Crustacea: non-cladoceran Branchiopoda

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INTRODUCTION

Branchiopod crustaceans are common inhabitants of temporary pools throughout the world. They are often divided by workers into the cladocerans (sometimes treated as the order Cladocera; see Martin and Davis 2001, for discussions on the classification of the cladoceran groups) and the non-cladoceran large branchiopods. This artificial division is unfortunate. It masks the large size that some cladocerans can attain, as well as giving the impression that the large branchiopods (traditionally, the orders Anostraca, Notostraca, and Conchostraca; Fig. 1, Table 1) are somehow more closely related to each other than they are to any of the cladoceran groups. The truth is that relationships within the Branchiopoda are still poorly understood, and division of the group into large branchiopods and smaller ones (cladocerans) is an obviously artificial grouping of convenience by those who work on the groups.

Few branchiopods have been reported from Southeast Asia (defined by us as including Myanmar, Thailand, Cambodia, Laos, Vietnam, Malaysia, Singapore, Indonesia, Timor-Leste, and the Philippines). No large branchiopods were reported from Malaysia prior to a recent report (Martin *et al*. 2003) of the clam shrimp species *Cyclestheria hislopi* (family Cyclestheriidae) from tin mine lakes in the vicinity of Kuala Lumpur. However, large branchiopods in general are widely distributed, and it is reasonable to expect that additional species might occur in Malaysia.

ORDER ANOSTRACA

INTRODUCTION

Anostracans, commonly called fairy shrimp or brine shrimp, are easily recognizable crustaceans that are often presumed to be primitive. The body is elongate and divided into three recognizable sections or tagmata: the head, the thorax (bearing the phyllopodous limbs and the genitalia), and the limbless abdomen (Figs. 1B, 2A). They lack a carapace, although it has been argued that a headshield is recognizable early in development (see discussion in Martin 1992). There are 19 to 27 postcephalic

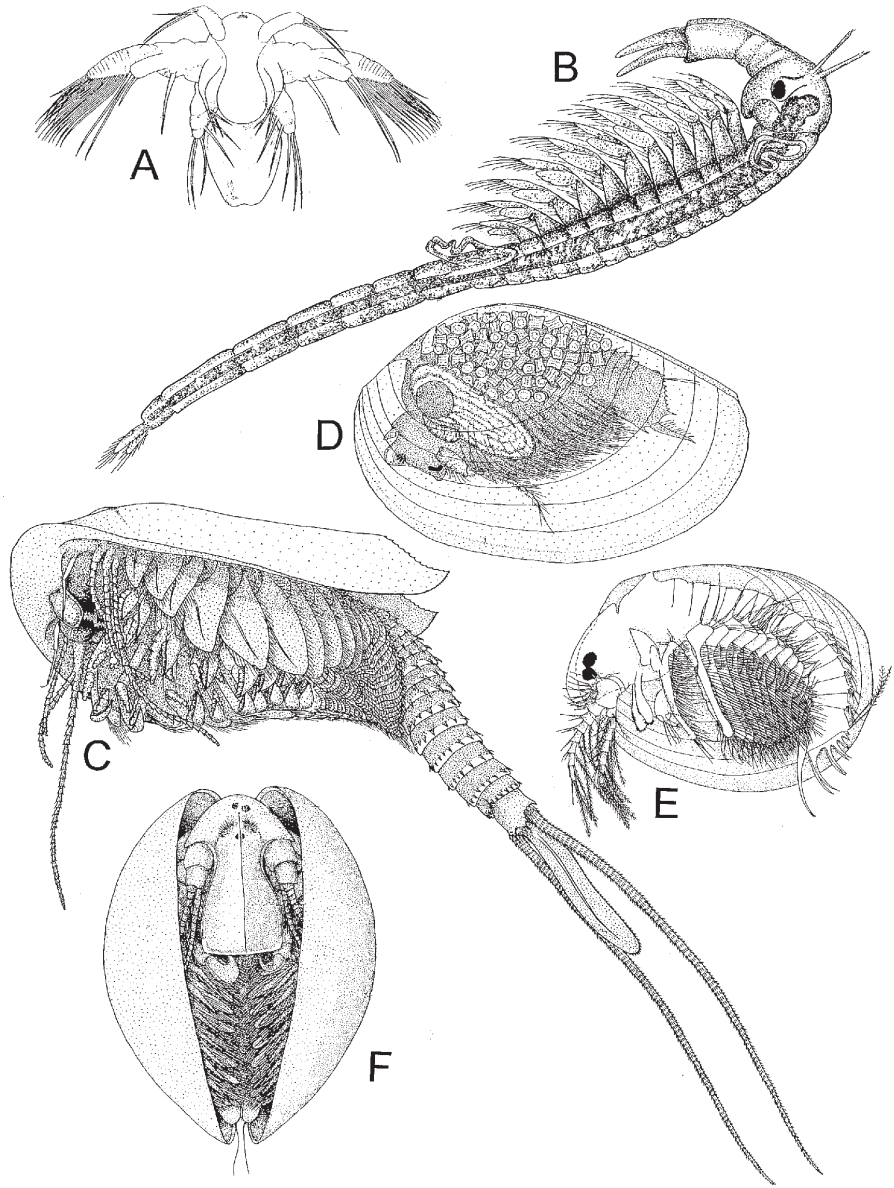

Figure 1. A – fairly typical branchiopod nauplius larva, the first stage nauplius larva of the anostracan *Branchinecta ferox*, ventral view; B – F: representatives from each of the "large branchiopod" groups: B – Anostraca, adult male *Branchinecta*; C – Notostraca, *Lepidurus packardi;* D – Spinicaudata, *Eulimnadia belki*, adult female; E – Cyclestherida, *Cyclestheria hislopi;* F – Laevicaudata, *Lynceus gracilicornis*. Not drawn to scale. (Sources: A, modified after Fryer 1983; B, from Martin 1992, after Sars; C, from Martin 1992–frontispiece; D, after Martin 1989; E, after Olesen *et al*. 1997; F, from Martin *et al*. 1986)

Table 1. Classification of the 'Large Branchiopoda' used in this chapter (after Martin and Davis 2001, with genera added following Martin 1992, and references therein). Relationships among, and classification of, the large branchiopods are uncertain, and the classification presented here is not agreed upon by many workers. See especially Belk (1996), Brtek (1997), Eriksen and Belk (1999), Naganawa (2001a,b).

CLASS BRANCHIOPODA	
Subclass Sarsostraca	
Order Anostraca	
Family Artemiidae	– 1 genus, *Artemia*
Branchinectidae	– 1 genus, *Branchinecta*
Branchipodidae	– 8 genera
Chirocephalidae	– 10 genera
Polyartemiidae	– 2 genera, *Polyartemia*, *Polyartemiella*
Streptocephalidae	– 1 genus, *Streptocephalus*
Thamnocephalidae	– 6 genera
Subclass Phyllopoda	
Order Notostraca	
Family Triopsidae	– 2 genera, *Triops* and *Lepidurus*
Order Diplostraca	
Suborder Laevicaudata	
Family Lynceidae	– 3 genera, *Lynceus*, *Lynceiopsis*, *Paralimnetis*
Suborder Spinicaudata	
Family Cyzicidae	– 4 genera, *Canestheria*, *Caenestheriella*, *Cyzicus*, *Eocyzicus*
Leptestheriidae	– 5 genera
Limnadiidae	– 6 genera
Suborder Cyclestherida	
Family Cyclestheriidae	– 1 genus, *Cyclestheria*
Suborder Cladocera	
(4 infraorders and 10 families, see Silva-Briano and Mirabdullayev 2004)	

body somites. The paired compound eyes are well developed and borne on movable stalks, a condition that is unique in the Branchiopoda. The antennae exhibit extreme sexual dimorphism, and the enlarged male second antenna, used in clasping the female during mating, is a diagnostic systematic feature. Additional distinguishing morphological features are given in Martin (1992). Most individuals are in the 15–30 mm size range as adults, but the group also includes the largest of the branchiopods, the predatory *Branchinecta gigas*, which can reach up to 100 mm long as an adult.

GENERAL BIOLOGY

Anostracans occur worldwide in ephemeral ponds, playa lakes, saline inland bodies of water, and occasionally marine lagoons (Martin 1992). Species are known from ultra-pure fresh waters in tundra habitats to extremely turbid and silt-laden puddles. Most species appear to be filter feeders or deposit feeders, but some are rapacious predators on other species of anostracans.

Life cycle

The typical life cycle of large branchiopods involves males, females, and sexual reproduction, resulting in eggs that may be carried briefly in modified brood pouches but that are eventually shed into the environment (with some exceptions), and a larval stage called a nauplius. This type of life cycle is exhibited by all anostracans. The nauplius larva is small and oval or pear-shaped, with three pairs of appendages (Fig. 1A); additional appendages are added as somites are added during growth. Development in anostracans is thought to be primitive (among branchiopods and among all other crustacean groups) because it is more or less anamorphic, meaning that growth is achieved through the addition of body somites but without any drastic

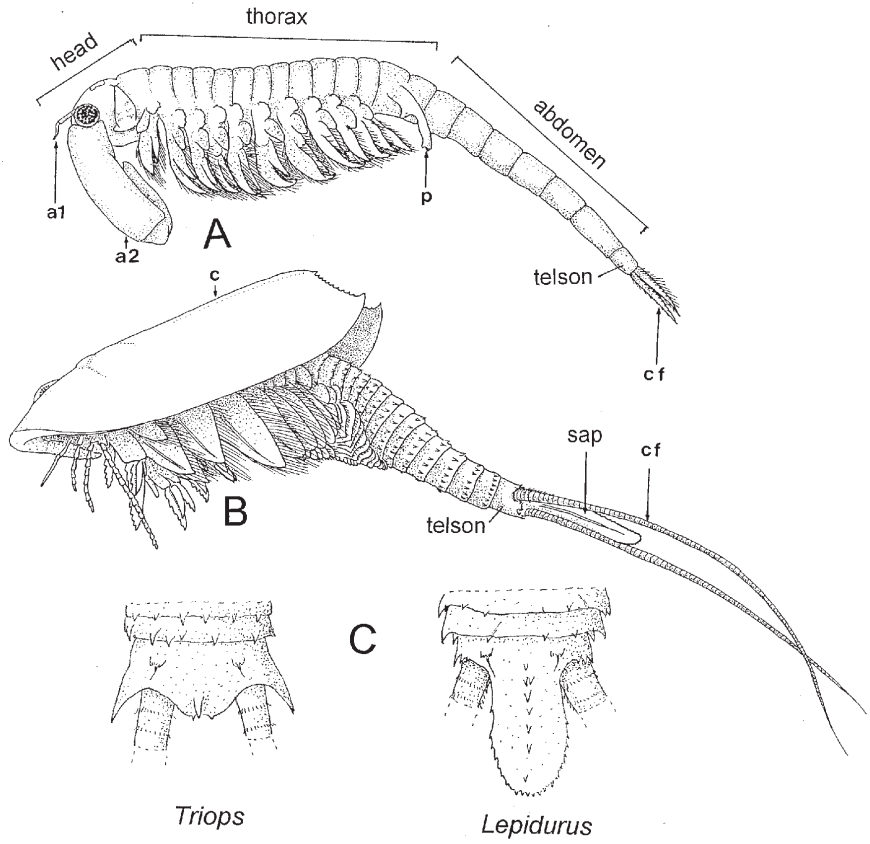

Figure 2. Schematic illustrations of A – a male anostracan (fairy shrimp) (the figure is inverted for purposes of comparison – all anostracans normally swim upside down, with their limbs directed upward) and B– a notostracan (tadpole shrimp). C – comparison of the telson and supra-anal plate of the notostracan genera *Triops* (on left) and *Lepidurus* (on right). Abbreviations: a1, first antenna; a2, second antenna; c, carapace (dorsal shield); cf, caudal furca (cercopods); p, penis. (Sources: A, B, from Martin 1992; C, heavily modified after Linder 1952)

change or metamorphic development. As many as 22 moulting stages (or instars) may occur before adult habits replace naupliar habits (Fryer 1983). Maturation in some species occurs at a size of about 15 mm, although this varies greatly with species. Mating in adult anostracans involves the use of the male's strongly modified second antennae (Fig. 1B, 2A) to grasp and hold the female during copulation. Egg development occurs within elongate brood pouches, the shape of which is often useful in systematic studies. Resting eggs (cysts) may be smooth and spherical or elaborately ornate, or even flattened and disc-shaped (e.g. see Martin 1992); these eggs can withstand dessication and persist in the environment for years until the next rain cycle provides the water that allows them to hatch and begin again. Because they inhabit ephemeral bodies of water, the entire life cycle of some anostracans is amazingly brief, with development, maturation, mating, and egg development sometimes occurring in a span of only a few weeks or less.

REGIONAL TAXA

Records of anostracans in East Asia, reviewed recently by Naganawa and Orgiljanova (2000a,c), are relatively rare. Several species are reported from India (e.g. Radhakrishna and Prasad 1976; Belk and Esparza 1995), Korea, Japan, and eastern China, Russia, and Mongolia, but hardly any from other regions of Asia. One exception is *Branchinella kugenumaensis*, a species that is known from the 'lowlands of south and east Asia, Japan, Korea, China to India' (Belk and Brtek 1995: 324). However, D. Christopher Rogers (pers. comm.) informs us that *B. kugenumaensis* is actually a Japanese species, that the Indian species is *B. madurai* (see also Brendonck and Belk 1997, where the species name is unfortunately misspelled as *maduraiensis*), and that there is a currently undescribed species of *Branchinella* in Thailand. *Branchinecta orientalis* and *Branchipodopsis affinis* were reported from Mongolia by Brtek *et al*. (1984); *B. orientalis* has since been reported from Nepal. There is at least one species of *Streptocephalus* known from Thailand, another species of *Streptocephalus* (possibly introduced) in Myanmar, and another *Streptocephalus* reported from Java, Indonesia (see Sanoamuang *et al*. 2000; Belk and Brtek 1995). Species of *Artemia* have been reported from India, China, Indonesia, Japan, Korea, Sri Lanka, and Taiwan (Battish 1992, Vanhaecke *et al.* 1987), so it would not be surprising to find *Artemia* in Malaysia.

CURRENT TAXONOMY AND KEYS TO IDENTIFICATION

As currently understood, the Anostraca contains seven extant families (e.g. Martin 1992; Belk 1996; Martin and Davis 2001, and Table 1) and over 260 species in about 23 genera worldwide. However, Brtek (1997; see also Brtek and Mura 2000) would recognize two additional families (Linderiellidae and Artemiopsidae). Reasons for not recognizing these families and for treating their genera as members of the Chirocephalidae are discussed in Martin and Davis (2001: 17). Various workers over

the years have recognized different numbers of families, and considerable work remains to be done on the taxonomy and systematics of fairy shrimp. Brtek and Mura (2000) presented keys to the known families and genera but unfortunately used some terms not previously used or defined, which we feel may lead to confusion. Thus, we use a somewhat simpler key (below).

KEY TO FAMILIES OF THE ANOSTRACA

This key is based on a previously unpublished key supplied to us by D. Christopher Rogers, and is restricted to only those families recognized in Martin and Davis (2001). Many of the key characters are illustrated and discussed by Eriksen and Belk (1999) and Brtek and Mura (2000).

1. Seventeen or 19 pairs of legs ..... POLYARTEMIIDAE
- Eleven pairs of legs (eleventh pair may be reduced or absent) 2

2. Two pre-epipodites (may appear as one deeply notched) ..... CHIROCEPHALIDAE
- One pre-epipodite 3

3. Penes directed ventrolaterally, widely separated at the base .... BRANCHINECTIDAE: *Branchinecta*
- Penes directed ventrally, with the bases closely united 4

4. Penes with one or two longitudinal rows of spines 5
- Penes without longitudinal rows of spines 6

5. Male second antennal distal segment shifted laterally, proximal segment with large distal cheliform appendage ..... STREPTOCEPHALIDAE: *Streptocephalus*
- Male second antennal distal segment not shifted laterally ..... THAMNOCEPHALIDAE

6. Penes with a pair of medioventral processes; male second antennal distal segment broadly triangular ..... ARTEMIIDAE: *Artemia*
- Penes with basal or distal processes; male second antennal distal segment not broadly triangular, basal segments fused ..... BRANCHIPODIDAE

ORDER NOTOSTRACA

INTRODUCTION

Notostracans, commonly called tadpole shrimp because of their superficial resemblance to frog larvae, are large (up to 100 mm in some cases, although most species are in the 30–50 mm range as adults) predatory and scavenging branchiopods. They are immediately recognizable by their large, horseshoe-shaped dorsal shield (Fig. 1C, 2B). The shield, often called a carapace, has a dorsal ridge or carina, but it is not truly hinged, and there are no adductor muscles for closing it (as seen in the bivalved clam shrimps, below). The compound eyes are sessile and are integrated into the dorsal shield, as is the entire head of the animal, a condition that differs from what is seen in other large branchiopod groups. The abdomen terminates in a pair of long,

filamentous caudal furca sometimes called cercopods. Additional distinguishing morphological features were presented by Martin (1992).

GENERAL BIOLOGY

Notostracans are known from temporary bodies of water on all continents and New Zealand, with the exception of Antarctica. They inhabit some truly inhospitable environments and temperatures; eggs of *Triops* have been shown to withstand boiling water and still develop normally later. Notostracans are not filter feeders, but instead appear to feed on detritus or on other organisms, living or dead, and have been reported to pursue and catch anostracans and even small fish.

Life cycle

Like fairy shrimp, all tadpole shrimp hatch as nauplius larvae. There are some morphological differences between tadpole shrimp nauplii and fairy shrimp nauplii, such as the conspicuous presence of the developing carapace in the nauplius of notostracans. Another difference is that notostracan larvae do not swim well and contain much yolk; apparently these early larvae do not feed (Fryer 1988). Some populations of notostracans are reported to be parthenogenetic and/or hermaphroditic, though most populations seem to have males and females present. Eggs produced by notostracans are always uniformly spherical and smooth to the naked eye, never elaborately ornamented or oddly shaped as in some anostracans and some spinicaudatan clam shrimp. As with anostracans, the entire life cycle can be extremely brief, with maturation, mating, and egg development occurring in a span of only a few weeks.

REGIONAL TAXA

Asian records of notostracans are scarce. Brtek *et al*. (1984) reported *Triops granarius* and *Lepidurus couesii* from Mongolia. However, Eurasian specimens of *L. couesii* apparently do not match the type material of that species (C. Rogers, pers. comm.; see also Rogers 2001). Naganawa (2001a) listed three species from Japan, and Vekhov (1992) described a new species, *Lepidurus mongolicus*, from the semi-deserts of Central Asia (Mongolia). To our knowledge, no species have been reported from Southeast Asia.

CURRENT TAXONOMY AND KEYS TO IDENTIFICATION

The Notostraca contains a single extant family, the Triopsidae, with two genera, *Triops* and *Lepidurus*, and about 10 species worldwide. The most salient distinguishing character between the two genera is the large supra-anal plate (= caudal lamina of Rogers 2001) seen in species of *Lepidurus* (Fig. 2C). (And apparently there is a very reduced supra-anal plate in about 40% of specimens of *Triops cancriformis*;

D. Christopher Rogers, pers. comm.). There is much morphological variation present in the group, even among individuals within a population, and some characters vary according to diet (see review on Nearctic species of *Lepidurus* by Rogers 2001). Understandably, this variability has caused much taxonomic confusion in the past.

KEY TO THE GENERA OF THE NOTOSTRACA (FAMILY TRIOPSIDAE)

1. Telson (anal somite) with large, posteriorly directed supra-anal plate extending back between and slightly above the long caudal furca (see Fig. 2C) ..... *Lepidurus*
- Telson (anal somite) lacking a supra-anal plate, instead terminating abruptly ..... *Triops*

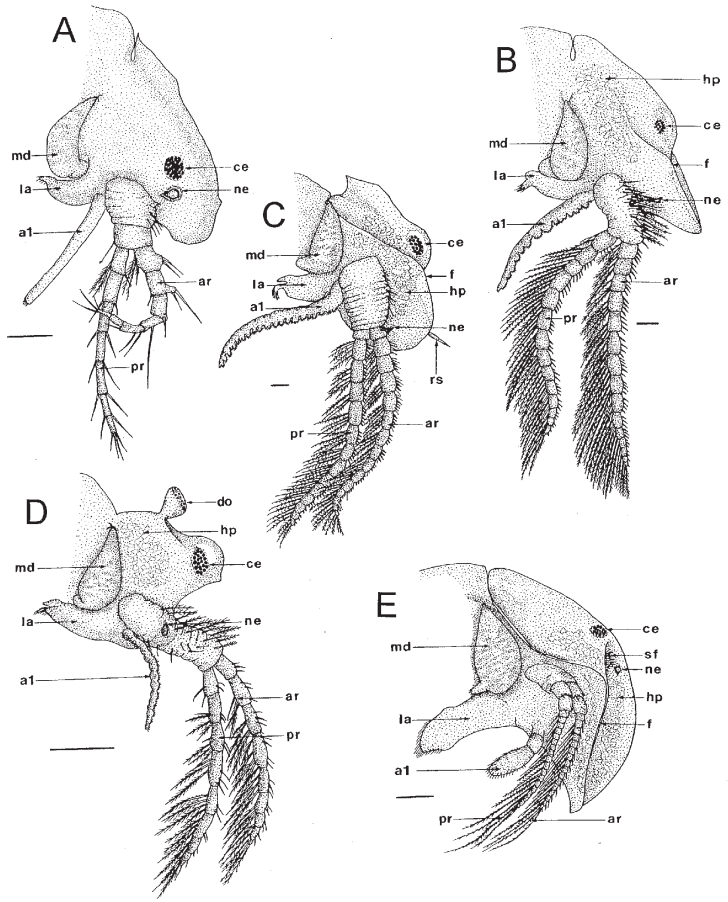

Figure 3. Lateral view of the head regions of representatives of the five families of clam shrimps. A – *Cyclestheria hislopi* (family Cyclestheriidae); B – *Caenestheriella setosa* (family Cyzicidae); C – *Leptestheria compleximanus* (family Leptestheriidae); D – *Limnadia lenticularis* (family Limnadiidae); E – *Lynceus gracilicornis* (family Lynceidae). Abbreviations: a1, first antenna; ar, anterior ramus of second antenna; ce, compound eye; do, dorsal organ; f, fornix (supportive ridge of rostrum); hp, hepatopancreas; la, labrum; md, mandible; ne, naupliar eye; pr, posterior ramus of second antenna; rs, rostral seta; sf, setal field. Scale bars = 0.25 mm. (Source: After Olesen *et al*. 1997)

"CONCHOSTRACA" – ORDER DIPLOSTRACA, SUBORDERS SPINICAUDATA, LAEVICAUDATA, AND CYCLESTHERIDA

INTRODUCTION

Conchostracans are commonly called clam shrimps because of their superficial resemblance to bivalved molluscs (Figs. 1D–F). The group contains five families whose relationships to one another (and to other groups of branchiopods) are unclear. Indeed, there are arguments for avoiding the use of the term conchostracan as a taxonomic name, as it might imply a relationship that does not exist (Martin 1992; Martin and Davis 2001). All conchostracans have a bivalved carapace, with the two valves joined by a dorsal hinge or fold and attached and manipulated by a strong adductor muscle. They differ markedly from anostracans and notostracans in their ability to be completely enclosed within the bivalved carapace, and in their correspondingly reduced abdomen. Generalizations beyond this point are difficult to make, as the families of clam shrimp are morphologically quite diverse (Fig. 3).

GENERAL BIOLOGY

Conchostracans occur on all continents except Antarctica, and they are almost always found in temporary waters. There are sporadic reports of species of the family Lynceidae in prairie streams (see Martin 1992), and *Cyclestheria hislopi* (the sole member of the family Cyclestheriidae) is known from some permanent bodies of water where it is invariably associated with aquatic vegetation; *Cyclestheria* is basically a circumtropical species. Although often described as filter feeders, clam shrimps actually do a large amount of scraping and tearing of their food, and they will scavenge just about any other organism in their environment.

Although habitat specifics differ by species, these taxa might be encountered in just about any ephemeral pool or similar habitat (such as troughs for watering animals), and their mode of distribution – with some species having drought-resistant eggs that can be carried by waterfowl or blown by the wind – is such that some species are quite widespread.

Life cycle

Like anostracans and notostracans, most conchostracans (clam shrimps) hatch as a pear-shaped nauplius larva with three pairs of appendages. Development is decidedly more metamorphic, with some species undergoing dramatic changes in morphology in a single moult. This is particularly true in the family Lynceidae (Laevicaudata), the unusual larvae of which have an enormous flattened dorsal shield and ventral labrum, and look nothing like the adult lynceid, and nothing like the larvae of any other branchiopod. Some populations are thought to reproduce parthenogenetically, as males are either absent or extremely rare, especially in the

monotypic Cyclestheriidae and in some limnadiid spinicaudatans. *Cyclestheria* is unique in that larval development occurs within the confines of the carapace valves. In those groups where mating has been observed, males used modified anterior thoracopods (claspers) to grab the shells of females and then hang on at right angles to the female's shell length. As with anostracans and notostracans, the entire life cycle in all the clam shrimp groups is quite brief, with development, maturation, mating, and egg laying sometimes occurring in a span of only a few weeks or days. Details of cyst morphology can be very useful in species identifications, especially in some of the spinicaudate clam shrimps, and particularly in the family Limnadiidae, where the resting eggs are elaborately sculptured. Eggs of the lynceids (Laevicaudata) and in most other spinicaudatans are smooth, spherical, and unremarkable. As in other groups, the eggs can withstand dessication and persist in the environment for years awaiting the water necessary for them to hatch.

REGIONAL TAXA

The suborder Spinicaudata in East Asia, reviewed recently by Naganawa (1999) and Naganawa and Orgiljanova (2000b), includes numerous records from Japan, Korea, and Russia (Naganawa 1999). Records of clam shrimp from Mongolia include *Eocyzicus davidi* and the laevicaudatan *Lynceus dauricus* (Brtek *et al*. 1984). Naganawa (2001a) listed four spinicaudatans and one laevicaudatan from Japan. Records from Southeast Asia include only the circumtropical species *Cyclestheria hislopi* (Fig. 4), reported from Thailand (Junk 1977), from unspecified localities in Java, Sumatra, and Sulawesi (based on a map provided by Olesen *et al*. 1997), and from Malaysia (Martin *et al*. 2003). Belk (1996) listed only *Cyclestheria* in Southeast Asia in his world list of conchostracan genera and their distributions. *Cyclestheria hislopi* has also been reported from India, Cambodia, the Americas, Africa, and Australia (Olesen *et al*. 1997; Martin *et al*. 2003). Nayar and Nair (1968) reported *C. hislopi* and *L. brachyurus* from southern India, and described two species of spinicaudatans (*E. michaeli* and *L. maduraensis*) from India as well.

The sole record of any clam shrimp in Malaysia is a recent report of a population of mature (many egg-bearing females) *C. hislopi*, collected in August, 2001, from hyacinth-infested tin mine lakes in Kepong, Kuala Lumpur, Malaysia (Martin *et al*. 2003). Other tin mine lakes containing *Cyclestheria* are mentioned in that report as well. Tin mine lakes are a potentially important habitat, as there are some 4300 artificially created tin mine lakes in Malaysia, as opposed to only two natural lakes on the peninsula, both riverine in origin (C. Yule, pers. comm.).

CURRENT TAXONOMY AND KEYS TO IDENTIFICATION

The most recent treatment (Martin and Davis 2001) recognizes three suborders (Spinicaudata, Laevicaudata, and Cyclestherida) which comprise, along with the suborder Cladocera, the Order Diplostraca. This scheme is not universally accepted

(see discussion in Martin and Davis 2001: 17–19). Some workers would combine the Cyclestherida and Spinicaudata, and some have suggested affinities between the Laevicaudata and Notostraca. Following Martin and Davis (2001), we recognize for now five families of conchostracans in three suborders: Cyclestherida (family Cyclestheriidae), Laevicaudata (family Lynceidae), and Spinicaudata (families Limnadiidae, Leptestheriidae, and Cyzicidae). The family Cyclestheriidae is monotypic (*Cyclestheria hislopi*). A second genus and species of the family Cyclestheriidae, *Paracyclestheria sinensis*, described from China, was possibly based on young stages of *C. hislopi*, according to Olesen *et al*. (1997). The family Lynceidae contains three genera and approximately 40 species worldwide (Martin and Belk 1988). The families Limnadiidae, Leptestheriidae, and Limnadiidae are more diverse, containing some 15 genera among them (Table 1). Some workers recognize the family Imnadiidae for the genus *Imnadia*, which we treat among the Limnadiidae.

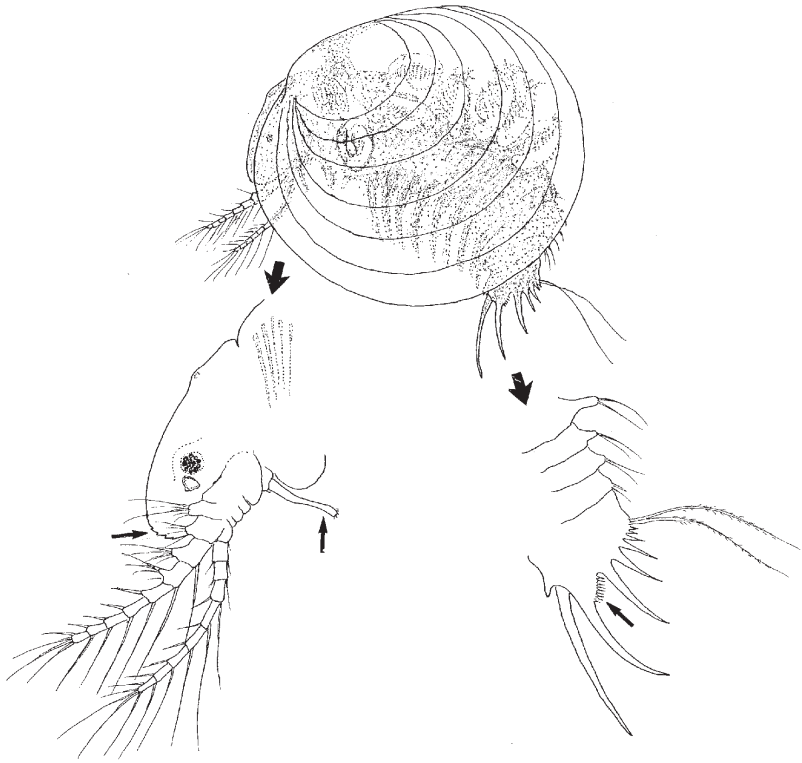

Figure 4. One of the large (3.1 mm) individuals of *Cyclestheria hislopi* from the Malaysian specimens (LACM CR 2001-011.1) reported by Martin *et al*. (2003). Large arrows indicate areas enlarged to show detail while the smaller arrows highlight characters unique to the species, such as the serrated anterior rostral border, tubular first antenna, and heavily spinose posterior region. Note also the nearly circular carapace valves and developing embryos within the valves, both of which are characteristic of *Cyclestheria.*

KEY TO THE FAMILIES OF CONCHOSTRACA (CLAM SHRIMPS)

1. Carapace valves without growth lines; inflated and nearly spherical. Pair of sensory fields on either side of rostral carina. First pair of thoracopods in male modified as claspers; second pair of thoracopods not modified, or if modified not as functional claspers. Dorsal joining of carapace valves recessed, appearing hinge-like. Caudal end lacking spines or spine-like caudal furca ..... LYNCEIDAE

- Carapace valves with obvious growth lines; valves laterally compressed, never inflated or nearly spherical. No paired sensory fields on either side of rostral carina. First, or first and second, thoracopods in male modified as claspers. Dorsal joining of carapace valves not recessed, appearing instead as a flat, simple fold. Caudal end with well developed spines and caudal furca 2

2. Rostrum compressed, bladelike, lacking a fornix (supportive fold or ridge on either side of rostrum) 3

- Rostrum not compressed or bladelike, and with well developed fornix on either side of rostrum 4

3. First antenna of female tubular, with setation restricted to distal tip. First male thoracopod modified as clasper; second male thoracopod unmodified. Head without stalked dorsal organ protruding anterodorsally. Embryos carried within valves of carapace ..... CYCLESTHERIIDAE: *Cyclestheria*

- First antenna of female not tubular, instead composed of lobes, with setation occurring on lobes and not restricted to tip. First and second male thoracopods modified as claspers. Head with obvious stalked dorsal organ protruding anterodorsally (though reduced in genera *Imnadia* and *Metalimnadia*). Eggs, often elaborately sculptured, carried on female thoracopods but shed upon dying; development never taking place within confines of carapace valves ..... LIMNADIIDAE

4. Distal extremity of rostrum bearing acute rostral spine in both sexes in adult ..... LEPTESTHERIIDAE

- Distal extremity of rostrum without acute rostral spine in adults ..... CYZICIDAE

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