca* 31 000 km^2) for example, at least 7 locations are known (De Meester, 1989; Symoens, 1953), two of which are situated in the Meuse River (Damas, 1938). I personally found polyps on submerged glass slides in the Sambre River, in 1973 (unpublished observations). These polyps strobilated young medusae in the laboratory. Between the upper Sambre (near the French frontier) and the Meuse lies the highly polluted, azoic industrial basin of Charleroi, such that the upstream population in 1973 could not – except by aerial dispersal – have been generated by the downstream population.

Dispersal with water plants (again largely aided by man) is also a factor. Parent (1982) found that *Elodea canadensis* may have been a vehicle for *Craspedacusta*, with a time lag of *ca* 50 years. The numerous occurrences of *Craspedacusta* (and in rare cases, of *Limnocnida*) in aquaria suggest that 'escape' from aquaria may mark the beginning of the conquest of a new area. A strong case was documented by Amemyia (1930), who found *Craspedacusta* in his aquarium in Japan about six months after importing some water plants from San Francisco. Stadel's (1961) detailed locality records up to 1960 show that of 140 records from Europe and North America, 21 (a conservative estimate, not including small outdoor artificial basins) refer to indoor aquaria, and ponds in botanic gardens. These included almost all records at the northern fringe of its present range (*i.e.* Scandinavia and Russia). It should be added that the only record of *Craspedacusta sowerbii* from India so far (Joshi & Tonapi, 1965) was also an aquarium occurrence.

Immigration into New Zealand presumably occurred late, in accordance with the isolated position of this pair of islands, and may have taken place only in the sixties (Fish, 1971). Southern Africa recently also became colonised: the first record was from temperate Lake Midmar (Rayner, 1988), but records quickly accumulated, and at least four sites were known by 1989 (Rayner & Appleton, 1989).

C. sowerbii now inhabits the subtropics and the warm-temperate-cool belt of the entire planet. Records are being added year after year, with, recently, the contribution by SCUBA divers showing by visual observation that classical plankton collecting techniques reveal only a fraction of the true occurrences (cf. Dodson & Cooper, 1983 for various lakes in Michigan; N. Lair, pers. comm., for Lake Tazenat, Central Massif, France). The polyp (*Microhydra*) form is even more rarely seen than the medusa, although it may be far more common than the medusa itself. Little is known about the exact conditions which induce production of medusae by these polyps. A high temperature is required, but this is certainly not the whole story.

Low diversity of limnetic medusae: the result of an osmotic problem?

The peculiar low diversity of limnic *Cnidaria* (and Ctenophores) has not been well addressed, neither conceptually nor experimentally. Three aspects appear relevant: (1) the spatial confinement of the limnic habitats, (2) the one-way (downstream) passive dispersal in lotic freshwaters and, (3) the necessity for osmotic regulation.

Confinement to closed (lacustrine) environments, rather than posing a problem, seems to be an asset in Cnidarians: explosive developments have been recorded from so-called marine lakes, like in the Palau archipelago, where brackish (salinity 17–27‰) karst lakes harbour large, permanent, swarm-forming populations of the wide-ranging marine Scyphozoan *Mastigias papua*, and of the cosmopolitan *Aurelia aurita* (Hamner & Hawri, 1981; Hamner *et al.*, 1982). Here, even a jellyfish-eating sea anemone, *Entacmaea medusivora* occurs (Fautin & Fitt, 1991). The non-marine Moerisiidae, sequestered in continental or coastal saline lakes (*Moerisia lyonsi* in Birket Qurun, Egypt, and *Moerisia pallasi* in the Caspian sea), as well as *Australomedusa baylii* (Bayly, 1971) have even become endemic to their saline biotopes. Finally, Cnidaria (e.g. *Odessia*, *Ostroumovia*) are common and diverse in semi-closed brackish-water marine basins like the Baltic Sea, the former Dutch Zuiderzee, and the Black Sea.

Downstream transportation in rivers and lakes connected to a river is common to all aquatic animals which cannot maintain their position by swimming alone. The solution to this problem in freshwater is to produce a drought resistant life-stage adapted to passive (upstream) dispersal by anemochoria or by zoochoria. Such a stage has evolved successfully in some *Craspedacusta* (see earlier) and to a lesser degree in *Limnocnida*. Bouillon (1957) describes the fragmentation of African *Limnocnida* polyps into (drought?) resistant buds.

In India, no *Limnocnida* polyp has ever been discovered (Gravely & Agharkar, 1912), but a zygote which attaches to substrates by means of sticky threads (Rao, 1932) may be capable of being transported in dry condition, if attached to plant parts or other movable objects. The sudden appearance of *Limnocnida* in an aquarium in Ranchi (Firoz Ahmad *et al.*, 1987) is suggestive of this type of phenomenon.

The most serious obstacle, however, seems to be osmoregulation (perhaps more correctly ionic regulation), but few studies on this aspect of Cnidarian life are available. Romanes (1880) showed that *Craspedacusta* is incapable of adjusting to seawater, in which it shrinks and dies within few minutes. A survival of 1–2 days was achieved only at dilutions of seawater of the order of 20 times. Fleming & Hazelwood (1967) made a more exact study of the osmoregulation of *Craspedacusta*, and changed the osmolality of the medium from that of pond water (7 m $OsMkg^{-1}$) to 9.2% sewater (92 $mOsMkg^{-1}$). The animals were found capable of adjusting their osmotic pressure to that of the environment, but only at the cost of a rapid decrease in volume above 39 m $OsMkg^{-1}$, roughly confirming Romanes' observations. In a later study, Hazelwood *et al.* (1970) showed that ionic and volume regulation are accompanied by voiding of a hypertonic solution via the manubrium. *Craspedacusta* is thus a hyperosmotic regulator. Marine species are to be considered osmoconformers, but those tolerant of considerable dilutions may have hyperosmotic regulatory capabilities. *Aurelia aurita* is even capable of regulation over a rather wide salinity interval, like down to 4‰ salinity in the northern gulf of Bothnia (Sandström, 1982).

An intriguing fact is that the Ctenophore *Pleurobrachia pileus* O.F.M., belonging to a group otherwise totally unrepresented in fresh or brackish water, is a dominant element of the plankton of the Bothnian Gulf. It is most abundant as an adult in the freshest parts, while its larvae tend to be common further south, where salinity is higher.

It would be extremely interesting to determine whether such oligohaline populations have been selected for an osmoregulatory system different from that of truly marine populations. The region of 1/20 seawater concentration seems to constitute a critical zone, and the conquest of freshwater by *Limnocnida* and *Craspedacusta* must therefore have involved a fundamental switch in osmoregulation.

In this context, and although this paper is not a taxonomical one, the remark may be made that the difficulty involved in this 'switch' makes, it unlikely that it occurred twice, independently, around the same time, and in the same area. Rather, it seems logical that both genera were descended from a common marine ancestor, which would mean that, phylogenetically, they are extremely close. Such a hypothesis should be testable by molecular methods.

Feeding ecology

All non-parasitic Cnidaria are predators. Sessile forms (including corals, and sea anemones) exploit the littoral or reef environment, while medusae hunt in the pelagial, and sometimes in the epibenthos. Again, deplorably little research has been devoted to food, feeding, and the position of freshwater medusae in the lacustrine food web, and data from the original range (Asia, Africa) fo the two main genera are virtually non-existent.

The feeding mode of *Craspedacusta* was discussed by Dejdar (1934) based on experimental feeding trials in the laboratory. He called this medusa an indiscriminate feeder, accepting a wide variety of planktonic as well as benthic prey, including fish eggs. Prey size was related to medusa size. However, only fully grown animals (up to 15 mm in diameter) fed on large prey such as *Tubifex*. A typical behaviour of both *Craspedacusta* and *Limnocnida* is to parachute down, with tentacles extended, after swimming upward, and 'rest' on the bottom. Hess & Kronfeldner (1988) report that, while doing this, medusae may catch individual tubificid worms from the benthos.

There is conflicting evidence on their daytime feeding on zooplankton. Dejdar (loc. cit) claims that few medusae collected during the daytime had a full stomach, and some medusae even refused to feed on live plankton in aquaria. Conversely, Dunham (1941) and Davis (1955) found medusae to feed indiscriminately on lake zooplankton.

The only recent laboratory study is by Dodson & Cooper (1983). They found that medusae with a mean bell diameter of 11.6 mm would feed on Cladocera and Copepods up to 2.0 mm in size. Larger crustaceans (*Leptodora*, and even *Streptocephalus* up to 8.8 mm long) were killed, but not eaten. Because many fish larvae are in that size range, medusae may pose a threat to fish, and there are indeed reports which testify to this effect (e.g. Shadle & Minthorn, 1939). Dodson & Cooper (*loc. cit.*) calculated that, at medusae densities estimated at 3 m^{-3} in a pond, *Craspedacusta* had a negligible effect on both zooplankton and fish. Yet, in an artificial quarry reservoir near Ulm, medusa densities of c. 30 m^{-3} were measured in August 1992 (G. Maier, C. Dierckens & T. M. Van Maele, unpublished observations). Virtually no zooplankton had survived here, and medusae were even feeding on allochtonous material, such as terrestrial insects (flies) which had fallen to the water.

Kramp (1950), discussing Chinese sources, states that medusae occur from late spring till late summer in lakes and pools flooded by the turbid Yangtze river and its tributaries. Because river fish (mainly cyprinids) spawn at times of flood, it is not excluded that there is a trophic link between the mass appearance of medusae and the timing of fish reproduction. No hard evidence is available in support of this hypothesis, but there are analogous cases. The marine (and brackish water) *Aurelia aurita* and *Aequorea victoria*, for example, are noted fish-egg predators. In the Baltic sea and offshore British Columbia, they may effectively eradicate whole egg populations of herring (Purcell, 1985, 1989), and feed on the remaining herring larvae as well.

Probably the best site to gain a better understanding of the trophic role of freshwater medusae is lake Tanganyika, where *Limnocnida tanganjicae* is perennial, and moves around in huge, vertically migrating swarms (Leloup, 1951; Coulter, 1991). The species may have co-evolved here with the tanganyika sardines *Limnothrissa miodon*, a littoral-pelagial, and *Stolothrissa tanganicae*, a strictly pelagial feeder. *Limnothrissa*, which has been successfully introduced to Lakes Kariba, Cahora Bassa, and Kivu, deposits its eggs on sandy bottoms in sheltered bays, while *Stolothrissa* (and the predatory *Lates*) have planktonic eggs, which sink at a rate of 5 cm h^{-1}, but hatch after less than 24 h, *i.e.* before they sink to the deep anoxic zone of the lake. Besides eggs and larvae of these fish, there is little food available for the medusae in the plankton, which contains no Cladocera, but is almost exclusively composed of a fast-swimming calanoid copepod, *Tropodiaptomus simplex* Sars. In December 1989, I conducted some experiments in Bujumbura, offering medusae a dense sample of live *Tropodiaptomus* as a diet. The medusae would perform their characteristic parachuting behaviour, especially in dim light, and some would at times capture a copepod with their tentacles. However, many prey managed to escape unharmed. I therefore doubt whether the local medusae can subsist on an elusive prey like *Tropodiaptomus*. By elimination, only planktonic and sedimented sardine eggs remain available as food.

Swarms ('layers') of *Limnocnida* were found to be situated at considerable depth and below sardine schools in the lake during daytime, and both migrated to the surface in sequence during the night (Coulter, 1991). If this phenomenon is of regular occurrence, it would make sense as a pelagic egg-collecting adaptation. In such circumstances, *Limnocnida* predation might explain the saw-toothed aspect of year-to-year catch diagrams of the tanganyika sardines (Roest, 1985, 1987; Coulter, 1991).

Furthermore, the 'bottom-resting' habit of both *Craspedacusta* and *Limnocnida* may be a benthic egg-search behaviour, and an adaptation of medusae to escape from their own predators. In June 1975, I found that in daytime all medusae of the famous desert population of Guelta Molomhar (Mauretania) were at the bottom (*ca* 6 m deep). The pool has four species of fish, two of which belong to the genus *Barbus*. Exactly the same behaviour (medusae lying on the bottom during daytime) was also found in Bujumbura, Burundi, in a *ca* 20 m deep embayment of lake Tanganyika. Quite a few medusae were seen floating near the water surface, but upon inspection proved to be injured or otherwise damaged specimens.

The question remains what preys on the medusae. It may be argued that medusae ar not worth being eaten: 99.26% of their bulk is water (Ludwig, 1977). However, the story may not be that simple. In the invasion area of *Craspedacusta sowerbii*, most fish are discouraged by its nematocysts, and will taste, but reject, and later avoid it (Bode, 1950; Dodson & Cooper, 1983). Whether this is also true in the native area of the genera *Craspedacusta* and *Limnocnida* (*Halmomises* being completely unknown ecologically) is doubtful, although no data are available. Protection by nematocysts may not be hermetic, and both transparency (reducing visibility to predators), and the deep daytime refuge of healthy medusae are suggestive of light evasion but also of predator avoidance. Parallel situations exist in the marine environment and the abundance of medusae in the Palau lakes may, in fact, reflect the low-predation nature of these biotopes. Larson *et al.* (1991), using direct observations from submersibles, concluded that in the Atlantic Ocean most medusae are to be found at e depth of 500–600 m; the majority were transparent, but many were dark red, purple-black, or brown pigmented. In spite of their defences, they were preyed upon by amphipods, mysids, decapods, and fish. Perhaps one might go so far as to speculate that the absence of medusae from Lake Baikal is the result of predatory exclusion due to the adaptive radiation of carnivorous amphipods in that lake.

Dodson & Cooper (1983) report that two American species of *Orconectes* (crayfish) did actively prey on *Craspedacusta* while this was sinking to the bottom of their aquaria. This indicates benthic decapods as likely consumers of medusae in Lakes Tanganyika and Malawi as well. However, the adaptive radiation of shrimp and crabs in L. Tanganyika is much more important than that of L. Malawi, yet *Limnocnida* does not occur in L. Malawi. Much therefore remains to be learned about the position of *Limnocnida* and, evidently, of *Craspedacusta*, in trophic networks.

As far as the scarcity or absence of medusae from Latin America is concerned, predatory exclusion by turtles should be considered as a possible causative factor. Marine turtles are known to actively feed on Cnidaria (Ates, 1991); if given a chance, freshwater species might behave similarly. In this respect, a statistical relation exists between the relative scarcity of aquatic turtle species (*ca* 10) in Africa, where *Limnocnida* is commonest, as compared to India (*ca* 20 species), where *Limnocnida* is less common, and tropical South America (*ca* 40–60 species), where medusae are absent, and large rivers abound, but deep lakes, which might offer refuges from predation, are rare or absent. Experimental work relating freshwater medusae to turtles would be welcome.

Acknowledgements

For permission to use unpublished locality records of freshwater medusae, I thank R. Margalef, J. Armengol and M. Alonso (Spain), R. Chengalath (Canada), A. Egborge, C. B. Powell, and G. Delincé (Nigeria), E. Balseiro (Argentina), B. Sket and co-workers (Slovenia), L. Forro (Hungary), R. Hart (Zambia), W. De Smet (Belgium; Namibia); D. Dudgeon (Hong Kong); Y. Ranga Reddy (India), A. el Moghraby (Khartoum), and A. Infante (Caracas).

Literature was provided by B. Goddeeris (Brussels), G. Hanazato (Japan), G. Maier (Ulm), D. Dudgeon (Hong-Kong); R. Kinzelbach (Darmstadt, Germany), N. N. Smirnov (Moscow), G. Balvay (Thonon), N. Lair (Clermont-Ferrand), S. Negrea (Bucarest), V. Sladecek (Prague), M. Arcifa (Ribeirao Preto, Brazil), and J. G. Tundisi (Sao Paulo). J. Mertens (Gent) provided the 'wild' idea of linking medusae to aquatic turtles.

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