

Parallel, paedomorphic evolutionary processes of the bivalve-inhabiting hydrozoans (Leptomedusae, Eirenidae) deduced from the morphology, life cycle and biogeography, with special reference to taxonomic treatment of *Eugymnanthea**

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SUMMARY: It is hypothesized that bivalve-inhabiting hydroids originated from colonial, free-living eirenid hydrozoans, initially appearing as an *Eutima* species with solitary hydroids producing immature medusae with tentacles and manubrium, and also with derived characteristics of the marginal warts of the mature medusae as the remnants of the tentacular bulbs of the ancestral eirenid, and decreased number of statocysts. The derivate eumedusoid-producing *Eugymnanthea* evolved then. Deduced from the morphology, life cycles, and geographical distributions of this group and of all the known extant *Eutima* species, it is proposed that parallel, paedomorphic evolution took place in the marginal regions of the area of distribution of the ancestral-like *Eutima* at least in the northern hemisphere of both the Pacific and the Atlantic Oceans. *Eugymnanthea* appeared as a polyphyletic taxon as a result of the parallel evolution of different species of *Eutima*. It is pointed out that *Eugymnanthea* and *Eutima* are to be merged into a single genus in the future.

Key words: bivalve-inhabiting hydrozoan, paedomorphic, parallel evolution, eirenid, *Eutima*, *Eugymnanthea*, life cycle, geographical distribution, polyphyly, taxonomy.

INTRODUCTION

The most derived bivalve-inhabiting hydrozoan, *Eugymnanthea*, is distributed disjunctly in the northern hemisphere: *E. inquilina* Palombi, 1935 has been found in the Mediterranean Sea (Palombi, 1935; Cerruti, 1941; Crowell, 1957; Uchida, 1964; Morri, 1981; Gili, 1986; Kubota, 1989; Piraino *et al.*, 1994; Bouillon *et al.*, 1995; Celiberti *et al.*, 1998; Benovic, personal communication) and *E. japonica* Kubota, 1979 in the North-West Pacific

(Kubota, 1979, 1985a, 1991, 1992b, 1999; Kubota *et al.*, 1999). By combinations of the two diagnostic features of the medusae, manubrium and statolith, the two species of *Eugymnanthea* can be clearly distinguished (Table 1). There are no records of introduction of *Eugymnanthea* in any places (Kubota, 1991), differing from the case of their most popular host, *Mytilus edulis galloprovincialis* Lamarck. In Japanese waters, for instance, *M. e. galloprovincialis* from the Mediterranean Sea settled at the beginning of the 20th century, then spread over nearly all the coasts of Japan except for those of Okinawa Prefecture (Kubota, 1989, 1992b;

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TABLE 1. – Morphological differences between the mature medusae of the two species of *Eugymnanthea* and their geographical distributions. Fm: frequency (%) of medusae with manubrium; Nm: number of medusae examined; Fs: frequency (%) of statocysts containing 1-4 statoliths (Stl); Ns: number of statocysts examined; Nl: number of localities examined.

Species	Fm	(Nm)	Fs				(Ns)	Nl	Distribution	References
			1Stl	2Stl	3Stl	4Stl				
<i>E. japonica</i>	97.9	(4597)	90.2	7.4	1.1	0.1	(12955)	21	Japan (West Pacific)	Kubota, 1991
<i>E. japonica</i>	95.2	(105)	93.0	4.3	0	0	(517)	1	Taiwan (West Pacific)	Kubota, <i>et al.</i> , 1999
<i>E. inquilina</i>	3.4	(183)	9.4	37.3	35.4	11.7	(1462)	4	Italy (Mediterranean)	Kubota, 1989

Kubota and Hayashibara, 1995; Kubota *et al.*, 1995; Kubota, 2000).

Kubota (1987, 1989, 1991), discussing the origin of the two species of *Eugymnanthea*, discarded both the species introduction and the Tethys Sea relict hypotheses, and proposed the parallel, paedomorphic evolution. Bouillon (1985, 1994) ascribed *Eugymnanthea* and bivalve-inhabiting *Eutima* to the Eirenidae, merging the Eutimidae into that family. Monophyly of bivalve-inhabiting hydrozoans is supported also by unpublished data by Kubota, Larson and Migotto who found Atlantic bivalve-inhabiting hydroids producing *Eutima* medusae. If *Eucheilota*-like mature medusae are produced in any bivalve-inhabiting hydroids, they will belong to the Eirenidae as is the same case of the *intermedia* form of *Eutima japonica* that was firstly described as a new species of *Eucheilota*, being then considered as one of the four forms of *Eutima japonica* (Kubota, 1984, 1985b, 1992a, 1993, 1997, 1999).

In this paper the evolutionary processes of bivalve-inhabiting hydrozoans leading to the origin of *Eugymnanthea* are deduced from morphology, life cycles, and geographical distributions. Furthermore, the phylogenetic patterns that led to *Eugymnanthea* species allow a re-appraisal of the taxonomic value of this nominal genus.

EVOLUTIONARY PROCESSES OF BIVALVE-INHABITING HYDROZOANS

Early process of evolution

The ancestral form of the bivalve-inhabiting hydrozoans is conceivable as a free-living eirenid resembling *Eirene menoni* Kramp (see Bouillon, 1984) or *E. lactea* (Mayer) (see Brinckmann-Voss, 1973), i.e. a colonial hydroid producing immature medusae with tentacles and manubrium at liberation. Two key character changes took place in this hypothetical ancestor: decrease in number of both

the marginal tentacles and the statocysts in the mature medusa (Table 2: 1). It is conceivable that the marginal warts of *Eutima* medusae are remnants of the tentacular bulbs of the ancestral eirenid medusae.

In Japanese waters, records of *Eutima* refer only to the bivalve-inhabiting species, *E. japonica* Uchida, 1925 (Uchida, 1925; Yamazi, 1958; Kubota, 1992a, b, 1998, 1999, unpublished data) and no free-living species have been known. Other free-living eirenids in Japan are referred to *Eirene*, *Tima* and *Eutonina* (see Kubota, 1998). *Eutima japonica*, representing what could have been the ancestor of *Eugymnanthea japonica*, is divided into the four forms that are parapatrically distributed, changing their morphology of the earliest matured medusae step by step (Kubota, 1992a, 1997, 1999). The medusa of *Eutima japonica* was also collected in the central part of the north Pacific (Kramp, 1965), Cochin Backwater, India (Santhakumari *et al.*, 1971), and in the Jiulong River estuary near Amoy, China (Zhenzu and Jiachi, 1983). It was never found in the east coasts of the Pacific, from where no bivalve-inhabiting hydrozoans have been recorded yet, in spite of recent surveys conducted in Central and Southern California, USA (Kubota, unpublished data). It is assumed that the water temperature is too low for this group to settle, since the coasts are usually washed by cold currents.

Some planktonic *Eutima* species have been described from the Mediterranean Sea (Boero and Bouillon, 1993; Fig. 1), but ancestral-like bivalve-inhabiting *Eutima* have not been found, even in recent surveys carried out in Italy, Croatia and Spain (Kubota, unpublished data). However, in the west coasts of the Atlantic Ocean, in both northern and southern hemisphere, bivalve-inhabiting *Eutima* have been reported (Mattox and Crowell, 1951; Narchi and Hebling, 1975; Kubota and Larson, 1990; Kubota *et al.*, unpublished data), though *Eugymnanthea* has not been recorded from this region.

TABLE 2. – Parallel evolutionary processes (1-3) producing the bivalve-inhabiting hydrozoans, showing some extant representatives. (1) Decrease of number of statocysts and tentacles; (2) Evolution of sucker-like hydrorhiza and disappearance of periderm; (3) Evolution of eumedusoids; * *Eirene hexanemalis* is another possibility.

Region (Oceans and their marginal seas)	Existence of ancestral-like free-living <i>Eirene</i>	Evolution of free-living <i>Eutima</i>	Evolution of bivalve-inhabiting <i>Eutima</i>	Evolution of derivative <i>Eugymnanthea</i> by progenesis
Atlantic Pacific	<i>Eirene lactea</i> <i>Eirene menoni</i> *	(1) <i>Eutima mira</i> (1) ?	(2) <i>Eutima sapinhoa</i> (2) <i>Eutima japonica</i>	(3) <i>Eugymnanthea inquilina</i> (3) <i>Eugymnanthea japonica</i>

The evolution of the most derived bivalve-inhabiting hydrozoan *Eugymnanthea*

From the free-living, colonial *Eutima*, the solitary, bivalve-inhabiting hydroid evolved without drastic modification of the medusa stage, and appeared as a specialized, distinct member in the Eirenidae as mentioned above. The hydrorhiza changed into a sucker-like structure from the stolon in order to attach to the surface of the living, soft body portions of the bivalve hosts. The periderm disappeared in these hydroids in relation to the endosymbiotic life within the mantle cavity of the hosts (Table 2: 2). Such an evolution occurred parallelly both in the Atlantic Ocean and in the Pacific and their marginal seas, producing primitive bivalve-inhabiting *Eutima* (Kubota, 1987, 1991). In the Pacific, a different hydroid morphotype, i.e. a branched, solitary one with hydrorhiza penetrating into the host tissues, appeared in specialised wood-boring host bivalves (Santhakumari and Balakrishnan Nair, 1969; Ramachandra *et al.*, 1974; Kalyanasundaram, 1975). The medusae of this species were recorded from the Cocin Backwater, India, where the hydroids were also recorded (Santhakumari, 1970), Bombay harbour, India (Santhakumari, *et al.*, 1971, 1977), and the Red Sea (Schmidt, 1973). Including *E. commensalis* Santhakumari, 1970, all the bivalve-inhabiting *Eutima* in the Pacific possess cirri in the medusa stage, contrary to the bivalve-inhabiting *Eutima* in the Atlantic Ocean (Kubota, 1987; Kubota and Larson, 1990; Kubota *et al.*, unpublished data).

Boero *et al.* (1996) hypothesized another possible origin of bivalve-inhabiting *Eutima*, i.e. from a free-living, solitary, planktonic eirenid hydroid resembling *Eirene hexanemalis* (Goette) (see Bouillon, 1983). Such floating hydroids are rare at present and the only other species with this feature is *Zelounies estrambourdi* (see Gravier-Bonnet, 1992). It is possible that both types of ancestral-like hydrozoans produced independently the special

hydrorhizas for the endosymbiotic life with bivalves. The invasive developmental stage of the bivalve-inhabiting hydrozoans is a solitary planula, therefore a particular ability of this larva to settle on the living tissues of bivalves, which are often covered by a mucous layer and moving cilia, should be acquired. However, this was accomplished during the course of evolution of this group like other endosymbiotic hydrozoans with ascidians, *Ascidio-clava* (see Kubota and Yamada, 1988) or with bryozoans (Boero *et al.*, 2000).

From the bivalve-inhabiting hydrozoans with sucker-like hydrorhiza, *Eugymnanthea*-like species evolved independently by progenesis, at least in the northern hemisphere of the Pacific and of the Atlantic Ocean and its marginal seas, appearing as the most derived and aberrant thecate hydrozoans (Table 2: 3). These hydroids produce eumedusoids without marginal tentacles and ordinary manubrium that go out from the mantle cavity of the hosts to quickly spawn in the sea (Palombi, 1935; Kubota, 1996). Their life span is short and all life is spent near the host. No bivalve-inhabiting hydrozoans producing sporosacs have been found, but at low temperature *Eugymnanthea* eumedusoids are not released (cf. Kubota, 1979, 1987).

According to Boero and Bouillon (1993), among the members of the Mediterranean hydromedusae with hydroid stage, the Indo-Pacific element is not abundant, i.e. only 28 species (8.0 %) out of 346. This geographical element is thought to be originated by the migration through the Suez Canal (the Lessepsian migration). However, the genus *Eugymnanthea* can not be included into this zoogeographical element, and the Mediterranean *Eugymnanthea* is considered as endemic by Boero and Bouillon (1993). The origin of the Mediterranean-endemic element is ascribed to essentially three causes: the relict of the Tethys Sea fauna; speciation from species that colonised the basin after the Messinian crisis; ‘false endemics’ due to lack of knowledge of zoogeographical and/or taxonomic informations.

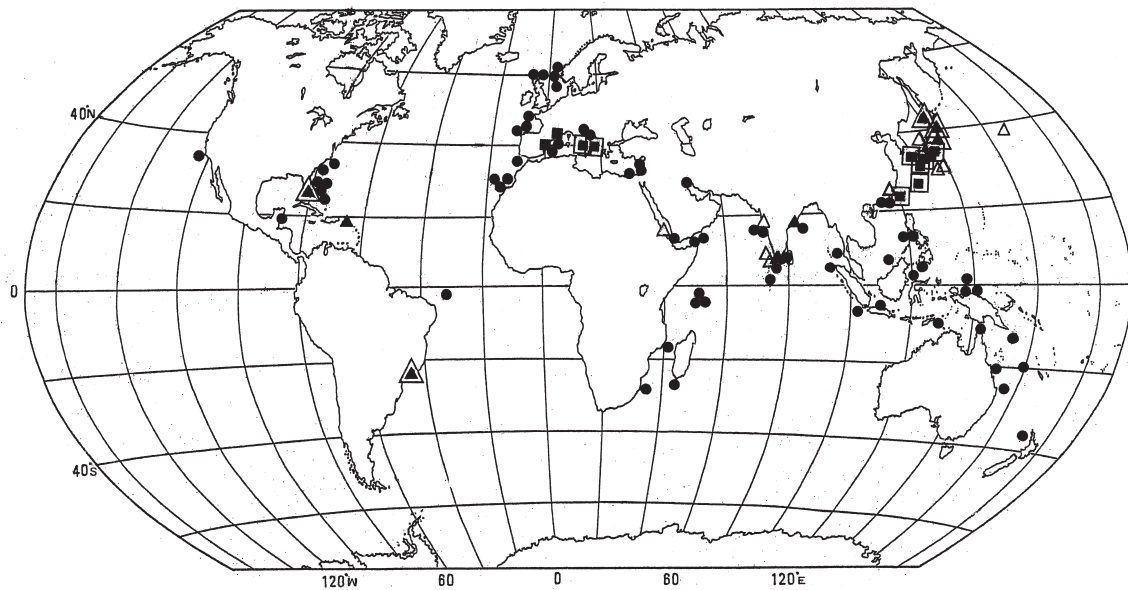


FIG. 1. – Geographical distribution of planktonic medusae of bivalve-inhabiting *Eutima* (*E. japonica* and *E. commensalis*: open triangles), hydroids of bivalve-inhabiting *Eutima* (at least 4 species: closed triangles), hydroids of *Eugymnanthea* (2 species: closed rectangles), and planktonic extant *Eutima* medusae (closed circles: after many references, but not cited everyone and confer van der Spoel, 1996). Doublefold symbols indicate mature medusae of the bivalve-inhabiting hydroids are known by culture.

However, the origin of the Mediterranean *Eugymnanthea inquilina* is entirely unknown. An ancestral type of bivalve-inhabiting hydrozoans, corresponding to the Pacific *Eutima japonica*, has not been discovered in the Mediterranean and also in the east coast of the Atlantic Ocean.

Deduced from the geographical distributions of the bivalve-inhabiting hydrozoans and all the known extant *Eutima* species, the above-mentioned processes of the parallel, paedomorphic evolution occurred in the marginal regions of the distributed area of the ancestral-like *Eutima* species (Fig. 1), although there is a problem that most of the hydroid stages of the extant *Eutima* are still unknown (Table 2). The center of origin of the leptomedusae, the Indo-Malayan region pointed out by van der Spoel (1991, 1996), may not be a suitable location to promote the progenetic evolution leading to the production of *Eugymnanthea* and there are no records of this genus in this region (Kubota, unpublished data; Ho, pers. comm.). Kubota (1987) speculated that this convergent evolution was induced in the Pacific and the Atlantic Oceans and their marginal seas by climatic changes, i.e. cool and/or cold environment in the Pleistocene. If this progenetic evolution produced identical morphological forms of *Eugymnanthea* in two or more different remote places, as the mosaic evolution of the hydrozoans often takes place in different taxonomic groups (Boero and Bouillon, 1987; Petersen, 1990), we deduce the origin of the

Pacific *Eugymnanthea* as a mere introduction from the Mediterranean Sea together with its host *Mytilus edulis galloprovincialis*.

***Eugymnanthea*, together with at least bivalve-inhabiting *Eutima*, could be merged into the one same genus**

The genus *Eugymnanthea* is traditionally defined on morphology (Bouillon, 1985, 1994). If the above-mentioned origin of this genus in the Eirenidae is demonstrated, then a taxonomic problem related to phylogeny turns out. General evolutionary processes producing bivalve-inhabiting *Eutima* and *Eugymnanthea* are acceptable, and the phylogenetic tree is depicted as shown in Fig. 2A (Kubota, 1983; Boero, Bouillon and Piraino, 1996). This phylogeny does not conflict to the hypotheses of the Tethys Sea relict and the species introduction, and no taxonomic problems turn out from this tree. However, in the case of parallel evolution a more precise phylogenetic tree is shown in Fig. 2B. In this tree the bivalve-inhabiting *Eugymnanthea* appeared as a polyphyletic genus. Taxonomic treatment of assigning all the bivalve-inhabiting *Eutima* and *Eugymnanthea* into the one genus is, therefore, reasonable. In this paper, however, formal taxonomic changes according to the international nomenclatural rules are not made until more biological studies are made and we confirm the origin of *Eugymnanthea* (Kubota *et al.*, in prep.).

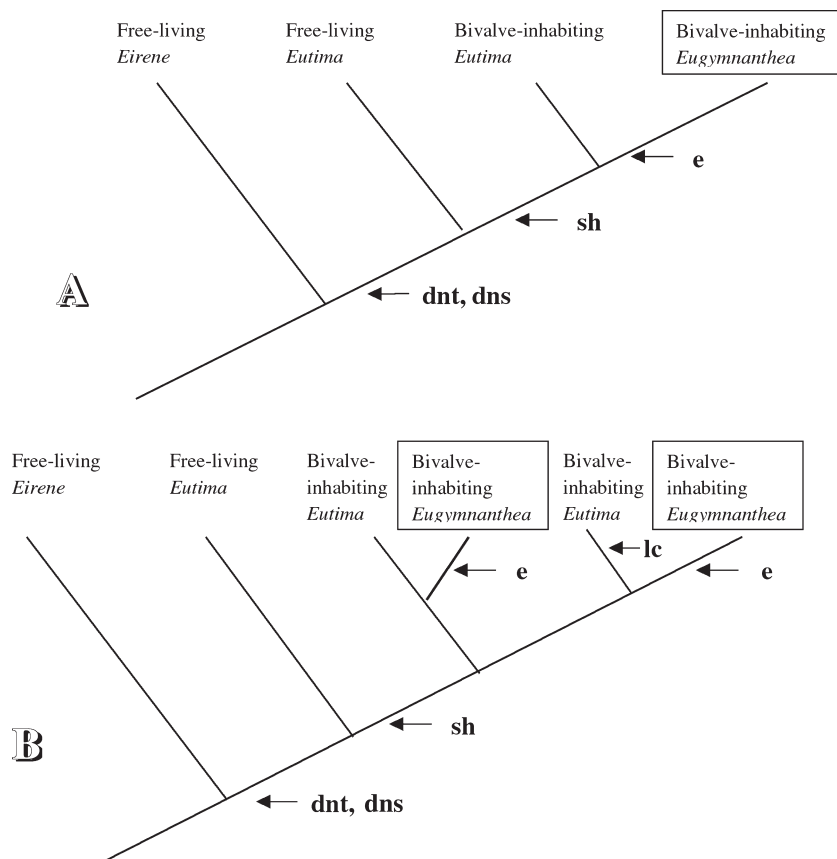


FIG. 2. – A: Phylogenetic tree showing general evolutionary courses of the bivalve-inhabiting hydrozoans in Eirenidae. B: Phylogenetic tree showing bivalve-inhabiting *Eugymnanthea* originated by parallel, progenetic evolution, resulting polyphyly. dns: decrease of the number of statocysts, dnt: decrease of the number of tentacles, e: production of eumedusoid, sh: production of sucker-like hydrorhiza, lc: loss of cirri.

It is generally admitted that the metagenic hydrozoans like bivalve-inhabiting ones are difficult to manage to establish an appropriate classification (Kubota, 1983; Boero and Bouillon, 1987). In the athecate groups producing eumedusoids, Petersen (1990) pointed out that production of either fixed gonophores or of eumedusoids is not a key character to define genera. Convergent evolution producing eumedusoids took place in many branches of diverse taxonomic groups. The same conclusion was obtained by a molecular approach on the Hydractiidae by Cunningham and Buss (1993). Therefore, similar studies are needed for bivalve-inhabiting hydrozoans, and they will shed light in the phylogeny and taxonomy of this group.

The phylogeny of Eirenidae, a family comprising 12 genera (Bouillon, 1985, 1994), is not easy mainly due to lack of knowledge of life cycles. Bouillon (1985) considered the related hydrozoans to the Eirenidae are Lovenellidae, Eucheilotidae and Cirrholoveniidae, therefore all these hydrozoans should be taken into account to clarify the

phylogeny of the present group. Much care is needed to select outgroups since such choices greatly change the resultant phylogenies, as pointed out by Boero *et al.* (1997).

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