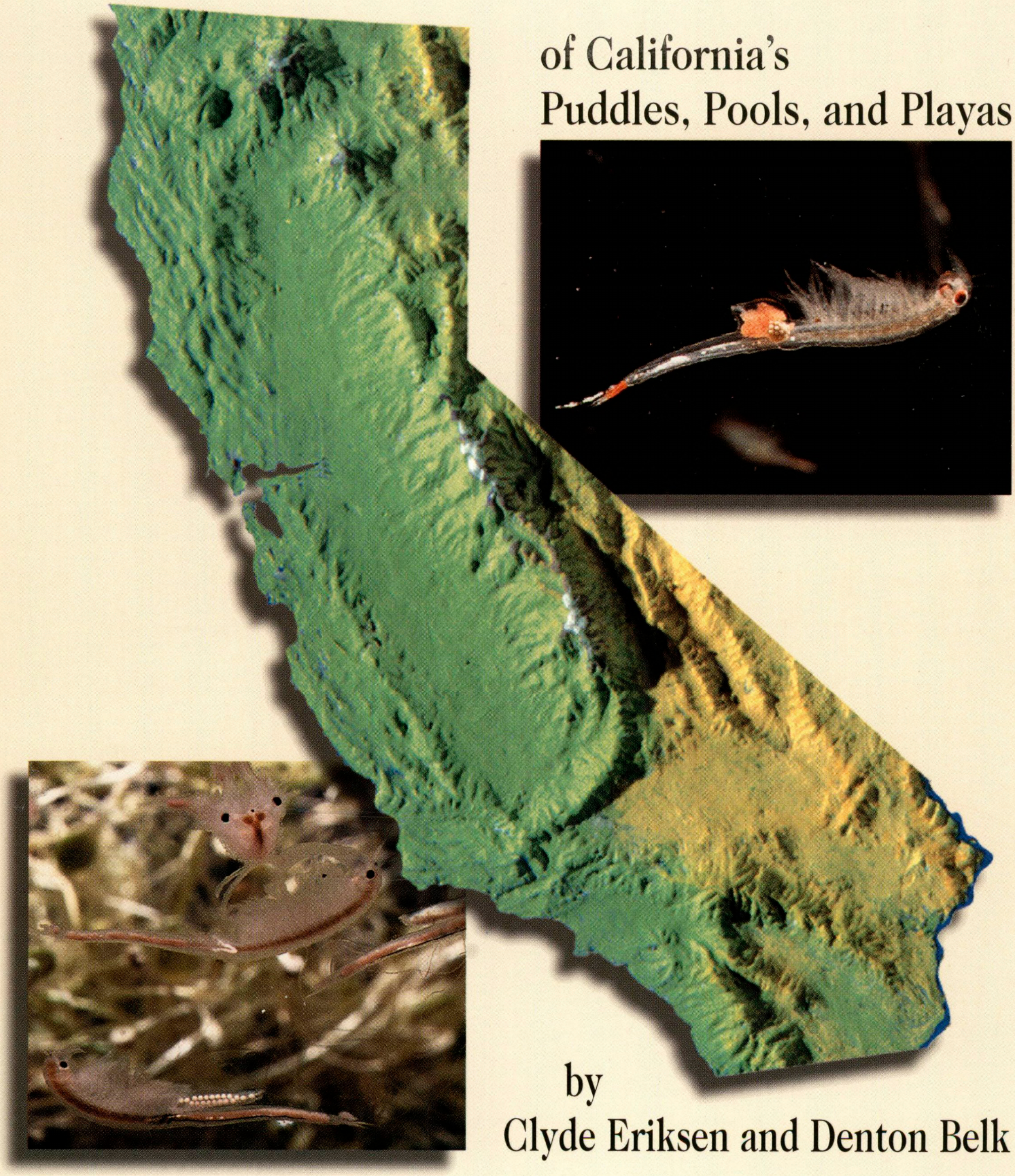
Fairy Shrimps



of California's
Puddles, Pools, and Playas

by
Clyde Eriksen and Denton Belk

The 25 fairy shrimps found in California

Artemia franciscana Kellogg, 1906	San Francisco brine shrimp
Artemia monica Verrill, 1869	Mono Lake brine shrimp
Branchinecta campestris Lynch, 1960	pocketed pouch fairy shrimp
Branchinecta coloradensis Packard, 1874	Colorado fairy shrimp
Branchinecta conservatio Eng, Belk, & Eriksen, 1990	Conservancy fairy shrimp
Branchinecta dissimilis Lynch, 1972	dissimilar fairy shrimp
Branchinecta gigas Lynch, 1937	giant fairy shrimp
Branchinecta lindahli Packard, 1883	versatile fairy shrimp
Branchinecta longiantenna Eng, Belk, & Eriksen, 1990	longhorn fairy shrimp
Branchinecta lynchi Eng, Belk, & Eriksen, 1990	vernal pool fairy shrimp
Branchinecta mackini Dexter, 1956	alkali fairy shrimp
Branchinecta sandiegonensis Fugate, 1993	San Diego fairy shrimp
Branchinecta sp. - 1	midvalley fairy shrimp
Branchinecta sp. - 2	winter fairy shrimp
Branchinecta sp. - 3	mountain fairy shrimp
Eubranchipus bundyi Forbes, 1876	knobbedlip fairy shrimp
Eubranchipus oregonus Creaser, 1930	Oregon fairy shrimp
Eubranchipus serratus Forbes, 1876	ethologist fairy shrimp
Linderiella occidentalis (Dodds, 1923)	California fairy shrimp
Linderiella santarosae Thiery & Fugate, 1994	Santa Rosa Plateau fairy shrimp
Streptocephalus dorothae Mackin, 1942	New Mexico fairy shrimp
Streptocephalus sealii Ryder, 1879	spinytail fairy shrimp
Streptocephalus texanus Packard, 1871	Great Plains fairy shrimp
Streptocephalus woottoni Eng, Belk, & Eriksen, 1990	Riverside fairy shrimp
Thamnocephalus platyurus Packard, 1879	beavertail fairy shrimp

FAIRY SHRIMPS OF CALIFORNIA'S PUDDLES, POOLS, AND PLAYAS

by

Clyde H. Eriksen and **Denton Belk**

art work by
Ina Rae Lengyel

cover and maps by
Jones & Stokes Associates, Inc.

Published by Mad River Press, Inc.
141 Carter Lane
Eureka, California 95503

Printed by Eureka Printing Company, Inc.
106 T Street
Eureka, California 95501

ISBN 0-916422-83-6

Dedication

As a student at the University of California at Santa Barbara in the early 1950s, I (Clyde Eriksen) often accompanied my professor, Dr. Donald M. Wootton, on collecting forays to terrestrial haunts, intertidal habitats, and, in the winter and spring, to rain pools. On one of my first visits to the magical world of a pool, Don showed me a net-full of gorgeous little red-eyed creatures he called fairy shrimps. Their beauty and graceful swimming behavior, combined with Don Wootton's enthusiastic field style, caught my attention. Our collecting sites on the coastal plain near the University are now but a distant memory. The pools were drained or leveled, the earth compacted and built upon to provide different living sites, this time for higher hominids meeting the higher demands of higher education.

During those college years of mine I spent parts of each summer back-packing the John Muir Trail along the crest of the High Sierra. In 1953 and 1954, I cajoled Don into going with me to "collect fairy shrimps". He agreed. We went. And the stories, from burro problems in the snow of Donohue Pass to apple fritters baked at the base of Fin Dome, are legendary – but for another telling. We did net fairy shrimps in many a pool. They were forwarded to the desk of an expert in Ohio, never to be seen again. But no matter, Don had "netted" me, and his fairy shrimps have kept my life-long interest!

In August of 1992, I was pleased to visit again with Donald Wootton and tell him of our plans for this book, a book that for me has been 45 years in the making, and for him will not be read. While outlining this manuscript in January of 1993, I received word that Don, like so many of the other of God's creatures that he studied and loved so well, took his last breath.

Though it is but a small token in appreciation of Donald Wootton's influence on so many young biologists, and in his retirement years on numerous "ordinary citizens", we dedicate this book to his service and memory. And may *Streptocephalus woottoni*, the Riverside fairy shrimp formally named after him in 1990, swim gracefully each rainy season as a tribute to his care for, and our care and consideration of, the life with which we humans share this small planet.

Donald Wootton

Reprinted courtesy of The Idaho Statesman

Contents

CHAPTER 3 31

ECOLOGY OF FAIRY SHRIMPS

CHAPTER 4 57

STATEWIDE DISTRIBUTION OF FAIRY SHRIMPS

CHAPTER 5 75

NATURAL HISTORY OF CALIFORNIA'S SPECIES OF FAIRY SHRIMPS

List of Figures

List of Maps

List of Tables

Preface

The graceful, almost ethereal, fairy shrimps swim, often in cloud-dense numbers, under the rain-splashed or sunlight-drenched surfaces of temporary pools. And although any of the kids amongst us who journey to the beach certainly know the "symbol of the sea", the starfish, few who splash through the water and mud of a rain pool see or are familiar with the "symbol of temporary waters", the **FAIRY SHRIMP**.

These small, delicate creatures ply pools filled by rain, snow melt, or flash flood. There they feed on microorganisms and organic particles, growing to 10-20 mm (0.5-0.75 inches) over a period as short as two to three weeks, to about 40 mm in some of the species that may live several months, or even 150 mm for the raptorial giant fairy shrimp. When these creatures become too aged as fairy shrimps go, or their home evaporates to the thirsty sky, they succumb, and the embryonated eggs that have been spewed to the pool bottom or left in the brood-pouches of stranded females dry, bake, or freeze as the vagaries of the weather dictate, and await the pool's next filling.

Unfortunately, there is often no "next filling" in today's world of consuming development for agriculture, roads, housing, and industry. By "next time" the land may have been leveled, drained, compacted, or covered. And in concert, of course, with a basin's demise is the destruction of another fairy shrimp population and all the other plant and animal creatures who for centuries or millennia called that particular spot on the face of this earth...home.

With their loss, once again humans have dominated; once again we have put ourselves first and counted the creatures in our way as "worthless". In justifying such extirpations, how many times have we heard or read the opinion that humans have been given dominion over the earth and its creatures, and what each of us wants to do on private or public land, no matter its effect, should take precedent over our neighbors, certainly over some worthless fowl, or flower, or in this case tiny green, or gray-white, or red-eyed, backbone-less fairy shrimp. Is it not true that in lunging ahead with single-purpose goals, either through lack of ecological knowledge or through lack of willingness to apply what ecological information humans possess, we continue to illustrate the erroneous "truism" that "what isn't known can't be important". Yet, to paraphrase Aldo Leopold (1953), how foolish we are to throw away some screws and springs of one of our machines because we do not know, or have not shown the interest to seek out, their function.

Knowledgeable individuals who study such things note that from 90-98% of Orange and San Diego counties' rain pools have been wiped away by development, and "Vernal pool habitat in Los Angeles County has been destroyed." (Federal Register 1993). As many as 60-85% of temporary waters in the Great Central Valley, and thus their fairy shrimp inhabitants, have also been lost to "progress" (Federal Register 1994). Sadly, the rate at which we humans further decimate these special places and thus these graceful creatures continues to escalate. What is truly disheartening is that this destruction slashes indiscriminately at the heart of the richest fairy shrimp diversity (in terms of species per unit of land area) on our small globe, outpacing #2, the former Yugoslavia, by 10%, and #3, Italy, by 17%. California's 23 species constitute 47% of the entire fairy shrimp fauna of North America (Mexico, U. S., and Canada). And of those 23 species, 9 are found nowhere else on the face of our planet, be it round or flat. This does not mean that, oh, all right, we can afford to lose a mess of shrimps because we have so many; it means that by impacting even small pieces of land we Californians are more likely to either exterminate some species altogether, or eliminate a significant amount of the genetic diversity needed for its long-term survival. The stimulus for this book emerged from these facts.

Your authors are scientists who, for more than 60 professional years between us, have enjoyed sharing the grassland swales, rock pools, desert playas, and alpine basins with the living things that dwell in and around them. We have attempted to take the threads of our experiences in "fairy shrimp country" and weave into the fabric of this small, relatively non-technical volume a presentation that will introduce fairy shrimps to anyone with a casual, vested, or scientific interest in these creatures. But obviously we can't "know it all", so we have included along our route through these pages enough citations of authors to get you into the scientific literature should you wish to venture that far. We are writing for an audience that we hope will include the general reader, landowners who may serve as landlords for some fairy shrimp tenants, young and budding naturalists who have been turned-on to the world of life about them, and also those already skilled in natural history. Although this volume was not designed for the classroom, as scientists we have striven to make it scientifically accurate so that students and their professors would find it valuable for their studies. We have attempted to make it more easily understandable by including a glossary containing terms not necessarily available in a standard dictionary. Also included is a new field-tested key to the fairy shrimps of California so that anyone with a dissecting microscope, or sufficient magnification, can attempt to determine which species they are viewing.

We hope that as you read this book, these wonderful creatures we call fairy shrimps will tantalize your interest and lure you to the fascinating temporary waters in which they dwell. Upon your arrival at a fairy shrimp oasis, we encourage you to bend down, and carefully observe and consider the rather small, sometimes tiny, world of a pool. In so doing, remember that five California species (*Branchinecta conservatio*, *B. longiantenna*, *B. lynchi*, *B. sandiegonensis* and *Streptocephalus woottoni*) are listed as endangered or threatened under the federal Endangered Species Act (Federal Register 1993, 1994, 1997), and cannot be collected without a permit. However, much can be learned by non-manipulative observation, and of course 18 other species remain freely available for closer examination and study. We hope that as you become familiar with fairy shrimps, you will develop an excitement about, an involvement in, and a camaraderie with them and the other fascinating creatures who dwell in your observation and study sites oblivious to the overwhelming growth and spread of the human population and its concomitant technological development, encroachment, and residue.

When awareness and understanding develop, concern soon follows. So we hope that all who read this book, no matter the perspective from which you come, will join voices and extend a cumulative hand to protect and preserve enough pieces of the important and necessary fabric of our earth, including rain pools and their creatures, so that not only our generations, but those after us, can enjoy their presence as well as benefit from it.

Acknowledgments

This book was a labor of love...a longer labor before its birth than either of us imagined at the outset. True, we already had full lives prior to conception of the idea, but several colleagues added to the gestation time by making helpful suggestions about organization and presentation that we took to heart. We gratefully recognize Bob Brown, Richard Hill, John Moeur, and our editors, Jim and Virginia Waters, for these midwife services.

Along the way several individuals and organizations were gracious in providing considerable amounts of unpublished data, both life history and distributional, that helped tremendously to fill information gaps thus aiding in making this book as complete as it is. Brent Helm, Richard Hill, John Moeur, Christopher Rogers, Jones & Stokes Associates, and Sugnet & Associates were vital in this regard. Many people far too numerous to mention individually, but nonetheless prominent in our thoughts, supplied collection data instrumental in compiling the species distribution maps. To all of you, our hearty thanks for your time, effort, and willingness.

The identification key contained between these covers evolved into its present form with the aid of the more than 140 biologists who used various earlier drafts in Denton's fairy shrimp identification classes, and made suggestions for its improvement. We thank you very much for these testing services.

In order to write a book about California's fairy shrimps and their often secretive, certainly transient, homes, the person putting pen to paper, or in this day and age computer keyboard to printer, needs a good deal of familiarity with California's terrain. As many thousands of miles by car that Clyde has amassed criss-crossing California in search of fairy shrimps, and the magnificent terrain that harbors them, nothing has aided as much in gaining a perspective of this state as the aerial wanderings piloted by colleague and friend, Harv Wichman. Thanks Harv for the magnificent views, and for your attentiveness to aerial safety.

Of course, many technical aspects are encountered in putting together a book. We thank Ina Rae Lengyel, who, as our biological artist, has labored a number of years with us. She has not only become a critical observer of fairy shrimp anatomy, but devotee of seeing to it that we, and you, perceive the magnificent architecture of these animals in a precise, representative, and understandable manner. We appreciate the graphic design and production expertise so willingly and amiably provided for the book's cover and maps by Christy Anderson, and Mary Engbring of Jones & Stokes Associates' graphic arts department. We thank Brent Helm for getting Jones & Stokes involved. A special thank you to Larry Serpa and Richard Hill for generously giving photographs for the cover. These pictures both beautify the book and offer wonderfully detailed views of fairy shrimp color and anatomy. Last, but definitely not least, were the hours of thoughtful attention given by Bob Brown to a seemingly endless stream of computer glitches. Many were the inopportune times that he set aside his own work to save Clyde's computer-limited mind from melt-down. What is there to say but "thanks, Bob"!

Research travels, artists, and supplies require funds, and we are grateful for various grants that have helped in the accumulation of data, development of graphics, and publication of this book. Those grants have come from The W. M. Keck Foundation, Pitzer, Scripps, and Claremont McKenna Colleges of The Claremont Colleges, and from the Joint Science Department which serves these institutions.

And finally, to those who excited us about fairy shrimps in our formative years, and to our students who have shared in the enthusiasm and pain of seeking and working with these creatures during our careers, we acknowledge your involvement with gratitude. Please know we are aware of your roles in this book. And as we have said somewhere in the text, we cannot know all there is to know about fairy shrimps, but we have tried to be as complete and as accurate as possible. The omissions and errors that will undoubtedly surface are solely the responsibility and property of the authors, and may not be reproduced without permission.

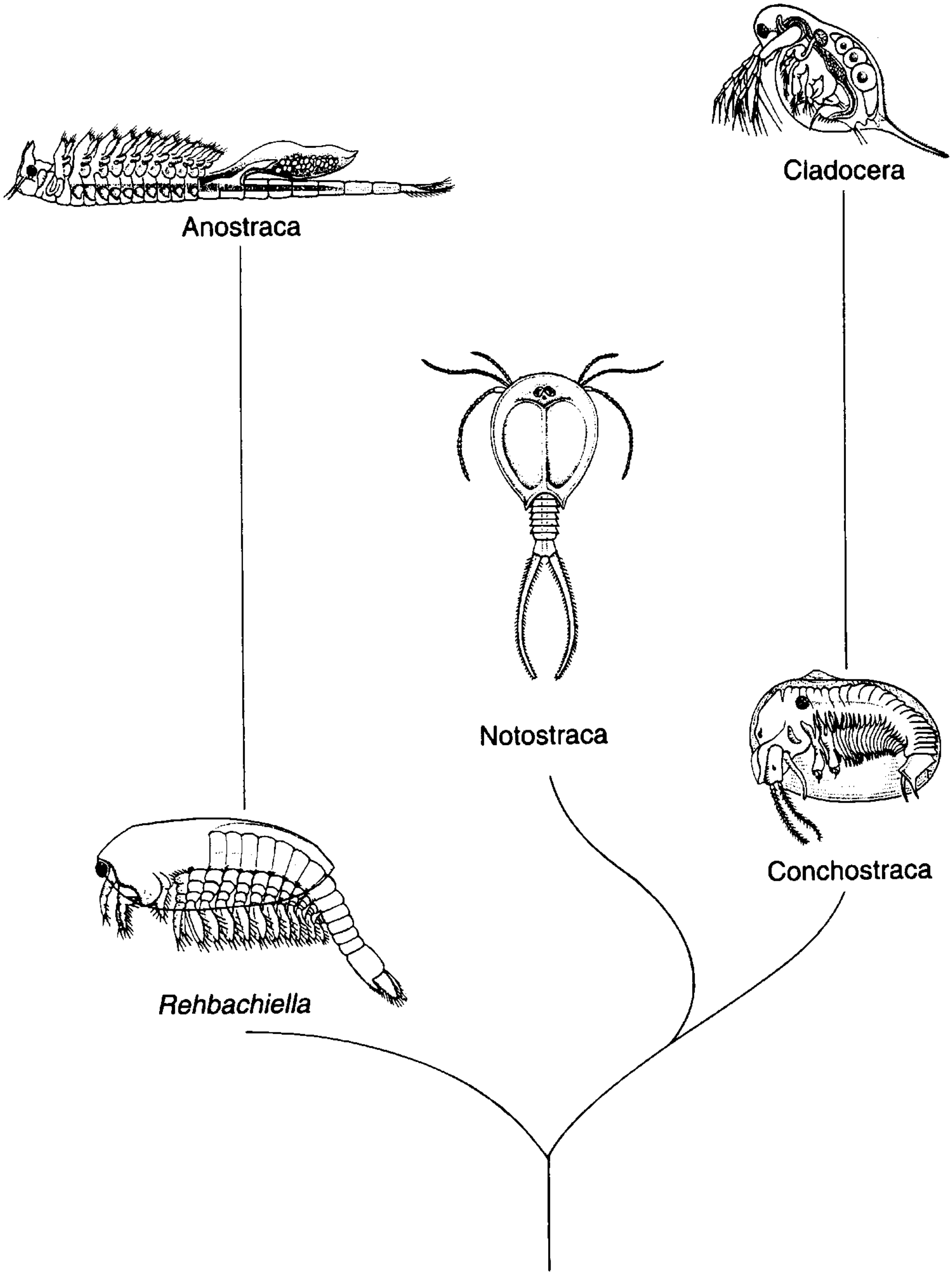


Fig. 1.1. Family tree of the branchiopods. The representative animals are positioned relative to each other at the approximate level of their group's origin based on fossil evidence. Except for *Rehbachiella* which is extinct, all the others are part of the biodiversity of our modern world. This scheme is based on Walossek (1995).

Chapter 1

INTRODUCTION

What are fairy shrimps?

In the early 1960s, having inherited a Montana mountain cabin where I (Clyde) began to spend the summers, I was putting my scientific inquisitiveness to work by studying the habitat complexity of two small pools. One was a dirty cattle watering-hole which was filled from the other, a clear-water, grass-lined reservoir. I dubbed these places Cow Paddy Puddle #1 and #2. Resident in both was the spinytail fairy shrimp *Streptocephalus sealii*, and I was fascinated by the fact that the fairy shrimps in the dirty Cow Paddy Puddle #1 were brown, while those from the grass-bottomed reservoir "next door" were apple-green. After a sampling run one day, I took some of the green animals with me to show the proprietor of Gnose Mercantile in the near-by village of Wise River. When I told Walter what they were he looked inquisitively at the animals, then at me, and said "fairy what"? "Fairy shrimps", I said again, and attempted a simple explanation of what they were and how they could be distinguished from other water creatures.

I also explained to Walter that the frozen lobsters he sold in his store are related to fairy shrimps as both are in the group (Phylum) **Arthropoda** (arthro = joint; poda = feet or appendages). This group must have jointed feet (appendages) for movement to occur because arthropods are covered with a rigid straitjacket called an exoskeleton.

Included in the Arthropoda are such familiar creatures as insects and spiders, centipedes and scorpions, and the **Crustacea**, a group (Subphylum) which contains crabs, Walter's lobsters, shrimps, barnacles, sowbugs (roly-polys), water fleas (*Daphnia*), **AND... FAIRY SHRIMPS** (e.g., Ruppert & Barnes 1994; Pearse *et al.* 1987). We have listed these familiar back-yard organisms and dinner-table delicacies in reverse order of their complexity. Thus, fairy shrimps are the most primitive living crustaceans except for a small group of tiny ocean creatures living among sand grains called Cephalocarida. Anatomically, crustaceans differ from all other arthropods by having two pairs of antennae, and several different kinds of appendages along the locomotor and abdominal portions of the body. Although a very small number of crustacean types live in wet or humid haunts on land, the great majority are adapted to spend their time in a watery milieu. Thus these creatures have gills for breathing in water, and the more primeval members are recognized by the paddle-like legs they use to swim through their liquid home.

Fairy shrimps possess such paddles, the insignia of their primitive nature, and, yes, they use them in swimming, but swimming which, interestingly, is accomplished **on their backs!** Their swimming appendages also double as gills because they present such a large surface area to the water and its dissolved oxygen. These leaf-like structures, attached to the underneath or ventral part of the body, are also the origin of their Class name **Branchiopoda** (branchio = gill; poda = feet). Additionally, the "gill-feet", along with a deep ventral **food groove**, form a postcephalic (behind the head) filter-feeding apparatus that sets the Branchiopoda apart from all other Crustacea

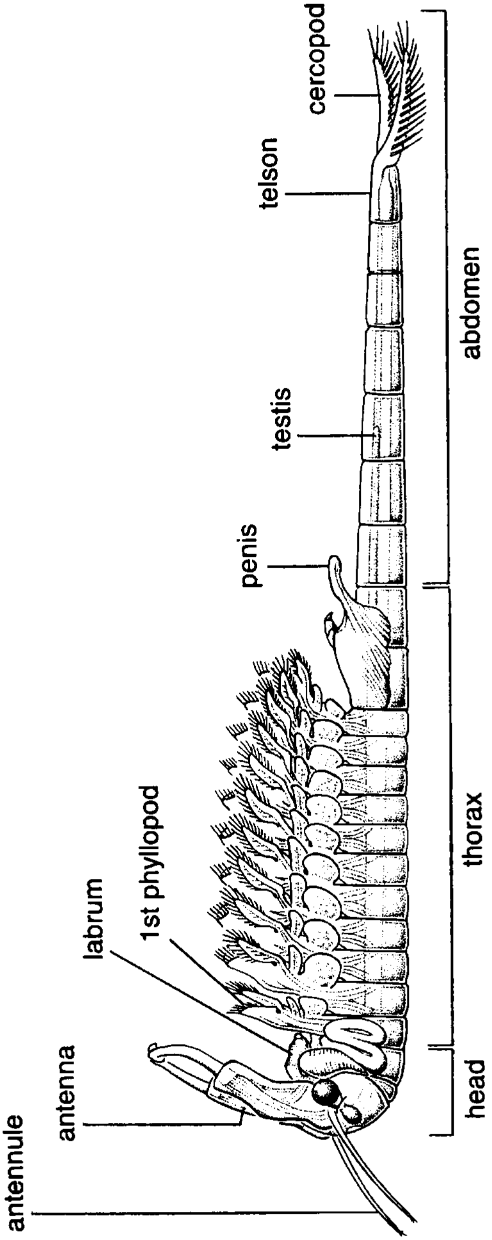


Fig. 1.2. Lateral view of a male *Branchinecta lynchi.*

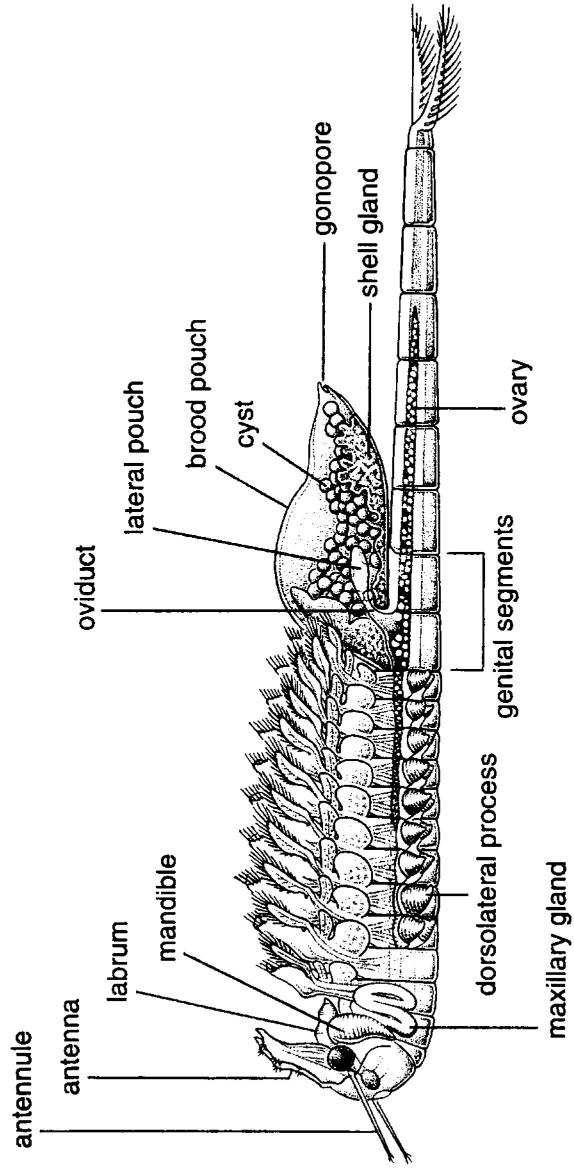


Fig 1.3. Lateral view of a female *Branchinecta lynchi*.

(Walossek 1993). Using this ingenious apparatus, fairy shrimps filter small gastronomic delights from the medium in which they swim, or scrape a comparable array of goodies off of rocks or sediments in their pool. And finally, believe it or not, certain cells on the surfaces of these appendages are responsible for salt exchange with the fairy shrimp's watery home, a strange circumstance indeed particularly in light of the fact that we humans think of salt regulation being a function of kidneys.

Lastly, fairy shrimps are included in the Order **Anostraca** (an = without; ostraca = hard plate or shell). Perhaps the best way to explain this bit of structureless anatomy is to compare a fairy shrimp with some familiar organisms, although considerably more evolutionarily advanced, that possess such a "bony plate". As you view a shrimp, lobster, crayfish, or crab, you will see a large piece of the exoskeleton that covers the back (dorsum) of the head and leg-bearing portion of the body (thorax); it is impregnated with calcium (thus "hard"). This dorsal plate, or shield (in older, inappropriate terminology, the carapace), is lacking in fairy shrimps. And a good thing too, for heavy armor is not a feature that complements a delicate body adapted to continuous swimming. Before moving on to compare our fairy shrimp friends with their equally fascinating closer relatives, let us not forget to draw your attention to the fact that up front, fairy shrimps see the world through stalked, compound eyes, and about the middle of the body, immediately behind the swimming appendages, males bear a pair of penes (Fig. 1.2, p. 2), while females possess a ventrally-protruding brood pouch (Fig. 1.3, p. 3) in which they produce their embryonated and shelled "resting eggs" called **cysts** (Fig. 3.2, p. 56).

Cysts are not just reproductive items deserving casual mention. Rather, cysts are the devices upon which anostracans rely to withstand adverse conditions such as drying, freezing, or the digestive system of animals. Being so exceptionally tolerant, cysts are not only the structures that lie dormant in dry pool soils awaiting the return of water, sometimes for years on end, but also serve as the fairy shrimp's mechanisms of dispersal.

Who are the relatives of fairy shrimps?

Amongst all the creatures referred to in the paragraphs just concluded, what relatives did we really have in mind? Well, we were thinking at least of "kissing cousins"; and by kissing cousins we mean members of the Class Branchiopoda whose leaf-like swimming appendages, called phyllopodia (phyllo = leaf; podia = feet), separate them from all other crustaceans. For those of us who faithfully visit rain pools each year to joy in the mix of creatures swimming about in them, we expect to see in one pool or another representatives of all the earth's living branchiopods, namely fairy shrimps (**Anostraca**), clam shrimps (**Conchostraca**), tadpole shrimps (**Notostraca**), and water fleas (**Cladocera**). In order to view the scientific classification of these creatures in one fell swoop, just refer to the "Classification of Fairy Shrimps and Some of Their Arthropod Relatives" (Appendix 4, p. 179).

The **Conchostraca** (conch = shell; ostraca = hard plate or shell), or clam shrimps, are so named because the animals give the impression of being small clams, perhaps 3-10 mm long (Fig. 1.1, p. xiv). Their appearance is derived from a shield which is large, laterally compressed, folded and flexible along its mid-dorsal hinge line, and is able to enclose the entire body. Such a form certainly seems the antithesis of an architecture suitable for swimming. Yet, although clam shrimps often lie on the bottom with "shells" slightly agape and appendages beating, more vigorous phyllopodial movements, coupled with beating antennae, propel them about the pool in energetic filter-feeding and mate-seeking activity. To test which of these devices was more important to locomotion, Denton once cut off the antennae of several clam shrimps and noted that the animals were unable to swim (unpublished observation).

Conchostracans live in temporary pools, many of which are warm, turbid, and often charitably provided with considerable processed biomass by grazing mammals. As you might expect, because warmer water leads to greater oxygen consumption by the myriad bacteria and fungi decomposing the mammal "contributions", such pools are short on oxygen, and under the worst of these conditions some species of clam shrimps may be seen swimming upside down with their phyllopodia paddling the more highly oxygenated water surface (Eriksen & Brown 1980a). Because we will not spend significant time talking of clam shrimps elsewhere, and so you may more easily make comparisons when necessary, we had best point out here that their paired eyes are sunken within the tissues of the head, where they either lie close together or are fused. Like the rest of the body, the head is usually covered by the shield, which also forms a cyst-containing brood chamber dorsal to the animal's leg-bearing segments (Fig. 1.1, p. xiv). For protection from predators, clam shrimps tightly close the clam-shell-like shield around their entire body. Denton has observed this behavior working effectively against tadpole shrimps and diving beetles, because when he removed a small part of the bivalved shield to expose a few legs, these predators zeroed in and chowed down (unpublished observation).

Tadpole shrimps took a quite different evolutionary tack in structure. Their name, **Notostraca** (noto = back; ostraca = hard plate or shell), refers to a shield which is large, flattened, and overarches the back of the animal above its phyllopodia-bearing segments and fuses with the dorsal covering of the head (Fig. 1.1, p. xiv). Like fairy and clam shrimps, notostracans also live in temporary waters and also produce cysts as the mechanism to get them through dry and otherwise unfavorable times. But unlike those two groups, our maternal tadpole shrimp carries her cysts in special brood pouches on a posterior pair of phyllopodia.

Notostracans swim ably through the water, and in conditions of low 0_2 they are commonly seen, upside down, with their hemoglobin-filled phyllopodia rippling the more highly oxygenated water surface. They are better known, however, for moving along the bottom filtering detrital material from the sediments, or macerating both plants and animals, including fairy shrimps, first with the grinding bases of their appendages, then with the cutting surfaces of their massive jaws (Fryer 1988). Given their flattened shape and tendency for living on the bottom, you can understand why it makes sense that the paired, stalkless eyes are located on the top of their head (Fig. 1.1, p. xiv).

Fascinating animals these! So you may well understand why, of all the terrific creatures which my (Clyde) adult-education class collected in the wet spots from Baker to Death Valley one March day, 65-mm-long tadpole shrimps, found in a muddy-water basin formed by a turn-of-the-century railroad causeway near the Dumont Dunes, created more of a traffic jam around the dissecting microscope by class participants (and my wife) than anything else in our loot.

Cladocera are tiny creatures less than 3 mm long. Except for biologists and aquarium enthusiasts, few people know them, because in our society, big, fuzzy, colorful, and warm animals (bears, bunnies, and birds) get most of the attention. Small, non-fuzzy, non-descript, and cold creatures, usually get short shrift – except perhaps by adult-education classes looking at fairy, clam, and tadpole shrimps, and by those who read this book! As for tiny life..., well, are you kidding? However, we challenge you to take a look at water fleas through a dissecting microscope or hand lens; if you will, you're in for an experience! You will see branched antennae jerking in spurts of motion, the shield folded clam-like to enclose the body but not the head (Fig. 1.1, p. xiv), and the fascinating motions of phyllopodia, heart, and intestine all visible through the thin exoskeleton. Talk about educational television! Water fleas obviously get their name because of small size and jerky propulsion. The latter is caused more by the rowing motions of their branched antennae (Cladocera; clad = branch; cera = horn) than by their reduced number of phyllopodia. The two compound eyes of these creatures are placed side by side, appearing as one in the head; and the brood chamber, as in clam shrimps, is located beneath the shield and dorsal to the leg-bearing segments (Fig. 1.1, p. xiv). Unlike most of their relatives, cladocerans continually produce living young until the onset of lousy environmental conditions. At such times each female forms one to several "resting eggs" which are encased by the walls of the brood chamber to form what is called an ephippium.

Before we leave this group of branchiopod relatives, there is still time for an important question, a question we humans seem sooner or later to want to know about the history of our own families. What are the interrelationships of this cast of characters? Do we know anything about the branchiopod "family tree"? Actually we do, and although some traits considered by scientists seem rather esoteric, for our general purposes form of the shield and position of the eyes are the more conspicuous main attributes suggesting position on the evolutionary tree drawn in Figure 1.1, p. xiv (modified from Walossek 1995). Note that the groups are thought to have radiated in two directions from the supposed common ancestor of them all. First along the anostracan line was a wonderful creature, *Rehbachiella kinnekullensis*, which swam at or near the bottom of a late-Cambrian sea some 525 million years ago. In seeming contradiction to today's group name, this early anostracan had a shield, but, as shown by the fossil record, it was reduced, then lost, in creatures along this lineage, while eyes on **stalks** were increasingly developed. The other branchiopod line first became differentiated by the sinking of eyes into head tissues, then by conspicuous differences in shield form. A broad dorsoventrally flattened shield was emphasized in notostracans, while the Cladocera-Conchostraca branch led to one that folded along the mid-dorsal line and laterally enclosed all but the head in cladocerans, and the entire body in conchostracans (Walossek 1993).

The where and whys of fairy shrimp haunts

Although the Crustacea as a whole are found in just about every type of aquatic habitat, the Order Anostraca is restricted to inland (non-marine), non-flowing, and, with some exceptions, temporary waters. In California, one such exception is the large, permanent Mono Lake. In it swims the Mono Lake brine shrimp *Artemia monica*, demonstrating that some Anostraca dwell in very briny places, three times the saltiness of sea water in the case of Mono Lake. At the other extreme, high-mountain species live in pools that have hardly anything dissolved in them at all. Their watery medium is as pure as the snow from which it melted.

Up and down the length of California environmental differences are dramatic, so pools which fairy shrimps call home differ considerably mainly because of changing elevation, latitude, and geology. As a result, water varies seasonally in presence, longevity, temperature, and chemical composition. Pools at higher elevations and latitudes form from melting snow and ice. Some evaporate with the advancing season, others remain until winter's cold turns the habitat solid again. At the lower altitudes and latitudes basins fill from winter and spring rains, as well as summer downpours and flash floods, then, like ghosts, disappear into the drying air.

We assume you noticed two paragraphs back, when speaking of the Mono Lake brine shrimp, we coupled it with its scientific name. Because common names are oftentimes confusing, and commonly vary with where you live and who you talk to, we will generally use the internationally-recognized scientific names throughout the text; but, if you get hung up with remembering who's who among fairy shrimps, just look inside the front cover for a list of California species, and our edict of what their common names should be.

What good are fairy shrimps?

The age-old propensity of humans to ask what good is something, or what is it worth, can obviously be, and is, aimed at fairy shrimps. Something with a name like that ought to be on the menu at your local gourmet restaurant or sushi bar...but isn't! Even though today Americans don't pull themselves up to a table with a plate of steaming fairy shrimps, melted butter, and a wedge of lemon, in days gone by, Indians living around California's Mono Lake made *Artemia monica* and the brine fly *Ephydra* a normal part of their diet. They may not knowingly have eaten these creatures as a protein supplement, but in reality that is what was accomplished. In an attempt to see what the Indians had going, Denton, our very own Texas gourmet, tried some fairy shrimps and found the flavor "similar to real shrimp, and quite pleasing".

Today we Americans do not take interest in fairy shrimps to satisfy our hunger pains, but should they be useful to some economic enterprise we would hear praises sung to their name. The praises given to now may not have made the "hit parade", but there are many individuals who are ecstatic over the economic services of fairy shrimps. In this over-crowded world of ours, we have more and more environmental difficulties with which to deal and, thankfully, technology increasingly applies affordable biological means, including the use of fairy shrimps. For example, intensive livestock rearing results in wastes that severely pollute local water supplies. Mitchell (1991) tested the idea that if these wastes were directed into a pond where they stimulated algal growth, and fairy shrimps (in this case *Streptocephalus macrourus*) fed upon the algae, waste contamination could be significantly, economically, and usefully reduced. His results demonstrated that *Streptocephalus* was able to efficiently convert such food items into fairy shrimp biomass. Because the animals can tolerate considerable crowding, a dense population of these creatures can convert an impressive amount of feces to fairy shrimps, exceeding even the ability of rotifers and water fleas, which are the other creatures utilized in this manner to date. We predict that soon on, some knowledgeable fairy shrimp entrepreneur will corner the pollution control market for feedlot wastes and make a pile, so to speak.

While on the subject of *Streptocephalus*, several individuals have written about the abundance of *S. sealii* in recently filled rearing pools at fish hatcheries (e.g., Anderson 1984; McCarraher 1970), and undoubtedly a few fish-hatchery managers who have such a ready supply use them as a tasty, though temporary, food source for their ravenous charges. Other managers find them a problem, but apparently only when they try to raise fish fry in newly-flooded rearing ponds (Moss 1978). The problems arise because fairy shrimps, being about the same size as fry, cannot serve as dinner for the baby fish, rather they compete for space, food, and oxygen. The idea of raising fairy shrimps on a scale suitable for freshwater-fish culture has been considered in Italy by Mura (1992a). But while the use of freshwater species may just be getting off the ground, Kinne wrote in 1977 that the young of brine shrimps (mostly *Artemia franciscana*, obtained largely from the Great Salt Lake in Utah) were being used as food for more than 80% of the marine fish and crustaceans cultured world-wide. In those days brine shrimp cysts were collected by shovel from the windrows piled up at the edge of natural and man-made evaporative salt ponds (Kinne 1977), then hatched for use in aquaculture. With fish and shrimp culture booming world-wide, one sees why the commercial supply of *Artemia* cysts, exceeding 110 tons annually in the late 1970s (Sorgeloos 1980), has since exploded to 2,200 tons annually (Williams 1995). Now, add to that the profits from sale of live, dry, or frozen adults, and one has considerably more than a boutique business venture going, and one that certainly no longer employs only shovels for cyst collection.

We mentioned evaporative salt ponds, or salterns, that importantly yield *Artemia* cysts, but the other side of the coin needs to be presented as well! It turns out the presence of these animals in such basins is so beneficial to the economic production of salt, that if they are not present, they are usually introduced. The rationale for this action lies in the fact that *Artemia* is a filter feeder, and each little animal can remove from suspension 6.4-10 million cells a day, and when there may be as many as 3,300 animals in a cubic meter of water (at least in Mono Lake; Mason 1963) you can understand why water clarity is enhanced with their presence. With clearer water, more light reaches the pool bottoms, greater heating is attained, and a higher evaporation rate achieved, obviously resulting in greater efficiency of salt production (Browne 1993). Of course, that means $$$. So, chalk up another chunk of "the economy" to *Artemia*!

Scaling down from salt lakes and evaporative salt ponds to the minuscule size of an aquarium, scientific researchers often maintain their aquarium stocks, usually fishes, with brine shrimps, and of course most aquarium shops have a supply of *Artemia* or "sea monkeys" to sell as live food for their customers' neon tetras and other exotic aquatic creatures. Anderson (1984) wrote in praise of the anostracan *Streptocephalus sealii* as a food for freshwater aquarium fish. He noted that, unlike *Artemia* which dies in a short time in fresh water and, if not eaten, must be removed before fouling the water, *Streptocephalus* lives just fine until devoured. Perhaps a similar rationale prompted Dallas Weaver, of Scientific Hatcheries in Huntington Beach, to mass produce the yummy beavertail fairy shrimp *Thamnocephalus platyurus* for a time for use by aquarium hobbyists. We don't know the average number of cysts a female made throughout her life in Dallas' production facilities, but whoever goes into the business of mass producing fresh-water fairy shrimps ought to consider involving the African species *Streptocephalus proboscideus*. Luc Brendonck (1991), using a recirculating rearing system with "intensive water control", coaxed one individual to live 103 days, produce 83 broods of cysts, and thus bring the almost unbelievable number of 15,189 new fairy shrimp propagules into this world. Of course all females, perhaps thankfully, cannot accomplish such a feat. However, such massive cyst production is reported nowhere else in the literature, and, if this be an especially amorous and fertile beast, we fully expect someone to "acquire" its services.

Eating of fairy shrimps is mainly undertaken by aquatic insects, and wading and diving birds.

Thus, in the ecological scheme of things, fairy shrimps are important links, even if transitory, in the food chains of many of our migratory fine-feathered friends (Silveira 1998). In turn, fairy shrimps typically get their food energy by filtering bacteria-laden particles and microscopic plants and animals from the "biological soup" in which they swim. So, should a pool be lost to development, or poisoned by toxic runoff, the birds find either no resting, nesting, and feeding grounds, or no fairy shrimp food-source in the polluted waters upon which they might unfortunately come to rest. In either case, less food means fewer birds. Toxic water may mean dead birds. Even if most of our citizens are not particularly moved by the corpse of a fairy shrimp, they do seem to understand that fewer birds, or dead birds, signal significant ecological disorder. Food chains can then be appreciated as important, and in this way issues of loss of habitat and species, or habitat degradation, are brought closer to home. Such issues may even be dramatized for some when a species which is the "apple of their eye" is seen to be vulnerable because of harm done to a "significant other"...such as a fairy shrimp population.

If harm is done to the creatures with whom we share this planet, we usually find it ultimately damaging to humans as well. In this regard, miners have long been known to take canaries into their underground tunnels to test the air for toxic gases. In a similar vein, concerned scientists have tested a number of the ecosystem's creatures, fairy shrimps amongst them (Centeno *et al.* 1993a,b; Mizutani *et al.* 1991; Moss 1978), to determine their sensitivity to pollution levels which cause stress or death. Few anostracans have actually been evaluated to date, so there is not yet a pronouncement concerning their importance for this purpose.

Hundreds and hundreds of scientific papers and reports record studies of the brine shrimp from egg to adult. Such a wealth of information has provided the most detailed look yet into the biology of any anostracan. Perhaps more importantly, investigations using *Artemia* as a model organism have illuminated the workings of a myriad of biological processes – from genetics to gerontology, sex to salt secretion, and dormancy to distribution.

Before leaving this topic of "what good are fairy shrimps", we take cognizance of the fact that many humans find value in things and activities that do not require selling, serving, or sacrificing something for the almighty dollar, or peso, or yen. Nurturing the soul with beauty certainly fits this category, and amongst pool life, fairy shrimps never fail to offer such a quality. Over the years that your authors have taken their students of many interests and ages on field trips, and peered into trays of lake or pool netting's, we cannot remember a time when the observers did not express a "WOW" at the beautiful appendage beat or fairy-like trajectories of the fairy shrimp's body. Those present when anostracans with orange tails dashed in front of them never refrained from exclaiming: "look at that"! Those who saw bodies of spectacular deep green-blue, apple green, or red never kept from stating pleasure in their viewing, nor did they tire easily and wish for a video arcade. Only the field trip's evening meal seemed a strong enough stimulus to drag the last of the lookers from the dissecting microscope mounted on the truck's tail gate. Of course not everyone who visits with fairy shrimps carries home a burning desire to study them, the world of life is too amazing and diverse for that. But a surprising number do, and because the involvement and enthusiasm of one individual seems to stimulate another, each of your authors has had more students studying fairy shrimps than can be counted on the fingers of both of your hands.

Certainly it is true that the world of academia has seen more scientists in white lab coats observing white lab rats than fairy shrimps; however, we cannot refrain from pointing out that a considerable number of biologists, with names you will see repeatedly in this book and in the literature dealing with Anostraca, like Sarane Bowen, Graham Daborn, Ralph Dexter, and James Lynch, "...have found the study of these interesting...animals a rewarding activity". It was Walter Moore, a biologist at Loyola University of New Orleans, who wrote those words in 1959. He also included some others that we could not resist reprinting here – you'll see why!

"BUT WHAT GOOD ARE THEY?? (Fairy Shrimps, that is). In the fifteen years or so that much of my time has been devoted to the collection and study of the branchiopod Anostraca the above question has been posed to me more times than I like to remember. I can expect to hear it whenever a farmer, field hand, or motorist has stopped to watch the curious spectacle of a middle aged man carrying a dip net and wading up to his waist in a muddy ditch or pasture pond. It follows inevitably after the initial question, What are you trying to catch?"

"Sometimes when I have grown tired of going through the same conversational gambits for the tenth time in a single day I take the cowardly way out and forestall further questions by announcing that I am dipping for mosquito wigglers. Everyone, apparently, is satisfied that dipping for mosquitoes is a legitimate and praiseworthy activity and further conversation is usually terminated after the exchange of a few pleasantries about how bad the mosquitoes are this year. More often, however, my bucket or jar of recent captures is resting on the bank, giving the lie to any such response. And, since I like to talk about fairy shrimps, I repeatedly find myself trying to explain to some skeptical passerby why I go to the trouble of collecting an animal I have no intention of using either as food or bait". "...if the fairy shrimps were suddenly to disappear from the face of the earth...I suppose few would even notice the difference. Among these, however, would certainly be numbered those biologists who have found the study of these interesting though much neglected animals a rewarding activity".

Let there be no mistake, in addition to Walter Moore, the scientist just quoted, and undoubtedly Donald Wootton, the educator to whom this book is dedicated, your two authors, Denton Belk and Clyde Eriksen, count themselves among those biologists who have been richly blessed by their travels, field work, and friendships with fairy shrimps.

Chapter 2

BIOLOGY OF FAIRY SHRIMPS: HOW THEY ARE PUT TOGETHER AND HOW THE PARTS WORK

External structures and their functions

The stereotypical fairy shrimp possesses a cylindrical body composed of a head, thorax, and abdomen. The **head** includes the brain, stalked compound eyes, first and second antennae, and mouthparts. Remember, it does NOT possess a shield in today's models, the last one having vanished with the demise of some now-fossil anostracan between 525 and 390 million years ago (Walossek 1993). A **thorax** adjoins the head and has paddle-like locomotor appendages, **phyllopodia**, and sexual structures attached. Last along the body is an **abdomen** which sports at its terminus a pair of fringed projections called **cercopods** (equal to cerci of other arthropods). When all of these parts are laid end to end (Fig. 1.2, p. 2) you would have a mature fairy shrimp 10-40 mm in length. There is one exception though, and that exception is the stretch-limousine of anostracans, the raptorial giant fairy shrimp *Branchinecta gigas* (Fig. 4.1, p. 73) which reaches the mind boggling length of 150 mm (almost 6 inches).

In hearkening back to an earlier discussion, let us reinforce the fact that fairy shrimps are among the most primitive living crustaceans, that status being indicated by the ancient type of paired appendages ("legs") on each of the first 11 (in California species) of the 13 thoracic segments (Fig. 1.2, p. 2). Because of the importance and antiquity of these phyllopodia, we have chosen to begin our more detailed discourse on fairy shrimp architecture with them and the portion of the body to which they are attached, the **thorax**.

You already know that these "legs" are paddle-like, thus used in swimming. The fact that they are referred to as phyllopodia, meaning leaf-feet, suggests a broad, thin form, and this is true. The extremity of the appendage is composed of two branches and therefore is said to be **biramous** (bi = two; ramus = branch). Both branches, the medially directed one called the endopod and the laterally placed one referred to as the exopod, are attached to a basal piece named the basipod. The basipod also possesses some small lobes which include 6 small medial endites, and a larger lateral preepipod (pre = before; epi = upon) and epipod. The latter is particularly thin and thus is said to be a gill (**branchium**). Except for this gill, all edges of a phyllopodium are adorned with **setae** and, in some species, **spines** (Fig. 3.1, p. 47).

Appendage movement begins at the front (anteriorly) and passes to the rear (posteriorly) in a series of continuous mesmerizing waves. Because of their large surfaces and rhythmic motion, these "paddles" propel the fairy shrimp in graceful trajectories through the water, a character of motion probably responsible for the "fairy" part of our subject's name. Because great surface area and thin coverings are also characteristics of surfaces through which oxygen and other chemicals are exchanged, the whole of each phyllopodium, along with its branchium, undoubtedly serves as a gill and, in the cases that have been studied, as a site of salt exchange as well. The long, thin, fringed setae bordering most of the edges of the phyllopodium form a delicate meshwork with a particular pore size, which probably varies with