

Global diversity of large branchiopods (Crustacea: Branchiopoda) in freshwater

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Abstract With about 500 known species worldwide, the large brachiopods are a relatively small group of primitive crustaceans. With few exceptions they live in temporary aquatic systems that are most abundant in arid and semi arid areas. As many regions remain unexplored and as especially the number of species in clam shrimps and tadpole

shrimps is underestimated due to difficult identification, the species list will increase with future surveys. The Branchiopoda are monophyletic, but inter-ordinal relationships, as well as many evolutionary relationships at lower taxonomic levels are still unclear. Ongoing molecular studies will more accurately depict species diversity and phylogenetic patterns. With the exception of some anostracan families, most families are not restricted to the northern or southern hemisphere or specific zoogeographical regions. Large branchiopods are used for the assessment of the quality and function of temporary wetlands. Due to the reduction in number and quality of temporary wetlands, several species became endangered and are red listed by the IUCN.

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Introduction

The crustacean class Branchiopoda (clam shrimp (Spinicaudata, Laevicaudata, and Cyclotherida), tadpole shrimp (Notostraca), and cladocerans [=Phyllopora] plus fairy shrimp [=Anostraca]) is a morphologically diverse group of ecologically important, largely freshwater organisms that has a fossil record extending back to the Upper Cambrian (Walossek, 1993). Breeding systems within the class

are highly varied, including dioecy, androdioecy, parthenogenesis, and cyclic parthenogenesis (Sassaman, 1995; Weeks et al., 2006a, b). Branchiopoda without cladocerans are commonly known as the “large branchiopods.”

Most large branchiopod species rely on seasonal wetlands such as playas, vernal (rain and snow-melt) pools, salt flats, and alkali pans, while other species occur in permanent playas, fishless alkali lakes, and salt lakes (Dumont & Negrea, 2002). These habitats are, for the most part, seasonal pools that are dry for a significant portion of the year, or several years (Dumont & Negrea, 2002).

The vast majority of anostracans are omnivorous filter feeders, indiscriminately filtering particles from the water column with their continually beating

thoracopods (Brendonck, 1993a, b). A few species are predators on rotifers, copepods, cladocerans, and other Anostraca (Boudrias & Pires, 2002; Rogers et al., 2006). The tadpole shrimp are predominantly benthic and omnivorous, feeding on detritus and living or dead organisms (Martin, 1992). Clam shrimp typically feed nonselectively on detritus and algae in suspension (Belk, 1982).

Branchiopod crustaceans rely on banks of resting eggs (or “cysts;” Fig. 1) to bridge periods of drought or frost (Brendonck, 1996) and to buffer against the effects of environmental variability. The eggs lay dormant in the substrate until the pool dries and refills during the subsequent rains. In the temporally fluctuating environment of temporary aquatic habitats, usually only part of the dormant eggs, if any,

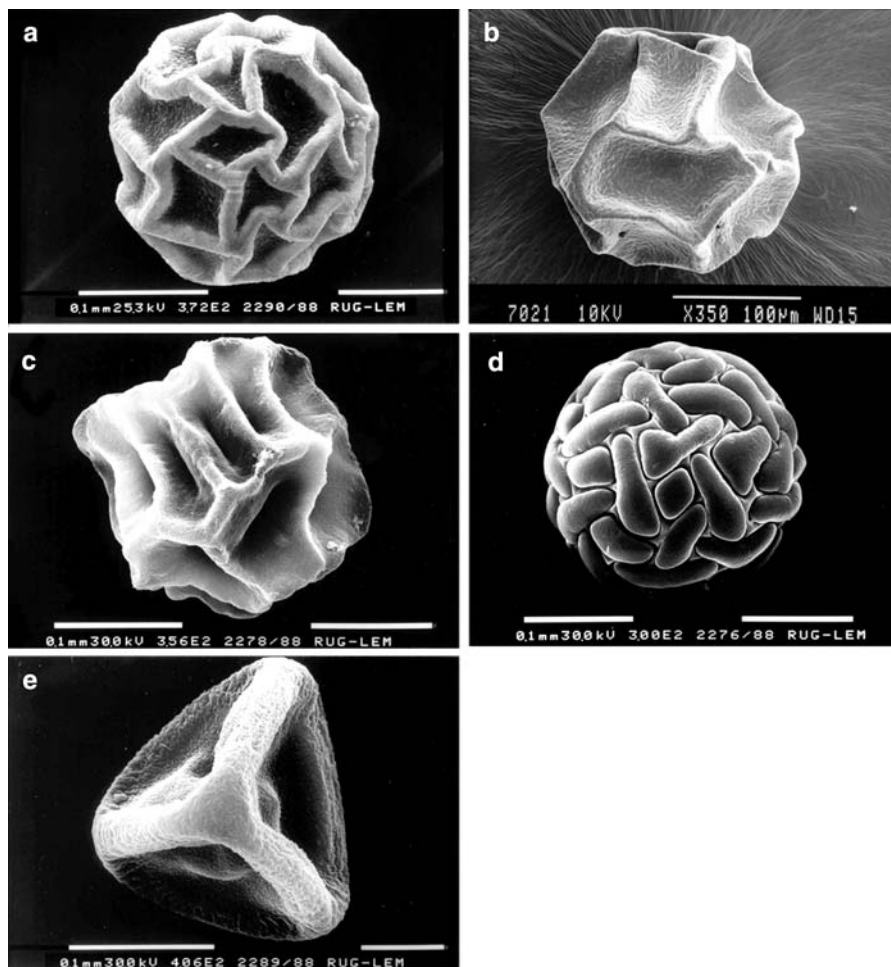


Fig. 1 Various large branchiopod egg morphology: (a) *Streptocephalus proboscideus* (Anostraca); (b) *Streptocephalus indistinctus* (Anostraca); (c) *Eulimnadia cylindrova* (Spinicaudata); (d) *Streptocephalus ovamboensis* (Anostraca), (e) *Streptocephalus zuluensis* (Anostraca)

hatches during each fill (Hildrew, 1985; Brendonck et al., 1998). This process can lead to the generation of an egg bank that can remain viable for decades or possibly centuries without re-hydration (Belk, 1998), and can harbor potentially great genetic and species diversity (Ellner & Hairston, 1994). The external morphology (shape and ornamentation; Fig. 1) of eggs is an important taxonomic tool (Mura, 1986; Belk, 1989; Martin, 1989; Martin & Belk, 1989; Brendonck et al., 1992; Brendonck & Coomans, 1994a, b). In many cases this allows the assessment of the temporary pool communities even when no water is present.

Large branchiopod crustaceans are arguably the least known of all macroscopic invertebrates in temporary inland waters even though they are the flagship group for these ecosystems and for temporary pool invertebrates in general (Colburn, 2004).

Species/generic diversity

In many areas of the world, the diversity, species composition, and conservation status of large branchiopods remain largely unknown. We therefore expect to discover and describe many new taxa in these largely unexplored areas (e.g., South America, northern, western and eastern Africa, Western Australia, and Asia).

Anostraca

Anostracans (Fig. 2a) are elongated crustaceans, which lack a carapace and are constantly swimming on their backs in the water column. The Anostraca are by far the most taxonomically diverse group at all levels (Tables 1, 2). There are ~300 species on all continents (including Antarctica; Belk & Brtek, 1995, 1997; Dumont & Negrea, 2002), currently arranged in 26 genera and eight families (Tables 1, 2; Weekers et al., 2002; Rogers, 2002b, 2006). Nearly 1/4 of these species are known only from the type localities, or from <3 localities (Belk & Brtek, 1995, 1997). Additionally, there are ~20 undescribed species and at least one undescribed genus.

Typically, anostracan species are differentiated based upon the form and ornamentation of the male second antennae, which are modified into large

claspers to grasp the female during copulation (Rogers, 2002a). Linder (1941) demonstrated the importance of copulatory structures, especially the male genitalia, in defining genera. Starting from this base, Belk (1991, 1995), Brendonck (1995), Brendonck & Belk (1997), and Rogers (2002b, 2006) established genital morphology as the defining criteria for anostracan genera. To date, most of the taxonomy and phylogeny has been based on the morphology of these antennal and genital characters.

Notostraca

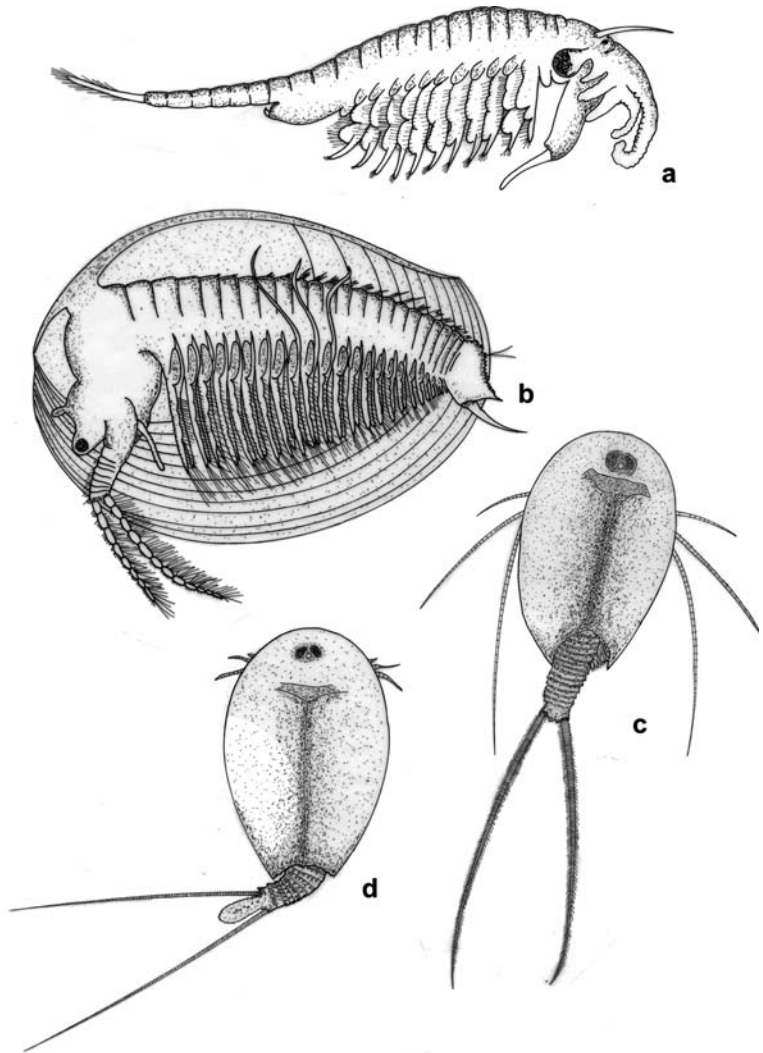
The order Notostraca (tadpole shrimp; Fig. 2c, d) is composed of the family Triopsidae and includes two genera (*Triops* Schrank, 1803 and *Lepidurus* Leach, 1819; Tables 1, 2) of “living fossils” which have undergone minimal gross morphological change since their divergence over 250 million years ago (Longhurst, 1955).

The Notostraca exhibit plasticity in external morphology, making the demarcation of species on this basis a difficult task (Rogers, 2001). The absence of well-defined criteria allowed taxonomists to describe many ‘new species’ in such a way that the nominal species of *Triops* and *Lepidurus* amounted to more than 70 in the 1950s (Longhurst, 1955). Linder (1952) and Longhurst (1955) reviewed the alpha taxonomy of the Notostraca and recognized only about 11 species with a wide geographic distribution. Until recently, this classification was extensively used “even attaining the status of dogma” (Sassaman et al., 1997). However, the genetic and molecular studies of Sassaman et al. (1997), Suno-Uchi et al. (1997), King & Hanner (1998), and Murugan et al. (2002) have demonstrated that Linder’s and Longhurst’s classifications have long obscured understanding of the real species-level diversity of the Notostraca.

Notostracan systematics is further complicated by the discovery of different modes of reproduction (Sassaman & Weeks, 1993; Sassaman, 1995). The determination of the mode of reproduction is important for the understanding of the variety of species.

Suno-Uchi et al. (1997) studied the three morpho-species *Triops cancriformis*, *T. granarius*, and *T. longicaudatus* from Japan, analyzing a segment of the mt16S rRNA gene. They proposed that there

Fig. 2 Habitus of large branchiopods: (a) adult male *Chirocephalus diaphanus* (Anostraca), (b) adult *Limnadia lenticularis* (Spinicaudata), (c) adult *Triops cancriformis* (Notostraca), (d) adult *Lepidurus apus* (Notostraca). (Drawings from: Brendonck, 1989)



are four, not three, phylogenetic species. King & Hanner (1998) studied a fragment of the mt12S rRNA gene in four nominal species of *Lepidurus* from Canada and the USA, and deduced that there are five, not four, reproductively isolated species, one of them recently described (Rogers, 2001). Using the mt12S- and mt16S rRNA genes, Murugan et al. (2002) studied five *Triops* populations from México and explored the phylogeny of the genus. Analysis of mt12S rDNA data was in agreement with previous allozyme studies (Sassaman et al., 1997), and showed the nominal (morphological) species *T. longicaudatus* to be a mixture of several species such that, of the seven *Triops* American populations studied, six phylogenetic species can be identified. These

molecular data, contrary to a phylogenetic proposal based on morphology (Maeda-Martínez et al., 2000), also indicated that two morphologically and reproductively divergent forms can be grouped into a single monophyletic clade, and that the Old World species *T. cancriformis* may represent a lineage that is independent from other species in that genus (Murugan et al., 2002).

Spinicaudata, Laevicaudata, and Cycletherida

These small, freshwater crustaceans have laterally compressed bodies enclosed by a bivalved carapace (Fig. 2b). Although clam shrimp are common

Table 1 Species ^a distribution of Anostraca, Notostraca, Spinicaudata and Laevicaudata per family in zoogeographic regions

	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Anostraca ^a	110	64	33	56	11	48	1	1	307
Artemiidae	6	3	2	1	1	1	1	0	9
Parartemiidae	0	0	0	0	0	13+	0	0	13
Branchinectidae	6	24	15	0	0	0	0	1	45
Thamnocephalidae	5	6	16	4	2	32	0	0	62
Streptocephalidae	16	15	0	24	7	2	0	0	56
Branchipodidae	9	0	0	26		0	0	0	35
Tanymastigitidae	8	0	0	0	0	0	0	0	8
Chirocephalidae	61	16	0	1	1	0	0	0	81
Notostraca ^a	7	7	2	1	2	2	0	0	15
Triopsidae	7	7	2	1	2	2	0	0	15
Spinicaudata ^a	~50	~15	~13	~20	~30	23	1	0	~150
Cyzicidae	~20	6	2	~7	~10	10	0	0	~90
Leptestheriidae	~15	1	~5	~8	~3	0	0	0	~37
Limnadiidae	~15	~10	~10	~10	~12	13	1	0	~55
Laevicaudata	8	7	13	4	4	2	0	0	36
Lynceidae	8	7	13	4	4	2	0	0	36

PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian; PAC, Pacific Oceanic Islands; ANT, Antarctic

^a Several taxa are known from more than one region

Table 2 Genus distribution of Anostraca, Notostraca, Spinicaudata and Laevicaudata per family in zoogeographic regions

	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Anostraca	16	11	10	6	6	4	1	1	26
Artemiidae	1	1	1	1	1	1	1	0	1
Parartemiidae	0	0	0	0	0	1	0	0	1
Branchinectidae	1	1	0	1	0	0	0	1	1
Thamnocephalidae	2	3	3	4	2	1	0	0	6
Streptocephalidae	1	1	1	0	1	1	0	0	1
Branchipodidae	2	0	4	0	1	0	0	0	5
Tanymastigitidae	2	0	0	0	0	0	0	0	2
Chirocephalidae	7	5	1	0	1	0	0	0	9
Notostraca	2	2	1	2	1	2	0	0	2
Triopsidae	2	2	1	2	1	2	0	0	2
Spinicaudata	9	5	5	4	6	5	1	0	12
Cyzicidae	3	2	2	1	3	2	0	0	4
Leptestheriidae	3	1	1	1	1	0	0	0	3
Limnadiidae	3	2	2	2	2	3	1	0	5
Laevicaudata	1	2	2	2	1	1	0	0	3
Lynceidae	1	2	2	2	1	1	0	0	3

PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian; PAC, Pacific Oceanic Islands; ANT, Antarctic

worldwide, they have not been the subjects of intense study. A few investigations have assessed their genetics (Duff et al., 2004), phylogeny and biogeography (Hoeh et al., 2006), and reproductive biology (Weeks et al., 2005, 2006a, b; Scanabissi et al., 2006), but most attention has been devoted to the morphological systematics of these animals and ~116 species are currently recognized. The three orders consist of five extant families and 19 genera (Tables 1, 2). Traditionally the genus *Cyclestheria* was considered to be part of the Spinicaudata, but Olesen (1998) and Spears and Abele (2000) suggested that spinicaudatans are paraphyletic, with respect to the Cladocera.

The systematics within the Spinicaudata has been problematic for centuries, and the principal difficulties are still far from being resolved. Presently, the Spinicaudata is subdivided into three families (Martin & Davis, 2001) (Tables 1, 2), but the monophyly of two of these (Cyzicidae and Leptestheridae) is highly uncertain (the monophyly of the third, Limnadiidae, is strongly supported; Hoeh et al., 2006). Similar problems can be found at both the genus and species levels in all three families. Spinicaudatans are well known for showing great ‘morphological plasticity’ making species identification exceptionally difficult in some taxa. The usual problems of poor descriptions and lack of type material add to the difficulties.

Belk (1989) re-emphasized the importance of the morphology of the outer covering of the desiccated resting eggs as a taxonomic character.

Phylogeny

The monophyly of the Branchiopoda has been strongly supported by recent phylogenetic analyses (e.g., Spears & Abele, 2000) but inter-ordinal relationships within the Phyllopoda, as well as many evolutionary relationships at lower taxonomic levels throughout the class, have not been clearly elucidated (e.g., Braband et al., 2002).

In last decades there were interesting rearrangements in the systematics of higher taxa of the Branchiopoda (Fryer, 1987; Walossek, 1993; Martin & Cash-Clark, 1995). Clam shrimps, formerly thought to be one order (the “Conchostraca”), have turned out to be paraphyletic with respect to the Cladocera (the water fleas; Olesen, 1998; Spears &

Abele, 2000; Braband et al., 2002), and probably also with respect to the Notostraca (tadpole shrimps; Stenderup et al., 2006). The “Conchostraca” are now divided into the Laevicaudata and the Spinicaudata (Fig. 2b) and the Cyclestherida.

Information on phylogenetic relationships in large branchiopods is most advanced, but still fragmentary in anostracans. The anostracan family Streptocephalidae has been subjected to morphological (Hamer et al., 1994a, b) and morphological-cladistic analyses (Maeda-Martínez et al., 1995a, b). To date there are only 5 phylogenetic studies using molecular data that focused on the Anostraca: *Branchinella* (Remigio et al., 2003), *Parartemia* (Remigio et al., 2001), *Streptocephalus* (Daniels et al., 2004), and two studies attempting to resolve familial relationships (Remigio & Hebert, 2000; Weekers et al., 2002) with one study focusing on the ordinal relationships (de Waard et al., 2006). These studies generated more questions about the relationships between the genera (Rogers, 2002b; Weekers et al., 2002).

Present distribution and main areas of endemism

Large branchiopods have a worldwide distribution (Fig. 3), including the polar areas (e.g., the anostracan *Branchinecta gaini* is rather widespread on the antarctic peninsula), but reach their maximum abundance and species richness in steppes and deserts, where temporary water bodies abound. The vast majority of species are fresh-water; however some species of *Branchinella*, *Streptocephalus*, and *Thamnocephalus*, as well as all species of *Parartemia* and *Artemia*, live in inland saline waters.

Family, generic, and species diversity of large branchiopods at the level of the main zoogeographical areas are presented in Tables 1 and 2. Some anostracan families are endemic to only one of the areas such as Parartemiidae to Australasia and Tanyastigitidae (Anostraca) to the Palearctic. Notostracan and clam shrimp families are always distributed over at least one of the zoogeographical areas. Except for the former families, not one is entirely restricted to the southern or northern hemisphere, which would reflect a Gondwanaland or Laurasia origin, respectively.

Some clam shrimp genera like *Cyzicus* and *Eocyclus* appear to be Laurasian, with their current

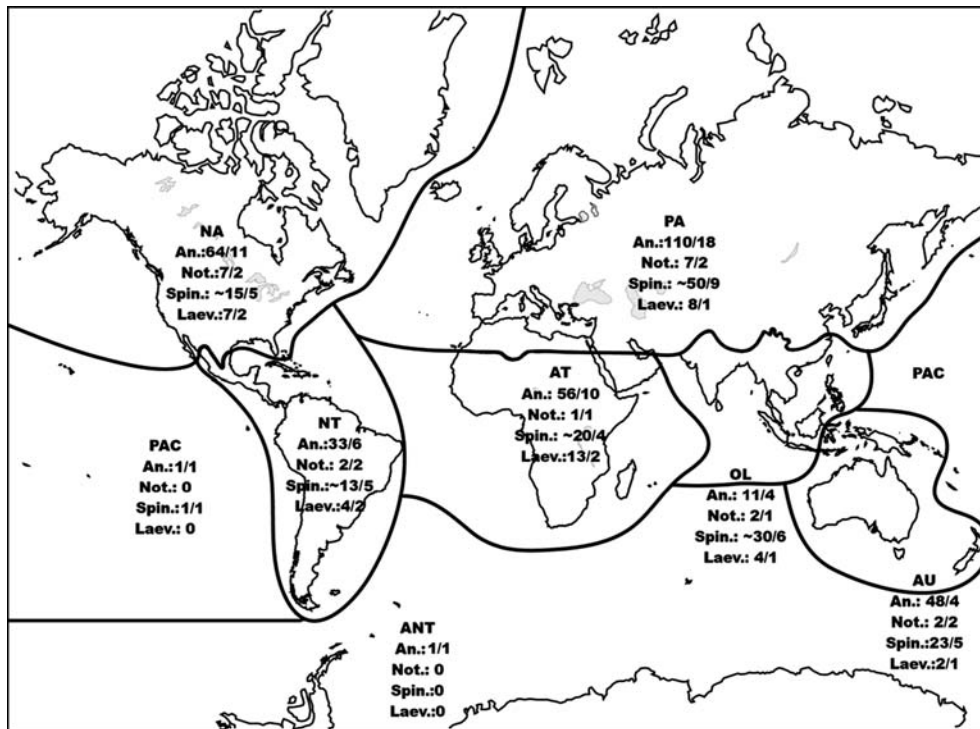


Fig. 3 Species and genus diversity of Anostraca (An), Notostraca (Not), Spinicaudata (Spin) and Laevicaudata (Laev) in each of the seven zoogeographical regions. PA, Palearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian; PAC, Pacific Oceanic Islands; ANT, Antarctic

ranges encompassing Eurasia, Africa, and North America. The genus *Lepthesteriella*, in contrast, seems Gondwanian, and occurs in Africa, Madagascar, and Asia. Lynceids are cosmopolitan, save in Antarctica. *Cyclestheria hislopi* (if representing only one species, which is uncertain) is pantropical.

Human related issues

Worldwide changes in land use, brought about mainly by agriculture and urbanization, has led to a global loss and deterioration of temporary pools. It has been estimated that during the post-war period in England, nearly 40% of ephemeral ponds have disappeared, which is a rate loss of ~1% per year. Several studies indicate a loss of between 50% and 90% of original Californian vernal pools (Bauder, 1986). For most regions of the world, and especially the developing countries, no such figures are available, but are likely to be as dramatic, due to

uncontrolled spraying with insecticides, mining, and agricultural activities (Brendonck & Williams, 2000).

Large branchiopods are used in the United States for assessment of ephemeral wetland habitat functions and values (Rogers, 1998), and five US species are currently listed as threatened or endangered in California and Oregon. Another anostracan species has been petitioned for federal endangered status and is protected as a “rare, threatened or endangered species” under the California Environmental Quality Act. Another species was proposed for federal listing in the state of Georgia, four species are proposed for endangered species status in New Mexico, one species is listed as vulnerable in Australia, and one in Brazil. About 32 large branchiopod species are red listed by the IUCN (IUCN, 2000). Furthermore, the world’s first large branchiopod preserve has been developed in Austria (Eder & Hödl, 2002) protecting the anostracan *Chirocephalus shadini*. Five of the six endangered fairy shrimp in California are endemic to that state, and were only discovered since 1990.

Some large branchiopod species are important economically, including species that are: harvested for aquaculture (*Artemia* spp.), for applications in aquatic toxicology (Brendonck & Persoone, 1993), for human consumption (*Streptocephalus sirindhornae*), or as pets (“Sea Monkeys” *Artemia “nyos”*) (Sanoamuang et al., 2000).

Some *Triops* forms (Notostraca) are pests in rice fields in at least seven countries on four continents (Grigarick et al., 1961). Alternatively, these shrimp have been used to control weeds in rice fields of Japan (Takahashi, 1977), and also have been proposed as a biological control agent of mosquitoes (Tietze & Mulla, 1991). Given their rapid growth, early maturation, and uniparental reproduction via resting eggs, two *Triops* forms are being studied for their potential use in aquaculture (Obregón-Barboza et al., 2001).

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