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

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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

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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 crisscrossing 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.

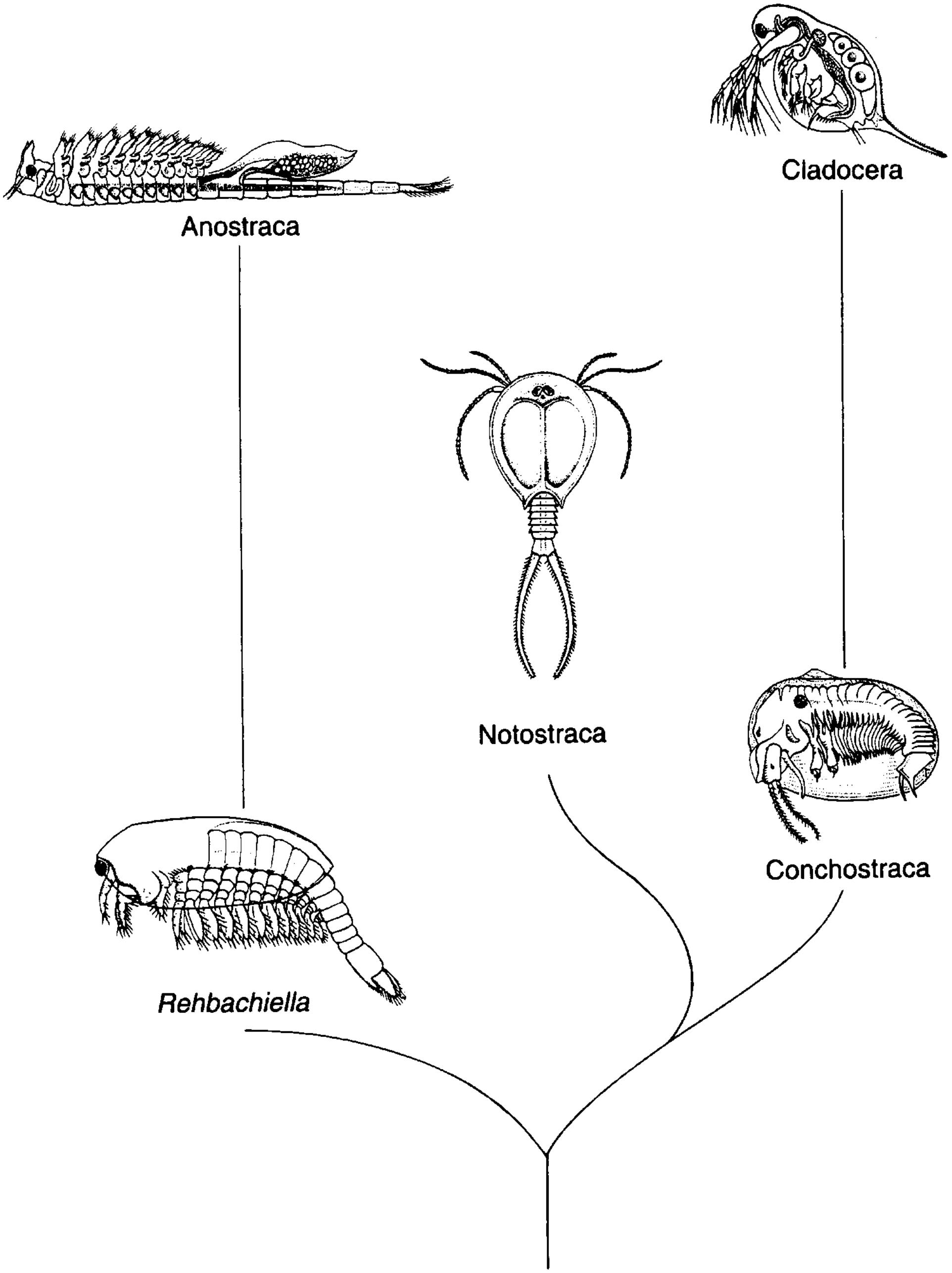


Fig. 1.1. Family tree of the branchiopods. The representative animals are positioned relative to each other at the approximate level of their group's origin based on fossil evidence. Except for *Rehbachiella* which is extinct, all the others are part of the biodiversity of our modern world. This scheme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

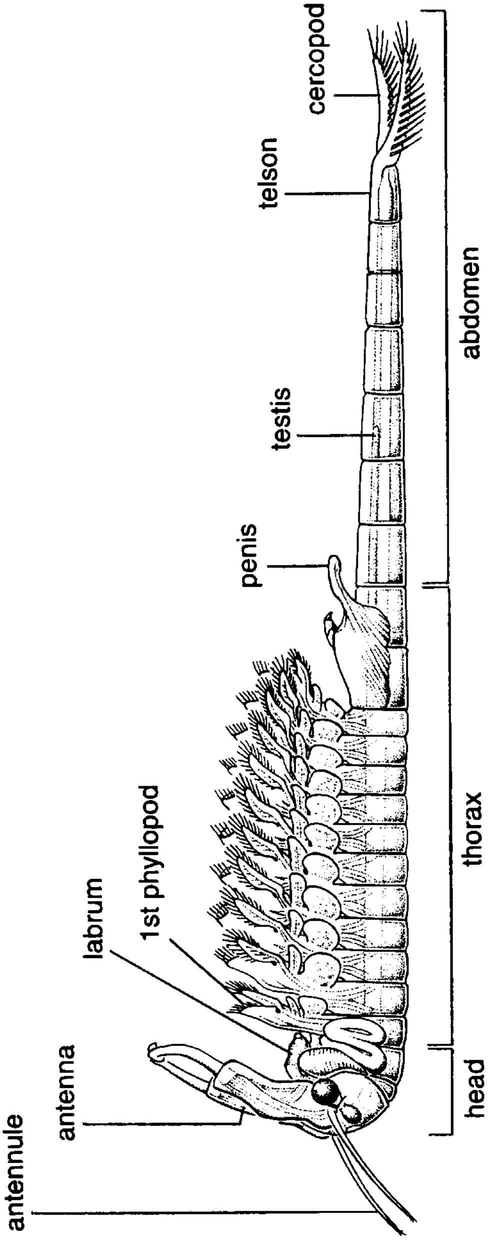


Fig. 1.2. Lateral view of a male *Branchinecta lynchi*.

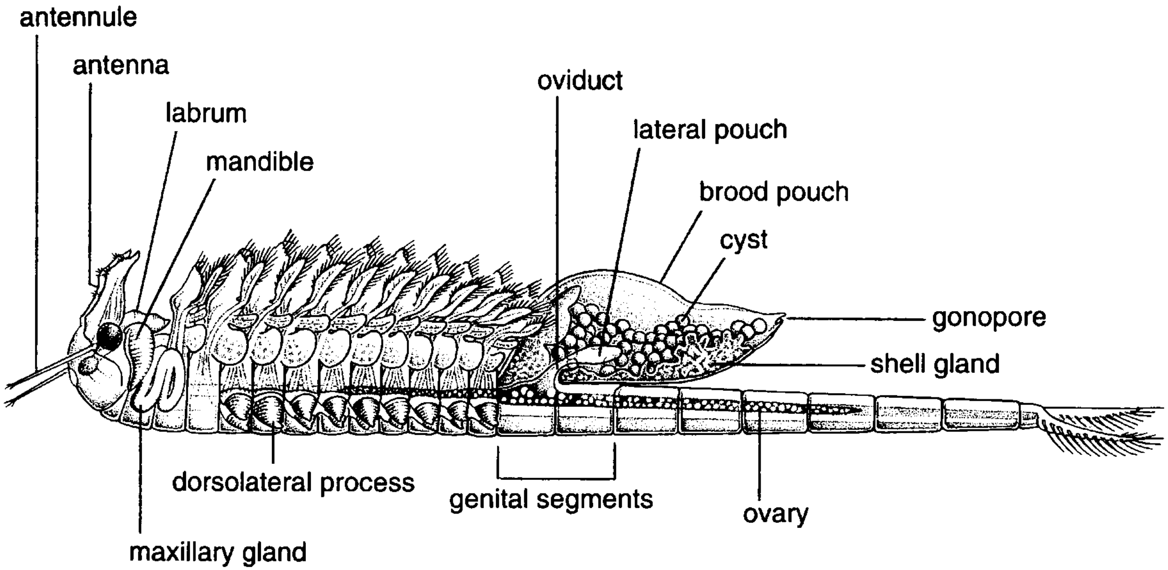


Fig 1.3. Lateral view of a female *Branchinecta lynchi.*

(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 life stage and species (Mertens *et al.* 1991). As appendages return forward from a beat, a low pressure is created between them causing water to flow in (be "sucked" in) with its dead particles, and living organisms too if they are unable to swim against the flow. When the phyllopodia beat once more, whether in graceful swimming or bottom scraping, increased pressure forces water through the setal meshwork and particles too large to pass through its pores are sieved out, whether living or dead, plant, animal, or mineral, nutritious or not. These particles are moved to a **food groove** between the bases of the phyllopodia, then passed along to the jaws and mouth by specialized spiny lobes at the base of each appendage. For an excellent discussion of anostracan feeding mechanisms, see Fryer (1983).

For those of you who enjoy history, it may be of interest to know that until just recently a fairy shrimp's **two fused genital segments** were thought to be part of its abdomen because, like that portion of the body, they lacked phyllopodia. However, certain perceptive and dogged scientists (e.g., Walossek 1993), noting that sex ducts of related fossil and living branchiopods all open on phyllopodia, that the embryology of the genital segments is more similar to thoracic than abdominal development, and that the penes of the male are actually derived through evolutionary modification of a pair of phyllopodia, have finally persuaded skeptics that the fused genital region truly belongs to the thorax! That issue settled, we can now rest in peace with the notion that the posterior portion of the thorax is the focal point for the reproductive organs and their accessory internal and external structures.

Internally, **ovaries** and **testes** are paired, blind tubules that lie alongside the gut, mainly in the abdomen, but in some species an anterior branch extends further into the thorax as well. The male's two **penes** protrude from the ventral surface of the fused 12th and 13th segments of the thorax (Fig. 1.2, p. 2). Yes, you read correctly, males actually have two penes. Each lateral testis empties through only the penis on its side of the body.

In females, **oviducts** extend from the ovaries and enlarge at their distal ends into what are called **lateral pouches**. These join one even larger structure called an **ovisac** which also receives ducts from several **shell glands**. The ovisac expands within the **brood pouch** which is a centrally placed and posteriorly directed protrusion from the ventral body wall of the fused genital segments (Fig. 1.3, p. 3). The opening of the ovisac to the outside is the female's **genital pore**, the site that male sexual behavior is aimed at entering for insemination. Rather detailed illustrations of this system can be seen in a paper by Brendonck (1991).

The **head**, the most anterior portion of the body, is situated immediately in front of the thorax, and bears the **mandibles** (jaws) and other tools. Rotating action of the mandibles helps crush and push food into the mouth (Fryer 1966). The grub is moved to the teeth-like mandibles from the thoracic food groove by two pairs of small head appendages located immediately behind the mandibles, the **maxillae** (Manton 1977). Unlike the teeth of humans and your pet goldfish, but similar to a grasshopper or lobster, a fairy shrimp's mandibles are not within its mouth cavity, rather they flank and ultimately cover the mouth. Immediately anterior to the mouth, and overhanging the mandibles, is a lobe or mound called the labrum, or "upper lip", which effectively prevents leakage from between the mandibles and serves as a backstop for food that might otherwise be pushed further forward. This device thus assures that mandibular action gets all of the food into the mouth. No messy face here!

More forward yet are one pair of large,

stalked, **compound eyes** and two pairs of antennae, referred to as **antennules** and **antennae** (Fig. 1.3, p. 3). In males, the antennae are large, and possess a variety of processes and appendages, as well as ridges and mounds which may be ornamented with spines or denticles (check out the many examples on pages 143-165). Because antennal shape and ornamentation apparently aid a female in choosing a mature mate, such features differ from species to species (Belk 1991a). As might be imagined, the crafty fairy shrimp taxonomists have learned to use the male antennae, with their bumps, processes, and acne-like ornamentations, as the main distinguishing characteristics of species.

The **abdomen** is continuous with the posterior end of the thorax and bears at its terminus a pair of setae-fringed, fluke-like **cercopods** (Fig. 7.1, p. 140). These cercopods are used in concert with abdominal musculature in turns as well as in rapid escape locomotion much as beavers, whales, or lobsters would employ their tails and bodies. Should you touch a cercopod you may stimulate a flurry of such behavior, so it seems these structures serve a rear-guard sensory function as well.

Circulatory system

So far our discussion has dealt with fairy shrimp parts that "meet the eye". But how about its "innards"? We begin with the circulatory system, a fascinating component of internal structure. Unlike your closed system of blood vessels, the fairy shrimp has an **open circulatory system** to transport oxygen, digested food materials, hormones, and wastes through its body. The system is said to be "open" because the long, dorsal, tubular heart pumps blood anteriorly into the head region, whence it flows posteriorly through body spaces largely under the force of muscles contracting for other body functions. In other words, there are no arteries, capillaries, or veins, and the heart is not the only propulsive force (Greene 1924). Blood thus surrounds and bathes all body organs, flows out into all appendages where the majority of oxygen uptake from the environment is thought to occur, then generally moves posteriorly where it re-enters the heart via valved openings called ostia.

If you want to see a thing of beauty and perpetual motion, isolate a fairy shrimp in a small volume of water (a clear-plastic box 2-4 cm across works fine) and observe it carefully with a magnifying glass or dissecting microscope. If you can take your eyes off the continuous motion of appendages and look inside through the thin, semitransparent exoskeleton, you will not see defined body spaces filled with blood. What you will observe above the dark, food-filled gut is the dorsal, elongate heart pumping rhythmically and continuously to the beat of its unseen metronome – the heart pacemaker.

The blood, called **hemolymph**, is usually colorless, and it contains cells, the movement of which will allow you to trace the general direction of blood flow (Greene 1924). At times the hemolymph may contain dissolved, not cell-bound, **hemoglobin**, which of course is a red, iron-based respiratory pigment. Because the exoskeleton is so thin, this internal color makes the animal appear reddish. Under conditions of plentiful oxygen hemoglobin is absent (why make it if you don't have to?), but in those species having the genetic ability, hemoglobin appears to be synthesized in response to low environmental oxygen levels, allowing the animals to increase the supply of oxygen carried to their tissues.

Oxygen: its procurement and regulation

Oxygen (O_2) is required for metabolic processes from which energy is released to accomplish bodily work like locomotion, growth, egg and sperm production, and all that sexual activity we will speak about with biological frankness later in the chapter. Aquatic creatures must not only take in sufficient O_2, but most must also maintain the rate of its intake, though some species may possibly just "tough it out" in the face of a pool's decreasing supply; and a reality of pool life is that the quantity of O_2 does rise and fall, sometimes drastically, even within a few hours. Oxygen, when in its greatest concentration in water, is present in minuscule amounts compared to air. While the atmosphere contains approximately 200,000 parts of O_2 for every million parts of air (ppm), water, at its maximum, is capable of dissolving only slightly less than 15 ppm, and the amount actually available dwindles from there! Scary, eh?

There is importance as well as fascination in understanding the physical and biological relationship between the amount of O_2 in an aquatic environment, and the latter's temperature, salinity, and susceptibility to being mixed by wind. Remember, these factors are among the most conspicuous and significant actors in the dramatically-changing conditions typical of temporary waters. Before we mention the effects of these environmental agents on species, an enthusiastic discourse on their interrelatedness seems warranted.

Most temporary waters are small in volume and possess large surface areas compared to their depths. These characteristics generally assure that the water is well mixed by wind and thus supplied with oxygen throughout. During winter and spring the atmosphere is cool and breezy, so the pools mirror these amiable conditions, and O_2 is seldom in short supply. However, warm, calm days in the environs of temporary waters are not uncommon, and, as the water heats at such times, its capacity to dissolve oxygen drops. Warming water also speeds up evaporation, consequences of which are the concentration of its dissolved salts and, therefore, the further reduction of its O_2 content – strikingly so in briny waters. The big problem is that in the face of these reductions the consumption of oxygen by pool creatures increases dramatically as their metabolic rate is elevated by higher temperatures. To make matters worse, atmospheric oxygen is not redistributed to the pool's volume at times of atmospheric calm. Should the habitat contain phytoplankton or submerged aquatic vegetation, O_2 is added to the water by photosynthesis during daylight hours; but at night all of the pool organisms, plants included, continue to consume the absolutely necessary but limited supply of dissolved oxygen. As a consequence, O_2 may decrease dramatically until the time "ol' Sol" begins again to brighten the morning sky.

Having said all of that, we must now advise that not much is known about how fairy shrimps gain their oxygen and cope with drastically changing concentrations. Of course most aquatic animals obtain O_2 from the environment via gills. Where then are the gills of fairy shrimps? We have already described how the phyllopod appendage is composed of several leaf-like lobes, one of which has been referred to as a gill. Undoubtedly these lobes serve in the intake of oxygen, but their combined surface-area is probably too small to account for the total volume of O_2 needed by a fairy shrimp given the energetic demands of constant swimming.

Large enough or not, Modlin (1985) suggests that species with a propensity for greater activity have larger gills than those which are less active. For example, he observed that *Eubranchipus holmani*, a constantly swimming, plankton-eating species, has gills 1.5 times the size of those of *E. neglectus* (misidentified as *E. vernalis*), which he suggests has a less energetic life-style because it sometimes feeds by scraping the bottom sediments and occasionally rests on the bottom while there.

Whatever the case, we believe that the surface area of the gills is still too small for sufficient O_2 intake when the fairy shrimp is faced, because of increasing temperature, with an escalating metabolic rate and scarce environmental oxygen supplies. Why do we say this with such authority? Well, partly because of some limited research on fairy shrimps, partly because of your first author's research on aquatic insects, and partly because of the characteristics that define a respiratory surface. Read on for the arguments.

Intuition tells us that a **large surface area** can allow more oxygen to pass through it per unit of time than a smaller one. The hemolymph within the **circulatory system** then courses through the gill to carry off the O_2 that enters. **Thinness** is a virtue because the distance that oxygen must travel from the environment outside to the hemolymph inside is minimized. Obviously the longer it takes to move O_2, via diffusion, to the circulatory system, the less the total amount that is transported to the tissues in a given period of time. And of course too much cellular bulk in a gill means that much of the O_2 would be used within the tissues and not be carried away at all. Oxygen needs to dissolve in water before it can pass through a respiratory surface; therefore, such surfaces must be **moist**. Maintaining moistness is not thought of as a problem for gills, of course, because only aquatic organisms possess them. However, it helps explain why gills do not function when they dry out. Finally, water containing the needed O_2 must be constantly renewed next to the intake surface, for with use the surrounding supplies dwindle into insufficiency. The renewal process is called **ventilation**, and may be actively accomplished by the animal, or passively provided by the environment flowing over the organism. When you breathe, you ventilate your lungs. The fairy shrimp breathes by beating its phyllopodia, a process which not only moves our favored creature through the water, but also passes water over its respiratory surfaces thus ventilating them as well.

Given these criteria for respiratory surfaces, one can see why a particularly blood-rich portion of an appendage might be considered a gill. But take note, as did Martin (1992), that the rest of the phyllopod is also thin, as is the exoskeleton and epidermis of the remainder of the body, particularly the thorax and abdomen; he concluded, therefore, that these surfaces undoubtedly also play a role in the uptake of oxygen. We confidently agree with Martin's conclusion for two reasons. Firstly, Gilchrist (1958, 1960) seems to have demonstrated that the male of *Artemia franciscana*, whose second antennae have very large blade-like portions, uses these surfaces for O_2 intake. Secondly, Eriksen (1986) and Eriksen and Moeur (1990) have shown that, for several aquatic insects, the general body surface, particularly the abdomen, is vitally supplemental to the gills in O_2 uptake.

No matter the extent of the respiratory surfaces, the ability to maintain a constant intake of oxygen through them in the face of a dwindling supply (**respiratory regulation**) is particularly important for organisms which dwell in habitats whose O_2 supply varies greatly throughout the day. If you wonder why regulation is so important, consider what would happen to your activity if your metabolism was yanked around by a drastically changing environmental O_2 supply because you could not increase or decrease your breathing rate in order to keep oxygen intake steady. Our guess is that you, and any other beast, would be at a serious disadvantage when in competition with creatures who, like Energizer batteries, "just keep going , and going, and going" at a constant rate.

The only anostracans whose O_2 intake have been determined over a range of environmental oxygen concentrations are *Branchinecta mackini*, the alkali fairy shrimp (Eriksen & Brown 1980b), and, yes, you guessed it, the brine shrimp, *Artemia franciscana* (Gilchrist 1954). Using these species as suggestive models, we can probably pronounce with some "ball park" assurance that fairy shrimps are respiratory regulators. You and the authors of this book regulate O_2 intake by changing the rate of our breathing as our needs vary. Fairy shrimps undoubtedly accomplish the same effect by varying the beating rate of their appendages. As useful as this ability might be over a range of oxygen concentrations, it has its limits at some genetically-determined low critical-level of oxygen. The particular level is "critical" because below that amount the animal is unable to obtain enough O_2 to sustain its metabolism and thus its necessary activities. For adult *B. mackini* tested at 12°C, this low critical-level lies between 1.4-2.9 ppm of oxygen, depending on the exigencies of the habitat to which the population is acclimated. Good ol' *Artemia* also falls within this range, 2.3 ppm, even though its test temperature was about 10°C higher (23.5°C). At lower temperatures, the critical level is undoubtedly lowered as well because the metabolic rate, thus the demand for O_2, declines. However, when water is below 10-15°C, low oxygen is seldom encountered.

To the contrary, when temperatures are higher, say 20° or 30°C, O_2 is more scarce and metabolic rate is considerably elevated, so the low critical-level of oxygen will undoubtedly be significantly higher. Perhaps this conflict of increasing temperature, metabolic rate, and O_2 need, in the face of a dwindling supply, is one of the reasons that most California fairy shrimp species appear during winter and spring. Among the 23 kinds of anostracans that swim in California's wet spots, only 5 might be considered "warm-water types", that is, fairy shrimps that will not hatch until water temperature exceeds about 15-17°C and which can do well as adults in temperatures exceeding 25-30°C.

If indeed cool- or cold-water fairy shrimps do not usually have a problem with the environmental O_2 supply, how is it that the few species whose little lights shine in warmer water succeed in what must be significantly lower O_2 concentrations? Once more there are few studies and therefore little in the way of definitive answers, but in reaching for at least some educated guesses to pass along to our readers, we return again to *Artemia* the brine shrimp, *Branchinecta mackini* the alkali fairy shrimp, and a warm-pool anostracan, the intriguing beavertail fairy shrimp *Thamnocephalus platyurus*, to serve as possible models.

Beginning with the last species, Hillyard and Vinegar (1972) noted that when pool temperatures were great, thus dissolved oxygen low, individuals of *T. platyurus* would repeatedly come to the surface where O_2 was assumed to be higher "...and appear to ventilate, with their respiratory appendages stirring the surface...." Thus when low O_2 is a problem, behavioral responses appear to keep fairy shrimps in the highest oxygen concentrations available. These same fairy shrimp enthusiasts determined that the metabolic rate of *T. platyurus* varied little with temperature change, particularly at the warmer conditions in which they often swam. Such thermal insensitivity is not at all common amongst organisms, but it does occur, and here we find it used to the advantage of a warm-water fairy shrimp.

More typically, metabolic rate doubles or triples for each 10°C increase. *Branchinecta mackini* is known to fit this scheme. Of course, like the world population, metabolic rate cannot keep doubling. At some temperature it reaches its peak, then declines, and finally the animal dies. For *B. mackini*, its peak metabolic rate is expressed around 8-10°C below its upper lethal temperature of about 32°C (Eriksen & Brown 1980b). Such a wide thermal span above its metabolic maximum suggests this desert anostracan, like some warm-water creatures, can "hang tough", that is, can tolerate the increasingly less favorable conditions as temperatures rise from those which are physiologically optimal. Such a conclusion makes sense because this fairy shrimp is one of the few California species that is occasionally found "doing its thing" in desert flash-flood-formed pools during summer when tolerance is undoubtedly a virtue. However, so as not to lead your thinking and conclusions astray, take note that *Branchinecta mackini* occurs over a temperature range unique among California Anostraca, and, in fact, is most commonly found hatching and swimming in cold and cool waters.

Without scientific studies of strictly cool- or cold-water fairy shrimps to demonstrate how their metabolic rates and tolerance physiologies might work differently, we are left out in the cold (so to speak) for an answer. Coincidentally, *Branchinecta mackini* and its notostracan relative, the tadpole shrimp *Lepidurus lemmoni*, sometimes occupy the same spring pools. If we were to use our research data from this cool-water tadpole shrimp (Eriksen & Brown 1980c) as a suggestive model for how a cool-water fairy shrimp works, we would expect to see little tolerance in the latter of environmental conditions that exceed those at which it demonstrates its maximum metabolic rate. In fact, once that magic temperature is surpassed, metabolic rate would decline catastrophically and the animal would soon die.

But back to survival in warm-water, low-oxygen habitats. As the last solution we can muster, remember that a supplementary method of obtaining and distributing O_2 is available in the form of hemoglobin; that is, hemoglobin binds far more O_2 than could be dissolved in blood without it. Hemoglobin-bound oxygen is picked up from the relatively high O_2 concentration at the body's surface and released in the lower-oxygen environments of tissues. Although hemoglobin has not been documented in all fairy shrimps, Denton has observed red coloration at one time or another in a number of species and, believing its source to be hemoglobin, feels that most species, if not all, can probably synthesize the pigment. If this be the case, then it appears that hemoglobin is made and utilized only over extended periods of tough times as is the situation with *Artemia* (Gilchrist 1954). Keep your checklist handy for recording such occurrences!

Water, salts, and liquid wastes: their regulation

Anostracans live in habitats with amazing extremes of alkalinity and dissolved salts. Combined, these are sometimes referred to as salinity, but we will use the more appropriate term **total dissolved solids** or **TDS**. Just as amazing is the fact that not all that much is known about how fairy shrimps accomplish the feat of dealing with this fantastic spectrum of ionic materials (the dissolved charged particles which in total result in the osmotic concentration of the medium: e.g., Na^+, K^+, Ca^{++}, Cl^-, $CO_3^=$, $SO_4^=$) and the influx or efflux of water that occurs as a result. As a generality, think of the problem this way. All organisms have a certain concentration of various materials in their tissues and blood. If that level strays very much from a given norm, the beast is in big trouble. You are probably quite aware of that for yourself, given all the emphasis your doctor undoubtedly lays at the altar of blood tests.

For an aquatic creature, like our fairy shrimp, water is the medium in which it lives, and that medium moves into or out of its body depending upon whether environment or organism has more water per unit of volume. If water outside is "fresh" and thus contains little dissolved material, water will move into the body where there are relatively more dissolved materials and therefore less water. If this process continues, our aquatic creature soon has a volume problem, and must make its "bladder gladder" by urination. If the surrounding briny medium contains more salts and less water than an equivalent volume of blood, water will move out of the organism, thus dehydrating it. This natural and passive process of water moving from its higher to its lower concentration, into or out of any living thing, is called **osmosis**.

To put all of this into the fairy shrimp's world, imagine the different osmotic consequences of dwelling across the full range of anostracan habitats: arctic-alpine, temperate, and desert pools. The former are typically environments with very little dissolved material of any kind. The fairy shrimp, on the other hand, is relatively loaded with salts, and so water moves into its body, soon presenting it with an excess. At the other extreme, evaporative desert pools often contain higher levels of dissolved chemicals than does the animal, water tends to move out, and dehydration is a danger.

How do anostracans compensate for these ranges of TDS and osmotic water movements? With the aid of the 9 species that have been studied in this way, four of which occur in California, we make the following general remarks. In order to maintain blood at ionic and osmotic concentrations different from that of the environment, that is, to transport substances in a direction opposite to their normal passive movement, fairy shrimps (yea, all animals) must expend energy in a process referred to as **active transport**. *Artemia franciscana*, which resides in California's most briny waters and "...can tolerate a wider salinity range than any other multicellular organism...." (Browne 1993), relies on this process to maintain the concentration of salts in its blood at a level lower, often considerably lower, than that of the environment. Referred to as **hypo-osmotic regulation**, this physiological ability requires several steps, and a relatively impermeable body surface so that the natural tendency of water to move out and salts to move in is considerably decreased (Croghan 1958b). First, *Artemia* drinks its salty milieu. Because the gut must be highly permeable to allow products of digestion to enter the hemolymph, salts from the water that it engulfed also enter. Second, because NaCl in the blood is maintained at an elevated level over that in the gut, active transport must be responsible for the difference. Because tissues generally have not evolved a mechanism "...that can...transport water against large osmotic gradients.", by actively taking up NaCl, the tendency for water to move osmotically from *Artemia*'s tissues to its intestinal fluids is lowered to "...a level that the active mechanisms for water uptake can overcome." (Croghan 1958d). In this way, the animal gains water from a very salty environment that otherwise would passively dehydrate it. Third, and lastly, because the increasing NaCl content of the blood cannot long be tolerated, *Artemia* must actively transport the excess back into its surroundings. It does this not at the gut surface but via specialized salt-secreting cells in the epidermis of the branchiae of the swimming appendages (Croghan 1958c).

Some California fairy shrimps, like *Branchinecta mackini, B. gigas*, and *B. campestris*, are found in pools which vary widely, both geologically and seasonally, in their dissolved salt concentrations. When the environmental TDS is low, individuals of these species maintain body fluids at a more or less constant osmotic level above that of their pools (**hyperosmotic regulation**). Regulation continues until the concentration outside equals the concentration inside (**iso-osmotic** point). As salts in their pool water rise further, the animals then **osmoconform**, that is they "mimic" the TDS of the fluid in which they swim. However, once the dissolved materials in the blood increase to a point that is no longer physiologically tolerable, the animals perish. A greater tolerance of salt in body fluids explains why *B. campestris* can be found in saltier environs than *B. mackini*, as well as why the latter may occur at times in more concentrated solutions than *B. gigas* (Brock 1988). California species have not cornered the market on this mode of physiological adaptation. In the land down-under, Geddes (1973) noted similar adaptations in two Australian species of fairy shrimps .

Finally, there are anostracans that live under the narrow constraints of water nearly as dilute as the rain. For these moderate- to high-altitude species, the problem is to get and keep salts, and to pump out the water that is constantly moving in osmotically. Although none of the California species living in dilute environments have had their water and body-solute regulation studied, several European fairy shrimps dwelling in similar habitats are known to maintain their blood at an osmotic level higher than the medium in their pools, which is to say they are hyperosmotic regulators (e.g., Panikkar 1941; Ralph 1967). These species have adapted differently from those just discussed in that they are able to regulate the concentration of their body fluids in waters of much lower salt concentration ("soft" waters), but die when the environment is saltier than themselves because to osmoconform means death. Horne (1968) believes that because all branchiopods have blood osmotic concentrations much lower than other crustaceans (Potts & Parry 1964), thus a lower osmotic gradient between body and environment, these creatures osmoregulate more easily in freshwater. Assuming this to be true, the ability would contribute significantly to the success of fairy shrimps in very dilute habitats.

In the process of osmoregulation, animals differentially regulate ions. In other words, while one ion in the blood is increased to some level, another may be increased or decreased to a different proportional concentration. Having said that, what do we know about the ion-regulatory ability of anostracans? Little! Six of the 8 species that have been investigated in this way dwell in California. Although ion regulation of K^+, Ca^{++}, Mg^{++}, and Cl^- has been briefly studied, most work has dealt with Na^+. For example, Horne (1968) demonstrated that Na^+ was actively taken into the body of *Eubranchipus bundyi*, even in waters very low in Na^+, and concluded from this that the species was well adapted to dilute habitats. *Branchinecta sandiegonensis* and *Streptocephalus woottoni*, also inhabitants of dilute rain pools, *Branchinecta mackini* which lives in much more concentrated alkaline waters, and *B. lindahli* which dwells in both kinds of places, are described as being regulators of Na^+ over certain environmental ranges. In habitat concentrations above and below their regulatory ranges, these fairy shrimps are Na^+ conformers until they perish (Gonzalez *et al.* 1996). These authors explain the different distributions of the three species by how well they tolerate Na^+ conformity at either end of their regulatory ability. For example, both *B. sandiegonensis* and *S. woottoni* sustain their blood Na^+ levels in the face of quite low habitat concentrations. However, following the cessation of regulation at higher environmental Na^+ concentrations, and as its level in the blood begins to rise along with that of its pool, individuals begin to die; and so these species are restricted to waters of rather low-Na^+. Although *B. mackini* is able to keep blood Na^+ from increasing as rapidly as that of its habitat, the animal is a poor hyperregulator of the ion. Absence of this species in low-Na^+ waters suggests that low levels in the blood are not tolerated; by contrast, comparatively high blood Na^+ is endured as it conforms to elevated environmental concentrations, and so relatively high-Na^+ waters are suitable habitat. Except for minor details, these same trends were mirrored by two Australian *Branchinella* species for Na^+, K^+, and Ca^{++} (Geddes 1973). Continuing with the Gonzalez *et al.* (1996) study, *Branchinecta lindahli* is viewed as a creature which reacts in the same way as *B. sandiegonensis* and *Streptocephalus woottoni* in low-Na^+ environments, and mirrors *B. mackini* throughout the rest of the range tested. You may not be too surprised to learn, then, that *B. lindahli* is found in pools similar to those occupied by the other three species.

When fairy shrimps typical of so-called "soft waters" regulate osmotically and ionically, where do they obtain the needed salts? Remember that brine shrimps spend energy in the process called active transport to **counter** the natural movement of ions from the briny water in which they live to their lower body concentrations. Assuming active transport can function whether the normal osmotic direction be out of, or into, an organism, then such a mechanism, evolutionarily honed for soft-water anostracans, could account for movement of salts from lesser amounts in the pool to greater levels in the animal. Panikkar (1941) thought this to be true for the European fairy shrimp *Chirocephalus diaphanus* and further claimed that branchiae of the phyllopodia were where this was accomplished. Add to the possibility of active uptake of ions the fact that a modicum of minerals is ingested in food, and we have the best guess as to how our soft-water fairy shrimp friends gain and regulate their salts.

When you and I think of kidney function we tend to think of eliminating urine, a solution of mainly water and urea, the latter being a toxic nitrogenous waste produced in the breakdown of proteins. Although fairy shrimps may eliminate a small amount of urea in the water they pump out, about 75% of their nitrogenous waste is ammonia (Bernice 1972). Ammonia is a highly soluble gas and rapidly diffuses away from the animal through the same surfaces by which it takes up oxygen.

Several times we have made mention of fairy shrimps pumping out excess water, yet we have not identified the pumps. Adult anostracans possess **maxillary glands**, so called because their ducts open at the base of these head appendages. Such glands are remnants of excretory organs, analogous to kidneys, used by ancestors of crustaceans. Apparently they play only a minor role in salt regulation of present-day fairy shrimps; however, the best guess is that they still function as bilge pumps by dumping excess osmotically-derived water (Croghan 1958d).

Reproduction

Those people who are gently touched by intently observing fairy shrimp mating behavior generally subdivide the process into a series of actions (Belk 1991a) which could probably define their own. Such beautiful steps, so coldly enumerated, are: detection, orientation, station-taking, clasping, copulation, ejaculation, and disengagement (sigh!). Perhaps before discussing the intimate details of these activities, we must admit that there have not been all that many scientists who have studied such behavior. In fact, the generalizations of what goes on in the sex life of fairy shrimps come from only 10 of the more than 260 species described world-wide (Belk & Brtek 1995). However, Belk (1991a) believes these generalizations are reasonable "...given the morphological similarity of reproductive structures in the Anostraca...."

Observers have noted that males seem always on the prowl for mates, and while they have demonstrated detection of females by males involves vision, nothing has been established concerning the role of chemicals or water-borne vibrations as cues to males about possible mates. Were we analyzing humans, a male who had detected a female might next be seen to "make a pass" at his prospect. By contrast, fairy shrimps are sorta dull. Orientation merely involves swimming over to the vicinity of any promising object; but with station-taking the activity becomes more intimate. The male of most species moves in below the female (remember, fairy shrimps swim on their backs) and positions his head next to the dorsal surface of her genital segments. Just to demonstrate not all fairy shrimps practice the same routine, males of *Streptocephalus* and *Thamnocephalus* will place their heads just above the female's ventral brood pouch. However, from either position the result is the same. The male aligns his body with hers and follows her every scintillating move.

Satisfied that this lovely creature is for him, the male quickly grabs the female from behind with his antennae by placing them around her body between her last pair of legs and the anterior end of her brood pouch. In typical female fashion, this lady fairy shrimp not uncommonly resists the male's embrace by briskly thrashing about, an activity which often results in her escape. This certainly illustrates that throughout the animal kingdom, including humans, not all males are acceptable to every female at any moment, and that females are involved in choosing a male rather than merely being overwhelmed by any one that happens by and demonstrates active interest. Although not all the cues used by fairy shrimps in choosing mates are known, evidence suggests species-specific antennal shape and ornamentation do aid the female in choice of a male (Belk 1984).

Once the procedures for evaluating a prospective mate are complete, and the male in question is found acceptable, clasping occurs, an activity which may last only a few seconds in streptocephalids, thamnocephalids, and the branchinectid *B. lindahli*; several minutes in *Eubranchipus serratus*; a few hours for *Linderiella occidentalis*; or days as seems to be the case in *Artemia franciscana* (whew!).

During these swimming soirées, with the male in firm clasp of the female, he curves his body around her abdomen then attempts to insert one of his penes through her genital pore and into her ovisac. She will generally not allow his entrance if already carrying fertilized eggs. However, when ripe eggs are present several struggling efforts may precede ultimate success. Not surprisingly, successful copulation, which lasts from only a few seconds to several minutes, is very stimulating to the male, and he soon ejaculates. For those so inclined, sperm can be watched flowing into the female's ovisac in slow-mating fairy shrimps like those of the genus *Eubranchipus*. Watched or not, once the ejaculatory act is finished there seems to be no biological sense for hanging around, and the pair soon disengages. In the inseminated female, "shutters", which separate the ovisac from the lateral pouches where eggs have been stored, now open, allowing eggs to flood into the ovisac, mix with the sperm, and be fertilized (Criel 1980). The male, as males are sometimes prone to do, swims off to detect another female whose delicately beating phyllopodia and enticingly protruding brood pouch lure him to repeat the sex-behavior sequence. Ah, those insatiable males.

If one were to try to draw meaning from variation seen in the reproductive process just described, unsurprisingly, ecological realities are probably at its root. For example, fairy shrimps typical of hot, short-lived, fast-drying pools might be described as of the "wham, bam, thank you ma'am" type. In pool's with an intermediate longevity, fairy shrimps are more deliberate as they proceed through the reproductive process. Finally, long-lived waters sport species which stay in each other's embrace for an extended period of time; and why not, there is no need for hurry.

Development of cysts

Immediately after fertilization not only does embryonic development begin, but the shell glands of the female secrete chemical substances into the mix of seminal fluid and fertilized eggs. Then an amazing thing happens. This material forms a thick, usually multilayered shell around each developing embryo. Talk about "better living through chemistry"! By the way, this layering is not at all analogous to dipping fish sticks in batter then congealing it in place by frying. Instead, as the material solidifies different layers develop, some spongy, some solid (De Walsche *et al.* 1991; Lee *et al.* 1994); and of course the elaborate structural details developed in the various species also vary wonderfully. What controls formation of architecturally different layers, the variation within species, and the intricate differences among species, lies in the realm of the unknown.

Adaptive significance of structural differences among shell layers has been the subject of some conjecture. Structure is not just for structure's sake, so the suggestions are based on the universal relationship between the way something is built and its function. With regard to the spongy layer, its interstices are of course filled with fluid when formed in the ovisac; but when the cyst is deposited and dries, the moisture is replaced by air. The suggestion has been made that these spaces, like those in a down vest, offer thermal insulation to the cyst. Frankly, we find this supposed benefit difficult to imagine given the tiny size of cysts (0.15-0.40 mm) and the long periods of time they must withstand high or cold temperatures or both. A much better suggestion it seems to us is that trapped air makes cysts buoyant when water returns, a condition which helps elevate them from the sediment and allows them to float. Floating not only makes them subject to passive dispersal within the pool (De Walsche *et al.* 1991), but also places them in higher O_2 concentrations necessary for the energetic hatching process. If the cyst walls of fairy shrimps function as do those of clam shrimps, and there is no reason to believe they do not, then they also provide some physical protection from abrading effects of soil particles being moved by water or wind, as well as from lethal effects of ultra-violet light (Belk 1970).

Although we have commented on the amazing cross-sectional structuring of the wall of the cyst, we would be remiss not to inform you that its surface-sculpturing is just as amazing, and varied, and often species specific! (See Fig. 3.2, p. 56). Richard Hill of the Environmental Office of CalTrans in Sacramento and Bill Shepard of Cal State University, Sacramento, are working on a scanning electron microscope (SEM) photographic catalog for cysts of all California species. Watch for this one! But in the meantime, refer to work by Mura (1991a, 1992b) where you can see most of the cysts of *Branchinecta* species from North America, and California's *Thamnocephalus* and several of its streptocephalids. The publications of Brendonck and Coomans (1994 a,b), where cysts of *Streptocephalus* species of Africa are displayed, give you a good idea of the variety exhibited in this genus.

Concurrent with shell development, embryonic development, which also began immediately after fertilization, proceeds apace for a day or two. During the process the embryo molts (sheds its exoskeleton) once or twice, adding the shed membrane(s), the last of which is called the hatching membrane, to the inelastic and protective shell, or tertiary envelope, surrounding it (Belk 1987). When development reaches a late gastrula stage, further maturation stops, metabolism is drastically slowed, and the embryo is isolated from the environment by a membranous barrier through which only gases and water freely pass (Drinkwater & Clegg 1991). So, the **cyst**, or "resting egg", is really a shelled embryo, analogous to the seed of a flowering plant, in a state of suspended development referred to as **diapause**.

At this point the cysts of most species are ejected through the genital pore to fall to the pool bottom, or, like the Titanic, the female carries them to the bottom enmasse at the time of her death. In some cold-water species, however, development takes a relatively long time with the result that some of the process occurs after the cyst is dropped into the pool (Mossin 1986). If the female survives for an extended period, she will continue to move successive clutches of eggs into her ovisac, each clutch being fertilized by a new mating, most likely with a new male. However, each batch of eggs undergoes development and ejection before the next clutch can be similarly processed. In long-lived species like *Streptocephalus sealii*, Anderson (1984) estimated that a single female, living for three months, may produce more than 1,500 cysts. Wow!

Both the Mono Lake and San Francisco brine shrimps may alter the typical reproductive pattern just described. Their fertilized eggs can remain unshelled and continue development in the ovisac until a larval stage is reached. Swimming young are thus expelled rather than cysts. For those who like to add to their vocabulary, the latter reproductive process is said to be **ovoviviparous**, while those with the more typical pattern are referred to as **oviparous**. Females of *Artemia* switch between the two depending on environmental conditions. And what are the environmental cues? Perhaps a favorable growing season, as indicated by sufficient oxygen, and water at an appropriate temperature and salinity, stimulates larval release, whereas more stringent environmental conditions trigger cyst development.

In large, comparatively static systems (e.g., Mono Lake), cyst production may be triggered when the length of day becomes too short, while in temporary waters high salinity, low O_2, and extremes of temperature are more likely the triggering factors. There is even evidence that individual females of *Artemia* differ in their genetic tendency to reproduce more commonly one way or the other (Lenz 1987; Lenz & Browne 1991).

When mature, cysts, like plant seeds, can withstand extreme environmental conditions. Because of their protective coatings built of materials not affected by the enzymes pepsin, trypsin, or lipase (Horne 1966), they are not digested when moved down the intestines of animals as long as they have not been punctured or smashed in the process. But it is when desiccated, and cysts are nearly free of moisture, that tolerance of real extremes begins (Clegg 1967). For example, they can now be subjected to temperatures near boiling (Carlisle 1968), be frozen for months, even withstand near vacuum conditions for 10 years without damage to the embryo (Clegg 1967). Of course these are the abilities which allow anostracan species to be distributed through alien environments and over great distances, as well as be adapted to a life in basins which dry or freeze solid sometime over the course of a year. And also as with plant seeds, cysts do not hatch until they receive **proper** environmental signals suggesting appropriate conditions for the species to successfully complete its life cycle.

In mountain snow-melt pools, the appropriate stimulus (perhaps cold, pure melt-water) presents itself unfailingly each spring, and cyst longevity need not be great. Having said that, no one knows what a cyst's life expectancy is for species living in predictable waters of this type. In the desert regions of California, one of the necessary stimuli, water, may not come for years on end. During such extended periods, cysts must also ride out temperature extremes that humans might see as verging on the ridiculous. During the summer, soil temperatures reach in excess of 65°C (150°F) day after day. Carlisle (1968) even describes temperatures of 80°C in the desiccated soils of African pool basins containing cysts of *Streptocephalus* and the tadpole shrimp *Triops*. During the course of winter, cysts may be warmed daily, but frozen each night. Still, under such conditions at least some of them survive 15 years, while others can probably make it more than 2-4 times that long. We say this with some authority because Clyde has stored dry soil samples from that wonderful Montana "Cow Paddy Puddle #1" (Eriksen 1966), containing cysts of *Streptocephalus sealii*, for 25 years, and had many successful hatches when water was provided. By contrast, Clegg (1967) noted viability of *Artemia* cysts decreased with time to the extent that only a few released larvae after 15 years and none were viable at 28 years. Although it may be folklore, Clyde swears he has read somewhere that a reasonable percentage of *Artemia* cysts hatched when doused with water after sitting in a vial on a museum shelf for about 100 years. Such a remembrance is given credence by the report that exploratory oil drilling near Utah's Great Salt Lake yielded buried *Artemia franciscana* cysts, carbon-dated at about 10,000 years old, a small number of which hatched when placed in water (Browne 1993). True or not, **ain't life amazing – and wonderful?**

Hatching

Cysts are usually dried, frozen, or both before even more cues finally break dormancy and the hatching sequence begins. An exception to this is the Mono Lake brine shrimp. Because Mono Lake is permanent, the opportunity for drying or freezing is small. Therefore, *Artemia monica* has developed a mechanism that makes environmental sense – a long period of fall and winter incubation at low temperature before the return of somewhat warmer water in spring induces hatching (Lenz 1980; Dana 1981).

In other anostracans, the return of water and any number of supplementary environmental stimuli, acting singly or in combo, are possible stimulators of the hatching process. Among them, temperature always exerts a fundamental controlling influence (Belk & Cole 1975). In at least two desert species, we know the rush of low-salinity water onto the dry, saline, playa lake bed where cysts lie dormant triggers hatching (Brown & Carpelan 1971; Daborn 1975), and when dissolved materials increase to around 1,000 ppm, hatching ceases. Brock (1965) claimed that low O_2 is the hatching trigger for *Eubranchipus bundyi*. However, Mossin (1986) convincingly refuted that notion by showing high CO_2 or low pH is actually the stimulus for a related species, and by arguing that sufficient oxygen must be available to allow the energetically expensive hatching process to occur. While hatching takes place only within a limited range of temperature (Belk 1977a), and clearly not the same range for all California species, those of us familiar with fairy shrimps readily admit that the real complex of environmental cues for hatching is unknown for most species.

No matter the state of our knowledge, once the appropriate environmental stimuli present themselves, and only then, does dormancy end and development begin again. Byproducts from this reinitiation of metabolism accumulate around the embryo, so water moves in osmotically and stretches the flexible hatching membrane. The resulting outward pressure breaks the inflexible outer membrane, if present, and the shell. Further expansion ruptures the hatching membrane and, voilà, the embryo is freed to meet the dynamic challenges of its aquatic world (Fig. 2.1, p. 25) (Belk 1972, Rosowski *et al.* 1997).

Mossin's (1986) studies of a species of *Eubranchipus* revealed a variation on the timing of this process that may be widespread among cold-water forms. Here, in late fall or early winter, the embryo falls free of the shell but remains in a quiescent state (referred to as "prehatched") in the small cocoon formed by the hatching membrane. Finally, when ice melts in early spring, additional environmental cues trigger activity, and the larva emerges into the larger volume of its pool.

Given genetic variability among cysts, and the microenvironment each occupies by chance in a pool basin, not all hatch at a given wetting. However, those that release larvae do so within a limited time span – at most a few days. And with the hatch, the cycle of events that leads from desiccated, embryonated cysts, through tiny larval stages, to gracefully swimming adults is repeated once again as it has since the early morning of crustacean time.

When hatching happens, out pops a one-eyed, egg-shaped young larval stage bearing three pairs of appendages called the **nauplius** (Fig. 2.2, p. 26). In some species a **metanauplius** appears, this being a slightly more developed stage in which the beginnings of thoracic phyllopods are visible (Fig. 2.2, p. 26). Both types of larvae swim jerkily using their three pairs of functional limbs. Although you certainly would not guess it at this early stage, these appendages are really the fairy shrimp's two pairs of antennae and its mandibles. Because growth is limited by the exoskeleton, the latter must be unzipped and cast off, that is, **molted**, for increase in size to occur. And so it is that at each molt these amazing creatures will enlarge in length and girth as they add segments with their attendant appendages. The process continues from nauplius, through metanauplius and juvenile, and into adulthood. Such gradual, incremental growth contrasts starkly with the metamorphic growth of butterflies whose form changes drastically as they pass from egg to larva to pupa then adult.

We don't think further elaboration of anostracan embryology is pertinent to our book, so we've

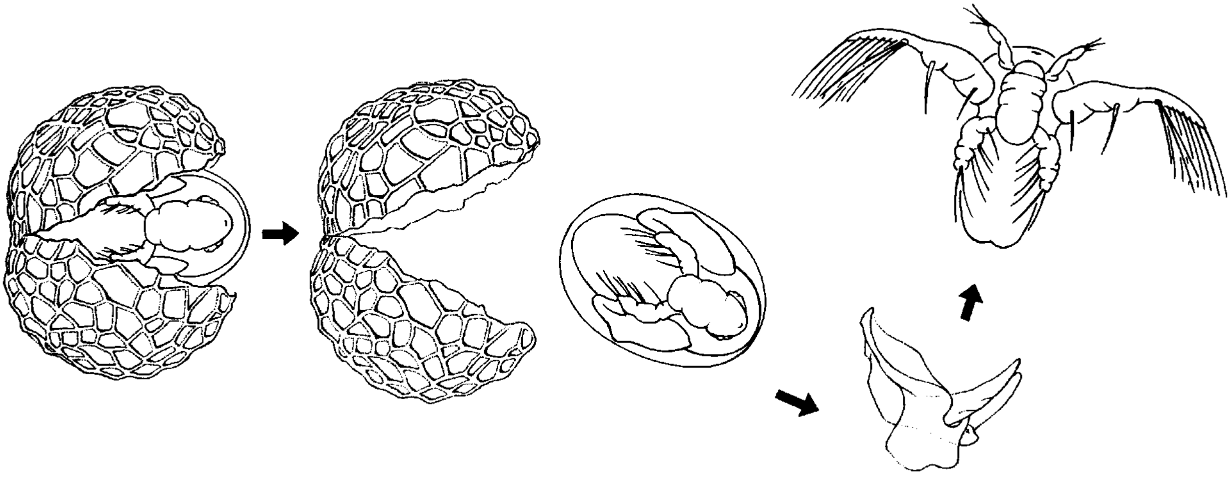


Fig. 2.1. Sequence of events in the hatching of a fairy-shrimp cyst.

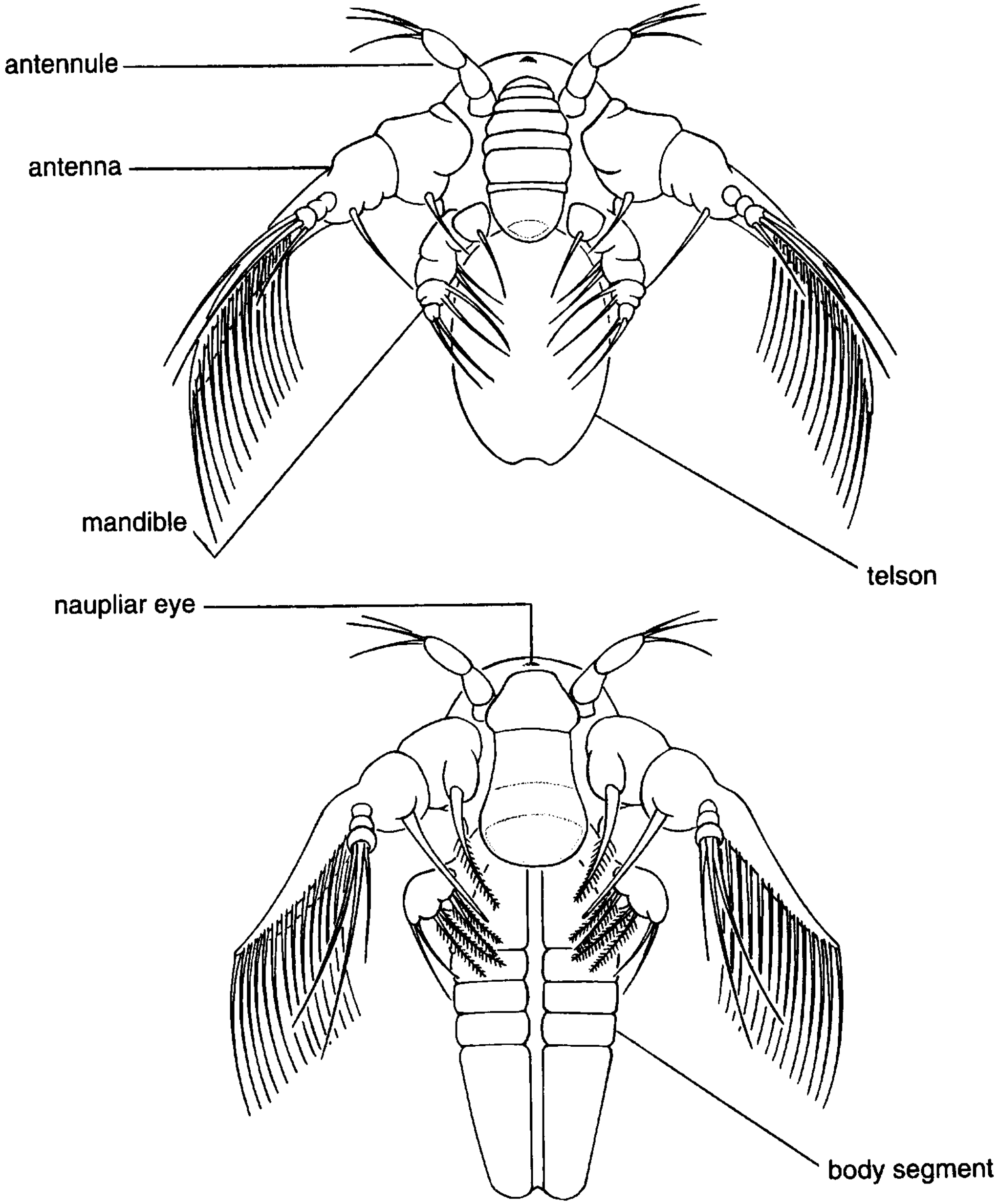


Fig. 2.2. Larval stages of fairy shrimps: Nauplius larva (above) and metanauplius larva (below).

neglected it entirely. However, should developmental details "tickle your fancy", the studies by Weisz (1946, 1947) of *Artemia*, and that of Fryer (1983) using *Branchinecta ferox*, will supply enough material, both external and internal, to satisfy most any appetite.

We encourage you to reserve for yourself some quiet time for inquiry over a minimum of three weeks, and watch the anostracan population in a near-by rain pool. You will not only be richly rewarded by seeing these changes occur before your very eyes, but you will be able to place these events in the real-life drama that is daily unfolding in the microcosm of your special pool.

Unfortunately for some of you, a rain-pool may be inconveniently far removed from your urban setting. Others may get the urge to observe and share these marvels of life with their kids at an ecologically inappropriate time of year (no rain). Some may be barred from a pool because it harbors endangered species (see Chapter 6). Not to worry, merely visit your local aquarium shop and there you can inexpensively, yea cheaply, purchase "sea monkey eggs" (*Artemia* cysts) or adults. Should it be the cysts you bought, merely follow some simple steps on the package, and watch the amazing developmental and reproductive processes anywhere at any time.

Color

Fairy shrimps are graceful and gorgeous, but conspicuously colored? Only sometimes. Most are semi-transparent and a nondescript gray-white. Of the variety of hues that may beautify these animals, the sources of many are unidentified, and the environmental cues that stimulate their production are largely enigmatic. But don't let that interfere with your sharing our delight in the startling range of colors exhibited one spring day by *Branchinecta lindahli* at Emerson Dry Lake, a playa in the western Mojave Desert once used by Marines for gunnery practice. In a bulldozed ditch filled with muddy water, my colleague John Moeur and I (Clyde) spotted brownish fairy shrimps. Such a color is not uncommon in turbid waters, but it is **not** because the animals are dirty, nor is it due to the clay particles which fill their guts; what the environmental cause and physiological source may be are unknown. In a bomb crater nearby, the fairy shrimps, though beige in this water of lesser turbidity, possessed a reddish cast. Dipping into the next turbid-water crater, our net yielded reddish males and pinkish females, probably a result of different amounts of hemoglobin in their blood. This was an interesting find because we had never seen *B. lindahli* with hemoglobin. The last site, another bulldozed trench with turbid water, produced females that appeared dark bluish-green, but this time the pigment was deposited in tissues along the ovaries and in extremities of the appendages. And what about the males? Paint them beige, much like the color of all shrimps from the initial site.

Branchinecta lindahli is widely distributed both within and without California, and is found in a wide range of turbidities and dissolved solids. Its California color variations, which also include red-orange and apple-green, seem to have no obvious connection with these physical factors, for in turbid and clear conditions, high and low TDS, and cold or cool waters, the animals' most common color is the signature milky gray-white of most fairy shrimps. The blue pigmentation we noted might hinge on a diet high in ß-carotene, for such a diet appears to result in blue ovaries in *Artemia* (Hata & Hata 1969) and *Thamnocephalus platyurus* (Maeda-Martinez *et al.* 1995b). We find this scenario unsatisfying, however, because water in all depressions was turbid and therefore must not have been oozing with phytoplankton, all of which possess ß-carotene. Besides, although all water holes had filamentous algae (which also contain the substance) tangled in the branches of brush that ringed the surface water, algal filaments have only occasionally been reported amongst gut contents of fairy shrimps (Maynard 1972; Belk & Ballantyne 1996), and only one pool had individuals decorated with blue ovaries. While reviewing this manuscript, Robert Brown of CSU San Luis Obispo reminded us that *Branchinecta mackini* also possesses a blue pigment in tissues of its oviducts and it too lives only in turbid waters. Whatever its cause, the blue substance may be canthaxanthin-lipovitellin, a material identified from yolk platelets of *Tanymastix stagnalis* (Zagalsky & Gilchrist 1976). Lastly, the cause of blue deposits in appendages remains unknown as well, but it has not been connected with ß-carotene in the diet.

Still on the topic of *Branchinecta*, we recently heard from Marilyn Myers, a graduate student at U. C. Berkeley, who netted *B. dissimilis* from a pool in the White Mountains, the highest known fairy shrimp site in North America (3,587 m). This unique anostracan, at this unique elevation, certainly possessed unique brood pouches because they "appeared phosphorescent to me, like they had light glands", Marilyn wrote. Talk about a "White Mountain high"!

Streptocephalus sealii is the most widely distributed anostracan in North America. In most habitats it displays the "typical" gray-white color of fairy shrimps with the addition that its cercopods are orange-red, a color attributed to trans-canthaxanthin (Murugan *et al.* 1995). Walter Moore (1955), the Louisiana scientist who has studied *S. sealii* more than anyone, transferred a dozen of his favorite beasts from a ditch habitat to a forest pool unoccupied by fairy shrimps. The pool soon dried and remained desiccated for over 6 months. When water returned, so did Walter. Yes, he found fairy shrimps, but rather than being gray-white like those he introduced, they were "...dark brown in color, tinged with deep green – typical coloration for forest pool shrimps." Environment certainly seems implicated, but what habitat clue or clues caused the change in coloration of the next generation was not pursued.

Like Walter Moore, both of your authors have reveled in the various colors of *Streptocephalus sealii*. For example, in a Tennessee pool Clyde described it as opalescent, while in a muddy cattle watering-hole in Montana the animals were the same light-brown color as the fluid in which they swam even though the source of the water was a clear, grass-lined "reservoir" in which all individuals were apple-green. In California, *S. sealii* is restricted to the high Sierra and Siskyou Mountains and thus usually to clear, although sometimes tea-colored, water. Animals in these populations are mostly a beautiful deep green-blue, but, in Lassen National Park, Clyde collected light purple individuals in one pool and green ones in another. In these cases the pigments appeared to be dissolved in blood and, to the esthetic detriment of all who would wish to view them, disappeared upon preservation. What the pigments were we do not know. However, Peeters, *et al.* (1994) described a blue substance (artemocyanin) in solution in the hemolymph of both *Artemia* (where it was first described by Krissansen *et al.* 1984) and *Streptocephalus proboscideus*. You might find it interesting that this blue pigment is a break-down product of hemoglobin. But if artemocyanin is truly the substance causing California-dwelling *S. sealii* to be green-blue, then we wonder why there should be a need to synthesize hemoglobin in the normally high O_2 levels of the cool pools in which they occur? We also wonder why no one has reported at least some red individuals, or possibly some strange-colored critters whose hemoglobin is mixed with the green-blue of artemocyanin?

Another *Streptocephalus*, the Riverside fairy shrimp *S. woottoni*, deposits an orange pigment in its cercopods and sometimes along the edges of its swimming appendages. Such a color pattern sounds suspiciously like that in *Thamnocephalus platyurus* placed on a yeast and ß-carotene diet (Maeda-Martinez *et al.* 1995b). In a control, animals given only yeast (no carotenes) were gray-white throughout. The authors suggested that since orange extremities are typical of most *T. platyurus* collected in natural pools, the color is "probably" due to algae in their diet. Sounds simple, eat algae, turn your appendages orange. However, such an explanation skirts the issue of whether algae can grow in the muddy waters typical of most habitats of *T. platyurus* and *S. woottoni*. In several pools near San Diego, not only the extremities, but the entire body of many females of *Streptocephalus woottoni* appeared bright red-orange. All males were gray-white with orange cercopods. The red-orange hue did not remind us of hemoglobin, but if it wasn't this material, or linked to dietary ß-carotene (which we would expect to affect males similarly), then we have no idea of its cause. If it was due to hemoglobin, it might be because females remain in deeper, more oxygen-poor regions of a pool, a characteristic behavior of females brooding fertilized eggs (Belk 1991a), while males spend more time in near-surface waters.

The fact that low O_2 stimulates production of hemoglobin, at least in some anostracans, is best demonstrated in brine shrimps. From the work of Barbara Gilchrist (1954), we know that in salinities less than about 3.5 times sea water (about 125,000 ppm), hemoglobin generally cannot be detected in the animals. However, at concentrations above that amount, animals become increasingly red. Remember, the greater the salinity of water the less O_2 it can hold. Therefore, *Artemia* increases production of hemoglobin, females more than males, as environmental oxygen declines, and by so doing transports more O_2 to the tissues than would be possible in its absence.

Thinking we "know it all" concerning red coloration may get us into trouble, however. For example, several scientists, studying *Artemia* ecology in salterns (ponds where sea water is evaporated to concentrate salts) along their Spanish coastline, noticed that only certain individuals were "a red color". So what, you ask? Why didn't they merely assume it was hemoglobin and go about their research? We suspect they reasoned as follows. If a low-O_2 environment makes the synthesis of hemoglobin advantageous, essentially all animals would possess the pigment, yet only **some** were pink or red. As it turned out, all pink individuals were parasitized by the cyst stage of a tapeworm. One finding deserves another, right? So analyses of body chemistry showed higher than normal lipids, probably related "...to carotenoid pigments conveying a red color...." (Amat *et al.* 1991). You might ask what the relationship is between being parasitized, body color, and lipid content? A reasonable hypothesis is that parasitization leads to castration of the shrimp, and thus loss of its reproductive hormones. A change in hormonal balance affects body chemistry widely, and probably causes the increases in lipids and carotenoids noted. Castration seems not to affect health of the shrimp otherwise; it merely allows energy normally directed into egg and sperm production to be utilized in development of the parasite(s). Red coloration makes the animal conspicuous and thus probably more susceptible to predation by birds – an advantage to the completion of the parasite's life cycle.

Robert Brown tells us of a similar situation he noted with *Branchinecta lindahli* from the Soda Lake area of San Luis Obispo County. In his case, when an unknown parasite filled the body cavity with its cells, the fairy shrimp became white, making infected individuals quite conspicuous. Bob also theorizes that birds feeding in the pools select these animals because they are easily seen – again a boon to the parasites.

Finally, *Linderiella occidentalis*, a small fairy shrimp typical of a number of California's grassland pools, though light gray-white in body color, has red eyes, a sharp contrast to the dark black eyes of all other Anostraca. In nature, most arthropods utilize black pigments to keep light from leaking between units of the compound eye, but why native populations of *L. occidentalis* swim in the face of this physiological generalization is not understood. Sarane Bowen and her compatriots at CSU San Francisco have been able to gaze into the red, garnet, and white eyes of mutants (produced by radiation treatments) of the normally black-eyed *Artemia franciscana* (Bowen *et al.* 1966). She and her co-workers determined that the various pigments were merely different chemical states of a substance called ommochrome (Kiykomoto *et al.* 1969).

You have undoubtedly noted that so far we have spoken only about adult fairy shrimps. Working our way backwards in the life cycle, we know of only three species in which larval color has been recorded for posterity. Dexter and Ferguson (1943) reported brilliant salmon-colored metanauplii of *Eubranchipus serratus*. Gilchrist (1954) noted that the bright red color of newly hatched *Artemia* nauplii is due to carotenoids in their fat stores and not to hemoglobin. As those stores are used over a period of a few days, the color gradually disappears. Lastly, Maeda-Martinez *et al.* (1995b) commented that nauplii of *Thamnocephalus platyurus* are "green-bluish". Denton (previously unpublished) observed that even embryos possess an array of colors. When he deshelled cysts to measure their contained embryos, to his pleasure he found gold embryos in cysts of *E. serratus*; rust, white, and purple ones inside those of *Streptocephalus mackini*; and cysts containing blue-green embryos of *T. platyurus* and *T. mexicanus*. We know of no definitive information about the source of these colors. Ah, embryonic Technicolor, but why?

Obviously many of the reasons for color variation in fairy shrimps are largely enigmatic. But, might this stimulate some of you to seek answers to the myriad of mysteries associated with color? For starters, how about determining the chemical nature of the pigments displayed? When that is done, perhaps other fascinated followers of fairy shrimps will ferret out the factors which signal an animal to mix its cauldron of bodily chemicals in such a way that colors appear which benefit the beast's survival in its ever-changing ecological world. In the meantime, many fans of fairy shrimps, including your authors, will merely remain in awe of some of the absolutely gorgeous colors carried about in the bodies of these gracefully-swimming creatures.

Chapter 3

ECOLOGY OF FAIRY SHRIMPS

Introduction to community ecology

As your mind's eye sweeps across the California landscape it "sees" the great variety of human communities through which you have traveled: from Alturas to Zzyzx, Red Bluff to Redondo Beach, and including Laytonville and Los Angeles. Ah, yes, how they vary: you remember their vast differences in land area covered, in human numbers, cultural diversity, complexity of economy, and esthetics. Some were nestled peacefully amidst the pines along a little-traveled mountain road; others lay pastorally on the rolling grasslands buffeted by winds and threatened only by afternoon thunderheads. Some were but an eyesore along a desert highway; unfortunately, too many were sandwiched and all but choked to death by urban sprawl and the ugly litter of excessive waste. And so it is with the communities in which fairy shrimps dwell, for many are the parallels should one want to pursue such anthropological-anostracan comparisons.

As with humans in their cities, fairy shrimps are often the most numerous "large" and, therefore, conspicuous animal inhabitants of their communities. "Most numerous" usually means these creatures occupy the **first consumer level** in **food chains**. Prudence suggests we explain these bits of jargon involving community economics. In fairy shrimp communities, just as in your own, there are a number of jobs or "functional roles" that when filled provide the "services" that allow the community to function. You may not interact with all your neighbors, but ultimately you and others depend on what they accomplish. For example, you may not know the trash collectors or the bankers, but you would be in a terrible fix were they to take their services elsewhere.

The Great Law for the universe and its living things (Second Law of Thermodynamics), the law that describes the constraints for everything, even the California Legislature, states that ultimately "there is no free lunch", that is to say everything costs something; for humans that might be paraphrased by saying that "using money, costs money". But for a more precise meaning, one which includes planets, people, plant life, pools, ...and fairy shrimps, it is better stated that "using energy costs energy". In other words, all things require and use energy. Because that energy cannot be obtained or used with 100% efficiency, living things are in an insidious, downward, and competitive spiral for the remainder.

Fortunately, one form of energy can be converted to another, like solar energy into food by plants or into electricity by humans, but, in accordance with the Second Law, when conversions occur some of the energy is changed to heat, and heat as we all know dissipates away from our bodies, our homes, and our cars, never to be recaptured. So, the nitty-gritty reality is that as our original energy supply is utilized, some is frittered away, and obviously new supplies need to be sought to replace both use and loss. The latter is a major cost of "doing business", a major controller of the human economy. And so it is with the rest of our universe, including our planet and its other living things, including the economy of the communities in which fairy shrimps dwell.

Fortunately, for humans and anostracans, the sun is a continual source of light energy that can be transformed to a type of energy useful to living things. Although it might strike at the ego of some engineers, conversion of solar energy was mastered more than a few years before their time by certain bacteria, then by lowly algae, and finally by land plants. By the process called **photosynthesis**, plants take the ecosystem's initial step in converting solar energy into the chemical energy of glucose; thus, they are referred to as **primary producers**. Plants then reconfigure glucose into various products to make their own structure (e.g., leaves and wood) and reproductive items (e.g., fruits and seeds). In so doing, plants set the limits for the amount of energy available in a community, for more cannot be used than is produced or imported.

Faced with an inability to convert solar energy to their use, many animals meet their energy needs by eating plants or plant parts which they are adapted to consume and digest. Such plant-eating animals (**herbivores**) are referred to as **secondary producers** or **primary consumers**. These plant-eating animals **use** energy to gain and process their food; therefore, they cannot possibly possess as much energy as they ate, and certainly not as much as is contained in the community's plants. This means that either the herbivore numbers are fewer, or their biological material, as measured by collective weight (biomass) or energy (calories), is less than in the plants.

We also know that the animals we call **carnivores** make a living by eating other animals, not plants. And if our previous argument is followed to its logical conclusion, the carnivores in the community should number fewer, or at least collectively contain less biomass or fewer calories, than the animals on which they fed.

The fact that plants provide all the initial fuel for a community's economy, and that certain animals eat those plants in order to gain their energy, and in like manner other animals eat the animals that ate the plants so that they too may have energy to drive their processes, is of paramount importance to humans, and to fairy shrimps! If you were to gather together all the threads that link the specific feeding requirements of all species in a pool-community, you would weave a particular pattern, yea structure, on the fabric of life that describes your particular fairy shrimp community. The relationships that have evolved among and between living things, in which the energy of some species is captured and processed by others adapted to do so, are what we call **food chains** and **food webs**. In nature, energy flow along these feeding interrelationships is the measure of the community's economy; and success is determined by the efficiency of energy use, **not** by the fantasy of an ever-increasing GNP!

Thus, because of constraints described by The Great Second Law, every creature gracing this earth is obviously concerned with continually "putting food on the table". As it does, it interacts with, or relies on, many creatures that provide other essentials which aid its, and its community's, health and survival.

The fairy shrimp's aquatic community

If we were to visualize the community in which a fairy shrimp lives, one where the ethnic and job diversity is **great**, just who are the participants providing the essential services that we are likely to encounter? Approaching this challenge as an ecologist might, we would first look at creatures who harvest the energy of sunlight. WOW, these come in a fantastic variety of shapes, sizes, and life styles – just as do humans in their communities. No surprise here!

At their simplest, there are the single- or few-celled blue-green bacteria and algae that live a life dispersed in the water column. Biologists call these **phytoplankton**. There are also algae that begin life attached to some stable surface such as the pool's bottom, including rocks and logs, or it may be other plants, living or dead, or even animals! The many creatures which share this way of life are collectively known as **periphyton**, and they are a tasty, nutritious smorgasbord for animals adapted to eat from this table.

Algae are among the most ancient and anatomically simple life-forms on earth; but in the evolutionary scheme of things some ancestors of these aquatic organisms gave rise to more complex terrestrial plants, adapted structurally, physiologically, and reproductively to a life out of water. Inevitably, like many animals (most notably insects), some plants reinvaded their watery origins. The ones who most commonly did so were the flowering plants, members of the community that make most of the "tenement houses" that root in the bottom of a pool and reach for its surface, sometimes piercing it. These flowering plants, from pond-weeds to rushes, create the structural complexity which provides the special habitats needed by many of the pool creatures. These are also the plants that are responsible for the late-season edge-bloom which defines, and colorfully graces, California Vernal Pools.

In their communities, humans watch birds, usually pigeons and house sparrows, circling the atmosphere between the tenements. In a pool, the aquatic "atmosphere" is filled with a much more culturally diverse and therefore pleasing variety of living things. Other than the countless numbers of bacteria and the phytoplankton already described, the midgets on the block include **Protozoa**, or single-celled animals. They teem in great abundance, occupying all levels of the consumer food chain. **Ciliates**, protozoans which possess a great profusion of cell membrane outgrowth which beat to cause rapid movement, are the speedsters of the microscopic world. Also included in this locomotor menagerie are those which have one or several long whips to propel them in spiraling trajectories. These are the **flagellates**. No simple classification of the eating habits of these tiny creatures exists, for many absorb dissolved organic materials while others eat organic particles, and thus are "animals". A number of flagellates possess chlorophyll, and, being plant-like in this way, are included in the phytoplankton as primary producers. Our tidy minds demand simplistic cataloging of community members; real life continually reminds us that to this end we fool ourselves!

Not much larger than protozoans, but many-celled in structure, are the Norelco shavers of the animal world. These microscopic creatures, usually with two rings of beating cilia at their head end that not only propel them through the water but sweep bacterial and algal food to their mouths, are called **rotifers**, or wheel animals. Although fairy shrimps need not concern themselves about collisions with such small-sized traffic, a different story might present itself with other pond creatures. The most common constantly swimming animals other than fairy shrimps are the water fleas (**Cladocera**; Fig. 1.1, p. xiv) and copepods (**Copepoda**). By comparison to adult anostracans, these creatures also are small (usually 1-2 mm). However, by virtue of their sheer numbers, the pool may seem like Times Square on New Year's eve to a fairy shrimp. Where the rub (pardon the pun) arises is most copepods, water fleas, and fairy shrimps are filter-feeders, that is, they filter small particles, including bacteria, protozoa, rotifers, and phytoplankton, from the water through which they swim. Similar feeding habits suggest competition for available "goodies", and so it may be. However, as with the human business world, specialists of all kinds abound which stake out and capture a sufficient piece of the economy. By possessing different-sized filters, or feeding in disparate areas of the pool, filter-feeders can specialize in only certain segments of the total resource and thus either minimize competition or out-compete generalists attempting to benefit from the same resource. Other small and constantly swimming community members include some wonderfully colored flatworms (**Rhabdocoela**), most of which probably use filter- and suction-feeding, and the spidery water mites (**Hydracarina**) adapted for sucking the body fluids of small crustaceans and insects.

Larger members of the community just might include some fascinating close relatives of fairy shrimps spoken about earlier. The clam shrimps, or **Conchostraca** (Fig. 1.1, p. xiv), often lie on the bottom, but as unlikely as it sounds they also spend a good deal of time swimming...and filter-feeding. And, if you are wary of the statement that "truth is stranger than fiction", you might change your mind when you encounter tadpole shrimps (Order **Notostraca**; Fig. 1.1, p. xiv) with rhythmically-beating hemoglobin-filled phyllopodia. These creatures, some upwards of 70 mm long, and feeders on bottom debris and predators on fairy shrimps when occurring together, look like something out of earth's fossil past. In fact, they have changed little from their own fossils, and, given their large, flattened shield and swimming legs, superficially resemble a fossil group of early arthropods, a resemblance that led to a fishery biologist's embarrassing misidentification. When accompanying an L. A. Times reporter to a desert lake to explain what life had burst forth following a rare summer rain, he gasped when he saw tadpole shrimps and exclaimed: "My god, Trilobites! Trilobites haven't been seen on earth for 250 million years". So, go look in **your** pool. Who knows what you will find.

Insects are common in some longer-lived temporary waters and, as you might expect given their fantastic variety in terrestrial habitats, have specialized along a number of aquatic life styles too. You will see snorkelers, aqua-lungers, and gill-breathers, and if such adaptations get the best of your curiosity, check out the chapter on **Respiration** (Eriksen *et al.* 1996) in *Aquatic Insects of North America*. Although many of these insects are small, several of the larger, highly mobile ones are notable predators on fairy shrimps and other pool life. Of these, the predaceous water beetles and their larvae (Family **Dytiscidae**) and a true bug called a backswimmer (Family **Notonectidae**) are the most common. The majority of the other pool insects live on or near a submerged surface, using the latter for resting, protection, and a place from which to launch a feeding foray. Such creatures include dragonfly larvae and their relatives the damselflies (Order **Odonata**), both of which can, and do, chow down on fairy shrimps.

Most of the other creatures which circumnavigate the pool have little direct interest in fairy shrimps. They make a living either by grazing on plants, or by scooping up dead remains enriched by a bacterial and fungal coating – a material you might call "gunk" but which ecologists refer to as **detritus**. Such creatures are called **detritivores** and include mayflies (Order **Ephemeroptera**), caddisflies (Order **Trichoptera**), seed shrimps (Order **Ostracoda**), and scuds or sideswimmers (Order **Amphipoda**). Also undertaking this way of life is a bug called the water boatman (Family **Corixidae**), a beetle called the water scavenger (Family **Hydrophilidae**), and pond snails called "pond snails" (Class **Gastropoda**). As if this menagerie of creatures is not enough with which to rub shoulders or cause traffic congestion, stand back for the "18-wheelers" of the pool. Although tadpoles of most frogs are herbivores, adults are predators, and salamanders and their larvae, long and lanky vertebrates, and also fairy shrimp predators, are big enough to run down and eat almost everything else on the "highways" of the pool.

Fewer, but unfortunate for pool animals, are the voracious wading and diving birds that come and go. Now we can understand the use of the broad and filtering bill of the Northern shoveler (duck) for collecting fairy shrimps. At an earlier and much more naive time of life, your senior author thought the long tubular bill of a wading American avocet was obviously adapted for probing mud flats, not for "filtering" anostracans from a pool's water column! Dare I admit I had a narrow view of the avocet's world? While "doing science" at many a fairy shrimp's home, I have watched in amazement as avocets waved their beaks back and forth in the water and grabbed whatever they hit. What they hit was most likely a fairy shrimp, but was also possibly something which ate a fairy shrimp. Ah, the ingenuity of life, and the beauty and symmetry of a pool's energy flow!

Fortunately for anostracans, circumstance rarely brings them together with fish. The ephemeral nature of fairy shrimp habitat obviously precludes fish in most cases. However, should flooding link permanent and temporary waters, as occasionally it does, and allow fish to enter the grocery store of a pool (e.g., McCarraher 1959; Pereira & Gonzalez 1994), they will find fine cuisine that has no protection but numbers, time, and the forest of pool vegetation in which to "get lost". Obviously this situation is not on-going, for the fish must find their way back to permanent water, or they too will be lost, in this case to the finality of drought for which most of the pool species are adapted, but fish are **not**.

What a complex community it can be! There are the producers (plants), and those animals that make a living eating plants, or eating those that ate plants, or eating those that ate those that ate plants. Finally, there are countless creatures which eat dead stuff – dead plant or animal material, dead of this year or last year, dead of what was produced in this pool or what was dropped or blown into it from afar. **Nothing** goes to waste in nature. Everything is sought and consumed by someone. Here is the true meaning of "**recycling**" which, if the organisms are left to do "their thing", forms raw products that allow production to continue. Here is the dynamic equilibrium of nature in action!

Some pools, like small human resource-based communities, are probably not so grand or complex as just described. Several are the reasons. As physical or chemical conditions become severe and cast a shroud of extremes to which only a few species are adapted, food webs become much simplified. One of the most striking examples is the salty and oftentimes warm waters in which brine shrimps like *Artemia franciscana* and *A. monica* flourish. Bacteria, an algal producer or two, the brine shrimps that filter these kinds of tid-bits from the water, and a detritivorous brine fly may be about the only cast of characters present.

Should you wonder if things can get even simpler, then consider Rabbit Dry Lake, an alkaline playa in the Mojave Desert. Here during dry times we see a hard, flat, expanse of clay shimmering in the summer heat. But when a storm dumps its contents on the encompassing mountains, soil- and organic debris-laden water rushes hellbent to the playa below to fill it with water so muddy it looks like a chocolate milk shake; water so muddy that light does not penetrate and photosynthesis cannot occur. Surprisingly to some, *Branchinecta mackini* hatches and thrives in enormous numbers. Such a prolific event makes it understandable why its major predator, *Branchinecta gigas*, may be present as well, albeit in expected smaller numbers, say one *B. gigas* to

40,000 *B. mackini*. Other than the ubiquitous bacteria, that's the cast of characters, friends! No other visible critters. But, you ask, "if there are so many alkaline fairy shrimps, what serves as their food?" We will provide an answer shortly in the section "What do fairy shrimps eat?"

Most pools, puddles, and playas probably lie somewhere between the extremes described. And should you follow the creatures in your favorite water-filled micro-universe, you will certainly see the comings and goings, searching and eating, reproduction and decay, that all add up to the particular economics of the community. **FASCINATING!**

As intrigued as you may be in your own "personal pool", we ask that you be of broad perspective. Do not get caught up in the simplistic mind-set of some poets, perturbed people, and politicians who believe, at least state, that "if you've seen one, you've seen 'em all", for nothing could be further from reality when dealing with temporary waters. To prove that point to yourself consider reading Balco and Ebert (1984) and Syrdahl (1993). They show, by comparing many features, that each pool is not only different, but usually uniquely so, even from its neighbor. Not only does the cast of actors change through the pool's duration, but the timing of those changes may also be strikingly varied!

Coexistence of species of fairy shrimps

In the previous section, we intentionally said little about different types of anostracans coexisting. Dogma has it that were two or more species to occupy "the same niche" (have exactly the same requirements and do exactly the same thing) they could **not** co-exist. The rationale is that, since by definition they are recognizably different, one of the species must be able to "do its thing" somewhat better, possibly only slightly better; but if so, it would have a competitive advantage, reproduce more, and ultimately predominate to the exclusion of the others. Species which are most likely to compete so intimately are those which are structurally and behaviorally most closely related.

Given such sage words, one might not expect several kinds of fairy shrimps, particularly those within a genus (e.g., *Branchinecta*), to compete equally and thus coexist while occupying what generally appears to be the same niche. **However**, although finding different kinds of fairy shrimps in the same pool is not a rarity, it is atypical, especially in cold-water habitats (Eng *et al.* 1990; Graham 1995; Maeda-Martinez *et al.* 1997). To our knowledge, three species is the record for California, while 6, collected in North Africa by Thiery (1991), is the world mark. So much for dogma! Or is it???

In order to begin our discussion of the intriguing problem of coexistence of species, "Return with us now to those thrilling days of yesteryear when out of..." Laurasia came the thundering phyllopod beats of the great *Eubranchipus* ancestor (Belk 1995), and probably the other ancestral anostracans of most of today's North American fairy shrimps (e.g., *Branchinecta, Linderiella, Streptocephalus*). When it was that founding populations arrived to settle pools in what we now call California is not known. What we do know is that some 10-15 million years ago California's earliest recorded fairy shrimp, a species of *Branchinecta*, plied the waters of an alkaline playa in a savanna or possibly basin-and-range setting near where Barstow (San Bernardino County) sprawls today (Belk & Schram in prep.).

Under similar climatic conditions, whether 15 million years ago or now, even closely-spaced pools often vary considerably as habitats; so, whenever founding populations arrived, natural selection immediately began the relentless process of selecting among different combinations of accumulating genetic variability at each site, thus initiating the continuous procedure of honing each population to its specific conditions.

Whatever the range of conditions was that prevailed around Barstow or throughout the rest of California so long ago, the land forms and climate were not what they are today. The Sierra at that time was perhaps 1,000 m high, and volcanoes spewed their contents across the landscape, particularly over the northern half of the range (Hill 1975). Narrow, shallow seas extended across the Central Coast Mountains in places and into the Central Valley. In what is now southern California, the South Coast Mountain Ranges, although still low, had begun to rise from the hills that preceded them (Oakeshott 1971), undoubtedly creating ever-increasing aridity across the lands to the east.

Now superimpose upon these circumstances considerable change in the geological landscape that began in the neighborhood of 10 million years ago. The Sierra began to rise, and the South Coast Mountain Ranges continued their progressive uplift, blocking further the movement of rain-bearing clouds to the east. Knowing this, we can begin to appreciate the increasing topographical and climatic isolation of pools, as well as California's increasing isolation from much of the rest of North America. Of course the general drying and warming trend since Pleistocene times about 10,000 years ago has further added to the increasing hindrance of gene flow between pools. And so fell the fickle finger of fate that gave us this laboratory called California, which not only offers genetically differing populations of the same species in different pools, but the evolution of a myriad of different species, including its great number of endemic organisms, among which are some of its fairy shrimps.

Isolation of California is not complete, of course, because of several methods for dispersal discussed in the section in Chapter 4 "How fairy shrimps got where they've got". In that context, it seems some species may get around more easily than others (e.g., *Branchinecta mackini, B. lindahli*), given their flexible physiologies and wide distributions, in both North America and California. In Australia, Williams and Busby (1991) note a similar broad occurrence of the tadpole shrimp *Triops australiensis*. But as admitted by these Aussies, and as is true of our two species of *Branchinecta*, no one has looked at their microanatomy with scanning electron microscopy, or protein dissimilarity as evaluated by electrophoresis, to determine if differences among populations exist or are developing. Using such techniques, people are accumulating evidence suggesting that dispersal is not successfully accomplished as often as might be imagined or thought (Belk & Cole 1975; Dumont *et al.* 1991; Fugate 1992).

Still, should chance introductions occur, transplants and residents may be different enough that they utilize separate fractions of the resources in a structurally simple puddle; or they may remain "isolated" from each other by occupying unutilized or under-utilized portions of a large, structurally complex pool (Hamer & Appleton 1991; Thiery 1991). To appreciate the fact that pools can truly be structurally complex, you may have to change your impression that an ephemeral water-body is merely a simple dimple full of water. Although such a view might approach reality in tiny potholes, puddles, and wind-swept turbid playas, deeper, longer-lasting habitats, particularly those containing areas of rooted vegetation, often provide great structural and thermal complexity. Hearken back to our discussion of "The fairy shrimp's aquatic community" (pp. 32-36) for a description of such a place.

With regards to coexistence of species, or lack of same, competition which excludes a species is most likely when the environment is predictable and the competitive advantage is expressed generation after generation. Should habitat conditions change slightly, or considerably, the advantage may be shifted from one type of anostracan to another. Temporary rain-pools and the environments in which they form are normally the quintessential example of habitat capriciousness. Important environmental factors can vary, often significantly, from year to year, and of course through the seasons of any given year (Dexter 1967). These include temperature, time(s) of pool filling, if they fill at all, and how long they hold water. Thus, in absence of a predictable environment that gives a competitive advantage to a particular species, a disturbance-based "dynamic equilibrium" is established between two or more forms, shifting the competitive advantage back and forth, and, as a consequence, allowing coexistence over time. Under these circumstances, competitive displacement (exclusion) occurs infrequently (Huston 1994).

If some level of competition does exist, then what are the structural and behavioral differences that explain its minimization among similar fairy shrimp species, you may ask? Perhaps these filter-feeders have evolved dissimilar filter size, allowing one species to utilize a different size-range of food particles from the total food resource than does another. That animals in different life stages have different sizes of filters, and therefore feed on different foods, seems intuitive. Perhaps different behavioral feeding strategies have come about so that one species feeds more on or near the bottom while another feeds higher in the water column. In other cases, temperatures at which cysts hatch may separate species by season, or if they hatch at the same time, perhaps because of different rates of development, young of one species do not mature until adults of another are on their last leg (or perhaps we should say phyllopodium). As the season progresses, and evaporation of pool water leads to increased salt concentration, one type of fairy shrimp may be stressed and see its population decline while another finds conditions much to its physiological liking and "comes on like gangbusters". In other words, although two anostracan species may be found together occasionally, there should be significant differences buried somewhere in their biology that account for their coexistence. Ah, for inquiring minds to dig in and ferret them out!

So, having explained some of the possibilities for coexistence of species, we must admit there is really nothing important known about the degree of competition among coexisting fairy shrimps. In most biological systems competition is difficult to demonstrate, and no experimental work has been undertaken with anostracans. When coexisting species show differences in structure, behavior, and ecology, we should probably best begin with the assumption that these are expressions of genetic selection which minimize competition between closely related species. However, not much is known about such differences among fairy shrimps. For example, we are aware of only 6 measurements of filter size (Fryer 1983; Mertens *et al.* 1991; Schrehardt 1987; Helm 1998), and four are for species not even found in the U.S., let alone California. What we know about anostracan physiology, tolerances of temperature and salt included, is also fragmentary. Observations concerning behavioral differences are minuscule in number, and reports concerning what life-cycle stages were present with coexisting species are fewer than that.

So much for refined theory, informed guesses, and what we do not know. What **can** we tell you about the coexistence of species of fairy shrimps? Well, we can note which ones have been found together (Table 3.1, p. 45), and we can cite several known examples that may explain how fairy shrimps could coexist in California's ecological settings.

We begin with the association of *Branchinecta gigas* (a predator reaching 150 mm in length) and *B. mackini* (its prey, about 30 mm long). These species obviously share physiological similarities that allow them to live in the same alkaline pools, in the same life stages, at essentially the same time. However, the predator has evolved gargantuan size, the greatest length and bulk by far of any fairy shrimp species, has its adult appendages modified for capture of large prey rather than for filter-feeding, and has evolved the behavioral patterns necessary to catch *B. mackini* for its food. *B. gigas* has also been infrequently recorded coexisting with *B. lindahli*, so its feeding behavior appears satisfactory should the latter be the significant food item in its habitat. Although the main food supply of *B. gigas* certainly consists of anostracans, hors d'oeuvres include various species of copepods which it devours as it swims through the turbid waters of its home (Anderson 1970; Daborn 1975).

Differences in feeding strategy, involving behavior and structure of appendages, have been cited (Modlin 1982) as the reason that two species of *Eubranchipus* coexist in the central and eastern United States. Because so little is known about California's species of *Eubranchipus*, a similar comparison cannot be made here. Yet the general differences in feeding behavior described in Modlin's paper have been recorded for a number of other species, including some in California, so they warrant mention. As we know, fairy shrimps are said to be filter-feeders, but not all are just "pure filter-feeders". Using Modlin's example, although *Eubranchipus holmani* remained in the water column sifting out what living and dead "particles" it encountered, *E. neglectus* (misidentified as *E. vernalis*) added to this repertoire by occasionally scraping the bottom with its phyllopodia and thus collecting a load of detritus. Modlin noted that the tips of appendages of the pure filter-feeder are edged by many fine setae, while the tips of the "scraper's" phyllopodia are armored with spines adapting it for this additional activity.

Also interested in limb structure and feeding differences, Graham Daborn (1979), a Canadian scientist, compared phyllopodia of a number of genera and species. Included among them were three that occur in California, two of which may co-occur (*Branchinecta mackini* and *B. lindahli*) and one of which (*B. lindahli*) has been found at one time or another with 7 other California anostracans. He noted that both *B. mackini* and *B. lindahli*, which attentive eyes have seen scraping at times (Daborn 1977; Tasch 1970; Eriksen, & Belk pers. obs.), also have spines along the outer edges of their appendages. Well, all do except *B. lindahli* females which possess fine setae instead. Could it be that not only are species separated by such behavioral and structural differences, but also that males and females of some species minimize feeding competition in this manner as well? Ah, more questions!

Before we run to the field or lab to look closely at our less-observed species, know that *Branchinecta longiantenna* may be a scraper as well, for some of our old drawings show the outer edges of its appendages adorned with spines (Fig. 3.1, p. 47). If this be the case, then some other mechanism must minimize competition between *B. lindahli* and *B. longiantenna* when they occur together, as in the area around Soda Lake in San Luis Obispo County. By contrast, *Artemia franciscana* is probably a pure filter-feeder, for the outer edges of its appendages possess only long setae (Daborn 1979).

Having just mentioned Soda Lake, let us tell you that this is a very salty place and *Artemia* therefore relishes the place. In late April of 1991, Larry Serpa, a regional manager for The Nature Conservancy, collected not only *A. franciscana* from Soda Lake but, for the first time and still the only time in California, *Branchinecta campestris* as well. Larry did not obtain data on the population structure of these two species, but our best guess is the population of *B. campestris* was declining while that of *A. franciscana* was beginning to boom. We say this because that is what Broch (1969) found in his study of populations of these two species in four lakes in the state of Washington. Broch felt the reasons for his observations were rooted in the different biologies of the species. For example, in Washington, *Branchinecta campestris* begins to hatch early in the season when water temperatures approximate 4°C and salinities are low because of snow-melt and runoff. Although *Artemia* can hatch in distilled water, it needs temperatures in excess of 10°C to stimulate the process. Because *B. campestris* cannot regulate hypo-osmotically, it is limited to the habitat's "low-salinity" phase. By contrast, the hypo-osmotic regulatory ability of *A. franciscana* allows it to live on in the grandiose quantities of salt that accumulate when wind mixes fresher surface water with deeper saltier water, and when evaporation concentrates salts in the later life of the pool.

Physiological separation of stages in the life cycle is also important when *Streptocephalus woottoni*, the endangered Riverside fairy shrimp, co-occurs with *Branchinecta lindahli*. Here is a "togetherness" apparently allowed by differences between the species in duration of development (Hathaway & Simovich 1996). What this all means is that *B. lindahli* hatches well, and in several days, from 5-15° and poorly at 20°C as demonstrated by Denton's work (Belk 1977a), then develops rapidly (1-3 weeks) to maturity. *S. woottoni* readily hatches between 10-20°C, with some larvae even appearing at 25°C, but the process takes 1-2 weeks. Development is slow as well, with maturity requiring 7-8 weeks. Thus, during the cool-water stages of a pool in winter, *B. lindahli* is the conspicuous resident, and it is still holding forth in late February or early March when *S. woottoni* attains sufficient size to be collected in a normal dip net. However, by the time most individuals of the latter species are mature, *B. lindahli* has disappeared, and temperatures no longer drop low enough to stimulate another of its hatches. Why this beast has taken leave when adults can probably tolerate the water temperatures, and almost certainly the water chemistry, is not understood. What we do know about its longevity suggests that age might be the reason. Yep, senile fairy shrimps; and more opportunity for research!

Although the previous story seems straightforward enough, life in the co-occurrence lane isn't necessarily all that simple. Consider that the situation just described occurs in western Riverside County. Yet, but a few miles away on the southern coastal mesas of neighboring San Diego County, the preponderant resident anostracan is *Branchinecta sandiegonensis* (Simovich & Fugate 1992; Fugate 1993). Of the many pools on the southern mesas, in only three deeper ones on the Miramar and Otay mesas have *B. sandiegonensis* and *Streptocephalus woottoni* been recorded together; by contrast, on the coastal mesas in northern San Diego County, where *B. sandiegonensis* is much less common than *B. lindahli*, the former has been collected with *S. woottoni* but twice, the latter a number of times. Furthermore, given that the distributions of the two branchinectids overlap, we find it intriguing that on only three occasions, and only in degraded puddles, have they been found together (Simovich & Fugate 1992; Moeur pers. comm.). We would not argue too heartily with the individual who feels this situation smacks of competitive exclusion, but for the real answer, it's time for some experiments.

By way of introducing you to the secretive escapades of another fairy shrimp endemic to California, we note that collections from the largest habitat of *Streptocephalus woottoni* and *Branchinecta lindahli*, a valley grassland pool in

Riverside County called Skunk Hollow, have never yielded a third anostracan in the flesh. Yet, hatched in the laboratory from cysts in its mud is a third species, *Branchinecta lynchi*. This creature is widely distributed throughout the grasslands of California but is seldom abundant anywhere (also a situation not understood), particularly where it co-occurs with other species. Although no published studies deal with specifics of its life history, Helm (1998) determined that it hatches, like *B. lindahli*, at cool temperatures. Why then has it not been seen swimming in Skunk Hollow? We can only guess. And our guess is that *B. lynchi* was present but, true to form, in such small numbers that it just happened never to be taken in reported collections; or perhaps sampling was not done early enough in the season to record its presence. Coexistence with adult *S. woottoni*, if it occurs at all, must be fleeting, because the latter does not mature until waters warm, usually in spring, by which time *B. lynchi* has probably come and gone. How *B. lynchi* gets on with *B. lindahli* is unknown, but it may be too similar in some way to the better-adapted *B. lindahli* to compete well, yet different enough to "hang in there" in a large, comparatively complex habitat like Skunk Hollow. We suggest this because in situations where pool size is recorded, the smaller and simpler basins housing *B. lindahli* have not yielded *B. lynchi*.

The wide distribution of *Branchinecta lynchi* generally includes the ranges of California's two species of *Linderiella* and that of *B. conservatio*, fairy shrimps which also seem to require deeper and larger pools. *B. lynchi* co-occurs with one or the other of the linderiellas with some frequency, but only twice has it been seen on stage with *B. conservatio*. However, in all situations where these associations were noted, *B. lynchi* was far outnumbered. Why? Maybe pond complexity is involved here too (although no such comparisons have been made); and maybe, at least for the linderiellas, the fact they are different genera means they possess sufficient structural and behavioral differences to allow co-existence. Maybe.

Whatever the case with *Linderiella*, the situation with *Branchinecta conservatio* remains unexplained. So, into the void steps Brent Helm, who informed us recently that he believes he knows why *B. lynchi* cannot tolerate this branchinectid. First, both species hatch when cold water fills their pool basins. Second, *B. conservatio* produces but one cohort of numerous individuals per year, while *B. lynchi* may muster several, each with many fewer individuals. Last, *B. conservatio* is "hyperactive" and consequently sets an amazing swimming and filter-feeding pace. On face value these similarities and differences may seem unimportant for the sparse individuals of *B. lynchi*. And in reality they may not be very important, at least when both species hatch and grow together in winter pools that last 6-7 weeks – a period of time in which each can produce but one clutch of cysts. However, Brent feels that if the two species were plunked together in longer-lived pools (the typical habitat for *B. conservatio*), then, were *B. lynchi* to launch a second cohort, those nauplii would be eaten out of existence by the hyperactive filter-feeding activities of the numerous *B. conservatio*. Great hypothesis, eh?! How about someone stepping up to test it? If someone does, they might begin with the observation that the only time these two species have been observed together was early in 1994 in two pools on the San Luis National Wildlife Refuge Complex in western Merced County. Most of the Refuge pools did not fill until February of that year, and were low or dry by mid-March. This period is long enough for both species to reproduce, but so short as to disallow a second cohort for *B. lynchi*. Perhaps this is a typical period of pool longevity here in the arid western edge of the Central Valley; if so, it might prevent *B. lynchi* from being "eaten out of existence" and thus allow co-occurrence.

Finding *Branchinecta lynchi* with the midvalley fairy shrimp (*Branchinecta* sp.) should not raise eyebrows since both can reproduce rapidly and thus live in short-duration pools. However, because they appear to have similar preferred homes, one might expect *B. lynchi* to have been spotted with our midvalley acquaintance more than the three times so far recorded. Given their close taxonomic relationship, the reason may lie in some form of competition so far unraveled.

Branchinecta lynchi's quite unexpected one-known stand with *B. mackini* occurred in a road-side swale pool where the rather different ranges of these two species happen to meet, at the edge of the Pixley National Wildlife Refuge in Tulare County. Habitat water registered next to the highest alkalinity, and the highest pH and TDS, for any pool known to contain *B. lynchi*, and it was near the low end of these parameters for *B. mackini*. Never being ones to shun hypotheses to explain uncommon events, we suggest such non-optimal conditions for both organisms may give neither a competitive edge and both may struggle in this habitat. Here is another of those myriad of real-world situations that would be fascinating to monitor through the season and over the years in the hope of answering some of our ever-increasing number of questions!

Fascinating stories undoubtedly wait to be told concerning the intertwined lives of fairy shrimps – if only someone would take the time to untangle them! In some cases, particularly in California, it is probably too late, for no one has any idea of what nameless faces were extirpated before we humans even knew who they were. But in the case of two of California's most common and wide-spread anostracans with similar distributions, *Branchinecta mackini* and *B. lindahli*, there are some interesting tales to spin regarding their co-occurrence or lack of same.

Branchinecta mackini, true to its name of alkali fairy shrimp, lives in a wide array of alkaline waters. Strikingly, if one were to consider information recorded from out of state, *B. lindahli*, the versatile fairy shrimp, is in fact more versatile. It is known from an even wider range of alkalinity, beginning in the nearly pure waters of the quartz-monzonite dome pools that Clyde studied at Joshua Tree National Monument, and extending to such a seemingly trying habitat as an "alkali soup" the color of "black ink" in Nebraska (McCarraher 1970). Nothing approaching the latter conditions has been stumbled upon in California.

We read in Gonzalez *et al.* (1996) that *B. lindahli* is a much better ionic regulator than *B. mackini*, at least of Na^+, at low environmental concentrations of Na^+, and as a consequence *B. lindahli* is found in soft waters (low alkalinity, low Na^+) while *B. mackini* is excluded. However, since these authors show Na^+ is treated similarly from moderate to high environmental levels by both species (they conform), apparently different ion-control physiologies are not what separates them throughout much of their range. Fine, you say; but if separation is generally not in the manner that salts are handled, then what, pray tell, does isolate them most of the time?

We begin our answer noting that when *Branchinecta mackini* and *B. lindahli* are found together in our state, their habitats are only moderately alkaline, and are always small, turbid, pools and road-side ditches in the Mojave Desert and southern Central Valley. In fact, when found alone, *B. lindahli* typically inhabits small, sometimes tiny puddles usually low in alkalinity. And given its distribution in the most arid parts of the southern half of California, "small" also translates as short-lived. By contrast, *B. mackini*, if in small bodies of water, occupies those tending to be deeper and therefore longer-lasting, and of greater alkalinity. Perhaps more typical habitats for this creature are playa lakes lying in desert basins.

Some of these playas are very large, and reasonably long-lasting when filled, like the 20 km-long Middle Alkali Lake located in extreme northeastern California, or Rogers Dry Lake, landing site for space shuttles (when dry).

Ah, the numbers of fairy shrimps that must filter their way through such large universes – they cannot but boggle the mind! And in those numbers lies one of the keys to our present story. Of course reproduction is paramount in order to be successful in the game of life, but then offspring must feed, grow, mature, and reproduce again, **all with the resources and within the life span of a specific pool**. If one species competes better and therefore reproduces more, it should ultimately swamp the community with its members and drive its competitor to extinction.

Now consider the reproductive biology of our two critters in question. As you have come to expect, growth rate and length of time to sexual maturity are related to temperature. According to Sharon Maynard (1977), during warm falls *Branchinecta mackini* takes 12-17 days to come to sexual maturity. By contrast, *B. lindahli* requires only 9-13 days. In the cooler temperatures of spring, 21-31 days are needed by the former, while 17-20 are sufficient for the latter. In other words, no matter the temperature, *B. lindahli* matures about 25% faster than *B. mackini*. However, there is a price for early reproduction, and that is one of smaller adult size, with a concomitant smaller clutch size. Of course the more transitory the pool, the fewer are the possible clutches.

It seems, therefore, that *B. lindahli* has a strategy of allocating much energy early in its life to get to maturity in a hurry, with the consequence of small adult size and therefore small clutch size. Because *Branchinecta mackini* spends its energy early on to grow and attain larger bulk, it cannot produce eggs until later. But when it does reproduce, its clutch size is big, often 3-4 times that of *B. lindahli*. In both species, multiple clutches can be assembled in a season – the number depends on the pool's longevity **that particular year**. These different strategies of course favor *B. lindahli* in short-lived pools which may have dried to oblivion by the time *B. mackini* is able to begin producing eggs. And seeing the comparatively greater number of cysts that can be generated by a population of the latter, it is no wonder that it predominates in longer-lasting waters.

Although we do not wish to digress too far from our California species, it seems appropriate to mention that the latter have no monopoly on this strategy. In his central Texas environs, Denton (Belk 1991b) watched *Branchinecta packardi* develop to maturity with both small adult and clutch size in 7 days at Texas summer temperatures, and thus could complete a life cycle in short-lived rock-pools atop the local geological wonder, Enchanted Rock. The slower-developing *Streptocephalus texanus*, common in longer-lived pools at its base, never made it onto the granite dome because by the time maturity was attained (11 days and longer), any moisture up there had been lost to the Texas summer sky. This "Texas two" contrasts with our California cool-water pair by hatching and holding forth under a hot summer sun. These species would have a tough time in California given our inhospitable lack of summer rain! And true to this notion, *S. texanus* has been collected in California only along the furthermost southeast border with Arizona, where Sonoran Desert thunderstorms occasionally fill basins along normally dry washes. And although there seems to be no good reason why *Branchinecta packardi* might not also occur in the same area, so far as we know, it doesn't!

But back to *Branchinecta lindahli* and *B. mackini* and their California homes. Given different development times, it is undoubtedly at the "overlap" of short- and long-lasting pools where the two species are found together. In years of drought *B. lindahli* predominates, perhaps even replaces *B. mackini* if dry conditions continue. In years of plenty the reverse may occur. Should the seasons see-saw back and forth over time, one can understand why both branchinectid species could continue to "hang in there" together in spite of being closely related competitors.

A variation on this theme, which may have its parallel in California although it has yet to be seen, is demonstrated by two anostracan species far away in the south of Europe. At an elevation of 1,600 m in some secluded mountain-pasture pools of Italy, Mura (1991b) concluded that *Tanymastix* and *Chirocephalus*, co-occurring fairy shrimps in her snow-melt study pools, shared the same hatching stimulus, cold water. Yet, one species or the other would dominate or be exclusive in different years. In unwinding the evidence in this thriller, Mura discovered that when the season remained cold, *Tanymastix* developed faster and matured earlier, of course being of smaller size than *Chirocephalus*. Not only that, *Tanymastix* was killed by abrupt thermal increases, a not uncommon occurrence in Mediterranean climates. Its co-inhabitant, *Chirocephalus*, was unaffected by abrupt temperature changes, grew at a faster rate in warmer water, reached larger size, and left a greater number of cysts than *Tanymastix*. So, who comes out "numero uno" in any particular year depends on the day-to-day temperature events in these tiny crustaceans' world.

Because of its wide physiological tolerances, and therefore its wide distribution both in and outside of California, *Branchinecta lindahli* is afforded the chance for many inter-species interactions. Never let it be said that this creature does not take advantage of its opportunities because it holds the record for California (7) as well as elsewhere in North America (7 more). Truly *B. lindahli* is the versatile fairy shrimp.

In the most southeasterly desert in California, the Sonoran, there is a paucity of aquatic biologists searching far and wide for summer fairy shrimps so the data we have are few. In any event, *Streptocephalus texanus* and *Thamnocephalus platyurus* dwell there in the summer heat should thunderstorms dump water on their pool sites. Except that these species are both large, both warm-water creatures; and both intolerant of cold (*S. texanus* being less so), fairy shrimp enthusiasts know little about them, including why, throughout their range, if you find *T. platyurus* you usually find with it *S. texanus* or some other streptocephalid (Maeda-Martinez *et al.* 1997). But, never lacking for a reasonable hypothesis to be tested, your authors guess that the fact these anostracans are in different genera suggests structural and behavioral differences which minimize competition and allow coexistence. Certainly *T. platyurus* is a beast of unique architecture (Figs. 7.1, 7.3, pp. 140, 142), but how its strange form might allow it to cohabit with streptocephalids only the creatures of their pools know at this writing.

In California, the distribution of *Thamnocephalus platyurus* also extends into the Mojave Desert, barely overlapping the range of *Branchinecta mackini*. Although the latter can hatch at summer temperatures, it typically makes its appearance in the cold winter waters more commonly presented within its range. And even though *B. mackini* can live in moderate alkalinity, *Thamnocephalus* is found only in waters of low to moderate alkalinity; so there is a window of opportunity for these species to co-occur, and sure enough they do, in Troy and Bicycle Dry lakes near Barstow in San Bernardino County. For the sake of simplicity, let us once again invoke differences in adaptive strategies and generic structural differences as the most plausible reason at this time for their togetherness.

As a final generalization, predictable, long-lasting pools, which occur in areas of snowfall and consistently greater rainfall in the Sierra and more northern reaches of California, tend **not** to support more than one species of fairy shrimp. The favored reason for explaining this phenomenon is that when pools are predictable and stable, individuals of one species must be better suited than those of another to the yearly-repeated suite of conditions, therefore, in time, the better adapted will outcompete others that have found their way into the pool (Maynard 1977).

Table 3.1. Coexistence of anostracan species in California

species	found swimming with
Artemia franciscana	*B. campestris*
Artemia monica	none
Branchinecta campestris	*Artemia franciscana*
Branchinecta coloradensis	*B. mackini*, *E. serratus*
Branchinecta conservatio	*B. lindahli*, *B. lynchi*, *L. occidentalis*
Branchinecta dissimilis	none
Branchinecta gigas	*B. lindahli*, *B. mackini*
Branchinecta lindahli	*B. conservatio*, *B. gigas*, *B. longiantenna*, *B. lynchi*, *B. mackini*, *B. sandiegonensis*, *S. woottoni*
Branchinecta longiantenna	*B. lindahli*, *B. lynchi*
Branchinecta lynchi	*B. conservatio*, *B. lindahli*, *B. longiantenna*, *B. mackini*, "midvalley", *L. occidentalis*, *L. santarosae*
Branchinecta sp. "midvalley"	*B. lynchi*, *L. occidentalis*
Branchinecta sandiegonensis	*B. lindahli*, *S. woottoni*
Eubranchipus bundyi	none
Eubranchipus oregonus	none
Eubranchipus serratus	*B. coloradensis*
Linderiella occidentalis	*B. conservatio*, *B. lynchi*, "midvalley"
Linderiella santarosae	*B. lynchi*
Streptocephalus dorothae	none
Streptocephalus sealii	none
Streptocephalus texanus	*T. platyurus*
Streptocephalus woottoni	*B. lindahli*, *B. sandiegonensis*
Thamnocephalus platyurus	*S. texanus*
species	**cysts in same basin, but not seen swimming together**
Branchinecta lindahli	*T. platyurus*
Branchinecta lynchi	*S. woottoni*
Branchinecta mackini	*T. platyurus*
Streptocephalus woottoni	*B. lynchi*
Thamnocephalus platyurus	*B. lindahli*, *B. mackini*

What do fairy shrimps eat?

We have said in several contexts that anostracans are basically filter-feeders. They are also described as non-selective particle-feeders. If we put those ideas together, we visualize an animal which indiscriminately removes any kind of particle from the water that its suction currents can bring in and its filter size can retain, be it bacterial, plant, animal, detrital, fine sand, or glass beads offered by some researcher. Digesting its treasures is another story. Because of their undiscriminating eating habits, fairy shrimps are best called **omnivores**, or opportunistic feeders, eating whatever is available. But what are the sizes, or variety of sizes of particles, retained and eaten by different fairy shrimp species? The simple answer is no one knows! The more involved answer which follows deals with what few data exist.

Size of mesh or filter in anostracans has been determined for only 6 species that we know of, and only two are found in California. One, *Linderiella occidentalis*, has the smallest filter recorded – an incredibly tiny 0.3-µm intersetal distance (Helm in prep.). Not much larger is the brine shrimp *Artemia franciscana* with a 0.5-µm mesh, and, with it, life stages from nauplius to adult retain individual bacteria (Schrehardt 1987). That's small food! But being so fine a mesh, it is not difficult to imagine these micro feeding mechanisms clogging if the animals' aquatic world was loaded with particles much larger than 0.3-0.5 µm. Perhaps we have here part of the reason that *L. occidentalis* dwells overwhelmingly in deep, clear-water vernal pools (Helm 1998) where vegetation impedes mixing thus the stirring up of clays, and *Artemia* lives in brines where clays cannot remain suspended because they precipitate if TDS exceeds about 3,000 ppm. Ah, physics!

What tiny or big particles exist in the homes of *Linderiella occidentalis* and are sieved out and eaten is presently being determined by Brent Helm at U.C. Davis. With regards to *Artemia*, the environment offers nothing large, for multicellular life (other than the benthic detritivorous brine fly), cannot live submerged in its salty habitats. Certain single-celled bacteria, blue-green bacteria, and green algae, all very tiny creatures, must therefore suffice for *Artemia*'s nutrition. In order to obtain these cells, a filter with a small enough mesh to sieve out such food was obviously evolved for the job. Ah, adaptation!

Now, what about the other extreme? How large a particle can *Artemia* collect and ingest? Schrehardt (1987) writes that maximum particle size increases from 10 µm for early nauplii, to 30 µm for mid-stage larvae, and 50 µm in adults. Because all life stages filter bacteria, it appears that mesh size does not increase with growth of the animal. Also, it looks as though the ability to consume larger and larger particles as *Artemia* increases in size may be determined by oral dimensions, and the effectiveness of mandibles in reducing larger particles or organisms to pieces that fit into the mouth.

When hollow glass balls of a variety of micro sizes were suspended in an aquarium and filtered by *Streptocephalus proboscideus* (an African anostracan with a mesh size of 3.5 µm), the exact same trend was recorded as for *Artemia*. Here the young engulfed particles from 5 µm (the smallest presented) to 17 µm, while adults managed particles from 5-79 µm (Brendonck 1993).

Well, how about the other Californians? Do we have any ideas about what they can stuff into their mouths? The contents of the guts of *Branchinecta mackini* were extracted by Maynard (1972), and amongst the treasures found were algal cells that ranged from 10-50 µm. Maynard was attempting to compare the diet of *B. mackini* with another branchinectid, *B. paludosa*. She

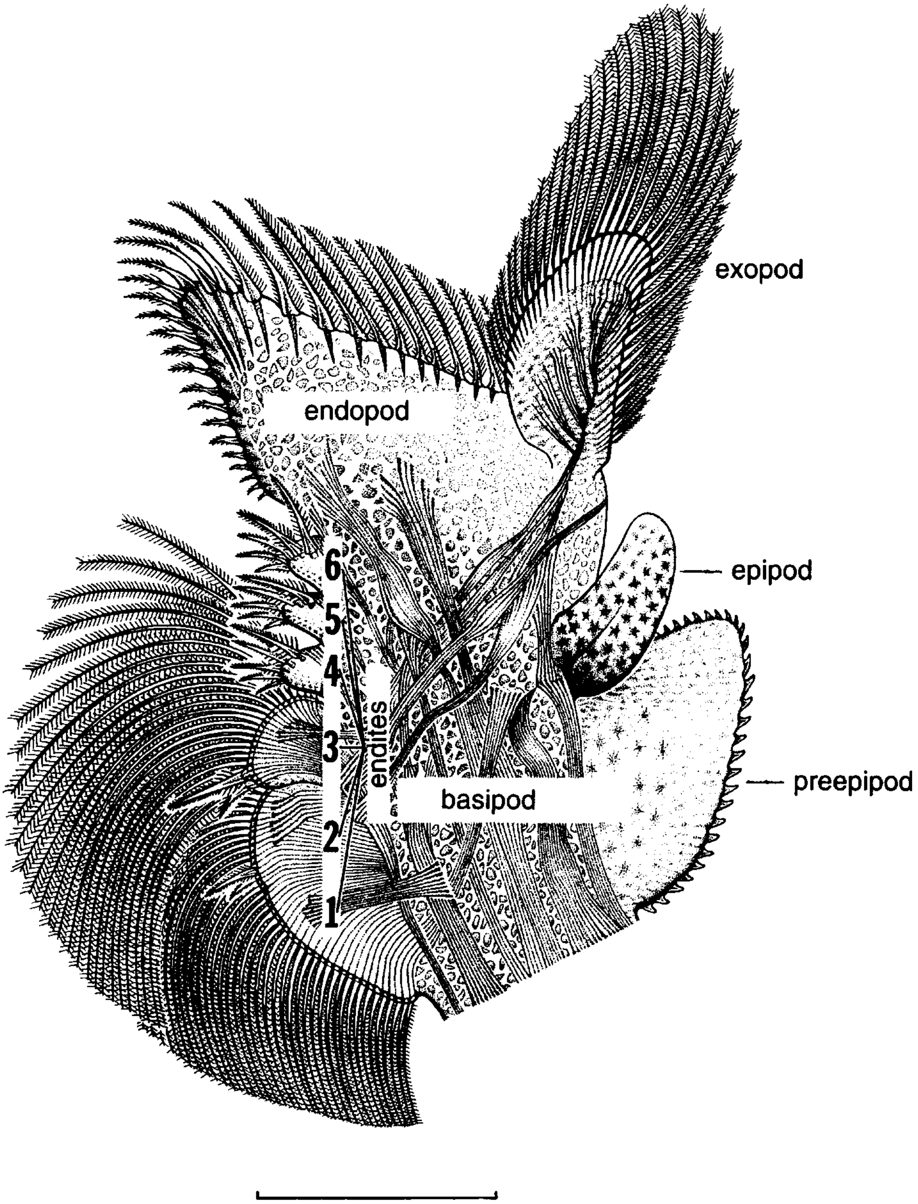


Fig. 3.1. View of the anterior surface of the right fifth phyllopod (leg) of a male *Branchinecta longiantenna*. The numbers 1-6 mark the endites. Endites are inwardly (medially) directed lobes of the unbranched basal part of the leg, the basipod. Scale = 1 mm.

commented that the latter had a coarser, but unmeasured, "filtratory net", a situation which correlated with cells 92-100 µm in size in its gut. Finally, Daborn (1979) counted twice as many setae in the filter area of an appendage from *B. mackini* as compared to one from *B. lindahli*, suggesting a finer mesh-size for the former. Problem! The *B. lindahli* he measured were half the length of the *B. mackini*. So naturally, for these data to be most useful we need to know whether or not setal number and spacing change with an increase in animal size.

How different are the size-ranges of particles filtered and ingested by the various anostracan species? A fascinating study which would begin to answer this question might involve the following. Into one aquarium stocked with similar-sized fairy shrimps of different species, and a second with different-sized individuals of the same species, mix an appropriately wide size-range of glass or plastic beads (industrially available; Brendonck 1993). After the animals stuffed themselves for awhile, ingested beads could be removed from their guts and measured under a microscope. The minimum and maximum diameters, and the size-ranges thus established for each age and species, could then be compared to the measured filter mesh-size of each. Such a study, possibly highly instructive about how the differences in food resources utilized by each species could minimize both inter- and intraspecific competition, has not been done. Will someone step forward to pursue this one? Whoever does, try to incorporate a great idea our editors proposed, color-code the beads for size, for that would make your evaluation so much easier!

Of course fairy shrimps are constant swimmers, so what they filter comes from the water through which they navigate – at least it does for *Artemia* and *Linderiella occidentalis*. Although we do not know how general the situation is, a number of species supplement their feeding by turning over (remember, fairy shrimps swim on their backs) to scrape the flocculent bottom deposits into suspension with their beating phyllopodia. Some return to their normal swimming position with a load of scrapings between their phyllopodia, others swim through the sediment cloud, apparently filtering appropriately-sized particles from it.

So, what are these particles they filter and engulf, and how nutritious are they? In a pool with "clean", clear water the particles are largely phytoplankton and bacteria, but they must include protozoa, rotifers, and tiny larval forms of a variety of species. From present information, we conclude that individual bacteria are probably not captured by the sieves of most species of fairy shrimps because mesh-size is too coarse. Much of the animal material ingested probably gets fully digested. By contrast, phytoplankton cells are surrounded by a cellulose cell wall which is not digestible by animals, but the wall is a rather small fraction of the total cell volume and is permeable to a fairy shrimp's digestive enzymes. Therefore, this array of foods, being mostly digestible, is undoubtedly a very nutritious smorgasbord for anostracans.

In a pool with muddy water, insufficient light penetrates to allow photosynthesis. Particles present may include the animal types already mentioned and bacteria, but phytoplankton is absent. Particles in greatest abundance are the clays that muddy the water. Clay is inorganic and indigestible. So what supports the energy requirements of the fairy shrimps and other community members? The answer is, directly or indirectly, the remaining type of particle, **detritus**.

Detritus is an exceedingly important particle type in pools, be they muddy or clear. It is dead organic matter, largely of plant origin. Its nutritious fraction has already been used by someone or, as with tea leaves, leached into the water as dissolved organics. What remains is composed largely of cellulose and lignin, which are not digestible by macroscopic life. Two questions are immediately obvious. First, if these materials are not digestible by fairy shrimps and others, why are we talking about them? And second, if the pool is turbid and cannot support photosynthesis, where does detrital plant material come from anyway? One question at a time, please!

Although the "large" creatures we visualize as making up the pool community cannot digest cellulose and lignin, bacteria and fungi can. By themselves, detrital fragments are about 5% protein, but after several days in water they are colonized by bacteria and fungi and the protein content of the "combo" rises to about 25% (Cummins *et al.* 1989). To paraphrase Ken Cummins, detrital fragments are like saltine crackers - not much nutrition by themselves, but when spread with peanut butter they become a very wholesome food. So, the organisms that can filter detritus particles from the water and eat them digest the nutritious bacteria and fungi. The still indigestible, but somewhat more fractionated, cellulose and lignin remains are then defecated into the pool where colonization begins anew. Isn't there a well-known saying that goes something like "from detritus to detritus"? Whatever the literary equivalent, detrital cycling is real, and very important!

All that remains now is to get "colonized detritus" into the water in appropriately sized particles and the fairy shrimps can "chow down". Mixing action of wind, and stirring up of the bottom by animal activity, including scraping by some anostracans, are the causative agents. With regard to our second question, detritus which originated outside a pool can be brought to it in several ways. In areas where there is little vegetation to impede movement, wind may blow dead material along the ground, only to have it trapped in a water-filled basin. In grassland areas, overland flow during times of excessive rain or flood, and possibly wind, are undoubtedly important agents of detrital transfer. Where surrounding vegetation is tall, leaves and branches may be blown down into a pool. In the desert, flash floods move not only fantastic quantities of rock particles, but the raging water also picks up leaves, twigs, even bushes that have accumulated in washes, and reduces them to smaller pieces as it grinds its way downhill to the collection basin, often a desert playa, below.

Irrespective of whether a pool is turbid or clear, there is yet another mechanism for transporting detritus. In today's California, cows, horses, and rabbits, probably in that order of abundance, are the main big grazing animals that come to pools to drink. Oh, yes, throw in a few sheep as well. Historically, elk, pronghorn, and deer roamed the California range instead, or go back a step further in time and add mastodons, camels, giant ground sloths, and all other such creatures that are no longer with us. All but the rabbits certainly did not or do not hesitate to wade on in to take a drink. In order to make room for that wet, cooling elixir, these animals are prone to dump their unusable products into their drinking water, yea into the fairy shrimp habitat! Their urine is a fine nitrogen source, and one that can be converted by bacteria to ammonium or nitrate and used by those bacteria, and algae, for growth; the "road apples", "cow-pies", fecal pellets, call them what you may, are fine sources of partially pulverized organic matter. And anyone who has walked through a pasture or along a favorite fishing meadow knows the prodigious amount of processed detritus this source can move (pardon the pun).

There is yet another story that merits telling. Although the process undoubtedly applies to all muddy-water habitats, the details were worked out with *Branchinecta mackini* in a desert playa, Rabbit Dry Lake, by Mike Patten and Louis Rappoport (1980), two students who were working with Clyde. After a steady but non-drenching rain formed shallow pools in the basin without the aid of significant run-off, analyses showed that playa water contained little particulate organic matter. Interestingly, and fortunately, no fairy shrimps hatched into these food-less waters. Shortly after the pools dried, a heavy winter storm created flash floods which brought water, mud, **and organic particles** from the surrounding mountains to fill the playa. Fairy shrimps now hatched and lived happily ever after, well, at least until the particulate organics ran out or the pool dried up. And why didn't the shrimps hatch in the first instance? Was it related to no food? We doubt that one; just how could a cyst determine whether or not food particles were out there? Or, was it the non-drenching rain? Come on now, how do fairy shrimp cysts distinguish between drenching and non-drenching precipitation if both supply puddles, pools, and playas with water?

Back in Chapter 2 we explained that the conditions which stimulate hatching of *Branchinecta mackini* are known, and were also worked out on the Rabbit Dry Lake population. Remember that fresh water, or at least a sudden decrease in dissolved salts, is required to begin coaxing nauplii from cysts. However, when the water's TDS exceeds 1,000 parts salt to a million parts water (1,000 ppm), hatching is inhibited. If we apply this information to the observations of Patten and Rappoport, we realize that the steady light rain which added water drop by drop to the playa's salty soil, plus the constant mixing action of wind on water, assured a high salt content in the pools that formed. The result, of course, was inhibition of hatching. In contrast, when flash floods descend the mountain slopes and fill the playa rapidly, although muddy, the water is large in volume and low in TDS. Hatching is therefore stimulated. Because of the large volume of fluid, several days of wind-mixing of water over playa soils are usually necessary to raise the dissolved salt concentration to a level that inhibits further hatching.

Mizutani (1982), using *Branchinecta longiantenna* (thinking it was *B. mackini*), did some creative lab work to establish what the animal eats. He labeled a common sugar and an amino acid, both of which occur dissolved in playa water, with radioactive tracers. These materials supposedly are leached from detritus brought by flash floods. Physicists tell us that dissolved particles are charged particles, and both of these organic molecules have positively charged ends. Clays, although not dissolved, are so small they too have surface charges, theirs being negative. Ah ha! The clay particles, present in such massive numbers that they make the water muddy, attract and bind dissolved organics, and "hungry" bacteria cluster around and grow on these nutrient-rich surfaces. Such a layering of goodies makes a particle large enough for at least some fairy shrimps to filter, and filter they do, for the radioactive organics were detected in their bodies. Although the clay center of such a concretion is non-digestible, the "peanut butter" on its surface, and dissolved organics held underneath, make for a nutritious morsel. So, fairy shrimps propel themselves through their dark, turbid milieu, seeing little, darting in another direction when they bump into something, but continue filtering nutritious "mud" (or should we also call it a type of detritus?) from the water. Not far down the gut its contents are acidified, and the charged organics are disengaged from the clay. The former, and the bacteria, are digested and absorbed, the clays are moved on and out, ultimately to become suspended particles once more, allowing the process to begin all over again.

You may think we have spent an inordinate amount of time talking about detritus and who eats it, for after all your favorite pool is probably not the color nor the consistency of a chocolate milk shake. For most folks, it is more romantic to think of living things eating living things under clear blue skies and in crystal clear water. However, to put detrital food chains into perspective, consider that probably as much as 95% of an aquatic community's energy flow ultimately passes along such a route; that's only about 5% for the romantics. **Pretty impressive,** or disquieting; depends on how close your esthetic and economic views are to ecological reality!

And speaking of ecological reality, you already know our description of anostracans as being filter-feeders is an over simplification, for many fairy shrimps also scrape detritus from pool bottoms. Further, there are two species which terrorize the crustacean world with carnivory. One, *Branchinecta ferox*, lives in North Africa and Europe and is a filter feeder when small. However, when a length of perhaps 15-20 mm is attained, the animal develops such strong suction currents that it is able to draw in copepods and cladocerans (Fryer 1983). Because this beast grows to lengths of at least 45 mm, it feeds on these animals for a goodly portion of its life.

Branchinecta gigas is the other carnivorous anostracan, and its distribution includes the Mojave and Great Basin Deserts of California. This animal is giant enough that it feeds on other fairy shrimps, particularly *B. mackini*, but *B. lindahli*, as well as cladocerans and copepods, may be significant food items as well. It turns out that *B. gigas* lives only in highly turbid habitats and thus is not a visual predator; in fact, it has by far the smallest eyes in proportion to body size of any fairy shrimp. Because it does not create suction currents that are strong enough to draw in large prey, this fearsome beast swims alertly through its murky medium and reacts immediately upon contact with a potential meal. By drawing its phyllopodia together, the tips of which then overarch the food groove, and at the same time flexing its abdomen over its appendages, our predator attempts to trap its much smaller prey in this "phyllopodial basket" (White *et al.* 1969). If it is successful, the niceties begin with the predator moving the prey forward with the spined bases of its appendages to the mouth area where it is "processed" by the mandibles for ingestion. Armed with sharp denticles, mandibles not only pierce the food when they close, but crush and move it forward as they rotate toward the mouth. Thus Fryer (1966) describes these mandibles not as tearing or chewing devices, but as "crushing rollers". For the trapped fairy shrimp or other crustacean food item, this process is "the end of the line" as the punctured and mashed body is ingested whole. Robert Brown reminded us that although the prey may have been moved into the gut in one piece, it had undoubtedly lost a significant amount of nutritious body fluid. Remember, this fluid, or hemolymph, circulates in large body spaces, not in closed vessels. The pressure which causes circulation also keeps the body "pumped up" thus giving it form, as with a balloon. So, when our predator punctures its food item and hemolymph rapidly spews out, the full caloric value of the prey goes unrealized. Because *B. gigas* cannot return to the drawing board to correct this problem, it gets busy groping for more prey to meet its energy needs, and grope effectively it does! Anderson (1970) demonstrated this fact with a simple and tidy experiment in which he placed 1,040 cladocerans, 200 copepods, and 20 *B. mackini* in 3 L of water with a single 75 mm-long *B. gigas* female. After 200 hours in this dark, 10°C meat market, only the female predator was left swimming.

Perhaps when food resources become scarce *B. gigas* casts around for alternatives; at least Fryer (1966) thinks so, for he suggests that scraping is used to supplement its diet. And just so you know this beast seems to take advantage of every option to enjoy a meal, Belk and Ballantyne (1996) observed some of these characters clustered around a wad of *Spirogyra* apparently "...pulling at the algal mass with their phyllopods." That they feed on this kind of material at times is suggested by the fact that algal filaments were found between the mouth parts and in the gut. Those times must be few, however, for as we have noted, *B. gigas* typically lives in waters so turbid that algae cannot grow.

What eats fairy shrimps?

The old adage that "those who live by the sword, die by the sword" even has meaning for anostracans. Although these graceful and seemingly passive creatures are hardly the sword-carriers for which the statement was written, they do live by eating considerable quantities of living things. And, in their turn, they die by the "swords" of birds, bugs, and beetles. Some also fall prey to jaws of relatives – another fairy shrimp or a tadpole shrimp, even dragonfly larvae, occasionally fish, amphibians, and, yep, humans. About who eats them from the inside (parasites) we know next to nothing except that they do fall prey from within. Amat *et al.* (1991) and Jarecka (1984) noted that the brine shrimp *Artemia*, and the freshwater fairy shrimp *Branchinecta gaini*, can serve as intermediate hosts for the cyst stages of hymenolepid tapeworms. The presence of these cysts has no effect on survival, but it does lead to castration, obviously a factor in the size of the next generation of shrimps. Long-time anostracan enthusiast Robert Brown collected a pot full of *Branchinecta lindahli* near Soda Lake in San Luis Obispo County and returned them to his lab at CSU San Luis Obispo. There he watched as an unknown micro-organism grew and occluded the anostracans' body cavities. Once filled with whoever it was, the fairy shrimps succumbed. As has been said before, there needs to be bread on every table!

So much for pleasantries, let's get down to naming names of those who eat whole fairy shrimps! How's this one: **giant fairy shrimp**, so named because it is! We just told you about this behemoth's eating habits, but feel free to check back on its culinary artistry.

Another predator of anostracans is the tadpole shrimp (Fig. 1.1, p. xiv). There are four species of these "Jurassic Park" creatures in our state. Three live in turbid, desert alkali playas like our giant friend *Branchinecta gigas*, the fourth dwells in pools of low dissolved solids in the northern Central Valley. Two of the desert alkaline-lake tadpole shrimps share the same food, *B. mackini*. However, they appear to divide feeding opportunities in these places by season. *Lepidurus lemmoni* eats *B. mackini* in winter and spring waters. *Triops newberryi* must "chow down" on them, possibly *Thamnocephalus platyurus* and who knows what else, during summer (no one has ventured into the heat of the Mojave at opportune moments to find out).

The intriguing question (yes, another question) is: how do *B. gigas* and *L. lemmoni*, whose distributions in California overlap significantly, divide winter and spring playa waters between them, given that they share *B. mackini* as their major food? Before the 1992-1993 rainy season we knew of no records that these species co-occurred, and we wondered who out there would find out why? Well, we still don't know why, but Marie Simovich and Richard Gonzalez (1993) found both species inhabiting sites scattered across Edwards Air Force Base in the Mojave Desert. In 8 of those pools, one species or the other was present; in 12 of them both occurred. However, in examining the Simovich-Gonzalez data, we noted that *B. gigas* was often present from November to January, while *L. lemmoni* did not usually appear until January or March and remained in the pools later into spring, in several cases much later. Perhaps thermal cues separate the hatching times of the two predators. When the earlier-hatching *Branchinecta gigas* appears, its nutritional needs are met by *B. mackini*. As the *B. gigas* populations bow out, *B. mackini* is then fed upon by the later-appearing *L. lemmoni*.

Lepidurus couseii has recently been recorded in the Great Basin Desert of the far north-east of our state, and although it has not yet had its eating habitats described, we'll bet it too eats anostracans.

Golly, desert waters seem to have phyllopod predators of fairy shrimps galore; but how about the rest of California? The fourth of the state's tadpole shrimps, *Lepidurus packardi*, dwells mainly in the northern and eastern Central Valley. Its distribution thus overlaps those of *Branchinecta lynchi*, *Linderiella occidentalis*, and several uncommon fairy shrimp species. In a Sugnet and Associates study (1993), *Lepidurus* was taken in 345 of about 3,100 locations checked, and at least 40 of these were occupied by *L. occidentalis*, many fewer by *B. lynchi*. Although we know nothing about the interactive private lives of these creatures, we must assume *Lepidurus packardi* enjoys eating tasty anostracans whenever they co-occur.

Other than those organisms exposed above, there are no others that prefer munching on fairy shrimps who dedicate their whole lives to pools. But, like children and relatives who take advantage of abundance, then leave when supplies run out, there are predators that fly, walk, hop, or swim into pools when such pastures are plentiful; then fly, walk, hop, or swim out (if possible) when pool resources dwindle or water disappears.

Studies with islands show the smaller the island, the fewer the colonizers that happen to find it and therefore occur there. In like manner, the more distant the island the fewer in number are the species in residence. Why talk of islands when our concern is puddles? Well, such places are aquatic "islands" in a sea of land, and if those pools are "next door" to permanent water, as is relatively common in the northern two-thirds of the Central Valley and the high Sierra, organisms which inhabit the latter find the pools in a short time. In areas where permanent water is scarce, and temporary pools are often quite distant from a permanent source, colonization is slower, possibly even out of the question for most species. A broad brush would paint California's southern mountains and deserts with this color.

Water birds, being highly mobile travelers, have got to be amongst the fairy shrimp's biggest concerns even in some of the most distant "islands". These birds are large and always hungry. They move easily into a habitat, take what they can get, then depart. In desert areas, American avocets are a particularly common sight wading in turbid, alkaline waters and swishing their sword-like beaks to and fro. Whatever they hit they attempt to grab. Given fairy shrimps' place in food chains, and thus their numbers, they are undoubtedly the most common morsels encountered by the avocet's beak. Kildeers, wading birds which also are known to eat fairy shrimps (Proctor *et al.* 1967), are a common sight around rain pools throughout California, and Lenz (1987) describes gulls and grebes as being avid eaters of Mono Lake's resident brine shrimp *Artemia monica*.

Swanson *et al.* (1985) and Eldridge (1990) have written that northern pintails and mallards, which come to rest on prairie pools along the midwestern flyway, feed on fairy shrimps because they are one of the first invertebrates available once the temporary waters form. Northern shovelers and blue-winged teals also are noted to have significant portions of their diet composed of anostracans. Undoubtedly these and other ducks that wing their way over California find fairy shrimps equally significant to their diet, but we are unaware of any research done in the state on the feeding habits of ducks. What we are aware of is that "The wetlands of the Central Valley provide wintering habitat for 19% of the wintering waterfowl in the continental United States. They support some of the highest densities of waterfowl in the country. Nationally, these are the highest priority wetlands for preservation of wintering habitat." (Secretary of Interior 1994). We also know that the Central Valley is California's richest fairy shrimp country. We suggest that these two facts are not unrelated! Further, an observational study of use by birds of vernal pools on the Santa Rosa Plateau in western Riverside County (Baker *et al.* 1992) demonstrated that, in the larger pools, mallards, northern shovelers, and northern pintails are frequent guests. In addition, green-wing and cinnamon teals are common, and the list goes on to include gadwalls, American wigeons, and ring-necked ducks. Since the waters of these larger pools are plied by fairy shrimps, we doubt the ducks come merely to float unaware of the shrimps' presence. For more information on avian uses of California's ephemeral pools, take a look at the review by Joe Silveira (1998).

Although insects are reasonable fliers, distance from their permanent-water refugia to temporary pools becomes a problem. Only adult insects fly, so they are the colonizers, and aquatic bugs and beetles are the most common of these. Having flown into the soup of a pool, they spend their time diving, often to some depth, in search of prey. Of the bugs, the most common are backswimmers (Family Notonectidae). Like all bugs, these have mouth parts for piercing their prey and sucking it "dry". Notonectids are aqualungers, so they may be seen hanging from the surface film where they recharge their air stores, then dive after food, including fairy shrimps. And eat fairy shrimps they do, at the clocked rate of 2.06 individuals per notonectid per hour (Woodward & Kiesecker 1994).

Predaceous diving beetles are another common sight. Like the bugs, they too carry an air store and also hang from the surface film, then swim rapidly through the water in search of prey! There are a variety of species and sizes, but some fall into the size range of anostracans, and some are even much larger, both as larvae and adults. Although both life stages feed in the same manner, larvae are particularly fascinating beasts. The mandibles are magnificently large, curved, and sharp. In fact, they are hollow and are not used in chewing. Like ice tongs, they close on their prey and impale it. Then digestive enzymes are pumped into the body of their food through these hollow structures and, when digestion has reduced the prey's internal parts to a slurry (exoskeletons are not digestible), it is sucked in through the beetle's mouth with gusto. Bob Brown points out that if the beetle is in no hurry, meaning that it must make the most efficient use of limited food reserves, this feeding strategy is a tidy way to go. However, he has watched many a diving beetle grab, pierce, suck, and run (swim off), suggesting that if food resources are plentiful, sucking a fairy shrimp's hemolymph, rather than waiting around for digestive enzymes to reduce tissue to a slurry, is the more efficient way to proceed.

If the pool is long-lived enough, offspring of these air-breathing colonizers may be seen in numbers, as may the aquatic larvae (also called nymphs or naiads) of dragonflies and damselflies. Adults of the latter groups are terrestrial insects, and are seen flying in the vicinity of pools looking for food and mates, but they are also there to lay eggs in the water. Because the larvae are aquatic and have gills, they always remain submerged, usually clinging to a surface, be it the bottom or aquatic vegetation. Although they move from place to place, they are not great swimmers like beetles and bugs, and thus are more the wait-see-and-pounce type of predator, some pouncing on fairy shrimps.

All these predatory insects must see to feed. Should the pools become occluded, vision is impaired, their way of life is obviously limited (Woodward & Kiesecker 1994), and these creatures disappear. Another way of saying this is that, if pools are muddy, visual predation is out of the question, and finding prey by bumping into it is "the way to go"! So we have come full circle in our feeding story; we are back to fairy shrimps and fairy shrimp-relatives eating fairy shrimps in the darkness of muddy pools! One last comment though about such environments. Because this bump-and-feed life style not only depends on a high density of prey but a large enough prey population to support a predator population, small pools and puddles, particularly those with small numbers of anostracans, do not sustain the predator level of this food chain. However, should the small pool be clear, it may also contain the visually-feeding bugs and beetles who can snatch up conspicuous and tasty morsels, then leave to gain sustenance elsewhere.

We have an uncommon but wonderful little example of free-market opportunism to share with you, although it is certainly insignificant to fairy shrimp biology. Our story involves a midge, a relative of the mosquito. As larvae, midges, like mosquitoes, are aquatic. Unlike mosquitoes they don't hang from the surface film; rather, they live on or just under surfaces, usually of the bottom sediments. And also unlike mosquitoes, some of them are predators. Anyway, Tim Graham (1994), a U. S. Biological Service scientist, was peering into potholes (the water-filled variety) in Utah when he noticed a fairy shrimp moving about erratically. "Good reason for such panic", he undoubtedly thought when he saw a midge larva clamped on the fairy shrimp's head. Because midge larvae are usually somewhat buried in bottom sediments, and fairy shrimps swim, little is the opportunity for such a predator-prey interaction to occur. Knowing this, Tim monitored the encounter until the midge had killed and consumed half of the fairy shrimp. How did a swimmer cross paths with a non-swimmer? Perhaps you will remember that some species of fairy shrimps have a habit of mucking around (scraping) in bottom sediments. Undoubtedly Graham's fairy shrimp was following that passion when the midge trap was sprung. Perhaps a more orthodox paraphrase of a common expression is appropriate here: "predation happens"!

As mentioned in the "Community" section of Chapter 3, fishes may occasionally enter anostracan habitats when flooding occurs, be it natural or agricultural. McCarraher (1959), Pereira and Gonzalez (1994), and Zemmouri (1991) have caught various fish species in the act and recorded it for posterity. When such an event occurs, the opportunistic fish will certainly eat fairy shrimps until they cannot find more, until they find their way out, or until they perish with the pool's drying. We can safely say that fishes are of little importance to modern-day fairy shrimp ecology; however, in the vast past of evolutionary time, after fishes first came into being, they must have encountered environments filled with tasty fairy shrimps. Kerfoot and Lynch (1987) and Wägele (1992) reason that the evolution of more versatile predatory methods by fish (read this over-kill by fish), particularly the development of suction feeding, ultimately exterminated fairy shrimps from all permanent waters by Mesozoic times, leaving anostracans only ephemeral pools as refugia against extinction.

Frogs, toads, and salamanders are also not usually thought of as inhabitants of temporary waters. However, in damper areas of California, and in wetter weather, adults of these creatures may migrate to pools to lay eggs, and, along with their immatures, use these wet places as temporary feeding sites. Frogs feed both above and below waterline, and how effective they might be in utilizing fairy shrimps is unknown, but instances of young bullfrogs filling their guts with tadpole shrimps are known from the Vina Plains near Chico (Federal Register 1994). Anostracans are a part of the diet of at least some salamanders and their larvae. We say this, even though no one has gone public with such information from California, because several scientists have spied on these beasts elsewhere (e.g., Sprules 1972; Thiery 1991; Woodward & Kiesecher 1994; Woodward & Mitchell in prep.) and found both adults and immatures to include fairy shrimps in their food supply. Finally, in California's more southern reaches where spade-foot toads hang out, they and their sometimes predaceous tadpoles may benefit from fairy shrimp feasts. Although no one has told of this drama being played out in California either, once more we rely on Woodward and Mitchell (in prep.) for the juicy information that adult spade-foots will in fact feed on *Streptocephalus texanus*. Interestingly, tadpoles of the spade-foot toad come in both predator and omnivore morphs (forms), sometimes in the same pool. In a fascinating piece of work by David Pfenning (1990), via astute observations and experimental manipulations he showed that "...morph determination depends on the ingestion of shrimp.... If a critical number of shrimp were ingested, the tadpole developed into a carnivore; if not, the tadpole developed into an omnivore." And who were these body-building New Mexican "shrimps"? Ah, those tasty tid-bits (steaks?) *Streptocephalus texanus* and *Thamnocephalus platyurus*, that's who. By the way, Simovich *et al.* (1991) also agree that fairy shrimps are "...an important component of the natural diet..." of spade-foot toad tadpoles in Arizona; so this issue seems to be settled!

The last of the vertebrate predators, with collecting equipment and behaviors capable of sampling both turbid and clear waters alike, are humans. Among them of course are those of us who study fairy shrimps, as well as the individuals who use these graceful creatures for the myriad of purposes already revealed in the Chapter 1 section "What good are fairy shrimps?"

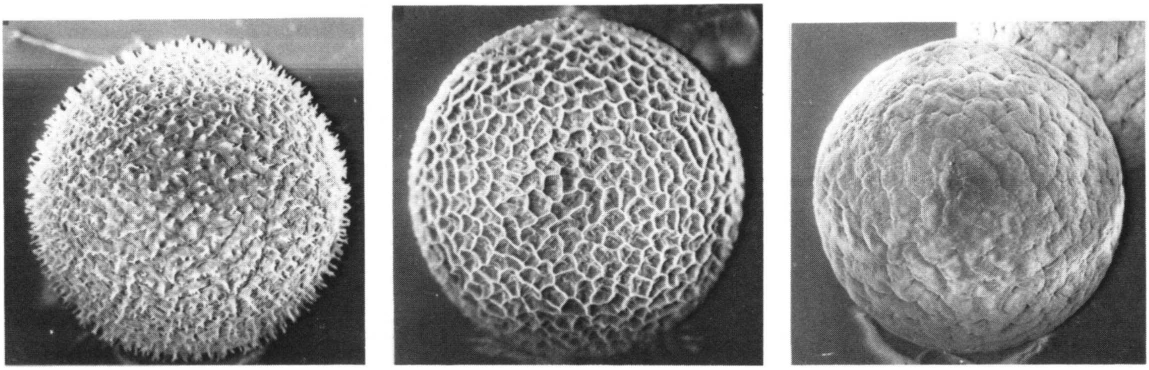


Fig. 3.2. Cysts of the California species of *Eubranchipus*. From the left, *E. serratus* 0.38 mm diameter cyst, *E. oregonus* 0.37 mm diameter cyst, and *E. bundyi* 0.31 mm diameter cyst. SEM photographs by Graziella Mura, Università degli Studi di Roma "La Sapienza", Italy.

Chapter 4

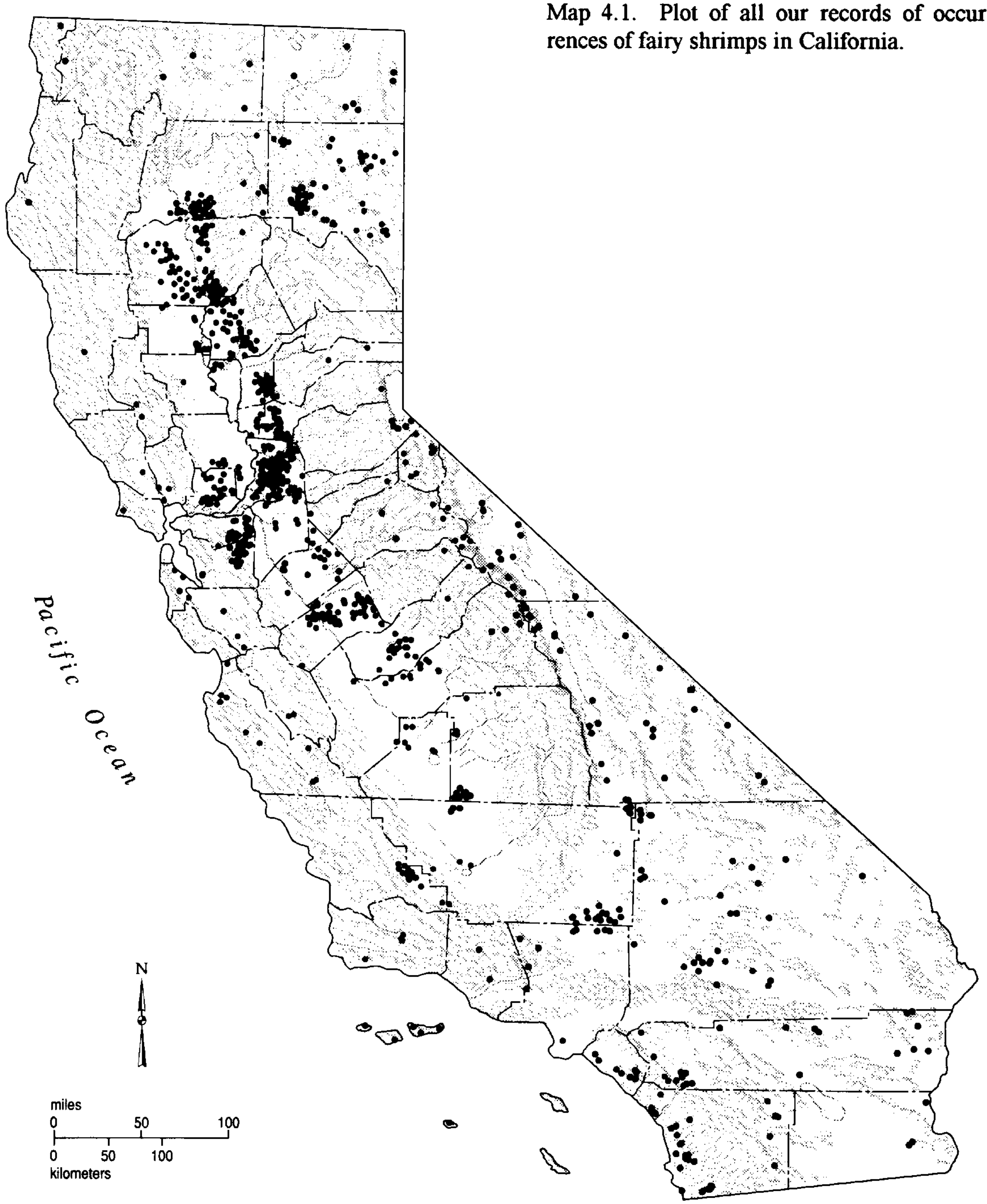
STATEWIDE DISTRIBUTION OF FAIRY SHRIMPS

Fairy shrimps aren't everywhere in California

California is certainly rich in anostracans. In fact, we can rightfully brag that, of the 23 known species that call our state home, eight are found only here (and in a northern sliver of Baja California, Mexico). These statistics are both North American and world records for the number of species of anostracans occurring in a comparable land area. No matter the reality, we sometimes hear silly and uninformed rhetoric about fairy shrimps on radio and TV by individuals hoping to harvest political hay. The printed page may be no different, as exemplified by the grossly inaccurate, almost hysterical disservice to truth by some unidentified author of a Wall Street Journal article dated October 17, 1994. The thesis of the article, entitled "A Fairy Shrimp Tale", was that all shrimps are the same, and all live in mud holes, and because mud holes are everywhere, fairy shrimps are everywhere. Ignorance is bliss they say, but in spite of this writer's bliss, **FAIRY SHRIMPS AREN'T EVERYWHERE!**

True, we have described our little subjects as "the symbol of rain pools", but they are not in every rainpool, or mud puddle, or stock-watering hole, or road-side ditch, or even everywhere in California as is attested to by Map 4.1 (p. 58), a compilation of all known locations of all of our state's fairy shrimps! Don Wootton used to tell your first author that even in the heart of the Central Valley's fairy shrimp country he could find no anostracans or tadpole shrimps west of the Sacramento River from Yolo County north. An intensive survey by Sugnet and Associates, Roseville, (1993), apparently blanketing all of the Central Valley and beyond, and including private lands often difficult to sample because of limited access, led to essentially the same conclusion. Further, they found the same general absence of anostracans and notostracans in the Central Valley west of the San Joaquin River from Alameda County south. Shawn Gallagher (pers. comm.) wrote of his impression of few fairy shrimp locations west of the Sacramento River when he sent us an unpublished "Vernal Pool Survey" (Alexander & Gallagher 1993), done while he was a student at CSU Chico, demonstrating that of 36 pools visited west of the river and south of Red Bluff only 10 contained shrimps, all *Branchinecta lynchi*. One might argue that there are few fairy shrimp sites west of the Central Valley's two main rivers because development has "done'em in". However, there is no less development east of the rivers where the great majority of the Valley's anostracans are found, so this is an unsatisfying suggestion.

Finding out what species reside on the less developed lands of wildlife refuges, no matter their location, would be a worthwhile endeavor since historically these places have gone largely unexplored. To its credit, the Federal Government has recently developed an interest in wetlands, and fairy shrimps, so managers of National Wildlife Refuges (NWR) have begun to look for species



Map 4.1. Plot of all our records of occurrences of fairy shrimps in California.

other than bovines and birds on their lands. In an aquatic survey of the Sacramento NWR **west** of the Sacramento River at the border of Glenn and Colusa counties, refuge biologist Joe Silveira turned up three species of fairy shrimps already known from the region, *Linderiella occidentalis, Branchinecta conservatio*, and *B. lindahli*. Unexpectedly, *B. coloradensis* also debuted in one of their pools, a location that is only its third known site of residency in the Central Valley. Further to the south, and west of Merced, lies the San Luis NWR Complex. Of 59 sites sampled in 1994, including both sides of the San Joaquin River, 15 pools **west** of the river yielded anostracans. Here too, most were *Branchinecta lynchi*, but the Kesterson area also produced *B. conservatio*, *B. longiantenna*, and *B. lindahli*. Do such collections suggest that wildlife refuges hold the remains of the aquatic resources west of the Central Valley's major rivers, or are these records, and the few we have from other surveys, "the exceptions that prove the rule" that fairy shrimps are scarce west of the major rivers in California's Central Valley? Let's ask the talk-show hosts, certainly they will have the answer!

While still peering westward, take a look again at Map 4.1 (p. 58). As you study it, you will probably be struck by the paucity of anostracans in the North and Central Coast Ranges and the near absence of our fine phyllopodous friends in all coastal counties from Santa Cruz to the border with Oregon. Why should this be? Our best guesses (yep, here we go again) are insufficient aridity and lack of pool sites, consequences of the area's generous rainfall. The sites we know about are in meadows, on a depositional flood plain, or along the San Andreas Fault, places which runoff from excessive precipitation could probably not soon erode or fill in. Pools, if present, probably don't freeze or desiccate sufficiently given the cool but not cold near-coast locations and frequent rains. As one trends southward, rainfall and its frequency lessen, and wave-cut terraces, which over geological time have been lifted above the sea, provide an increasing number of pool basins, most numerous in southern-most San Diego County.

Further evidence that fairy shrimps aren't everywhere is presented in a report by Sugnet and Associates (1993). They demonstrated that only about 27% of possible habitats in the northern two-thirds of the Central Valley contained anostracans (830 pools of 3,092 visited). Interestingly, in Sacramento County where 20-30 pools were sampled in each of several clusters of pools, about 75-85% yielded fairy shrimps. These high frequencies were clearly the exceptions for, not uncommonly, **none** were taken in areas where, for example, 95, 86, and 56 sites were visited. That these results closely portray reality is supported by the work of Brent Helm at Jones and Stokes Associates, Sacramento (in press). Brent sampled 5,565 seasonal wetlands in the same region; fairy shrimps paddled their way through only 31.7% of them.

The story is no different in southern California. Near Oceanside in San Diego County, pool basins lie scattered across the coastal plain. While many are natural, a substantial number are considerably deepened by human activity, or are man-made. Some are habitats for anostracans, others not. Truly baffling is the oft-repeated situation where one site will contain fairy shrimps while its seemingly identical neighbor a meter or so distant harbors **nothing**.

These kinds of perplexities are repeated on the grassy slopes of Cachuma Canyon in the backcountry near Santa Barbara where, for 40 years, Clyde has casually kept track of four earth-slump pools within a km of each other. To the eye, all basins are formed in the same soil type. They fill faithfully each year, yield similar water chemistries, and probably dry up at about the same time. All are frequented and dumped upon by cattle. Two pools with milky-colored water contain fairy shrimps. The clam shrimp *Cyzicus californicus* lays claim to a more turbid habitat. Several meters from the latter is a pool of clear water, somewhat smaller but just as deep, harboring no anostracans, although a few clam shrimps were seen in it once. Clyde led Don Wootton to this area in 1954. We collected two kinds of fairy shrimps. One with red eyes was then called *Pristacephalus occidentalis*; you know this little beauty today as *Linderiella occidentalis*. We had no idea what the other species was, and rightfully so, because *Branchinecta lynchi* was not formally described until 36 years later by Eng, Belk, and Eriksen (1990). At any rate, the contents of these pools, one containing both species but the other with only *B. lynchi*, have apparently not changed over the years. What's going on? Since these species not infrequently co-exist, why aren't they together in both sites in Cachuma Canyon, and why haven't they invaded the other pools? Similar questions have been expressed in the scientific literature by scientists whose intellectual curiosity has been challenged by these rain-pool critters. So far, in this regard, all of us have met our match.

Because small basins of water are largely inaccessible from view along the few roads in the Santa Barbara backcountry, and in hopes of finding more rain pools in topography similar to that in Cachuma Canyon, Clyde cajoled his psychology-professor friend and pilot, Harv Wichman, to fly him over the slopes of the San Rafael Mountains from Fillmore to Santa Maria (and ultimately over much of California south of Monterey). Ecstatically we noted a grassy hillside north of Ojai which sported about a dozen pools. They appeared to be formed as earth-slumps, just as were those in Cachuma Canyon; in fact, this hillside could have been mistaken for Cachuma Canyon! On the ground, and wondering which species would be found where, we began dip-netting the pools. After several hours of diligent work, disappointment set in because we collected nary a shrimp. Even water fleas (Cladocera), creatures "typical of almost every pool", were absent. This was a strange place! Or was it? Remember, fairy shrimps are not found everywhere, even in the heart of "fairy shrimp country". The question remains ...**why**?

Road-side ditches serve as homes for fairy shrimps; well, that is to say **some** do. **Most don't!** On one trip in the Alturas area of far northeastern California, Clyde dip-netted every ditch he saw, and not one fairy shrimp was found. By contrast, in the northern portion of the Central Valley, that is, in the heart of "fairy shrimp heaven", of 218 road-side ditches sampled, 55 (25%) had fairy shrimps, most of which were *Linderiella occidentalis*, but 11 harbored or co-harbored *Branchinecta lynchi* (Sugnet & Associates 1993). Interestingly, these data are heavily skewed by the situation in Sacramento County, where 30 of 37 ditches possessed *Linderiella*, including two which also harbored *B. lynchi*. What this means is that, elsewhere, fairy shrimps occur in only 14% of road-side ditches – hardly a preferred habitat type it seems. According to the Federal Register (1994), most, if not all, of Central Valley ditches containing anostracans are probably remnants of vernal pools. If true, then man-made road-side ditches, by themselves, seem to be lousy residences for our selective subjects.

In our experience, the general absence of anostracans in ditches is related to soil, which in turn affects water chemistry. Ditches are usually constructed by scooping away the topsoil. The leached, more acidic sub-soil seems to provide inappropriate habitat. However, we, and others we have spoken with, have noted that where the top 6-8 cm of material have been carefully returned and kept in place, or carried in by erosive waters, for example along desert roads, fairy shrimps occur more commonly, although still infrequently.

Several studies in the Midwest and one in Canada have demonstrated that an anostracan's presence or absence one year is not necessarily the situation forever (e.g., Dexter & Kuehnle 1951; Donald 1983). Remember, fairy shrimps respond to distinct, species-specific environmental clues that, when received, result in hatching of some of the cysts in the pool's sediments. If a species of fairy shrimp is not present in any one year, we cannot say with certainty that none dwell in that particular place. Perhaps rain or temperature patterns proved to be unsuitable that season. Similarly, if fairy shrimps are present one year, it is just as inappropriate to claim they will be there forever, as for example in a pool constructed for mitigation. The rationale is that species may survive for a year or so in a marginal habitat, only to be eliminated by continuing poor conditions.

Certainly some pools seem to have had fairy shrimps "forever"; for others, we do not usually understand whether their absence suggests inappropriate environmental clues, extinction due to a series of "bad years", or a just plain unsuitable habitat. Likewise, how often such "barren" pools are successfully reinvaded is another unanswered question. My gosh, if humans are so unpredictable, how can we expect fairy shrimps to be otherwise? And if there are so many unanswered questions, let us humans of all ages, abilities, and backgrounds, get on with the fascinating sleuthwork of ferreting some of them out.

How fairy shrimps got where they've got

Okay, so fairy shrimps aren't in every pothole, puddle, pool, pond, pan, or playa you can shake a stick at, but they are found in some of the most "out of the way" places! Consider the miles of water between the mainland and California's Channel Islands, where, yes, *Branchinecta lindahli* swims in rain pools (Soiseth 1994)! Then visualize the myriad of wilderness-area snowmelt-filled basins along the Sierra crest, far from road ends or trail heads, that are graced each year with fairy shrimps paddling in isolated splendor and oblivious to human wonderment about how they got where they got. Several hundred miles away in the far northwest corner of the State, the Siskiyou Mountains harbor, as far as is known, two populations of *Streptocephalus sealii*, isolated by distance, topography, climate, and who knows what else, from others of its species, and populations of other species. Contrast these wet coastal mountains with the hot, comparatively desolate, and seemingly inhospitable expanses of California's deserts, and one is amazed to find that when suitable conditions present themselves, fairy shrimps are often in residence.

How did our anostracan friends get to these places given what seem to be improbable odds, given such distances, and given such inhospitable territory and seasons in between? And when did they arrive, yesterday, or in ancient times? If it was long ago, and under conditions scripted by different land forms, were the distances as great, the territory in between as inhospitable? These are fascinating questions about which any of us can conjecture on a rainy afternoon, but, whether pool sites be near or far, remember, fairy shrimps are adapted to those which desiccate, and the mechanism anostracans use to withstand desiccation is the cyst. Being resistant and tiny (about 0.15-0.40 mm in diameter), cysts are the structures that get transported from place to place.

The major agents of dispersal are two. First, cysts are known to pass undamaged and undigested through the digestive tract of birds (Proctor *et al.* 1967). The "how-I-got-there-from-here" story begins when mature female anostracans, containing cysts in their ovisacs, are eaten by birds. When our fine feathered friends take wing and fly to other aquatic locales and there charitably void their intestinal holdings, the result might be inoculations of sites new to fairy shrimps. But then the pools must desiccate, be refilled, and finally present the appropriate mix of temperature and water chemistry to prompt hatching. Undoubtedly a number of such "inoculations" go nowhere because the suite of conditions are, and remain, unsuitable for some of the species that just happened to be deposited. Obviously some are successful, and the sprinkling of the arctic fairy shrimp, *Branchinecta paludosa*, down the Rocky Mountain chain is thought to reflect the effectiveness of dispersal by bird-discharge (Saunders *et al.* 1993)!

A second mechanism, with most of the same limitations and possibilities for success, is the transfer of cyst-containing mud on the feet or feathers of birds. Mud, particularly if attached to migrating waterfowl, offers the possibility of long-distance transport before it is washed off in some distant pool along the flyway. By contrast, cysts passing down a bird's gut will be discharged, perhaps in an aerial bombardment far from water, within about 1.5 hours after feeding, although a small number may still be in the feces for up to 24 hours (Proctor *et al.* 1967).

Although aquatic birds are the most likely agents of dispersal, large, migratory mammals are also known distributors. Many of these beasts "wallow" in dirt, using the dust as a sort of desiccant for lice and other skin-infesting creatures. Wallowing in the same place deepens the basin and maintains a dust supply by continually abrading the soil, activities which discourage growth of plants which would bind the soil if present. Known in the Midwest as "buffalo wallows", these basins had their equivalent in California until the turn of the century in the form of elk wallows. Such depressions fill with rain and often harbor fairy shrimps. Thus cysts, when present, may get caught in the fur of rolling animals and be transported to another wallow where some may be left behind. Mud embedded in an animal's hooves, possibly containing cysts, could also be carried from water hole to water hole (Thiery 1991). And, finally, hearty gulps of water, perhaps containing gravid females, could allow gut-transfer, for if cysts are passed through the digestive system of birds unaffected, undoubtedly they can make safe passage down the guts of other vertebrates. Of course, "deposits" are made whenever and wherever the urge strikes, possibly in a basin suitable for fairy shrimps, possibly in a watershed where flooding carries cysts to a suitable home.

Various other creatures in addition to birds and mammals also eat fairy shrimps, and also indiscriminately purge themselves of the indigestible remains of their meals. What about these creatures? Well, it turns out that some inquisitive souls have delved into this more private aspect of frog and salamander biology. Both a French and a Louisiana scientist fed gravid fairy shrimps to lab-bound frogs, then succeeded in hatching nauplii from cysts recovered from their excrement (Mathias 1937; Moore 1973). Out in the real world, Thiery (1991) found viable cysts in the gut contents of salamanders which he caught in Moroccan pools inhabited by fairy shrimps. We were unaware of crayfish waltzing through California vernal pools until Brent Helm told us of seeing them on several occasions in pools in Sacramento and Yuba counties, so merely as a reminder that we should not overlook any possible mechanism of movement, we inform you that a wonderful father of fairy shrimpology, Walter Moore, teamed up with a student to see if Louisiana crayfish (crawdads in their vernacular) might be distributive agents. They fed cyst-bearing female *Streptocephalus sealii* to crayfish, and, guess what, out came cysts, still viable after their seemingly inhospitable journey down a gut containing one of the more formidable grinding structures known in the animal world, the gastric mill (Moore & Faust 1972).

Other transfer agents do exist, although their occurrence must be much less common, their direction random, and their success definitely obscure. Still, here are some remote possibilities. Unusual flooding, particularly in flood plains adjacent to large rivers (e.g., in California's Central Valley à la January 1997), may overwhelm pools and sweep cysts or wriggling fairy shrimps across the landscape or down water courses. Certainly most are buried or stranded in unsuitable places, but by some remote chance, should they end up in shallow basins, a new population may develop if the suite of conditions necessary for success is ultimately and appropriately presented.

In deserts, where winds are strong and vegetation sometimes minimal, an unlikely possibility is that soil and cysts may be bounced relatively unimpeded across the desert floor to a different site. A more plausible distributive agent is the so-called "dust devil", a small cyclonic wind that is strong enough to swirl fine soil particles, debris, and undoubtedly cysts, high into the desert air and carry them erratically across the landscape. Once again, blind chance may find an ideal spot for the cysts, though more probably they will be lost in the desert's unsuitable vastness.

Under historical conditions, wind-transport of desert species was probably less likely than today. Although cysts are deposited on top of a pool's bottom, being larger and heavier than surface clays they get worked into the sediment by water movement caused by persistent winds. Therefore, when the pool dries, cysts are trapped and bound in the soil about 5 mm below its surface (Eriksen *et al.* 1988a), inaccessible to the force of the winds. However, in today's world of ORV, military, and commercial use of dry desert basins, surface sediments are constantly abraded. Such abrasion and compression not only destroy some of the buried cysts, but loosen the soil to such an extent that removal by wind is far more successful (Eriksen *et al.* 1988a).

These same vehicles, forcing their way through mud in one wet basin then heading out for more challenges at another, must also carry, and drop, cyst-containing mud along their route, possibly in another basin, certainly on the floor of the garage. And to prove that the latter is not a facetious statement, Steiert (1995) recounts the story of a woman, living on the Texas High Plains, collecting a jar full of fairy shrimps from a rain puddle in her concrete driveway.

That transfer of cysts from pool to pool or success of cysts once transported are not particularly common events (Belk & Cole 1975) is suggested by the following: Certain species are highly restricted in distribution; adjacent pools may have different or no fairy shrimps; pools observed year after year seem always to house the same species, or mix of species; and structural and genetic studies demonstrate population differences between regions (Dumont *et al.* 1991) and sites (Baskin 1994; Fugate 1992; King *et al.* 1996). The fact that fairy shrimps are not everywhere is also possible evidence for the uncommon nature of transfer.

How often species have reached a habitat, then been lost to drought, competition, or some other ecological reality, only to be reintroduced once more, is certainly grist for the inquiring mind and for research.

Categorizing California's environmental diversity: An overview

We hope we have made it clear that we know where some fairy shrimps are sometimes, and where others seem to be all of the time. In an attempt to make sense out of the differential distributions of California's anostracans, and the ecological reasons for those distributions, we have developed a classification of **pool-basins** (p. 66), and grouped our state's 23 species according to what we call **habitat categories** (Table 4.1, p. 70). These are defined by pool characteristics which add to the general ecological conditions found within the eight **geographic-vegetational regions** of California (Map 4.2, p. 68).

But first, if you are not particularly conversant with California's host of environments, it certainly behooves us to introduce you to them! Such a task is not an easy one, however. Many individuals have wrestled with a way to organize the state's incredible ecological diversity into some conceptually useful framework. For others the task seemed rather simple. As an example of the latter, if you were to ask even long-time residents about the state's climate and space, many would give you the usual PR about "endless summer", sandy beaches, the hills of San Francisco, and maybe the geological and meteorological reasons for last year's vintage of late-harvest Zinfandel in the Napa Valley. Like a couple of dots on your TV screen, these few dots on a map of the state are but a tiny part of the picture of California, meaningless as far as fairy shrimps are concerned, for none of these fine creatures dwell any longer on such prime real estate. Additionally, by themselves, these fragmentary descriptions give a distorted view of this grand state and offer no hint about the juxtaposition of different land forms, the variations in climate that these conditions help create, or the distribution of anostracan species determined to a great extent by them.

Those who do see the complexity would tell you California is an amazing piece of this planet! And it probably contains, somewhere, a microcosm of most of the geological wonders found spread over the face of earth. It is more diverse in topography, geochemistry, climate, and vegetation than any similarly-sized chunk of our globe's crust. The isolation of its many living things by ocean, elevations, and deserts has produced a rather amazing and enviable list of fascinating plants and animals, including fairy shrimps, that are found nowhere else!

Those same knowledgeable people would also add that traveling across California is like riding a giant roller coaster, no matter which route is chosen. Were you to select the central two-thirds of California to test that point, and hop aboard your car where the mighty Pacific pounds against the land, almost immediately you must traverse the Central Coast Mountains, 900-1,500 m high, to get to the enormous Great Central Valley. Once the Central Valley is crossed, 75 km wide, almost 700 km long, and most of it less than 150 m in elevation, the lofty Sierra Nevada awaits to be scaled. The "Range of Light" forms a giant backbone along a considerable length of the state. Over 600 km from end to end, and most of it 2,750-4,250 m in height, it is topped by 4,418-m Mt. Whitney. This gigantic monolith of granite rock juts skyward more than any other point of land in the lower 48 states. Amazingly, only 140 km by air to the east, near the Nevada border, our roller coaster will plummet into the lowest spot in North America, Death Valley, some 86 m below sea level! However, no simple single slide, this one. First, there is a descent of over 3,050 m in only 20 km into the deepest part of the Owens

Valley. Then it's back up again to 3,368 m and the top of Telescope Peak, crown jewel of the Panamint Range, before dropping into the finality of Badwater, Death Valley's lowest spot.

While mulling over the changes in elevation just described, try to imagine the changes in temperature, rainfall, length of seasons, or any other environmental condition that parallels such drastic differences. Then, let your mind retrace the variation in land form from the Pacific Ocean to Death Valley. Over this distance, temperatures will range from year-around mild conditions near the 1,600 km-long coast, to subfreezing winters in the Sierra Nevada, to oppressive summer heat in Death Valley. Precipitation will vary drastically, from almost rain-forest amounts near the north coast to trace amounts in Death Valley, and most of it comes from winter storms of arctic origin. Virtually none falls during summer. The low desert of southeastern California is the sole exception, with the majority of its minimal rainfall arriving with summer storms which have their origin in the Gulf of Mexico (Major 1977).

Now that your roller-coaster ride has acquainted you with some of the fantastic geographic changes that California presents, how do you organize it all in your mind? As an aid, let us note some of the attempts that others have made to consolidate the state's overwhelming geologic and biotic diversity into some conceptually useful scheme. Various researchers have divided California into "provinces" based upon differences in landform (Durrenberger 1968), in vegetation (Stebbins & Major 1965; Munz & Keck 1973; Major 1977), and in fauna (Van Dyke 1919). With regard to such classification schemes, and for the purposes of this book's topic, the known distribution of California fairy shrimps correlates best with a modification of the vegetational subdivisions utilized by Stebbins and Major (1965). Those subdivisions and their modifications were described by Eng, Belk, and Eriksen (1990), and comprise eight **geographic-vegetational regions**: North Coast Mountains, Cascade-Sierra Nevada Mountains, Great Basin Desert, Great Central Valley, Central Coast Mountains, South Coast Mountains, Mojave Desert, and Colorado Desert (elaboration beginning on p. 67; Map 4.2). These eight regions can be geographically and vegetationally defined because they are generally set apart by topographical boundaries (mountains). Our presentation of these regions is organized along the continuum from high elevations and latitudes with cold temperatures, to low elevations and latitudes presenting high temperatures.

Reasonably superimposed upon the geographic-vegetational regions are what we call **habitat categories**. These help define the pools in which fairy shrimps actually dwell by adding to the gradients of the regions' characteristics the variables of low to high dissolved salts, greater to lesser predictability of filling, and long to short duration times (Table 4.1, p. 70). We champion these habitat categories for an important reason. All too commonly, little, and often fragmentary, specific habitat information is available for many of the California species. However, one might reasonably judge at least the general suite of conditions which a species faces by knowing the properties of the particular habitat category in which it is found. Let us illustrate. Some of the California species are rare; others occupy remote areas. In both cases, little is known about physical and chemical properties of their pools, and often not even casual descriptive information is available concerning their habitats. Additionally, some fairy shrimps occupy several types of basins, but existing habitat data, including out-of-state information, may represent those types unequally thus biasing one's perception of a species. By knowing the habitat category applicable to a particular species, one can make a reasoned guess about the spectrum of environmental conditions that exist there, in spite of a lack of specific data. Additional information describing conditions in which anostracans dwell can come from knowledge of the soils or rocks underlying these **pool basins** and of the way the basins were formed.

Because the subject of our book is the **Fairy Shrimps of California's Puddles, Pools, and Playas**, it may sound as though we are adhering to a commonly accepted scheme of defining, and therefore classifying, smaller bodies of water. If so, what **are** the differences between puddles, pools, and playas, and where do ditches, stock tanks, solution pits in rocks, and gas chambers in lava flows fit into the scheme? You might feel that such a question is unimportant, for after all these words are colorful and conjure up pictures in the mind that do a good job of portraying some types of seasonal water bodies. Problem! Speak to a rancher, Fish and Game biologist, university ecologist, or even your authors, and you will undoubtedly encounter a diversity of descriptions and definitions that may not include your own. If there is not a universally accepted classification, then how can we usefully talk about which fairy shrimp species are found in what kinds of aquatic habitats? Eng, Belk, and Eriksen (1990) attempted to deal with that problem by constructing a classification of temporary waters that was suited to the ecology of anostracans. In the next section of this chapter we present that scheme.

But first, please note, we organize the types of **pool basins** and **habitat categories** as we do even though we recognize that some fairy shrimps are generalists and are not constrained by the way our tidy minds group the places in which they dwell. When we consider such a widely-distributed species, we will do so in the context of the habitat category in which it **most commonly** occurs in California, with mention of course of the range of localities and basin types in which it is known to appear. In these ways, then, we will describe in Chapter 5, **Natural history of California's species of fairy shrimps**, what we know, and what we hypothesize, about the biology and the ecological requirements of the Anostraca of California.

A classification of pool basins where fairy shrimps might dwell

Our classification scheme of possible fairy shrimp waters is not necessarily dependent upon, or restricted to, specific geographic-vegetational regions or habitat categories. This three-tiered plan allows flexibility in accommodating special characteristics of specific sites. The tiers are hydrological, formational, and locational/descriptive.

In the **hydrological** tier we recognize three types. **Seasonally astatic** pools are those that fill and redry one or more times during any year, depending on the seasonal nature of precipitation and drought. **Perennially astatic** sites fluctuate significantly in level during the year, and as a result a portion of the bed dries out, but the entire body of water does not disappear completely every year (Decksbach 1929, translated by Hartland-Rowe 1972). **Aestival** habitats are shallow and semi-permanent in the sense that they retain some water year-long, but freeze to the bottom during winter (Daborn & Clifford 1974).

Understanding the **formational** origins of pool-basins is often important to the understanding of their water chemistry and seasonal change, and perhaps ultimately to putting damaged or destroyed systems back together. Therefore, recognizing that a temporary pool is **not** just any simple dimple or subtle puddle on the face of the land that receives and holds water for a period of time is of paramount importance!

Although formational origins of pool basins are varied and complex, they are usually either a result of geological processes (**geogenic**), some of which are no longer active in California (e.g., glaciation), or of organisms "doing their thing" (**biogenic**). Categorizing pool basins under these two headings gives us a colorful list of descriptive names like: lava flow dam pools, sag ponds, cirque lakes, swale pools, animal wallows, stock ponds, borrow pits, and bomb craters. For a wonderfully readable survey, we refer you to Norwick (1991) who has described, largely from the standpoint of geological processes, how an array of pool basins came or may yet come into being in California.

The **locational/descriptive** tier within our classification allows general and inclusive comments which describe conditions at a particular site (e.g., desert, grassland, coniferous forest, alpine, snow-melt, or rain-pool). However, they may also refer to unique regional pool-types like the famous **California Vernal Pools**, identified by their largely endemic annual plants (Thorne 1984). We ask you to take note of this distinction, for many of California's temporary bodies of water, though referred to casually and incorrectly as vernal pools, are **not** because they form at times other than spring, or have no resident endemic plant species.

Although this scheme offers a way to classify the types of basins in which pools form, and knowing the origin of a basin and its soils is an ultimate goal, we do not want to leave the impression that every, or even any, collector of fairy shrimps will be able to decipher all the various clues that place each pool into each hierarchical category. As is usual in environmental matters, some things are known, others are reasonably guessed at by those with appropriate expertise, and much lies in the realm of the unknown. Still, we offer this classification for your consideration in an attempt to be inclusive, understanding that California fairy shrimps may not yet have been found in all possible types of basins.

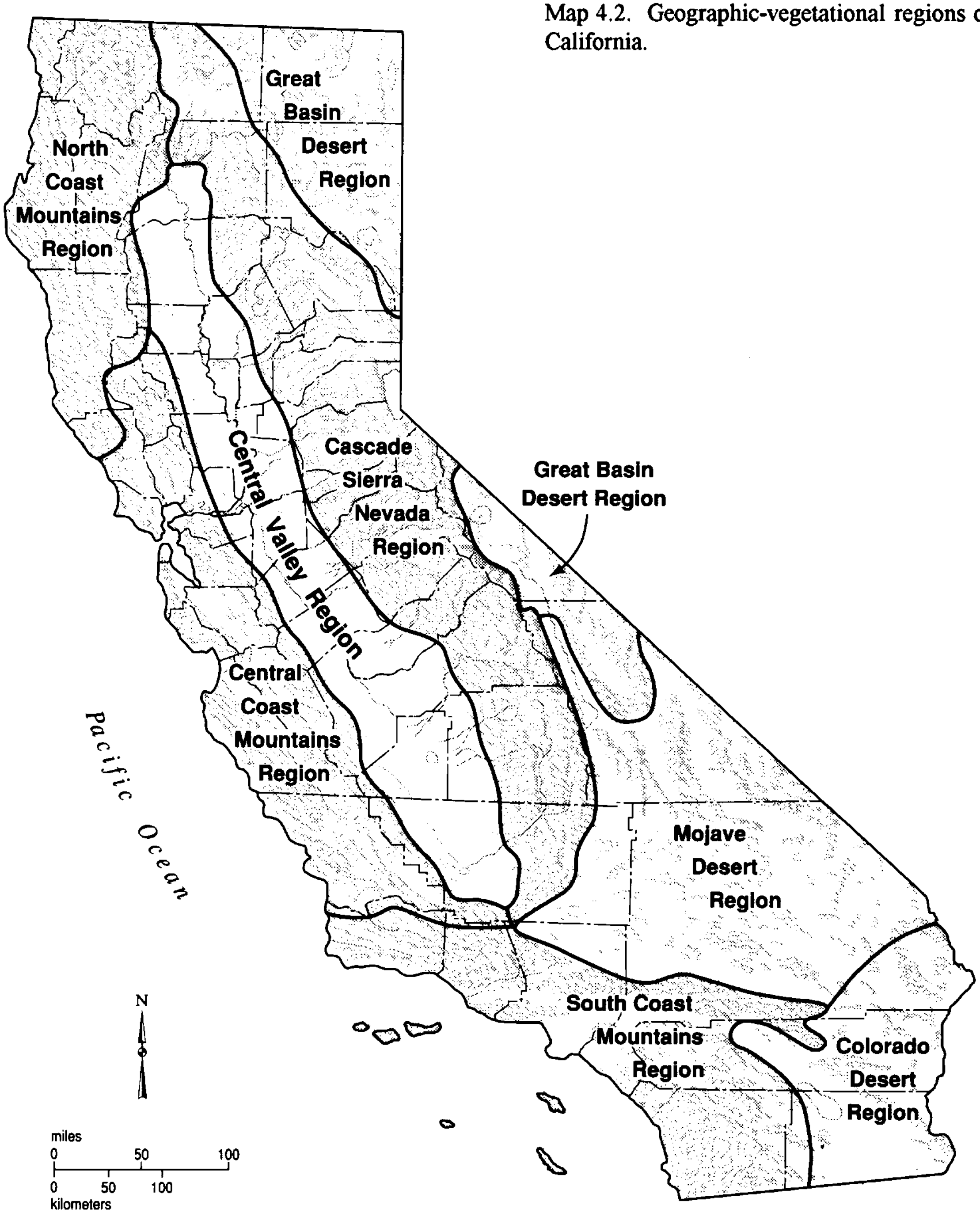
Geographic-vegetational regions of California

In describing the geography, climate, and vegetation of the state's eight geographic-vegetational regions (Map 4.2, p. 68), we rely heavily on Major (1977).

The **North Coast Mountains Region** (Klamath Mountains and part of the Northern Coast Ranges including the Siskyous) is a rugged coniferous-forest-covered land rising from the coast to heights exceeding 2,200 m. It receives the greatest annual precipitation of any area in California (278-440 cm). At the more coastal, lower elevations, temperatures are cool in summer and only slightly cooler during winter. Higher elevations may experience winter freeze.

The **Cascade-Sierra Nevada Region** (Cascade Range, Sierra Nevada), much of which is 2,750-4,250 m in elevation, separates the Central Valley from the deserts it has created in its rain shadow to the east. The term "rain shadow" reflects the fact that as weather systems rise up mountain ranges they cool and atmospheric moisture must be dropped, leaving little for the land "over the hill". So, on the windward western slopes of the range, precipitation increases with elevation but only to about 2,500 m; greater heights receive less moisture because little is left to fall, and of course the leeward eastern side receives less yet. Much of the precipitation falls in the form of snow, sometimes accumulating in drifts 20 m or more deep; and frost can occur on any day of the year (Williamson *et al.* 1986). These changing environmental conditions with elevation, and the differential adaptations of plants to them, help explain why Chaparral (a plant community dominated by low-growing woody shrubs with tough evergreen leaves), which is typical of the foothills, grades gradually into deciduous oak forest, then coniferous forest, and

Map 4.2. Geographic-vegetational regions of California.



finally into grass-amongst-rock, or nothing-but-rock, above tree line.

The **Great Basin Desert Region** (Modoc Plateau, Great Basin Desert) occupies the area east of the Sierra Nevada and Cascade Ranges in the extreme northeast and east-central parts of the state. Elevations are mainly 1,500-2,000 m, and precipitation ranges from about 10-50 cm. Most moisture comes in the cold winter, but the Region has more summer rain than do parts of California with a Mediterranean climate (areas where warm, dry summers and cool, wet winters are the norm). The climate of the Great Basin Desert favors sagebrush (*Artemisia tridentata*) and bunch grasses.

The **Central Valley Region**, varying in elevation from near sea level to about 300 m, lies in the rain-shadow of the Coast Ranges. Annual precipitation, reflecting this rain-shadow phenomenon as well as a north-to-south decrease in the frequency of storms, ranges from around 96 cm in the north to about 15 cm in the south. A Mediterranean climate is typical of this region. The yearly repetition of rain followed by drought, when combined with the Valley's fine soils, tells us why this region was once a vast grassland. Of course, for all intents and purposes, the Central Valley is presently clothed only with agricultural crops, houses, and asphalt; and even agriculture is losing out to urbanization in places.

The **Central Coast Mountains Region** (Southern Coast Ranges and part of the Northern Coast Ranges) comprises a series of mountains largely covered with Chaparral and grassland valleys, extending from about 80 km north of San Francisco to Santa Barbara County. The Pacific Ocean borders this region on the west, while the Central Valley bounds it on the east. Elevations from 500 to 1,000 m are common, and several peaks exceed 1,500 m. The climate is primarily Mediterranean; the annual rainfall ranges from about 27-90 cm.

The **South Coast Mountains Region** (Transverse and Peninsular Ranges) is similar in many respects to the Central Coast Mountains Region. However, it has stronger affinities with the desert, and at lower elevations the Chaparral is replaced by Coastal Sage Scrub, a community of more sparse, less woody, and often summer-deciduous plants. This region is also bounded by the Pacific Ocean on the west, but by deserts on the east. Much of the land within its borders is 500-2,000 m in elevation, but several peaks ringing the L. A. Basin exceed 3,000 m. The climate is largely Mediterranean, with annual precipitation at less than 32 cm.

The **Mojave Desert Region** is in many ways a transitional area between the colder, more northern Great Basin and the hotter, more southern Colorado Desert. In this and other hot deserts, creosote bush (*Larrea tridentata*) and a number of other sparsely distributed shrubs, like burro brush (*Ambrosia dumosa*), predominate. Although a number of isolated peaks occur in the Region, elevations are usually between 500-1,500 m. Annual precipitation, mostly occurring in winter, is generally more than 11 cm but less than 25 cm. Death Valley, while lying within this region, is ecologically quite different, with high temperatures more typical of the Colorado Desert and an annual precipitation of only 4-5 cm!

The **Colorado Desert Region** (a subdivision of the Sonoran Desert) is restricted to extreme southeastern California, being bordered by the Colorado River on one side and foothills west of the Salton Sea on the other. This desert is generally less than 500 m in elevation and includes the other area in California that lies below sea level. One might expect it to be hotter and drier than the more northerly Mojave and Great Basin deserts, and this stretch of land does not disappoint! Annual precipitation, its pattern highly irregular, is generally less than 11.5 cm, and much of this meager rainfall drops from summer storms originating in the Gulf of Mexico.

Habitat categories and their associated species of fairy shrimps

A discussion of conditions required by fairy shrimps could be approached in a number of ways. We feel that presenting information based on an alphabetical listing of species would lead to a random discussion of habitats, and "Dullsville", as they say! A regional approach would certainly be better, but given such varied topography at that level, we could probably not avoid a similar pitfall, and "Dullsville II" would be the result. We believe our purpose will best be served by describing what we know about habitat requirements of the various species that live within what we call **habitat categories**. Because these categories approximate the eight geographic-vegetational regions just described, and will be noted in the same sequential manner, a comparison can readily be made between the two.

Remember, we have placed our habitat categories (Table 4.1) into a continuum which generally grades from cold to warm, and low- to high-salinity waters. Although predicting whether a

Table 4.1. Habitat categories and their representative species

Habitat category	Representative species
Cold-water pools which are low in dissolved solids, predictable, and long-lived	*Eubranchipus bundyi*, *Eubranchipus oregonus*, *Eubranchipus serratus*, *Streptocephalus sealii*
Cold-water pools which are low to moderate in dissolved solids, predictable, and long-lived	*Branchinecta coloradensis*, *Branchinecta dissimilis*
Cool-water pools which are low to moderate in dissolved solids, moderately predictable, and long-lived	*Branchinecta coloradensis* (suggested two new species), *Branchinecta conservatio*, *Linderiella occidentalis*, *Linderiella santarosae*
Cool-water pools which are low to moderate in dissolved solids, less predictable, and short-lived	*Branchinecta lindahli*, *Branchinecta longiantenna*, *Branchinecta lynchi*, *Branchinecta sandiegonensis*, *Branchinecta* sp. (midvalley fairy shrimp)
Cold- and cool-water pools which are moderate to great in dissolved solids, predictable to less predictable, and long-lived	*Branchinecta mackini*, *Branchinecta gigas*
Warm-water pools which are low to moderate in dissolved solids, less predictable, and long-lived	*Streptocephalus woottoni*
Warm-water pools which are moderate in dissolved solids, less predictable, and short-lived	*Streptocephalus dorothae*, *Streptocephalus texanus*, *Thamnocephalus platyurus*
Cool-to warm-water pools which are great to impressive in dissolved solids, predictable, and temporary or permanent	*Branchinecta campestris*, *Artemia franciscana*, *Artemia monica*

pool will fill with water each season is a risky proposition, it is also true that, in California, the general continuum described also leads from more to less predictability of the presence of water as well as its duration.

Our organization leads us to begin with fairy shrimps requiring cold habitats, that is those in rather predictable pools occurring in or near areas of coniferous forest at high to moderate elevations in the North Coast Mountains, Sierra Nevada, and Great Basin Desert regions. Next come the low-elevation cool-weather species, most of which live in grassland pools in northern and central parts of the Central Valley where rainfall is moderate and reasonably predictable. Then we move south to species inhabiting more arid grass- and shrub-lands where rainfall is less in amount and predictability. Following the trend to greater aridity, we describe cold- and cool-weather forms that dwell in desert alkaline basins. Next come those that are found in desert waters of low alkalinity during warmer times of the year. In various regions of California, low rainfall, saline geology, and periods of high temperature produce salterns with a unique fauna. Because of their peculiarity they are our final consideration.

As for how cold "cold water" really is, or what the limits are for "moderate" amounts of dissolved solids and "low" pH, or where in the continuum of conditions "long-lived pools" might fall, we have set some limits so that when no information for California species is available, at least a reasonable "guesstimate" can be made of the conditions that actually prevail. By the way, the boundaries chosen (Table 4.2) have bases in the data presented by Eng, Belk, and Eriksen (1990).

Regarding water temperature we make two points. First, in California's northern and mountainous localities winter cold turns aquatic environments solid if water is present, and snow covers the landscape, sometimes in exceptional amounts. The species of fairy shrimps that live there are adapted to hatch as soon as snow melts and pool sediments thaw, that is at or near 0°C. Secondly, cold waters do warm with the season, and collections, along with temperature measurements, normally have been made later in the season when animals are partially, if not totally, developed, and during the warmth of the day. We must recognize, therefore, that elevated temperature readings, possibly those near maximal, are more likely to be the data we have to describe the thermal environment. For example, later-season events occasionally boost pool temperatures as high as 25°C for a brief afternoon period, but if they do, night-time cooling inevitably swings the temperature back into the neighborhood of 10-15°C (Daborn 1976; Eriksen unpubl.). Given these realities, "cold water" habitats are best con-

Table 4.2. Quantification of pool habitat categories for California's fairy shrimps

Environmental Measure	Quantification Range
cold water	0 - 15°C 0 - 10°C for hatching
cool water	5 - 25°C 5 - 20°C for hatching
warm water	17 - 35°C 17 - 30°C for hatching
low alkalinity	few - 100 ppm
moderate alkalinity	100 - 300 ppm
high alkalinity	300 - <10,000 ppm
impressive alkalinity	>10,000 ppm
low TDS	few - 300 ppm
moderate TDS	300 - 600 ppm
high TDS	600 - >175,000 ppm
low pH	4.8 -7.0
moderate pH	7.0 - 8.3
high pH	8.3 - 10.5
short-lived pool	<3 weeks
long-lived pool	>3 weeks

sidered as places where temperatures normally fall between 0-15°C, but where short-term highs of 20° or even 25°C may be recorded. Utilizing similar arguments, we also provide "typical" temperature ranges for our other habitat categories (Table 4. 2, p. 71).

Total Dissolved Solids or **TDS** (dissolved gases go unmeasured), sometimes also referred to as salinity, is a commonly-determined environmental measure because dissolved materials are not only the nutrition source for plants and ultimately animals, but also determine the osmotic conditions to which an organism must be adapted. When materials dissolve, they normally form charged particles (ions). Because charged particles can carry an electric current, measurement of the amount of current conducted can be recorded as **conductivity**, usually in µmhos, or alternatively as ppm of TDS. Because the µmho unit is foreign to most folks, we have chosen to convert such measurements to ppm TDS using a conversion factor of 0.65 (Lind 1979). Certain soils and rocks (e.g., limestone) dissolve comparatively readily resulting in high-TDS water; other soils and rocks (e.g., granite) dissolve only grudgingly yielding "soft" water with little dissolved material. Certain of the dissolved substances affect the constancy of the acid-base relationships within the aquatic environment. **Alkalinity** (mainly the total of bicarbonate, carbonate, and hydroxide ions), or the acid-combining ability of water, is the normal measure of the acid-base stability (buffer capacity) of an aquatic environment. In pools with "low TDS", alkalinity typically falls within the range of a few to perhaps 100 ppm. When waters are scantily buffered as these are, carbonic acid (from the solution of CO_2 in water) and organic acids (particularly tannic acids, tea-colored substances derived from plant materials) may overwhelm the buffering capacity and make the **pH** acidic, that is, below the neutral value of 7.0 (e.g., pH readings in the 5-6 range). Also typical of pools with little buffer is a considerable shift of pH over a daily cycle (e.g., 4.9-6.2, 6.8-8.6; Eriksen unpubl.) brought about by the often substantial fluctuation in CO_2 as it is produced in respiration and consumed in photosynthesis. Increasing TDS, whether due to evaporative concentration in a single pool or exhibited in a series of pools, normally is associated with increasing alkalinity and, therefore, with increasing buffer capacity; pH thus generally rises, sometimes considerably above neutral, and, as it does, demonstrates less and less change through a 24-hour cycle.

Pool **predictability** is a tough category to define, but a reasonable generality to which we can adhere is the further north and the greater the elevation in California, the more predictable the pool. The reverse, of course, follows. All of us are well aware that California is faced with years of drought erratically strewn over time. Even so, most pools at higher elevations faithfully form from the melting of whatever snow volume accumulated over an entire winter. However, when rain events are responsible for filling a basin, pools are less predictable because storms must be reasonably heavy and of some duration, or back-to-back. Such conditions certainly occur more frequently in northern California than they do further south, and, given rain-shadow effects, pool filling in the deserts is not only inconsistent but often problematic.

Pools that dot California's landscapes may be fleeting or permanent. However, those that are of interest to anostracans have certain defined periods of containing water which are specific to each species. Our classification of pool **duration** has as its basis the fact that some species of fairy shrimps have the genetic capability of completing their life cycle in less than three weeks (sometimes as little as 11 days), while others require a greater period than that (although temperature considerably affects the actual time to cyst production). Thus we define "short-lived pools" as those which exist for less than three weeks, while "long-lived" describes waters that endure from three weeks to perhaps as long as 6 months.

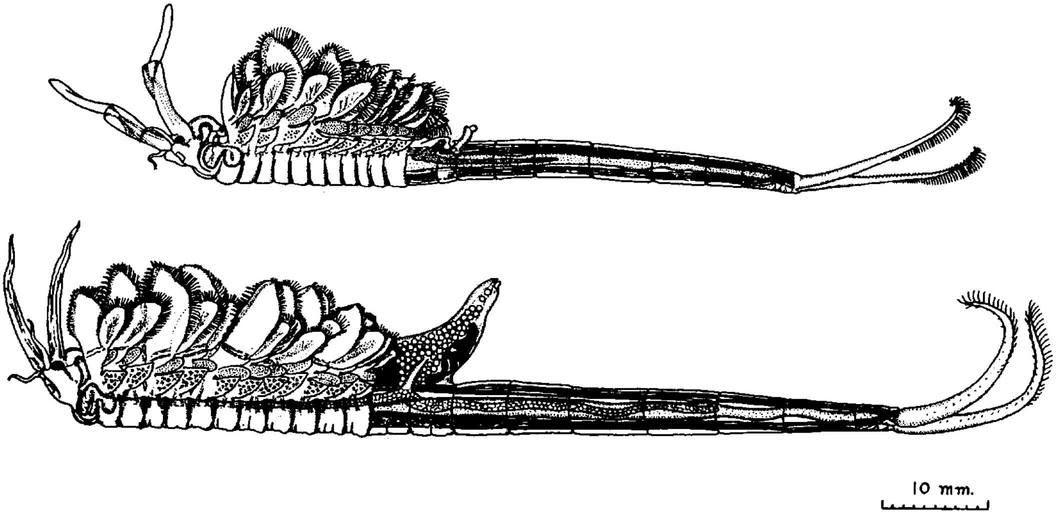


Fig. 4.1. Male (above) and female (below) of *Branchinecta gigas* from Lynch (1937); reprinted courtesy of the Smithsonian Institution Libraries.

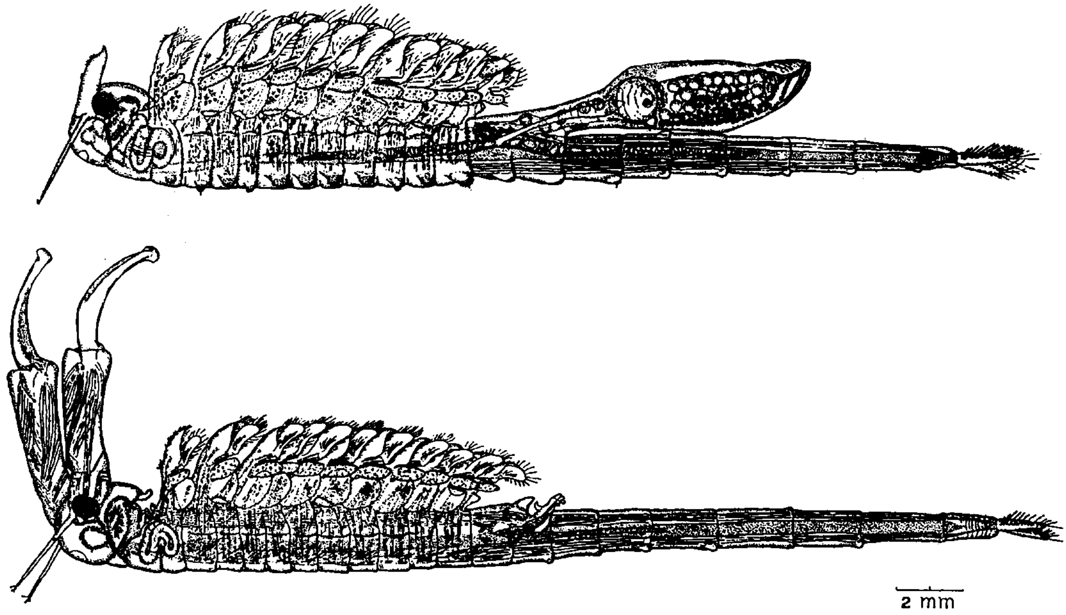


Fig. 5.1. Female (above) and male (below) of *Branchinecta campestris* from Lynch (1960); reprinted courtesy of the Smithsonian Institution Libraries.

Chapter 5

NATURAL HISTORY OF CALIFORNIA'S SPECIES OF FAIRY SHRIMPS

Much of what is known about the natural history of the anostracan fauna of our state was summarized in 1990 by Eng, Belk, and Eriksen. For some of the California species, little further information is available today than was at hand then, so the following discussions may take freely from our 1990 summaries; for their liberal use, we thank both Larry Eng and the *Journal of Crustacean Biology*! However, we do know a good deal more about where fairy shrimps occur, and to help you visualize those locations we have provided Maps 5.2-5.12 (pp. 118-128) which indicate pools or pool clusters supporting each species. To place these sites into the geo-political world of counties, and into the ecologically-meaningful geographic-vegetational regions of the state, refer to Map 5.1 (p. 117) and Map 4.2 (p. 68), respectively.

Information about California's fairy shrimps is unequally available for species and topic. For some, certain facets of their biology are totally unknown. Conditions under which data were collected in the field or experiments were conducted in the lab vary "all over the map", so in most cases it would be impossible to develop tables which present data in a comparative and summary manner. For these reasons, we have chosen to "spin a story" about each species, usually beginning with a unique feature of its life, then let the tale progress from there through what is known and what is surmised about its biology. In the process, we tell you what we can about each animal's **life history**, and use terms that have sometimes been applied with different meanings by different researchers. Our meanings are presented in the following sketch of the stages of a fairy shrimp's life. To begin with, suitable conditions are necessary to trigger **hatching**, an event that is normally completed within a few days of cysts being submerged in water. All individuals which emerge during this time are considered a **cohort**. If appropriate conditions recur, another hatch may yield another cohort to swim with the first. Hatching produces a larva which develops through juvenile stages to a **sexually mature adult**, recognized by the possession of one or more cysts in the female's ovisac. A batch of cysts in the ovisac is referred to as a **clutch**. Some species generate only one clutch during their life; others can produce clutch after clutch until they die. A female's **fecundity** is measured by the total number of cysts manufactured over her lifetime. The length of that lifetime (birth to death) is referred to as **longevity**.

As a final consideration before we discuss the natural history of California's fairy shrimps, you have undoubtedly noted that temperature has arisen repeatedly as an environmental measure of great consequence to the differential distribution of fairy shrimps. Among other things, cysts hatch only within a certain temperature range for each species; metabolic rate, and thus rapidity of growth to sexual maturity, are also sensitive to temperature, and are species-specific. Finally, the number of cysts per clutch seems directly related to temperature, while the size of cysts, as well as the size of newly hatched larvae, appear to be inversely related to the temperature to which the species is adapted. That is, fairy shrimps of cold water make fewer but larger cysts, and thus larvae. We explain this by example. When we averaged all of Belk's (1977b) data relating to 19-20 mm-long females, the following picture emerged: rainpool anostracans produced 547 cysts measuring 0.26 mm in diameter, and larvae 0.36 mm in length at hatching. By comparison, individuals from snow-melt pools came forth with 98 cysts of 0.35 mm diameter that resulted in larvae 0.62 mm long. Striking differences, but the adaptive rationale? This is Denton's work, so let's quote what he has to say: "...production of small eggs...maximizes the number of offspring in a (less predictable) food-rich pond, and the generation of larger eggs...increases the survival chances of each larva in a food-poor (predictable) melt pond." (Belk 1977b). More recently Mura (1991c) has corroborated, with Italian anostracans, the relationship of increasing cyst mass with increasing elevation of the populations that produce them. However, she offers the important caveat that because of the intraspecific variation now on record, an average cyst size is not meaningful and, therefore, such a measure can no longer be considered a valid species trait. Still, as information of general comparative value, you will find cyst measurements reported as we busy ourselves exposing available details about the wonderful lives of California's fairy shrimps!

Fairy shrimps of cold-water pools which are low in dissolved solids, predictable, and long-lived

In California, predictable pools containing cold water are found in the North Coast Mountains and Cascade-Sierra Nevada Mountains regions. Here, basins usually fill by snow-melt to yield waters that are typically "crystal clear", although possibly tea-colored. We know essentially nothing about the chemistry of these places, but if they are like the smattering of pools in similar western regions about which we have some information, we would expect somewhat acidic waters very low in alkalinity and TDS.

Our stories about the fairy shrimps that are restricted to these mountainous habitats begin with California's three species of *Eubranchipus* and one of the state's streptocephalids, *Streptocephalus sealii*. The *Eubranchipus* species are known only from 1,250-1,650 m in elevation where they stake their claims in meadow pools surrounded by coniferous forest. At somewhat higher altitudes (mainly 2,000-3,000 m), and within the heart of the coniferous forest, lie the vast majority of known residences of *Streptocephalus sealii*.

Eubranchipus bundyi

(Map 5.2, p. 118)

Eubranchipus bundyi is well known for dwelling in pools scattered along the northern states and into Canada, even Alaska. But does California possess habitat conditions suitable enough to support this creature? That intrepid field man Christopher Rogers answered this question in the early spring of 1990 (May 8) when he brought forth the first California collection of *Eubranchipus bundyi* from a 30-cm deep portion of Grass Lake in Siskiyou County. Now this far-northern California jurisdiction covers a large piece of variable terrain, so where, pray tell, is Grass Lake, and what kind of a place is it? Well, it lies along U.S. Highway 97 between the coniferous forest slopes of Goosenest and Deer Mountains of the Klamath National Forest, 35 km northeast of the town of Weed. Rogers (1996) notes that the lake is seasonally astatic, covers about 3 km^2, has a maximum depth of 0.5 m, and lies at an altitude of 1,535 m. The basin is largely covered with sedges and perennial grasses (hence its name???), and receives water from snow-melt.

How *E. bundyi* got to Grass Lake is conjectural, because not only did Coopey's (1946) collection of branchiopods from southeastern Oregon, including the Cascades, not reveal this species, but the closest known populations are in the Uinta Mountains of Utah and Medicine Bow Mountains of Wyoming at elevations exceeding 3,000 m, and on the Kaibab Plateau of Arizona where altitudes range from 2,100-2,700 m.

Eubranchipus bundyi is best known from pools in non-montane coniferous and deciduous woodlands (e.g., Broch 1965; Dexter 1953, 1967) but has also been taken in tundra, flood-plain, swamp, prairie sandhill, and high-desert salt-bush sites. Most of these habitats suggest clear water of very low TDS, alkalinity, and pH. However, the only data recorded when fairy shrimps plied the pools come from four sites that appear to span habitat types: alpine, mixed deciduous woodland, prairie, and high-desert. In these places alkalinity ranged from 1-513 ppm, pH from 6.9-9.0, and turbidity from clear to opaque (Daborn & Clifford 1974; Horne 1967; Maynard 1977; McCarraher 1970). The higher values all come from Nebraska's sandhills and seem atypical of its more common sanctuaries, although Chelberg (1973) affirms *E. bundyi* does reside in hard-water pools on limestone soils of Minnesota's prairie counties .

Where California's Grass Lake population straddles the known chemical range for the species is uncertain. In his article documenting *E. bundyi* in Grass Lake, Rogers (1996) reports some unpublished data collected by the California Department of Water Resources in the 1950s and averaged for all annual lakes in the Shasta Valley. The data (showing very high levels of Na^+, Cl^-, aluminum, boron, and pH), if true for Grass Lake, and we believe they are not at least in early season when fairy shrimps are in residence, suggest the place is a strange water-hole indeed. Strange too is that surrounding soils contain "high amounts of granite and lava rock", geological types which should yield soft water as did soils of the same description in northeastern Minnesota (Chelberg 1973). Before we admit this odd chemical soup is the actual liquid in which *Eubranchipus bundyi* swims, we would wish for analyses soon after snow-melt fills Grass Lake and individuals hatch and ply its icy waters. Richard Hill took such samples on 10 May 1995 and recorded a pH of 6.5 and a TDS (from conductivity) of 91 ppm, values more in line with what we would expect. However, Richard was unsure about the calibration of his meters, so more data are necessary to determine what kind of a chemical habitat Grass Lake really is.

Broch (1965), Daborn (1976), and Maynard (1977), studying pools full of these creatures near Ithaca, New York, Edmonton, Alberta, Canada, and Salt Lake City, Utah, respectively, observed that metanauplii averaging 0.69 mm in length hatched as soon as bottom sediments thawed in spring. Belk (1977a) confirmed the latter observation by experimentally showing that larvae from a population on the Mogollon Plateau of Arizona emerged well at 5°, poorly at 10°, and not at all at 15°C. Maynard (1977) observed that maximum longevity of her animals was 40 days, while Daborn (1976) counted 41 for males and 44 for females although most lived only 30-35 days. Broch described females dying at 49 days after producing but one clutch of cysts. Daborn (1976) and Maynard (1977) agreed that only one clutch (averaging 22 and 21 cysts, respectively) is normally produced before death, although a few females may turn out a second clutch with a greater number of cysts (a situation perhaps verified by data from Linder 1959). In some of Daborn's females, eggs that ultimately became cysts began to appear in the brood pouch at 10 days, and, after 20 days, 70% of females carried them. However, Maynard's individuals were probably cold-inhibited, for they did not begin to reproduce until 28 days after hatching.

Showing that published observations and pronouncements are not always the final word, Denton, the eager graduate student that he was at the time, counted 78 cysts crammed into the brood pouch of a female *E. bundyi* from Arizona. This number is 3.5 times the totals recorded above. Even so, 78 cysts are not that many when compared with the 846 he removed from a female *Streptocephalus dorothae* (Belk 1977b). Maynard (1977) determined that the average cyst size for her Utah shrimps was 0.36 mm, but Denton's Arizona animals could only manufacture cysts averaging 0.34 mm in diameter, while those from California came in with a comparatively wimpy 0.31 mm average (Hill & Shepard in press).

In contrast to *E. bundyi*'s 7-week maximal longevity in the field, would you believe 20 weeks in the laboratory? Yes, Chelberg (1964) pushed life-span that far by maintaining some Minnesota shrimps at their hatching temperatures of 1-2°C; and no, such conditions are not realized in nature. By contrast, when *E. bundyi* is warmed too much, that is to a constant 25°C, more than 50% of them succumb (Belk 1977a). Similarly, young larvae which survived only 2-3 days when subjected to 22-23°C, grew to maturity when maintained on a fluctuating regimen of 16 hours at 2°C, then 8 hours at 22-23°C (Chelberg 1964). These latter data support our earlier statement that cold-water fairy shrimps, though occasionally collected during the day in waters as warm as 25°C, do not face those conditions for long because they live in areas where temperatures drop drastically at night.

As seems typical of fairy shrimps from predictable pools, *Eubranchipus bundyi* seldom occurs with other anostracans. When that does happen, *E. bundyi* does not share equally; it either numerically dominates or shows up as a small fraction of the total fairy shrimp population. In California's Grass Lake, Christopher Rogers netted it swimming alone.

Eubranchipus oregonus

(Map 5.2, p. 118)

Our mention of the town of Weed calls to mind the first known locality for *Eubranchipus oregonus* in California. Ken Beatty of the College of the Siskiyous sent us his collection of 28 February 1986 from a pool south of town which is situated at approximately 1,250 m elevation. You note we said that this was the first "known locality". Actually, the U.S. National Museum of Natural History holds a collection made in February 1956 by F. Flammer, taken from an "ephemeral pool south of Brocot, California". We have pored over maps, even made a name search, but can locate no such place. So, if any of our readers can direct us to the elusive Brocot, perhaps we can better follow the route of this fairy shrimp into California.

Actually, its approximate route is probably not all that secret. Coopey (1950) believes the species has a general distribution in the valleys of western Washington and Oregon, for he collected it as far south as Cottage Grove, Oregon, some 200 km as the duck flies north of the California border. We are of the opinion that "Brocot" would be an interesting place to locate and fit into the dispersal path of *E. oregonus*, for Brian Quelvog established (27 March 1995) that this species resides in Abernathy Meadows (1,350 m in elevation), immediately north of Yosemite National Park in Tuolumne County. More recent yet, a collection of this beast was taken near Schoettgen Pass at 1,450 m, some 35 km to the northwest, in a snowmelt, silty-bottomed, meter-deep pool. These locations place the species 415 and 450 km by air southeast of the Weed population.

Knowing if and where any stepping-stone pools are located along the Cascade-Sierra chain became an interesting challenge for CalTrans biologist Richard Hill. Perhaps the phantom locality of "Brocot" lies between Weed and Abernathy Meadows, he reasoned, so maps were scrutinized and a creative possibility emerged. West of Lassen National Park lies the village of Viola in Shasta County. Departing southeast from Viola is Broke Off Meadows Road which traverses country from 1,500-2,000 m in elevation, and southeast of road's end is Brokeoff Mountain (yes, different spellings). Given the seemingly appropriate elevation, and that the meadows are on a straight-line flight path between the known sites, maybe, just maybe, Richard found the phonetically-misunderstood "Brocot".

Bird flight paths are not all straight lines however. Nor do all of our feathered friends fly along the Cascade-Sierra chain. Obviously waters of the Central Valley and lagoons along the coast are some of their favored resting and feeding grounds. Perhaps cysts of *E. oregonus* were transported along their coastal trade-routes from Oregon to California, for almost 7 km south-east of the twin cities of Rio Dell and Scotia, in the valley of the Eel River, supposedly lies a pool, its nature undescribed, from the bowels of which our subject is said to have been seined. We have the collection, but if from a pool in this area we have a unique find, so unique that several expeditions (unsuccessful) have been mounted to confirm it. And why is it unique? Not only would this be just the fourth known location for the species in California, but it would be one of **only four anostracan sites in the North Coast Mountains Region** (Map 4.2, p. 68). One could assume fairy shrimps are not common in these wet climes, so until someone is led knee-deep into this otherwise unknown pool we consider the record anecdotal. With Brocot not forgotten, we recently learned that also in this general area and immediately to the east of Arcata Bay is a spot on the map labeled Bracut. Could **this** be the elusive "Brocot"? And does *E. oregonus* live in its vicinity?

The *Eubranchipus oregonus* site near Weed is seasonally astatic and does not form every year. When it does fill, snow-melt provides the water, usually in February, and it lasts through April. The pool is held by deep clays in a natural drainage under a railroad span which crosses a wet meadow surrounded by coniferous forest. At maximum the basin is about 8x3x0.2 m and holds clear water with poor buffering capacity (Beatty pers. comm.). Being a biology professor in Weed, Beatty describes these conditions from many seasons of observation. However, on 10 May 1995, Richard Hill found a "huge pool", at least a football field long and 10-12 m wide, backed up along the railroad bed. Although unable to wade to its center, he netted *E. oregonus* in areas where his boots were safe from filling. The clear water had a pH of 6.5 and a TDS (from conductivity) of 91 ppm, corroborating Ken Beatty's verbal description of conditions.

In Abernathy Meadow, which is also surrounded by coniferous forest, a "spring pothole" in granitic soils houses *E. oregonus* (Hill, pers. comm.). Whether or not water remains in the basin when winter arrives is unknown, but if it does, certainly it freezes. And whether the pool is filled mainly by snow melt or by the spring is also unclear. What we do know is that in the spring of 1996, when the site was brimming with fairy shrimps, the clear water was 11°C and had an alkalinity of 68 ppm (Hill again). These conditions are not at odds with what Coopey (1950) felt was characteristic habitat of *E. oregonus* in western Washington and Oregon. He described a site near Seattle, Washington, as a "temporary, *Typha* bordered pond" with a maximum depth of 1.3 m that contained much detritus and "yellow to brown stained water". It filled in late November and was dry by late June or July. During his studies, temperatures were 1°C (under ice) to 16°C, and the water was mildly acid (pH 5.8-6.2) .

Coopey's work also demonstrated that cysts (0.35 mm in diameter; Hill & Shepard in press) began to hatch three days after pool-filling; and though the process continued for 5 weeks, 75% of the metanauplii appeared within the first 10 days. Although hatching occurred at temperatures of 4-9 °C, water of 10-15°C was required to bring females to maturity. At maximum female size, ovisacs commonly possessed 150-250 cysts. Coopey watched females doing their reproductive thing until temperatures reached 26.5°C. Armed with this information on clutch size and longevity, he estimated a female's fecundity at 300-400 cysts. Apparently a good deal of this production was accomplished without pestering males, who had succumbed when temperatures attained only 16.5°C. Whether thermal limits were surpassed, or the sexes merely lived out their genetically allotted time, is not known. In any event, female longevity of 23-25 weeks appears to be one of the longest for North American Anostraca.

Eubranchipus serratus

(Map 5.2, p. 118; back cover)

Eubranchipus serratus, reported by Eng *et al.* (1990) as known only from McCoy Flat, 6 km west of Eagle Lake in Lassen County, has now been collected by Richard Hill and Christopher Rogers from additional sites in the same general region. Pools in this Cascade Range area lie at elevations from 1,500-1,750 m in small meadows surrounded by heavily logged coniferous forest which, immediately east of Eagle Lake, grades into Great Basin Desert. About 120 km north is California's border with Oregon, and about 20 km into Oregon is a pool identified by Coopey (1946) as containing *E. serratus*. Because this species spans the continent, with the U.S.-Canadian border being about its northern limit, dispersal routes along the Cascades from British Columbia through Oregon and into California were undoubtedly used to establish the populations in Lassen and Shasta counties. Although there are more southern populations in Virginia, Oklahoma, and Arizona, we consider it unlikely, given intervening habitats, that *E. serratus* arrived in California from the south and worked its way north along the Sierra and into the Cascades.

Information from California specific to this species is pretty much limited to the knowledge that it occurs where winter freeze is long and hard. However, in early October of 1995, Clyde ventured forth to find the McCoy Flat site in order to determine if it was anything like the Montana, mountain-meadow pools where, for a number of summers, he had pursued *E. serratus*, and in turn had been pursued by mosquitoes. Results were positive in all aspects, including mosquitoes. Here was a partially mud-bottomed basin, still holding clear water (1995 was wet!), and, although lacking fairy shrimps, was replete with *Carex*, *Juncus*, and *Ranunculus*, filled with the typical later-season menagerie of aquatic insects and frogs (*Hyla*), and surrounded by cow dung, aspen, and conifers, in that order of proximity.

Of the two dozen or so California collections, only the one from McCoy Flat was made in fall (early December). This probably means the pool was filled by rain, although if 1995 is any indication, the possibility exists that water remained year-long, and in the fall became cold enough to stimulate hatching but remained liquid long enough to allow development before winter solidified the habitat.

Studies outside California (Belk 1977a; Coopey 1946; Dexter & Ferguson 1943; Prophet 1963a; Eriksen unpubl.) indicate that *E. serratus* is typical of seasonally astatic waters in forests, meadows, and grasslands that are subject to winter freezing. Autumn, winter, and spring collections have been reported at water temperatures usually between 1-17°C. In one instance the surface of a pool reached 23.5°C, but near its bottom the water was a cool 15.1°C; it is doubtful that individuals experienced the surface temperature, for *E. serratus* is known to congregate in and around vegetation and to swim removed from the surface, perhaps selecting cooler water in such places. We say this because McGinnis (1911) showed shrimps select temperatures of 15-17° C, will not voluntarily swim into water over 17°, and die at 28°C. Belk (1977a) was able to acclimate adults at 25°C for 24 hours, but 50% of them succumbed within an hour when transferred to 31°C. Given such information, the fact that fairy-shrimpologist Richard Hill found *E. serratus* in a number of pools around Poison Lake (Lassen County) at temperatures from 21-24°C should not raise too many eyebrows. However, he also saw "huge numbers...in a cut off pool adjacent to the lake" at 26.8°C, which suggests that either this population might soon be terminated by elevated thermal conditions, or such daytime highs were only fleeting because of substantial nighttime cooling, or colder bottom water was available. Place a check opposite your favorite hypothesis!

Although pools inhabited by *Eubranchipus serratus* are usually at least partially mud-bottomed, they also possess significant amounts of living and dead vegetation and thus contain clear, though often tea-colored, water. The result is very low TDS, poor buffer capacity (low alkalinity), and a slightly acidic pH, although values from 4.9-8.2 are on record.

Cysts of *E. serratus* will not hatch at 20°C, do so poorly at 15°C, but yield larvae well at 5-10°C (Belk 1977a; Prophet 1963b). 0°C must also be suitable because Dexter and Ferguson (1943) reported metanauplii swimming amongst flooded ice as their pool began to thaw, and development continued for several weeks under heavy ice cover. As is typical, length of the life cycle, and time to maturity, depend on temperature. For example, individuals have been known to survive almost 9 weeks, reaching sexual maturity after 5, under "moderate temperature conditions" (Dexter & Ferguson 1943). But Coopey (1946) noted that individuals subjected to what he supposed were cooler than average temperatures did not reach maturity until 6-8 weeks had passed, and lived a total of 11.5 weeks. In his Kansas lab, and at a constant 15°C culture temperature, Prophet (1963b) noted that a female's ovaries began producing eggs about day 13. Over a life span, the average female made 366 cysts, but the variability (42-640) was considerable, as was the number per clutch. Prophet's recorded range of 1-290 comfortably encompasses the 157 cysts counted by Denton in a 22.8-mm Arizona female (Belk 1977b). As is typical of species living in snow-melt pools, cysts were large (average 0.37 mm), in fact the largest of those Denton measured in his study. This did not surprise Hill and Shepard (1997) who found cysts of *E. serratus* to be the largest (0.39 mm) among California Anostraca (except for the giant fairy shrimp). Also contained in Denton's study was the fact that larvae of *E. serratus* hatch as big metanauplii (0.58-0.73 mm), as do other snow-melt pool species.

Although both Christopher Rogers and Richard Hill have found *Branchinecta coloradensis* in several pools containing *E. serratus* in the vicinity of Poison Lake in Lassen County, the latter far outnumbered the former. Because it seldom has been collected with other anostracans elsewhere, *E. serratus* seems to follow the pattern of cold-water fairy shrimps being "loners".

Streptocephalus sealii

(Map 5.3, p. 119)

This often strikingly-colored species occurs in a number of sites in California. All but two are within the coniferous forest belt of the moderately high, glaciated, Cascade-Sierra Nevada Mountains Region, from Siskiyou County at the California-Oregon border to just south of the Mammoth Lakes area, barely into Inyo County, somewhat over 500 km to the south-southeast. The two exceptions to this distribution are located in the Siskiyou Mountains of the North Coast Mountains Region some 200 km west of the northernmost Cascade-Sierra sites. A pool near Sanger Lake, about 7 km south of the Oregon border in Del Norte County, appears typical of those occupied by other populations of *Streptocephalus sealii* in that it is rock-strewn, mud-bottomed, filled with clear water, and rests in a small meadow surrounded by coniferous forest and guarded by Steller's jays. Another 40 km due south, and barely east of the mountain crest that separates Del Norte County from this Siskiyou County location, lies a truly remote and undescribed *S. sealii* hideout. These pools are of note because they harbor two of the three proven anostracan populations in the North Coast Mountains Region. Additionally, at elevations of almost 1,600 m, these and the two sites in eastern Siskiyou County at 1,200-1,400 are the lone locales in California where *S. sealii* has been documented below 2,000 m, although more will undoubtedly be discovered, most probably in this general region. Populations of *Streptocephalus sealii* in the Cascade-Sierra Nevada Region are typically at elevations from 2,100-2,500 m, although several lie at 2,770, 3,032 (Tioga Pass in Yosemite National Park) and 3,219 m (the only known Inyo County site).

In California, this species has been netted from late June to mid-September – with one exception, that being an interesting and historical one! A collection, given credit as the first record of the species in California, was made "March of 1930 in the High Sierra Mountains". A local placement of this population is obviously impossible, but a low-elevation site in the high Sierra, though a contradiction of terms, may be responsible for the much earlier collection date.

Information concerning the California habitat of *S. sealii* is all but absent. What little we know from recorded data shows it swims in waters from 10.6° (and certainly much lower) to 23.4°C in seasonally astatic, perennially astatic, and aestival pools where winter snows lie deep. The most common habitat is a meadow basin surrounded by coniferous forest, and strewn with granite outcrops or boulders, and often fallen trees. Such pools are glacially formed, probably kettle holes, mud-bottomed, and have clear, though often tea-colored water because of dissolved organic matter leached from meadow grasses or conifer needles. The perennially astatic waters are a small crater lake, a cirque lake, and several 1-2 m-deep glacial basins covering 987-8,195 m^2, at elevations around 3,200 m (Jim Muck pers. comm.).

These general habitat conditions suggest slightly acidic, soft-water of low buffering capacity. The only data from California support such generalities and come from the perennially astatic Lower Inyo Crater Lake in Inyo County. This unique-sounding habitat is lightly turbid from volcanic clays derived from pumice, has very low buffering capacity (20-40 ppm alkalinity), and a pH of 6.8-7.1 during the time shrimps and Clyde were present together (Eriksen *et al.* 1988b).

Outside California, *S. sealii* has been dipped from clear, snow-melt pools in high mountains as well as from low-elevation "mud holes", turbid cattle-watering sites, and summer-rain-filled, tea-colored, forest waters. Charted temperatures range from 0.5-35°C (one record of 42°C) in waters of low to moderate alkalinity and conductivity, and a corresponding pH variation of 4.9-8.7.

This species is the most widely distributed fairy shrimp in North America, occurring from southern Canada to Mexico's southern most state, and from coast to coast across the U.S. Such a distribution involving a wide diversity of habitats would require a fantastically labile physiology. We wonder if it is not more reasonable to think of this anostracan as being at least two, if not more, sibling (cryptic) species. We say this because, first, the high mountain pools of Arizona and California, fed by snow-melt, are quite different from plains and bayou basins to the east and south which fill by rain. Second, different hatching mechanisms are indicated in those contrasting conditions. Cysts of "lowland" *S. sealii* are said to release nauplii only from 10-32°C (Moore 1963; Prophet 1963b). Cysts of plateau and mountain populations presumably hatch in snow-melt waters. But Denton, who had no trouble coaxing nauplii from Louisiana cysts, had no luck hatching high-elevation ones from Arizona, nor was Richard Hill's brief attempt successful with cysts from several Sierra populations.

Although Denton's search for a reason that might explain the dichotomy in laboratory hatching success between high- and low-elevation populations of *S. sealii* was unsuccessful, he did discover some significant reproductive differences between the two (Belk 1977b). For example, he noted that Arizona animals possessed significantly larger cysts (0.34 vs. 0.24 mm in diameter) which contained embryos more than twice the volume of those from low-elevations, and consequentially the high-altitude *S. sealii* produced fewer cysts per clutch on a size for size basis. To illustrate, the largest Louisiana female had 315 cysts in her ovisac; she was 19.4 mm long. By comparison, a slightly larger Arizona female (23.0 mm), the high-altitude specimen closest in size with a filled ovisac, bore only 86 cysts. Strikingly, the largest Arizona female (34% longer than her biggest lowland counter part), possessed 22% fewer cysts (only 246). With interest whetted, Belk *et al.* (1990) did a follow-up study with other low-land populations and some from the high Sierra. Although this time the average size of cysts of lowland forms was 0.26 mm, mountain cysts continued to average almost 0.34 mm, with none smaller than 0.31 mm. The hypothesis seemed confirmed! Or was it?

As scientists, we generate ideas freely from data at hand. However, not uncommonly, some of those data seem at odds with what we think we know and thus cry out for resolution. A case in point is some measurements sent to us by Hill and Shepard (1997). Their cysts of *S. sealii* from the Sierra had a composite average diameter of 0.27 mm, obviously a size more reminiscent of those from low-elevation rainpool animals, but their diameters ranged from 0.24-0.31 mm. That the mass of cysts is considerably more variable among populations than was previously imagined is undeniable. Still, we wonder if any of the Hill and Shepard samples came from populations with which Denton dealt? Did they come from animals living at comparatively low elevations? Are the differences recorded really the result of variation between populations, or are sample sizes for any of the studies large enough to establish a meaningful average? What we all know is that the hypothesized relationship originally conceived by Denton (pp. 75-76) requires that additional inquiring minds probe its ramifications and possible exceptions.

Before we leave these data on cyst, clutch, and larval size, there are several more comparisons to consider, and, you guessed it, more questions to ask. Anderson (1984), knowing that a single female *S. sealii* from low elevations can produce multiple clutches, estimated that, if this normally long-lived creature survived three months, her fecundity could top 1,500 cysts. Prophet (1963b) had already proved such an estimate reasonable, for one of his lab-reared females actually manufactured 1,791 cysts!

Are such levels of fecundity attainable by *S. sealii* populations residing in western mountains, or are reproductive characteristics of the latter more like those of other high-elevation, snow-melt pool species we have already considered? Well, for starters, larvae of mountain *S. sealii* emerge from relatively large cysts to swim in melt-water-filled basins. Are these larvae released as metanauplii as with other high-elevation species possessing large cysts, or do nauplii pop out as in rainpool forms of *S. sealii*? No one knows. And how long do high-elevation animals live? How many clutches can they generate in a season – one, as do other snow-melt pool species, or from 3-14 as per low-elevation forms (Prophet 1963b)? If more, what is their maximum fecundity? Ah, questions, but few answers. At least we know their clutch size is relatively small!

We also know that the temperature tolerances of adults differ. Belk (1977a) recorded a one-hour LD/50 (a comparative lab measure of the temperature at which 50% of the experimental organisms survive and 50% die within one hour) of 38°C for mountain populations in Arizona, while Moore (1955) reported 44.5°C for animals from Louisiana. Moore also noted that several hours at 42°C was lethal for bayou beasts, as was 40°C, but only after 18 hours of exposure. Finally, Moore showed that "warm-water" (low-elevation) *S. sealii* could not be acclimated to cold water, being sluggish even at 7-8°C. Given conditions in which California individuals swim, we assume they are physiologically like *S. sealii* from the mountains of Arizona and unlike their low-land counterparts.

Streptocephalus sealii, which has not been observed in California coexisting with other anostracan species, is yet one more example of a cold-water, predictable-pool fairy shrimp which swims alone.

Fairy shrimps of cold-water pools which are low to moderate in dissolved solids, predictable, and long-lived

Branchinecta coloradensis

(Map 5.4, p. 120; Fig. 5.2, below)

Branchinecta coloradensis, named in 1874 for its collection site in the Colorado Rocky Mountains, conjures up thoughts of high terrain and snow-melt pools embracing crystal waters. We might think of it as the stereotypical organism of such places, for this species has been taken from 2,900-3,530 m in mountains of a number of western states, including California. Our four known high-elevation sites, 15 km from each other on either side of the Sierra crest in Inyo and Fresno counties, lie at 3,150-3,530 m. The problem with thinking of this fairy shrimp as a resident only of mountains is that what we presently call *B. coloradensis* also appears in some prairie pools in Oklahoma, Wyoming, Alberta, and Saskatchewan, and it frequents high deserts throughout the West, including those in Oregon and California. A number of havens for this animal are scattered along a 100-km stretch of Great Basin Desert, 1,300-1,600 m in elevation, between Alturas and Susanville in Modoc and Lassen counties. Westward toward the Sierra-Cascades, and on the Modoc Plateau of Lassen County, *B. coloradensis* inhabits meadow pools down to around 1,000 m (Christopher Rogers, Richard Hill, pers. comms.).

Fig. 5.2. Female of *Branchinecta coloradensis* from Lynch (1964); reprinted courtesy of *The American Midland Naturalist* (scale = 2 mm).

Its crystal-clear Sierra haunts, with surface areas from 49-355 m^2 (Jim Muck pers. comm.), are of glacial origin; many localities in the high desert are road-side and railway-side ditches holding turbid water; and those in forest meadows are largely clear-water basins whose dimensions and origins are unknown but which commonly lie on soils of volcanic origin. Whatever the site, most of these waters are seasonally astatic, a few aestival, and all are filled initially by snow-melt.

Because its habitats seem so environmentally different, the obvious question is: what traits do these places share that *Branchinecta coloradensis* requires? Freezing winters and a pulse of water of very low osmotic concentration from melting snow appear to be the obvious factors. Simple, right? **Perhaps wrong,** for *B. coloradensis* has popped up in several California habitats which look quite different from those described so far. One, Panamint Dry Lake, occupies a 475-m-high basin one valley west of Death Valley. "Dry lakes", or playas, are usually quite alkaline, and the fact that the alkali fairy shrimp *B. mackini* dwells here as well is living proof of the conditions in this habitat. Interestingly, when Clyde dipped into the turbid and alkaline water of Panamint Dry Lake during the plentiful rain-year of 1995, *B. coloradensis* was conspicuous by its absence, only *B. mackini* graced his net. Obviously conditions here aren't always just right for the Colorado fairy shrimp.

Although the Panamint Dry Lake area may prove cold enough during most winters to satisfy what was thought to be a hatching requirement for the species, there are three other known sites containing *Branchinecta coloradensis* that do not normally receive intense cold, all in the Central Valley. These include a very large, turbid vernal pool, 70 m in elevation and about 15 km from the Sierra foothills, which lies east of Hickman in Stanislaus County. A second site is on the Sacramento NWR in Glenn County at its border with Colusa County. Joe Silviera, wildlife biologist at the Refuge, collected *B. coloradensis* early in 1993, and again in 1994, though not in 1995, in a pool he described as being turbid and alkaline, and 50 m in elevation. The most recent find, a collection taken in March of 1996 from an undescribed site a few km south of Colusa, was given to Christopher Rogers by William Beckon. If our Colorado fairy shrimp requires water the temperature of snow-melt as a hatching stimulus, this implies that a relatively harsh cold-snap settles in on these otherwise cool pools often enough to stimulate hatching and thus maintain their populations.

Richard Hill told us of transferring some *B. coloradensis* to his Sacramento lab from a site 1,700 m in elevation on the Modoc Plateau. His animals, kept at 10°C, went about their reproductive business and ejected many cysts into their aquarium habitat. Of course biologists are prone to experiment, and Richard observed that every time he lowered the temperature to around 5°C, presto, many of the cysts hatched. Drying was not required! Whether this scenario fits the "lowlander" populations we do not know. Lab experiments and continuous measurements of pool temperatures are called for to find out.

A hypothesis has recently been developed to explain the occurrence of this fairy shrimp in such diverse environments, and here it is for your consideration. Perhaps, in a situation analogous to that seen in *Streptocephalus sealii*, we are dealing with populations which developed from *B. coloradensis* cysts that were deposited in what at the time were atypical environments. Then because some individuals in these founding populations successfully adapted to the new conditions, they started down the ever-diverging path toward new species status. This idea is not without accumulating evidence. Intrigued by the problem, Christopher Rogers set about to study the morphology of these different populations in some detail. On the basis of preliminary observations, he felt that what we now call *B. coloradensis* may actually be a complex of three species, one from high mountains, one from the Great Plains and Great Basin Desert (including Panamint Dry Lake), and one from the Central Valley of California.

As we go to press, Christopher's hypothesis is having problems with variability in several taxonomic characters, both within and among populations. Help might come from protein analyses (electrophoretic studies), comparison of cyst sizes, and determination of hatching temperatures for the various populations. We must await the final evaluations and their review by other scientists. Should Christopher be correct, it could solve the questions pertinent to how this "species" is able to inhabit such diverse environments.

We have presented habitat data in such a way that should *B. coloradensis* ultimately be divided into three species you will be able to refer the appropriate information to the correct one.

Whatever the outcome, *Branchinecta coloradensis* (or its species complex) is a fairy shrimp that has been known for a long time, but about which we are only beginning to be informed. The range of temperature over which cysts from its various populations hatch is undocumented, but Maynard (1977) observed rather large metanauplii (0.73 mm in length) appearing in water accumulating from melting snow. In her study pools 2,900-3,100 m high in the Uinta Mountains of Utah, growth to maturity took 18-26 days, the longer period being required when melt-down occurred earlier in the season (the temperature relationship holds true again!). Females produced one clutch of 12-33 large cysts (0.39 mm) during a life that spanned the tenure of their pools (45-60 days). Hill and Shepard (1997) measured cysts from 6 California populations. Their data fell into two groups. One averaged only 0.27 mm, but the mean of the other (0.35 mm) was nearly as large as that for cysts from Utah – the same great variability seen for *Streptocephalus sealii*. Still, the overall average of 0.31 mm shows that *B. coloradensis* makes a rather large cyst. Wouldn't it be interesting to know if the populations producing smaller cysts come from lower elevations, and whether their cysts yield nauplii instead of metanauplii?

This species is usually collected between March and July, but Maynard's (1977) statements suggest that her high-elevation Utah shrimps persisted until mid-September. Similarly, individuals seen on October 6 in an icing-over aestival lake in the high Sierra (Pioneer Basin) were probably from a late hatch as indicated by the 3,400-m elevation. This seems a reasonable conclusion given that dates of all collections from our state correlate directly with elevation.

In California, *Branchinecta coloradensis* has appeared in basins from 20 m^2 to 2.6 km long, and all snow-melt ones were annually predictable. Properties of the high-mountain waters have rarely been measured, but what data exist show low pH (5.3-6.8), and very low alkalinity (1-11 ppm) and TDS (10-33 ppm) (Horne 1967; Maynard 1977; Hill pers. comm.). The few records from its Great Basin Desert waters (California and Oregon) show the animals tolerate pH from 7.5-8.5 and alkalinities of 86-290 ppm (Coopey 1946; Lynch unpubl.; Eriksen unpubl.). Even though the water chemistries of Panamint Dry Lake and the alkaline pool on the Sacramento NWR were within these ranges when Clyde sampled them in 1995 (except that the playa was higher in alkalinity, 366-520 ppm), this species was absent. Although most populations of *B. coloradensis* hatch in cold water, all face later-season temperatures as high as 26°C. And like other cold-water anostracans, *B. coloradensis* has been seen in the same California pools with other species of fairy shrimps only a few times (once with *B. mackini*, several times with *Eubranchipus serratus*).

Branchinecta dissimilis

(Map 5.5, p. 121)

This uncommon fairy shrimp seems to have similar requirements and distribution in Oregon and California as does *B. coloradensis*. In the Great Basin, *B. dissimilis* is known only from alkaline pools in Deschutes, Harney, and Lake counties, Oregon (Lynch 1972; Eriksen unpubl.), and Storey County, Nevada (Handelin pers. comm.). In the high Sierra Nevada, somewhat over a dozen of its glacially-formed domains have been located between Monitor Pass south of Lake Tahoe and the high country southwest of Bishop in Inyo and Fresno counties, a total distance of only 150 km. All were at or above timberline from 2,540-3,450 m in elevation. East of Bishop is the only known site for a fresh-water anostracan amongst the non-glaciated topography of the White Mountains. Marilyn Meyers, a graduate student at U.C. Berkeley, netted *B. dissimilis* in a pool 9 km south of White Mountain during the summer of 1995. At 3,587 m, this is the highest recorded anostracan locale in both California and North America.

We commented above that *B. dissimilis* is an uncommon fairy shrimp, but as is often true in ecological matters, such a conclusion may be an artifact of where people have looked. For example, both Karen Wilson and Christopher Rogers went looking for fairy shrimps on the Modoc Plateau in Shasta and Lassen counties, and found populations of this species as low as 1,000 m near Fall River Mills.

Sierra Nevada haunts of *B. dissimilis* are mud-bottomed, yet filled with clear but sometimes tea-colored water, and have measured surface areas of 49-12,800 m^2 (Jim Muck pers. comm.). Because they are in alpine, glacially-scoured granitic basins, these pools and lakes are seasonally astatic or aestival. At the White Mountain site, the 7x5x0.6 m, cobble-bottomed pool contained "very pigmented, reddish-brown" water (translation: high in tannic acids) (Meyers pers. comm.).

Collections were made in March in the Fall River area, and from June to mid-September in the high Sierra and White Mountains. Temperatures were 7.5-23°C. The few data available show that pH of 5.5-6.5 correlates well with low TDS (10-40 ppm), and alkalinity (1 ppm) of the mountain sites. The Great Basin desert habitats of Oregon, though seasonally astatic and filled by snow-melt, differ by being turbid, displaying a pH of 7.5-9.0, and occurring at elevations around 1,500 m (Lynch 1972). Somewhat intermediate conditions were noted by Mark Handelin in a Great Basin Desert pool lying at 1,969 m in Storey County, Nevada, a few km southeast of Reno. Mark sampled several times over the 1995 season, and recorded temperatures from 5.2-20.3°C, low TDS (about 30-160 ppm, from conductivity), and pH of 5.8-7.8.

Because of its distribution, *B. dissimilis* is suspected to produce large cysts which release metanauplii into cold waters yielded by melting snow. However, conjecture is the name of the game for there are no pertinent field observations, and Hill and Shepard (1997) provide the only measurements of cysts. These averaged 0.27 mm, the same as they determined for Sierran *Streptocephalus sealii*, and one of the larger produced by California's fairy shrimps.

Although the range of *Branchinecta dissimilis* in the Sierra Nevada overlaps the southern end of the distribution of *Streptocephalus sealii*, it was the dominant fairy shrimp at elevations exceeding 2,500 m. However, four collections of *B. coloradensis* from above 3,000 m show the latter to be up there as well. *Branchinecta dissimilis* has not been collected with other anostracan species in California, but in a pool in the Great Basin Desert of Oregon it was recorded once with *B. mackini* (Lynch 1972).

Fairy shrimps of cool-water pools which are low to moderate in dissolved solids, moderately predictable, and long-lived

Branchinecta conservatio

(Map 5.6, p. 122)

Branchinecta conservatio was the first organism to be named in honor of The Nature Conservancy, an organization in the forefront of conserving natural diversity, and whose Vina Plains and Jepson Prairie preserves protect two of the few pool clusters which sustain this rare creature, Federally listed as endangered.

This fairy shrimp is found in grasslands of the northern two-thirds of the Central Valley, spanning a north-south distance of about 300 km, at elevations of 5-145 m. Within this limited range, its populations are even more restricted, occupying only a few disjunct localities: the Vina Plains of Tehama County; Sacramento NWR in Glenn County; Jepson Prairie Preserve and surrounding area immediately east of Travis Air Force Base, Solano County; Mapes Ranch west of Modesto, Stanislaus County; near Haystack Mountain northeast of Merced, and the San Luis NWR, in Merced County.

Rumor has it that a highly disjunct population occurs about 340 km to the south near the Ventura County village of Stauffer, at the also anomalous elevation of 1,700 m. This information came from Mike Fugate who raised animals from cysts contained in a dirt sample given to him when he was a graduate student at U.C. Riverside. Clyde attempted to verify this seemingly uncharacteristic location on April 1, 1996; he found a wet meadow, but no pool basin – and that's no joke! Until this population is further documented, we consider its existence anecdotal.

All known pools containing *B. conservatio* are seasonally astatic. In the Vina Plains, basins that hold vernal pools are of the Northern Hardpan type and occur in swales of old braided alluvium derived from the volcanic Tuscan Formation. Jepson Prairie basins are of the Northern Claypan type and form as large playa-like depressions on deep alluvial soils of Pescadero Clay Loam (Keeler-Wolf *et al.* 1995). Origins of the other pools are unknown. All sites are filled by winter and spring rains and usually last into June.

Branchinecta conservatio has been taken from November to late April, when pool temperatures were as low as 5°C early in the ponding cycle, to as high as 24° near the end of the season (Syrdahl 1993). Little other ecological information is available for this species. However, the type locality was studied by Barclay and Knight (1984). They describe Olcott Pond on the Jepson Prairie Preserve as covering about 4 ha with a maximum depth of 30 cm. Clays from its bottom are swept into the water by wind-mixing and the activity of animals, resulting in such turbidity (a white disc disappears at 5 cm) that rooted vegetation is absent except in shallows around its edges. All pools containing this species were at least moderately turbid and most were rather large; the smallest was 30 m^2. Barclay and Knight's data, and Syrdahl's (1993) and ours from the Vina plains, show habitat pH straddling neutral (6.8-7.5), with a few readings of 8.0, and TDS (mainly 20-60 ppm) and alkalinity (16-47 ppm) are both very low.

Brent Helm (1998) provides almost all the information about the biology of *Branchinecta conservatio*. He notes that hatching occurs in the week after pool filling at temperatures around 10°C, and that at least 19 days are required to reach maturity if pool temperatures slowly increase to at least 20°C. However, the average time to maturity, 49 days, demonstrates not only that cooler temperatures slow development, but that this species normally requires a longer time to mature than do others found within its realm. Its cysts (mean diameter of 0.23 mm; Hill & Shepard in press) are comparatively small for California fairy shrimps, and are produced in rather large, though uncounted, numbers. Individuals have lived as long as 154 days in Brent's back-yard rearing pools; however, 123 days was the average longevity. Because only one cohort is produced each year, both sexes normally disappear long before their native pools dry, apparently males first, because they appear to be less tolerant of stressful conditions than females (Serpa, pers. comm.)

Branchinecta conservatio occurs sympatrically with *B. lynchi* and *Linderiella occidentalis* on the Vina Plains (Tehama County), at the Jepson Prairie in Solano County, and near Haystack Mountain and on the San Luis NWR Complex in Merced County. Though it seldom appears in the same pools with these species, one of its rare co-occurrences with the pair also included *B. lindahli*, this at the San Luis NWR Complex. We hasten to remind you that *B. conservatio* not only occurs in great numbers by comparison to these other species, but that it is an especially hyperactive swimmer and filter feeder. You might wish to refer to page 41 to review how these factors are thought to influence the co-occurrence of *B. conservatio* and *B. lynchi*.

Linderiella occidentalis

(Map 5.7, p. 123; front cover)

Ah, *Linderiella occidentalis*, that wonderful red-eyed California endemic fairy shrimp (check out its picture on the front cover) that wiggled in our dip-nets, swam gracefully in the gallon pickle jar that Don Wootton always carried to the field to display our catches, and stimulated Clyde's career-long interest in these graceful creatures! It is the most common inhabitant of cool, soft-water pools of California's Central Valley grasslands. Here, at elevations from 40-168 m, it ranges from near Redding in the north to as far south as Fresno County, mainly to the east of the Sacramento and San Joaquin rivers. In the Sacramento area, it crosses the Valley and enters the Central, then the South Coast, Mountains Regions where it appears in a series of disjunct populations from Willits and Boggs Lake (430 and 850 m in elevation, respectively) in Mendocino and Lake counties north of San Francisco Bay, to Ventura and Santa Barbara counties far to the south. In the last county, where housing for the University of California at Santa Barbara now sprawls, Don Wootton and Clyde collected *L. occidentalis* just back from the sea cliffs, 10 m above the surf; and in the nearby backcountry, on the wildflower-painted slopes of Cachuma Canyon, they dipped this little gem from the highest pool (1,159 m) in which it is known.

Linderiella occidentalis has been netted from late December to early May, at 5-29.5°C (Syrdahl 1993). According to Helm (1998), it is the most tolerant of warm water, and consequent low dissolved oxygen, of all fairy shrimps endemic to the Central Valley. In fact, *L. occidentalis* may thrive in some of these pools until they perish, not from heat stroke, but from desiccation. This species occurs in basins with a variety of geological origins (e.g., Northern Hardpan in old braided alluvium, Northern Volcanic Ash Flow, earth slumps, depressions in lava flows and sandstone caused by weathering) which are filled by winter and spring rains and are seasonally astatic. Most of its residences are vegetated California Vernal Pools (Helm 1998), and contain clear though often tea-colored water. However, not uncommonly, *L. occidentalis* swims in mud-bottomed habitats with lightly turbid water. Although the basins vary in size from a sandstone depression of one m^2 to the 40-ha Boggs Lake, Helm (1998) says that this anostracan typically occupies reasonably large pools; in the Central Valley, only *B. conservatio* frequents larger and deeper habitats. Data on water quality show *L. occidentalis* is a species of poorly buffered soft waters (low alkalinity and TDS, 13-170 and 33-273 ppm, respectively) a consequence of which is that pH varies about a unit to either side of neutral (6.2 to an occasional 8.5).

Cysts of *Linderiella occidentalis* average 0.26 mm in diameter (Hill & Shepard in press). These hatch at most temperatures below 20°C, but the best hatching rate is achieved around 10°C, a common early-season mean temperature throughout its range (Lanway 1974; Helm 1998). Of the Central Valley endemic fairy shrimps, *L. occidentalis* requires the greatest minimum time to reach maturity (31 days), although its 45-day average time to maturity is about four days less than *B. conservatio* which takes the longest. Finally, it holds the record among these species for longevity, 168 days or 6 months, though the mean time of its tenure is 139 days (Helm 1998).

Linderiella occidentalis has been collected infrequently with *Branchinecta conservatio*, but it often co-occurs with *B. lynchi*, in which case *Linderiella* heavily predominates.

Linderiella santarosae

(Map 5.7, p. 123)

This species, restricted to the grassland pools atop the 625-m-high Santa Rosa Plateau in Riverside County, has only recently been described (Thiéry & Fugate 1994). Eng, Belk, and Eriksen (1990) thought these fairy shrimps were *Linderiella occidentalis*, isolated by some 300 km from their nearest populations in Ventura and Santa Barbara counties. Accordingly, habitat information for Santa Rosa Plateau pools were lumped with all the rest of the field data for that species. Once the few facts pertinent to the Santa Rosa Plateau were separated, and data for both species compared, their habitats appear similar – as perhaps one should expect. That they are sometimes shared with *Branchinecta lynchi* should perhaps be expected as well.

Linderiella santarosae resides in Southern Basalt Flow Vernal Pools (Keeler-Wolf *et al.* 1995; Zedler 1987) ranging from 25 to just over 100,000 m^2 in area. These basins are filled by winter and spring rains, and the water is usually clear to lightly milky, although one disturbed pool contained red-turbid water. Recorded temperatures span 9.5-21°C, while pH is 6.3-8.5 and TDS (from conductivity) is low (90-195 ppm; Collie & Lathrop 1976; Keeley 1984; Eriksen unpubl.).

Nothing is known about the biology of this species except that its cysts are moderate in size (average 0.28 mm; Hill & Shepard in press). Until further information is accumulated, we should probably assume its life requirements are similar to those of *L. occidentalis.* Even though the range of *L. santarosae* is small and its pools are but a handful, The Nature Conservancy's Santa Rosa Plateau Preserve protects this most restricted of California's endemic fairy shrimps.

Fairy shrimps of cool-water pools which are low to moderate in dissolved solids, less predictable, and short-lived

Branchinecta sp.

(Map 5.8, p. 124)

This new species of *Branchinecta* is presently being formally described. Because it has been found only in the center of the Central Valley (at elevations around 20-90 m in Fresno, Madera, Merced, Sacramento, San Joaquin, and Solano counties), it is referred to as the "midvalley fairy shrimp", a name we will use in absence of the publication of its formal scientific handle.

Except for cyst measurements (diameter of 0.27 mm; Hill & Shepard in press), Brent Helm (1998) has provided all our information on the natural history of the midvalley fairy shrimp. Like other Central Valley grassland endemics, cysts hatch in the first week of pool filling if water is in the neighborhood of 10°C. When conditions are optimal, that is when temperatures slowly increase to at least 20°C, maturity is reached in 16 days, the shortest time for any of the California fairy shrimps. However, its average of 45 days to maturity, indicates that *B. lynchi* (typically 41 days) and *B. longiantenna* (mean of 43 days) normally attain this stage more quickly. As to its maximum time on earth, some midvalley fairy shrimps have hung in there for 143 days, or just a little over 5 months, although the mean was 123 days. Amongst California endemics, only *B. lynchi* displays a lesser maximum longevity. However, the midvalley fairy shrimp could seldom live so long because it typically occurs in small, unpredictable, grass-bottomed vernal pools and puddles in the most ephemeral of seasonal wetlands (Helm 1998). In such transitory real estate, a new cohort will hatch each time the basin refills with water of approximately 10°C. This species has been collected from late January to early April, and only three times has it been taken with another anostracan (*B. lynchi*).

Branchinecta longiantenna

(Map 5.5, p. 121; front cover)

Now here is an interesting-looking creature (check out its mug shot on the front cover; also see Fig. 7.19, p.158). Because its antennae are far longer than any other North American species, it is referred to as the longhorn fairy shrimp.

Branchinecta longiantenna also has an interesting and restricted distribution. The few known sites lie near the eastern edge of the Central Coast Mountains Region, and it is one of four California endemics Federally listed as endangered. Beginning at the northern end of its range, in the foothill grasslands west of Tracy, it has been dipped from 8 clear-water depression pools in sandstone outcrops. The first of these hauls was made in 1937, long before this beast was even scientifically described. In 1981-1982 Larry Eng and his associates made all but one of the remaining collections. All these localities are within 10 km of each other, spanning the border of Contra Costa and Alameda counties.

Located about 100 km to the southeast, in the Central Valley but only 25-30 km from the eastern foothills of the Central Coast Mountains Region, in Merced County, is the Kesterson NWR. Here, at an elevation of 23 m, Michael Peters first found *B. longiantenna* in 1993 swimming in 8 of 70 or so clustered grassland pools. However, in a beautiful demonstration of environmental capriciousness, during the dryer winter and spring of 1994 it appeared in only one.

Another jaunt, 235 km to the south-southeast, brings us to the southern most sites harboring our longhorn friend. Around the borders of Soda Lake in San Luis Obispo County are many vernal pools of the Northern Claypan type (Keeler-Wolf *et al.* 1995). From 1983-1988, Bob Brown, then Bob and Clyde, found at least 13 basins which serve as home for *B. longiantenna*. It also lives in a number of pools on The Nature Conservancy's Preserve in the Soda Lake area (Larry Serpa pers. comm.). These sites are in lightly alkaline soils and are scattered amongst grassland and Valley Saltbush Scrub (Keeler-Wolf *et al.* 1995), near the eastern edge of the Central Coast Mountains Region, at elevations around 590 m.

Branchinecta longiantenna has appeared from late December to mid-May in basins filled by winter and spring rains. In its tiny clear-water depression pools in sandstone, temperatures from

10-18°C have been recorded but no water chemistry was undertaken. However, given some work that Clyde did in a rock pool elsewhere, and the fact that sandstone is very low in soluble substances, we can reasonably assume that pH is in the neighborhood of 6.5-7.0, and TDS and alkalinity are very low. By contrast, *B. longiantenna*'s clear to rather turbid, clay- and grass-bottomed pools, 1-62 m in diameter, exhibited temperatures from 10.0-28.0°C. No observations have been made on predictability or longevity of these waters, however, given their positions in the rainshadow of the Central Coast Ranges, they are undoubtedly less predictable, and probably short-lived (Bob Brown estimates about three weeks). TDS (130-590 ppm) and alkalinity (58-156 ppm) are low to moderate, as they are in habitats of other grassland fairy shrimps, but the range of values is slightly greater. A median pH of 7.2, with a range of 6.7-7.9, is similar to that of other grassland species as well.

Branchinecta longiantenna certainly vies for the distinction of being one of the least known of California's fairy shrimps. Several of Clyde's students studied it, two of its tolerance of heavy metals (Mizutani *et al.* 1991), another its filter-feeding rate (Patten 1980). Mizutani (1982) also used this species to develop a model demonstrating how a clay particle, dissolved organic molecules, and bacteria form a complex large enough to be filter fed by anostracans (see p. 50 in section: What do fairy shrimps eat?).

Once more Brent Helm (1998) provides our only information on natural history. Like other Central Valley endemics, larvae of *Branchinecta longiantenna* hatch soon after winter and spring rains fill their swimming pools with water hovering around 10°C. We assume they emerge as nauplii because the average cyst diameter of 0.26 mm (Hill & Shepard in press) falls within the size range of others which do so. In any event, whatever pops forth, these shrimps need temperatures of 15-20°C to attain maturity. If conditions are optimal, maturation is reached in 23 days, more typically it requires 43 days. If their pools remain for an extended period of time, then individuals of *B. longiantenna* are known to swim right along for up to 147 days.

The preceding is interesting and ultimately useful information, but none of it helps much to explain why the distribution of this species, and its co-occurrence with other anostracans, is so restricted. We do not know why it is tucked away only in or near the eastern foothills of the Central Coast Mountains, nor do we clearly understand why it and *Branchinecta lynchi*, which also lives in the three major areas where *B. longiantenna* occurs, have only twice been found together. For example, in its small rock pools, with but one exception, *B. longiantenna* apparently swims alone, although these are very close to other seemingly identical sites that contain only *B. lynchi* or *Linderiella occidentalis*. *Branchinecta conservatio* and *B. lindahli*, as well as *B. longiantenna* and *B. lynchi*, share the Kesterson pool complex, but each claims its separate residences. In the Soda Lake area, only once were *B. lynchi* and *B. longiantenna* taken together. The latter has been found a few times with *B. lindahli* around Soda Lake, but co-occurrence has not been observed at Kesterson. Ah, as yet there still remain some very private lives amongst fairy shrimps!

Branchinecta lynchi

(Map 5.9, p. 125; Fig. 1.2, p. 2)

Branchinecta lynchi is an uncommon, common fairy shrimp. How's that for a seeming contradiction? Consider the beast common because it appears to be rather widely distributed in the grasslands of the state, from near Red Bluff in Shasta County, south through much of the Central Valley, and ultimately via several disjunct populations to the Santa Rosa Plateau in Riverside

County in the South Coast Mountains Region. Deem it uncommon because *B. lynchi* is not abundant anywhere; and when it co-occurs with other fairy shrimp species, which is reasonably often, it is always far outnumbered.

Throughout its range *Branchinecta lynchi* has been taken from early December to early May. In and near the Central Valley, its residences range from about 10-290 m in elevation; in the South Coast Mountains Region some are as high as 1,159 m. Habitats are of two major kinds. One, which includes the type locality, is restricted to the Slanted Rocks area west of Byron Hot Springs in the southeast corner of Contra Costa County. There, clear water is held in small depressions, usually less than 1.0 m diameter, in sandstone outcrops which are surrounded by foothill grasslands. These puddles each contain only a few shrimps which face unknown water quality, though alkalinity and TDS are undoubtedly quite low. The more common habitat is a small swale, earth slump, or basalt-flow depression basin with a grassy or, occasionally, muddy bottom, in unplowed grassland. Normally these are smaller pools than those occupied by other Central Valley anostracans (except the mid-valley fairy shrimp). These are predominantly the California Vernal Pools discussed by Holland (1978), Keeler-Wolf *et al.* (1995), Thorne (1984), and Zedler (1987). However, their pool basins display the greatest diversity of origins found amongst Central Valley fairy shrimp haunts, and this variety includes disturbed and constructed sites unfavorably received by other species (Helm 1998). These places of residence vary dramatically in size, from one exceeding 10 ha, to an uncommonly small puddle only 3 cm deep and covering but 0.56 m^2. *B. lynchi* occurs in waters at least 4.5-23°C, with low to moderate TDS (48-481 ppm, mean of 185) and alkalinity (22-274 ppm, average of 91), and a mean pH of 6.8 with a range of 6.3-8.5 (Collie & Lathrop 1976; Keeley 1984; Syrdahl 1993; Eriksen unpubl.).

Branchinecta lynchi can beget cysts speedily, which places it in the company of the midvalley fairy shrimp and *B. lindahli*, both of which have similar hurry-up-and-reproduce adaptations. For example, Gallagher (1996) and Helm (1998) observed that *B. lynchi*, which hatches soon after water of 10°C or less fills its pools, will reach maturity in close to 18 days under optimal conditions, that is when daytime water temperatures rise to at least 20°C. However, 41 days are more typical if the water remains in the vicinity of 15°C. Helm's records also divulge that, of the Central Valley endemic anostracans, *B. lynchi* has the shortest maximum longevity at 139 days, although 90 was the mean longevity in his artificial backyard pools. Sean Gallagher (1996) studied a cluster of natural pools in Butte County and watched most individuals disappear around 70 days, and vanish completely after about 84 days, even when water remained in their basins.

The number of cysts produced per clutch, and how many clutches can be generated during a life span, are unknown quantities. However, once cysts have been dropped, all that is necessary for another hatching is a frost or major storm which lowers water temperature to around 10°C (Helm 1998). Gallagher (1996) reports three separate hatches in a season, while Helm has observed 6! This ability of being ready and able to launch more than one cohort per year sets *B. lynchi* and the mid-valley fairy shrimp apart from other Central Valley endemic anostracans.

These biological realities certainly paint a telling picture of why *Branchinecta lynchi* dwells in some of the shortest-lived of fairy shrimp settings – pools which persist for only 6-7 weeks in winter, and perhaps three weeks in spring. Since *B. lynchi* develops faster in warmer spring pools than in colder winter ones, it probably averages about a week of cyst production unless individuals dwell in deeper longer-lived pools. In the latter situations they commonly co-occur with *Linderiella occidentalis* and, on the Santa Rosa Plateau in Riverside County, with *L. santarosae*.

The wide general distribution of *Branchinecta lynchi* overlaps or interfaces with the ranges of a number of other anostracans. Even so, we are aware of *B. lynchi* rubbing phyllopods only once or a couple of times with *B. mackini, B. lindahli, B. longiantenna*, the midvalley fairy shrimp , and *B. conservatio*. Brent Helm believes he knows why *B. lynchi* can't tolerate the last. To refresh your memory of the intimate details, refer to page 41 in the section on "Coexistence".

Branchinecta lindahli

(Map 5.10, p. 126; Fig. 5.3, p. 116)

If you thought *Branchinecta lynchi* had a knack for getting around the state, then consider *B. lindahli*. In the Great Basin Desert of California this vagabond has staked a claim to some turf near Ravendale in eastern Lassen County at around 1,600 m elevation. Further south it has set up shop mainly in the western two-thirds of the Mojave Desert (500-1,200 m elevation) and across the Tehachapi Mountains it is established in the arid portions of the western half of the Central Valley less than 90 m in elevation. The species is also found west of the Central Valley in disjunct, low elevation, arid areas where pools are short-lived; known sites in the Central Coast Mountains Region are near San Jose in Santa Clara County, at Fremont and Livermore in Alameda County, and around Soda Lake in San Luis Obispo County. In the South Coast Mountains Region, our amazingly versatile fairy shrimp dwells in all coastal counties from Ventura to San Diego. Of course, everyone "knows" fairy shrimps were wiped from the L.A. Basin long ago, but, guess what, Mark Angelus just reported a fugitive population of *B. lindahli* hanging tough at the Madrona Marsh Nature Preserve in Torrance. Knowing it had been reported from Santa Cruz Island off the southern California coast, Chad Soiseth (1994) set sail to Santa Rosa, San Miguel, and San Nicolas Islands where he found populations as well. *Branchinecta lindahli* is also widespread outside of California, being known from Baja California, Mexico, including Guadalupe Island, and from all states west of the Rocky Mountains except Idaho, and on the Great Plains from southern Alberta to Kansas.

Our subject has been seen "doing its thing" from late November to early June in seasonally astatic pools and puddles which collect water from winter and spring rains. These habitats are typically unpredictable, often quite small, and short-lived. They vary considerably in type and origin, from playas, to arid grassland swale pools, small water-filled gas pockets in old lava flows, and depressions created by weathering of sandstone and quartz monzonite domes. Some of the sites, although natural to begin with, have been highly disturbed and modified by a menagerie of ORVs, and by junk heedlessly dispensed by a coterie of users. Excavated depressions, where sub-surface soils are exposed to water that overlies them, are seldom suitable habitats for fairy shrimps. However, in arid environments where surface clays readily erode and are carried by wind and water into road-side ditches, quarries, bulldozed watering holes, even tire ruts, these human-constructed habitats may suffice for the seemingly ever-tolerant *Branchinecta lindahli* (another of Clyde's and Denton's observations).

Given its preference for arid lands, you should not be surprised that their milieu is typically turbid, yet *B. lindahli* also swims successfully through clear-water pools. Individuals of this species are equally flexible with water chemistry. Not only do they appear in very soft waters, as low in TDS and alkalinity as for any California anostracan, but they also frolic, though much less frequently, in pools that have measured as much as

3,000 ppm TDS in California, and even 23,000-37,440 ppm (from conductivity and specific gravity) in Wyoming and Nebraska (Horne 1967; Lynch 1964; McCarraher 1970). Alkalinities up to 763 ppm (one at 2,406 ppm) have been recorded for California, while McCarraher (1970) lists the astonishing value of 10,030 ppm for By-Way-Ranch Pond which lies amid those strange sand hills of Nebraska. These are ionic levels tolerated routinely only by *Artemia franciscana* and *A. monica*, and occasionally by *Branchinecta mackini* and *B. gigas*.

Gonzalez *et al.* (1996) have explained *Branchinecta lindahli*'s apparent indifference to habitat by its ability to regulate hemolymph concentration (at least of Na^+) considerably above that of the environment in water of very low TDS (up to 460-690 ppm of Na^+), while, in contrast to obligate soft-water species, above that amount it tolerates increasing concentration of Na^+ in its blood to at least 2,300 ppm (from mmol/L) (pp. 19-20 in section on: Water, salts, and liquid wastes...).

While the range of pH measured in its habitat (6.7-9.8) was greater than for any other fairy shrimp in California, *B. lindahli* is not so versatile with temperature. Thermal conditions in which it has been recorded (1.5-22.2°C) must certainly be considered moderate. Habitat records from outside California demonstrate a wider tolerance, however. For example, in Wyoming, Horne (1967) found *B. lindahli* at temperatures from 1-32°C, and Denton, who as a Texan is not prone to heat stroke, collected some in an Arizona pool with a temperature of 34.5°C (Belk 1977a). And, with regard to pH, back in those enigmatic Nebraska sand hills McCarraher (1970) netted *B. lindahli* in a "strongly alkaline pond with water the color of black ink", and at a pH of 10.0. Perhaps we have here California's fairy-shrimp equivalent of the "renaissance man".

Many of the habitat preferences of *Branchinecta lindahli* can be explained, of course, by others of its biological abilities. For example, hatching happens best from 5-20°, poorly at 25°, and not at all at 30°C (Belk 1977a). This means that although nauplii can emerge readily in cold temperatures, cysts also hatch in cool water typical of spring in arid portions of California. At the other end of its temperature spectrum, Denton recorded a one-hour LD/50 (remember, this is not an ecological measure, only a lab comparator) of 36°C, this being intermediate among the coldest- and warmest-water Arizona species with which he worked. Thus, the temperature physiology of *B. lindahli* explains, at least in part, its occurrence from mid-December to mid-May in the milder portions of California. An inability to hatch in warm water accounts for its absence in summer.

The wide range of ionic concentrations in which nauplii of *B. lindahli* appear (up to 3,000 ppm; Horne 1967) is certainly another of the reasons for why this species occurs over such a broad array of TDS. It also demonstrates that the mechanism for suppressing hatching is unlike the one for *B. mackini*, a species with which it may coexist, and for which hatching is arrested at TDS levels greater than 1,000 ppm (Brown & Carpelan 1971).

Hatching of *Branchinecta lindahli* cysts yields nauplii averaging 0.25 mm in length, and, not unexpectedly, the rate of their further development is controlled by temperature. In inland North America, at low elevations along the Rocky Mountain front, 17-20 days are required to attain maturity in the cold and cool of spring (April-May), but only 9-13 days in the warmth of summer (June-September) and fall (October-November) (Maynard 1977; Donald 1983). On bluffs overlooking the Pacific Ocean near Oceanside, San Diego County, on January 16, John Moeur (pers. comm.) found rather large fairy shrimps swimming at 11°C in rain water which had filled an "industrial-sized tire rut" between January 2 and 3. What daytime temperatures these denizens of the rut had basked in for two weeks is not known, but remember that winter here is not a bone-chilling experience. During those 13-14 days, not only had *B. lindahli* made its appearance, but so had *B. sandiegonensis*; and both had passed through adolescence and already had the opposite sex in mind.

Maynard (1977) noted that most pools in which *B. lindahli* lived lasted only 5-30 days, with the shrimps succumbing only when pools dried; however, she did indicate that some individuals survived up to 106 days when water remained that long. Maynard's work also indicates that *B. lindahli* invests much energy in early development and maturity but does so at the expense of the sizes of its body, clutches, and cysts. For example, in a summer puddle lasting only 10 days, individuals reached maturity at an average length of 6.7 mm, a size that severely limited the number of cysts produced per clutch (minimum of 3) even though the cysts were of moderate size (0.28 mm average; Arizona cysts 0.26 mm, Belk 1977b; those from California 0.24-0.27 mm, Hill and Shepard 1997, and Moeur pers. comm.). As a consequence, the average fecundity was only 16. Spring pools generally lasted longer, and as their duration increased so did the sizes of females and their clutches, and the number of clutches, so fecundity was greater. Maynard drew her conclusions from the following data: while females 8-12 mm long generated around 25-50 cysts per clutch, females 20 mm long (the largest in her study) averaged 150. As a consequence, in a pool which lasted 14 days, female fecundity averaged 192 cysts; in a 33-day pool, 213 cysts; and at a 77-day site, females yielded a mean of 326 cysts.

For the sake of perspective and ecological comparison, remember that *B. lindahli* is often found in habitats similar to those of *B. mackini* but shorter-lived. Maynard's data show us that *B. mackini* takes so long to develop it can not reproduce in the more temporary habitats, like the 14-day site just noted. However, when pools containing these two species persist around 30 days or longer, females of *B. lindahli* muster only one-third as many cysts as their competitor. Maynard argued that these biological differences work to the disadvantage of *B. lindahli* in longer-lived waters, while such a strategy offers them the upper hand in smaller and more temporary habitats, and in drought years. Also, the possibility that drought one year enhances hatching the following year (Donald 1983) provides an explanation for the occurrence of *B. lindahli* in some of California's smallest, most temporary, and unpredictable puddles and pools.

Not only is *Branchinecta lindahli* especially tolerant of a wide array of physical and chemical conditions, it shows the greatest flexibility in acceptance of other species of fairy shrimps. Check out Table 3.1 (p. 45) where we name names.

Branchinecta sandiegonensis

(Map 5.8, p. 124)

When Eng *et al.* (1990) wrote their paper on California Anostraca, *Branchinecta sandiegonensis* had not yet been described. At the time it was thought to be *B. lindahli*. But with Mike Fugate's (1993) description of the species, and his and Denton's review of all southern California collections originally thought to be *B. lindahli*, we now know that our San Diego critter is the most frequently found fairy shrimp in a 50 km-wide coastal strip of San Diego County where pool elevations most commonly range from 15-125 m but do reach 500 m. Yes, *B. lindahli* occurs in this strip as well, but, no, it is not common! And, yes, *B. sandiegonensis* has been reported elsewhere. For example, it is known from two pools lying on coastal mesas of Baja California, Mexico, within 70 km of the international border (Fugate 1993; Brown *et al.* 1993), and recently it has been found living with *Streptocephalus woottoni* in a disgusting stock pond in what remains of ranching country that borders suburbia in southern Orange County. In addition, it lives in shallow pools on a mesa perched above the Santa Ana River, also not far from the ocean, and also in Orange County. Although *B. sandiegonensis* has not been reported from Los Angeles or Ventura Counties, there is one report of it (one female only) at Isla Vista, adjacent to the U.C. Santa Barbara campus (Fugate 1993). Because the latter account has not been redocumented, no one knows whether it represents a remnant population in a California distribution that once extended from Santa Barbara to the border with Mexico, or is the result of an inadvertent confusion of samples. Why *B. sandiegonensis* has not made it to the off-shore islands of California and Baja California, a feat which *B. lindahli* performed, is one of those fascinating questions which we hope will tickle the fancy and tantalize the talents of some future watcher of fairy shrimps. If so, perhaps one more unsolved mystery about these worthy creatures can be deciphered. And if it is, perhaps the answer will throw some light on why the distribution of this species is so restricted.

Even though we describe *B. sandiegonensis* as "the most frequently found fairy shrimp within its limited range", do understand that this is a relative phrase, for the animal is under such threat of development, that in February of 1997 the San Diego fairy shrimp was placed on the Federal Endangered Species List (Federal Register 1997).

Branchinecta sandiegonensis may appear when late fall, winter, and spring rains fill their small, shallow (usually less than 30 cm deep), unpredictable, and seasonally astatic puddles and pools (Balco & Ebert 1984). Although there is no consensus on how the basins in which this species swims were formed, there is agreement that they have been with us "...probably at least since late glacial times – 25,000 years or more.", and that they occur on coastal terraces which emerged from the sea as its level fell and the land rose between 100,000 and one million years ago (Zedler 1987). Keeler-Wolf *et al.* (1995) describe both San Diego Mesa Hardpan and Claypan basins as typical of those on the coastal mesas of San Diego County. The former are identified by reddish-colored soils with a cemented iron-silica layer that prevents the percolation of water; they are most numerous on the mesas north of the city of San Diego. These soils are commonly associated with chamise Chaparral, although Coastal Sage Scrub and annual grasslands are occasionally present. The claypan pools are formed in quite fine gray soils which largely support annual grasses. These are concentrated on the Otay Mesa, which lies along the Mexican border, east of the city of San Diego.

In laboratory cultures, females produced 164-479 cysts over their life time (Simovich & Hathaway 1997). These cysts are relatively large (0.27 mm, Fugate 1993; 0.30 mm, Hill & Shepard in press), strikingly larger than those of their closest relative *B. lindahli*. Hathaway and Simovich (1996) note, from lab and field findings, that larvae appear in cool water of 5-15°C, but not at temperatures between 15-20°C. Moeur says "they write as if it's a simple task to hatch cysts of *B. sandiegonensis*...but it isn't! I had one helluva time getting a few nauplii to pop out, and I don't know what signaled those few to make their appearance". In actuality it wasn't such a simple task for these researchers either as is indicated by one of their later papers (Simovich & Hathaway 1997). In it, they specify that just 6% of cysts hatch at first wetting (range of 0-33%), and by the end of three hydrations a total of only 28% had released nauplii. They go on to say, however, that these numbers underestimate hatching success, for, in an analysis of a separate batch of cysts, only 50% contained embryos. Whichever low number you prefer, there is a bright side to having so few emerge at each wetting. Because the pools in which *B. sandiegonensis* resides are small and shallow, and because heavy rainfall in southern California is anything but predictable, the water that accumulates may vanish before the animals reach maturity. Under such circumstances, not having a high percentage of your cysts hatch with the first alluring presence of water makes a lot of ecological sense.

The few data we have on the subject show that nauplii emerge and develop to adults sometime between mid-December and early May. At these times water temperatures vary between 10-26°C (Simovich and Fugate 1992), though John Moeur told us of a sauna-like 31°C reading. pH is moderate (6.5-8), and alkalinity (40-55 ppm) and TDS (mean of 75 ppm, as measured by conductivity) are low (Balco & Ebert 1984; Gonzalez *et al.* 1996; Moeur pers. comm.). The reason for these chemical preferences seems to be that individuals of *B. sandiegonensis* strongly hyperregulate the ion concentration of their hemolymph in waters of low TDS. However, when concentrations in the habitat rise above normal body levels, the animals are no longer able to regulate, their hemolymph Na^+ elevates, and they die (Gonzalez *et al.* 1996).

Only Hathaway and Simovich (1996) have delved into the reproductive and developmental biology of *Branchinecta sandiegonensis.* They note that cysts require 8 days to hatch at 5°C, but that period is shortened to 3-5 days at temperatures between 10-15°C. Higher temperatures do not result in a hatch. Once larvae appear, they will ultimately die if maintained at 5°C, but if the lab temperature is raised and kept at 20-22°C, they mature in 7-10 days. In the field where temperatures oscillate, 10-20 days must pass before animals become mature. Once that happens our little bundles of joy live on for as much as another three weeks (maximum longevity being 42 days). Such biological limits fit this species well to its small, unpredictable pools in coastal, sunny southern California.

Branchinecta sandiegonensis, unlike its "cousin" *B. lindahli,* usually swims in the absence of other anostracans. And even though *B. lindahli* and *Streptocephalus woottoni* are the only fairy shrimps that occur within its range, another of those intriguing questions is why, when *B. lindahli* is so ubiquitous and apparently tolerant of other species, has it been collected only a couple of times with *B. sandiegonensis*? Competition seems the most likely reason, but no one really knows. *Branchinecta sandiegonensis* has been noted a bit more frequently with *S. woottoni*, but even this seems odd, because while the former is more typically a resident of shallow, shorter-lived habitats, *S. woottoni* lives in deeper, longer-lived pools.

Fairy shrimps of cold- and cool-water pools which are moderate to great in dissolved solids, predictable to less predictable, and long-lived

Branchinecta mackini

(Map 5.11, p. 127)

Branchinecta mackini is not at all like the red-eyed fairy shrimps that swam in grass-lined pools of clear water with which Professor Donald Wootton entrapped Clyde's life-long fascination with anostracans. To the contrary, the eyes of these guys are black, and the shrimps see next to nothing as they ply alkaline waters made brown with clay stirred up from the soft mud bottoms of their pools and playas. Colorful? An inhabitant of pastoral settings? It depends on how you view muddy water that lacks aquatic vegetation; but *Branchinecta mackini* is a cherished favorite none the less, for this is the fairy shrimp with which I, Clyde, entrapped my own students, the first of which was Robert J. Brown. It all began in 1962 on a field trip I was leading. We were dipping nets into a sag-pond along the San Andreas earthquake fault (to the chagrin of several class members) when up came a haul of wriggling fairy shrimps. I got excited, Bob seemed fascinated, and in response to my invitation he relinquished his semester break and we began the studies that took us on many a storied trip to alkaline basins in the Mojave and Great Basin deserts, consumed untold hours on experiments in the lab, and spanned 18 years. Among the end results of these efforts were a PhD for Bob, several co-authored scientific papers, a friendship that finds time even today...for fairy shrimps, and a story involving *B. mackini* that shows you the world is really a small place.

Allow us to digress a bit to spin this story. In the spring of 1964, Clyde was in the backcountry of Santa Barbara collecting fairy shrimps. Wanting access to a pool on private land, I struck up a conversation with the cowboy who managed the area. His eyes lit up as did his hand-rolled cigarette when he stated that fairy shrimps were familiar to him. He told me he was in the desert some years back when a news reporter, and a biologist from CSU Los Angeles, showed up to record creatures swimming in the muddy water of Bicycle Dry Lake. Given the time frame, this was apparently the "adventure" that led to the article in the L.A. Times describing trilobites in the desert (see p. 34 in "The fairy shrimp's aquatic community"), and also yielded a collection that fell to the hands of Ralph Dexter, the scientist who, in 1956, mentioned this locality along with other known harborages when he described *Branchinecta mackini* as a new species.

Bicycle Dry Lake is an alkaline playa, and *Branchinecta mackini* is a fan of alkaline pools wherever they last long enough that the animal's life can undergo its complete cycle. For example, the Great Basin Desert, which incorporates parts of Modoc and Lassen counties in the far northeast corner of California and a relatively small piece of turf from Mono Lake to immediately east of Mammoth Mountain in Mono County, has a number of waters which contain *B. mackini.* These areas lie at elevations from 1,200-2,100 m where most of the pools are probably predictable and seasonally astatic, although a few are perennially astatic and aestival like the 20-km-long Middle Alkali Lake. Basins of internal drainage, also high in alkali chemicals, exist throughout the northwestern three-quarters of the Mojave Desert between elevations approximating 400-1,200 m. And here too *B. mackini* paddles its canoe, but this time in unpredictable pool and ditch habitats, typically associated with playas, where water is present long enough for the animals to mature. *Branchinecta mackini* also spans the Tehachapi Mountains, finding harborage at elevations from 17-99 m in the Great Central Valley, particularly its arid southern third. However, one can find scattered populations in seasonally astatic alkaline waters along the Valley's western edge as far north as Glenn County.

And how alkaline are the waters in which these little beauties swim? And what about the other physical and chemical aspects of their habitat broth? Eng *et al.* (1990) list a mean pH of 8.7 (range 7.0-9.8) which dramatically demonstrates the alkaline nature of its habitat and should prove to you that the alkaline fairy shrimp is pretty well named. In fact, *B. mackini* dwells, on average, in higher alkalinities (maximum of 2,810 ppm, mean of about 1,600 ppm) than any other North American anostracan except *Artemia monica*, which is restricted to Mono Lake. (To find out how much of an exception it is, you will have to read its biography beginning on page 115). *B. mackini* has appeared in alkalinities as low as 146 ppm, but such a low value is rare and may have been the result of runoff temporarily diluting the basin's chemical mix. Known TDS of this creature's pools varies from 486-4,800 ppm (mean of 1,364).

You've got to take your hat off to *B. mackini* and its ability to deal physiologically with the magnitude of these environmental challenges. How does it do it? Opinions vary. Robert Brown (1972) says the animal handles low levels of TDS by regulating its hemolymph hyperosmotically. Broch (1988) agrees, but says the animal doesn't do a very good job of it. He also believes that once the iso-osmotic or isoionic points are reached, *B. mackini* then conforms to increasing environmental concentrations until it dies. Gonzalez *et al.* (1996) appear to corroborate Broch's conclusions although they measured only Na^+, the most common ionic component in this animal's milieu. By contrast, Brown (1972) says that *B. mackini*, both adults and nauplii, can deal with elevated environmental dissolved solids by regulating hyposmotically. Although we may be comparing apples and oranges here, or dealing with different levels of precision because of the methods involved, resolution of what seem to be different scientific findings awaits yet another inquisitive mind.

Because *Branchinecta mackini* is obviously a species of deserts, or areas with desert affinities, it goes without saying (although we're going to say it) that the species does not occur in any of the mountain regions of the state. However, the lowest, hottest desert in California, the Colorado, does not know *B. mackini* either. Consider these possibilities as to why: habitats of sufficient alkalinity are rare to non-existent there; but, should they occur, individuals probably cannot tolerate the extended periods of high temperature which come with the territory; and finally, winter and spring rainfall is probably too slight to provide pools which last long enough for these creatures to reach maturity.

In the Great Basin Desert portions of California, nauplii of *Branchinecta mackini* emerge in the snow- and ice-melt waters of spring where they mature, and remain until their pools disappear through evaporation, or the shrimps reach maximum life expectancy (as long as 107 days; White & Hartland-Rowe 1969). Although the Mojave Desert can get downright cold at night, cold enough to form ice cover on pools, the water in these basins comes not from melting snow and ice but from rain. And when those blessed raindrops fall and coalesce into the runoff of flash-floods, low-lying basins are rapidly filled with water of limited TDS (less than 1,000 ppm), the signal for cysts of this animal to hatch (Brown & Carpelan 1971). These flood and hatching events typically occur in the cold of winter or cool of spring, but on rare occasions a summer storm may lead to a hatch in a tepid pool. Individuals of *B. mackini* that dwell here during summer would not normally achieve maximum possible life expectancy, for water temperatures can become lethal (39°C has been recorded by Brown & Carpelan 1971), or the bath will all too soon climb the evaporative ladder to the bright sunny sky.

Given that *Branchinecta mackini* ranges from southern Alberta and Saskatchewan, south into Nebraska and Wyoming, and westward into most intermontain basins containing alkaline soils from the Rocky Mountains to California's Central Valley, no one should be surprised to learn that its temperature physiology demonstrates the lability just indicated. Although more typically hatching in near-freezing water, and developing to sexual maturity in 21-31 days under cold spring conditions (Maynard 1977), *B. mackini* is sufficiently flexible to produce populations in the warm water of fall and much warmer water of summer. For example, although not mentioning temperatures preceding hatch, Maynard (1977) wrote that only 12-17 days were required for *B. mackini* to reach sexual maturity in her fall study pools near Salt Lake City, Utah. Brown and Carpelan (1971) said nothing about hatching temperatures either, but did indicate that water in a summer puddle formed in Rabbit Dry Lake, a Mojave Desert playa, varied from 12°-32°C during the tenure of *B. mackini*. Although these extremes are experienced only fleetingly in any 24-hour period, that living during a season when water temperatures approach 32°C may be hazardous to this fairy shrimp's health (and survival) is suggested by the observations of Eriksen and Brown (1980b). We placed a small aquarium of water at 22°C containing cold-season animals in a controlled-temperature room set at 34.5°C and let the combo warm. No shrimps survived 10 hours. Five weeks later we followed the same recipe with cool-season forms from the same pool. This time quite a few hung in there for 11 hours, demonstrating that the physiology of *B. mackini* adjusts (acclimates), in this case its upper lethal temperature is raised, as the pool warms through the season.

No matter the time of year, *Branchinecta mackini* matures at about 10 mm in length (Maynard 1972), grows to lengths of 30-32 mm, and produces cysts which average 0.31 mm in diameter (Maynard 1977). Of California's anostracan species, those with such large cysts are basically forms which dwell in predictable snow-melt pools, and hatch as metanauplii. Although *B. mackini* does reside in predictable snow-melt pools, unpredictable rain-formed habitats are more typical, and Maynard says that it pops out of the cyst as a nauplius, albeit a large one (0.56 mm). She also says that variability of cyst size, even in the same clutch, is considerable, citing measurements of 0.22-0.38 mm. Such variability undoubtedly also accounts for the significant size difference recorded by Hill and Shepard (1997) for cysts from California *B. mackini* (0.14-0.32 mm, mean of 0.26 mm). Because the latter diameters are more typical for cysts which release nauplii, we would like to know the length of larvae hatching from them. We think, too, that the person(s) whose curiosity gets titillated by Denton's hypothesis concerning pool temperatures at time of hatch, cyst size, and larval length and developmental state at hatch (see pp. 75-76), would find *B. mackini* a fine experimental animal. This because, like *Streptocephalus sealii* whose physiological and ecological variability stimulated Denton's hypothesis, *B. mackini*'s habitat and physiology span a similar range of conditions. Whatever the outcome of such work, this animal demonstrates the truism that variability is often, if not usually, great! And separating what is genetically caused from what is environmentally influenced is the difficult, but fascinating task for whoever will grapple with the challenge.

With regards to hatching, just what are the conditions that initiate the process? As described above, larvae will appear in water near 0°C, as well as in desert pools during summer; however, no one has worked out exactly what higher temperatures shut down the process or to what degree temperature is involved. According to Brown and Carpelan (1971), the major controller of hatching for this species is not temperature, but osmotic shock from low-TDS water supplied to the alkaline environs of cysts. Such a shock is experienced when melting snow or ice adds pure water to a basin, or when heavy run-off events like flash-floods deliver large volumes of low TDS water. Hatching begins, and continues, until dissolved materials reach about 1,000 ppm. TDS increases as salts in the soil dissolve and are mixed throughout the water by wind action, and as a consequence of evaporation. Where pools are subject to flash-floods, heavy rainstorms may repeatedly fill basins and create a hatch each time, or they may dilute the water that remains to also stimulate release of nauplii. In the latter case, two or more cohorts may swim phyllopod to phyllopod for the pool's duration.

In some cases, *Branchinecta mackini* may swim phyllopod to phyllopod with *B. lindahli*; more commonly they merely occupy the same "neighborhood". In either case, because of similar physiologies and perhaps presence one year and not another, competition between them may be a way of life (see p. 43 in the section on "Coexistence..."). The following life history traits are relevant to this possibility. As is typical of other species, clutch size increases with female length. Although variability is the name of the game, smaller females of *B. mackini* (10-16 mm) produce in the neighborhood of 2-50 cysts, these numbers being fewer than for *B. lindahli* of equivalent length. By about 20 mm, both species generate around 150 cysts per clutch. But as the length of *B. mackini* females increases above 22 mm, their brood pouch dramatically enlarges in volume allowing them to carry many more cysts (up to 450) than would be accounted for by a typical incremental addition to length (Maynard 1977). The upshot of these species' differences for *B. mackini*, dwelling in pools that last from 1.5-3.5 months, is a fecundity far greater than that of *B. lindahli* even though females of both species continue to produce clutches over their lifetime. For example, Maynard determined that *B. mackini* generated from 832-1,208 cysts (mean of 988) over a 77-day study period, but in another pool, during the same period, females of *B. lindahli* produced only one-third that number (mean of 326 cysts). The following year, in the same two habitats, but over a 33-day period, *B. mackini* females realized a mean of 545 cysts each, to 213 for *B. lindahli*. The relationship held! In the arena of competition, this means that longer-lasting pools favor *B. mackini*, but they lose out to *B. lindahli* in waters of short duration. Where these species coexist, a year of plentiful rain must favor *B. mackini*, while drought conditions would boost the other.

Because *Branchinecta mackini* is the major prey species of *B. gigas*, the two are often found together in playa habitats. In one Mojave Desert playa it was unexpectedly found with *Branchinecta coloradensis*, and in two others the cysts of both *B. mackini* and *Thamnocephalus platyurus* have been found, but coexistence is probably uncommon because the latter species hatches only during the heat of summer and early fall. In one instance, *B. mackini* was surprisingly found with *B. lynchi* in a roadside swale pool at the edge of the Pixley NWR in Tulare County.

Branchinecta gigas

(Map 5.6, p. 122; Fig. 4.1, p. 73)

Were you visiting with *Branchinecta mackini* in its western North America alkaline-basin homes, we believe you would gasp in amazement, or jump back in disbelief, should you net a 150-mm-long anostracan. We would! Still, our reaction would be tempered by the previous knowledge that this sasquatch of the fairy shrimp world, *Branchinecta gigas*, does exist, and almost always swims in the company of *B. mackini*. Well, perhaps "company" is not the most appropriate word to use, because *B. gigas*, as you know, is a predator, and *B. mackini* is its sushi of choice.

Because of this association, the distribution of *B. gigas* is similar to that just described for *B. mackini* (Map 5.11, p. 127). And because there is about a 1:40,000 ratio of the former with the latter (Brown & Carpelan 1971), the giant fairy shrimp lives in comparatively giant habitats. In other words, this predator's world must be expansive enough to house very large numbers of prey if its own population is to be big enough to assure survival. In California, this means that habitats of *Branchinecta gigas* are usually large pools associated with playas, or occasionally even the whole of the playa, and because such places must be of sufficient longevity for the completion of a life cycle requiring at least 40 days (Daborn 1975), this species is restricted to winter and spring (California collections are from late January to early May) in the Mojave and Great Basin deserts, from 700 m up to about 1,400 m. At the highest elevations, several aestival habitats are known, the largest being the 29-km-long playa called Middle Alkali Lake in Modoc County. At lower altitudes, all waters are unpredictable and seasonally astatic. You will note that this distribution and elevation range excludes the Central Valley.

Inasmuch as *Branchinecta gigas* occurs in many of the same alkaline habitats as *B. mackini*, the two obviously tolerate some of the same range of water chemistry. However, because the homes of the former are large, they are not as subject to extremes in concentration as the season progresses as are those in which *B. mackini* dwells alone. Brock (1988) reported that *B. gigas* disappeared at a TDS 25% less than when *B. mackini* populations went belly up a week or so later. The possibility exists that *B. gigas* did not survive because prey populations were rapidly declining, but Broch did not report population densities. Another scenario, this one consistent with ecological observations, is that *B. gigas*, in spite of being broadly tolerant of chemical and most physical conditions, cannot tolerate as high a temperature as *B. mackini*, for this giant predatory fairy shrimp has not been collected in waters warmer than 21°C. Whatever its limits might be, we must describe *B. gigas* as a species of relatively cool, if not cold, waters, which have high pH, alkalinity, and TDS (7.7-9.7, 300-960 ppm, 800-2,000 ppm, respectively; Eng *et al.* 1990). The occurrence of *B. gigas* in such a wide range of dissolved materials is at least partially explained by its ability to regulate body fluids hyperosmotically at low TDS, and survive high TDS by osmoconforming to a certain upper limit, one which is apparently less than for *B. mackini* (Broch 1988; Gonzalez *et al.* 1996).

In studies where both *B. gigas* and *B. mackini* were found together, they were noted to hatch at the same time. Therefore, Daborn (1975) assumed they utilize the same environmental clue as a dormancy breaker—a low TDS osmotic shock. How low the dissolved solids must be to stimulate hatching can vary between species and obviously does. Whatever the maximum stimulatory TDS value for *B. gigas* might be, we suggest it is lower than that for *B. mackini* (which approximates 1,000 ppm). We also propose that *B. gigas* has a lower maximum temperature for hatching, perhaps only 8°-10°C, whereas *B. mackini* will appear under considerably warmer conditions. Those willing to test these hypotheses can begin by considering the observations upon which they are based. First, *B. gigas* does not occur in summer pools even when its cysts are present and *B. mackini* has made its appearance (e.g., in Rabbit Dry Lake; Brown & Carpelan 1971). Second, *B. gigas* did not show up one year in a spring pool with an initial TDS considerably greater than usual, and yet *B. mackini* did (Broch 1988). And third, none of the authors we have cited reported more than one cohort of *B. gigas* per season, even though *B. mackini* can have several.

You may not be surprised to find that the giant fairy shrimp *Branchinecta gigas* produces giant cysts—the largest of any California anostracan (0.55 mm, Daborn 1975; 0.53 mm, Hill & Shepard in press). But because to now we have seen metanauplii emerging from large cysts, you may be surprised that nauplii, albeit large nauplii 0.90-1.10 mm in length, actually exit those of *B. gigas*. Daborn says the young feed on detritus, but upon reaching 7-10 mm they turn to carnivory and attain growth rates of 2.5-3.0 mm per day. Ovaries begin egg production when females are about 30 days old. At this age they are approximately 45 mm in length; given another 10-15 days, they average 60.6 mm but may exceed 70. Over this size range, 75-400 cysts are produced per clutch, the actual number being proportional to length of female, but the average will vary between years depending on available food. During one year of Daborn's study, females lived a maximum of 60 days, took 10-14 days to process each of their three clutches, and in the end demonstrated an average calculated fecundity of 630 cysts. Because the largest single clutch he recorded was 1,076 cysts for an 82.8 mm female, just imagine what the fecundity of the record-size 150-mm female might have been given her additional clutches over an extended life span...it must be mind boggling!

Fairy shrimps of warm-water pools which are low to moderate in dissolved solids, less predictable, and long-lived

Streptocephalus woottoni

(Map 5.3, p. 119; back cover)

Streptocephalus woottoni, first described by Eng *et al.* (1990), was given the name Riverside fairy shrimp because it was then known from but 5 pools about 45 km from the coast only in Western Riverside County. These included Skunk Hollow, the largest valley vernal pool remaining in all of southern California. Shortly thereafter, one of its refugia became the site of a gravel pit, the type locality was scraped for a housing development, and Skunk Hollow was slated to become a permanent lake surrounded by houses. Because of its limited occurrence, and further threats from construction, *Streptocephalus woottoni* was declared endangered by the Federal government in 1993. Thankfully, since that time several pools in Orange County, and some pool clusters on several mesa systems in western San Diego County, have been shown to house this rare beauty. Additionally, a couple of sites are now known on mesas immediately south of the international border in Baja California, Mexico. Even with these added locations, this species has one of the most restricted distributions among fairy shrimps endemic to the West Coast. With the exception of the remaining three in western Riverside County, all populations are within 15 km of the ocean over a north-south distance of about 140 km.

All pools benefiting *Streptocephalus woottoni* lie at elevations from 30-415 m in seasonal grasslands, some of which are interspersed among Chaparral or Coastal Sage Scrub vegetation. Several sites on the Chaparral-covered mesas immediately north of San Diego are considered San Diego Mesa Hardpan pools, while the two San Diego Mesa Claypan pools known to house this animal lie in the much finer grassland-supporting soils on the Otay Mesa east of the city (Keeler-Wolf *et al.* 1995). The remaining sites, including the pools on the coastal mesas near Oceanside, and Skunk Hollow of western Riverside County, have not yet been classified.

All of the swimming holes in which *Streptocephalus woottoni* plies its trade are seasonally astatic and are typically quite large, some exceeding 750 m^2. All have felt the impact of human activities, a number of them enlarged or deepened. They fill whenever late fall, winter, or spring rains generously bless the land, and because these basins are covered by 30 cm or more of water when full, they are comparatively long-lived, sometimes persisting into April or May (one record of early June). Such extended periods of wet soils usually allow the emergent rush *Eleocharis* to colonize the basins (Eng *et al.* 1990; Simovich & Fugate 1992). Although the water may be clear, more typically it is moderately turbid. Its very low TDS and alkalinity (means of 77 and 65 ppm, respectively) are corroborated by pH at neutral or just below (7.1-6.4) (Eng *et al.* 1990; Gonzalez *et al.* 1996; Moeur pers. comm.). Its appearance in waters with so few dissolved substances is explained in part by the fact it is an excellent hyperionic regulator, at least of Na^+, in very low TDS water. Once the environmental concentration reaches that of its blood, the animal dies. Additionally, *S. woottoni* can not tolerate 800-1,000 ppm of alkalinity for 24 hours. Although such amounts are much higher than any to which this species is naturally exposed, they are modest when compared to those with which several other southern California anostracans must deal every day (Gonzalez *et al.* 1996).

Very little is known about any biological aspect of this fairy shrimp. Among what we do know is that, in the laboratory, female *S. woottoni* will produce from 17 to 427 cysts over their lifetime (Simovich & Hathaway 1997). Cysts of *S. woottoni* will hatch, at least in certain situations, when placed in locales sometimes far from their natural pools. Clyde put some soil containing cysts in a newly-constructed basin on the Robert J. Bernard Biological Field Station of The Claremont Colleges in Claremont, and Denton added his aliquot of the same soil to a child's wading pool in San Antonio, Texas. When the rains came and conditions were appropriate (whatever those were), *S. woottoni* made its appearance. We assume that the cysts, with mean diameters of 0.27-0.31 mm (Hill & Shepard in press; Moeur pers. comm.) released nauplii, but neither of us checked this out.

Some of the pools in which *Streptocephalus woottoni* is found are known to contain *Branchinecta lindahli* or *B. sandiegonensis* as well. However, collections have shown that these species are usually mature or absent when *S. woottoni* is first taken. The prevailing explanation for this was that *S. woottoni* required a higher temperature for hatch and therefore did not emerge until later in the season (Eng *et al.* 1990; Simovich & Fugate 1992). Several years ago, John Moeur told us he believed that cysts actually hatch at temperatures in the vicinity of 10°C, but because development is so slow below 15°C, and the typical sampling net does not trap tiny animals, *S. woottoni* may merely be missed rather than be absent. Good reason for his reasoning, we thought, for on a fine January morning, when John took big *B. lindahli* and *B. sandiegonensis* from a mesa pool north of Oceanside, he noticed lots of dinky shrimps passing through the mesh of his net and back into their 11°C home. After 13 days, the precocious branchinectids were still there, but the baby shrimps had grown enough to show the undeniable traits of *Streptocephalus woottoni*. Demonstrating that such informed guesses (hypotheses) are sometimes correct, Hathaway and Simovich (1996) have now shown in lab experiments that *S. woottoni* hatches in 7-12 days if water temperatures are between 10-20°C, with some even appearing at 25°C. They also note that, depending on conditions, maturity of this relatively large fairy shrimp is attained in 48-56 days, and animals may remain as long as 120 days, although John Moeur (pers. comm.) has seen one population hang in there for 150 days. Such extended development and long tenure are certainly reasons for *S. woottoni* to reside in long-lived pools, some of which last into late spring when individuals may tolerate temperatures in excess of 25°C.

Just because these pools are described as "long-lived" does not mean they persist for extended periods each and every year. In fact, rainstorms in southern California are often highly problematic. If this animal hatched in a partially-filled basin, the water may disappear before *S. woottoni*'s long period of development is fulfilled, a situation that Simovich and Hathaway (1997) have observed up to 5 times in a year. It is not surprising then that many cysts do not respond to the first, second, or even third wetting. In fact, after three hydrations, a total of only 2.8% had hatched (range 0-13). This is the lowest reported hatching rate for any anostracan (Simovich & Hathaway 1997), but it certainly assures that cysts will remain for the blessed event of a filled pool.

The last of our observations is a colorful one. On a field trip to some deeper, near-coast pools, John Moeur dipped surface waters to show Clyde that here swam grayish male *S. woottoni*. By sweeping his net through the depths of the pool, John hauled in orange-red females. Denton and others believe the red is due to hemoglobin which better enables fertilized females to swim, undisturbed by amorous males, in areas of lower O_2, but this might not be the only scenario (you may wish to review again p. 29 in the section on "Color").

Please remember that if you contemplate MS or PhD research on this endangered animal, you will have to tackle some paper work for the USFWS; but don't fret, like the research itself, the chore is surmountable.

Fairy shrimps of warm-water pools which are moderate in dissolved solids, less predictable, and short-lived

Streptocephalus dorothae

(Map 5.3, p. 119)

Streptocephalus dorothae is the only one of the state's 23 species of Anostraca that has never been observed swimming in California pools. How do we know it's here? Well, Marie Simovich of the University of San Diego has a propensity for wandering around southern California and collecting dry soil from what appear to be pool basins. In the lab she subdivides each sample into containers which will be placed at several different temperatures, then follows that old directive "add water and stir". If cysts are present, they should hatch at appropriate temperatures. Hatchlings can then be raised to adulthood for identification. This approach does not require her to visit each and every pool during the limited time when adults are present.

Among Marie's dirt collections was a sample from Sunset Crossing in Banning. This scenic site, some 750 m in elevation, and along the route out of the L.A. Basin toward Palm Springs (or vise versa), lies at the crossing of the Southern Pacific Railroad tracks by Sunset Avenue. Here, in a rail-side ditch, *Streptocephalus dorothae* must swim in all its glory when runoff from rare summer thunderstorms fills its tub. Unless there was a mix-up in samples, we know it seeks asylum there, because back in the lab, sometime in 1992, out popped nauplii which grew to be adults of this animal when the soil was hydrated at 25°C.

Why did *Streptocephalus dorothae* settle down only in Banning? Where did it come from, and how did it get there? Good questions! No answers. However, thanks to Denton's work on the zoogeography of Arizona fairy shrimps (Belk 1977a), we may have a clue. *Streptocephalus dorothae* is reasonably widespread in Arizona, and the Southern Pacific Railroad connects Banning with the southwest of Arizona via Yuma. If it didn't get here via the suspected bird route, perhaps it rode the rails, or was smuggled in on the underbelly of some off-road vehicle. Perhaps. Maybe. No one knows. But such speculation may not be as wild as you might think. Maeda-Martinez *et al.* (1992) reported on another highly disjunct population of *S. dorothae*, the first record of this species in Mexico. It was found in a man-made roadside pool near La Paz at the southern tip of Baja California. The authors note that this too may be an example of "a recent man-assisted immigrant".

In an article that included some facts about the biology of *S. dorothae*, Denton (Belk 1977a) determined that hatching happens from 15-35°C, with 20° being about the best temperature and 35° not being very good at all. This information of course corroborates Marie's success at 25°C noted above. In addition, it supports the fact that *S. dorothae* is a summer species, a status also confirmed by its one-hour LD/50 of 40°C. Worthy of note is that such indulgence in high temperatures places this animal within one degree of the most heat-tolerant of Arizona Anostraca. Maeda-Martinez *et al.* (1992) supplemented Denton's information with the laboratory-derived observations that hatching begins to yield nauplii 24 hours after cysts are covered with water of 20-23°C, and continues for 48 hours. After 9 days, both sexes reach maturity at a length of about 8.5-

13.0 mm.

Man-made stock tanks or road-side ditches were the sites of 22 of Denton's 27 Arizona collections. Therefore, since this species apparently got as far as Banning, Sunset Crossing seems like appropriate harborage to us. How long water must remain in order for *S. dorothae* to complete its life cycle at summer temperatures is unknown, but, living as it does in unpredictable habitats, when it reproduces it does so with gusto. To illustrate, Denton patiently counted 846 cysts in the ovisac of a 20.5 cm-long female. Given such numbers it is no wonder that they are the smallest cysts (0.22 mm) of the Arizona fairy shrimps (Belk 1977a). Hill and Shepard's work (1997) demonstrates that, at 0.19 mm, they are among the smallest in California as well. The fact that so many cysts are generated, and that they seem to have a low hatching success at any one wetting (about 25%; Belk 1977a), bodes well for the survival of *Streptocephalus dorothae* in summer pools which at times may not last long enough for larvae to enjoy the fruits of growing to maturity.

Streptocephalus texanus

(Map 5.3, p. 119)

Collection records aren't much more numerous for *Streptocephalus texanus* than for our previous gem, but at least adults were encountered in the wild, though only at four locations in the extreme southeastern portion of California. The case of *S. texanus* is also a bit different because none of its populations made it very far into our state. One of its residences is in Imperial County, along the same Southern Pacific Railroad route that *S. dorothae* may have used and only 54 km from the Arizona border. The other three lie 2-38 km from the border in Imperial and Riverside counties. All sites are within 85 km of each other.

Being in the Colorado Desert, these locations are low in elevation (100-400 m) and particularly hot in summer when most of the year's meager rain descends on this parched land. In accord with such atmospheric timing, and the fact that *S. texanus* hatches at 15° and above but less than 32°C (Prophet 1963a; Horne 1967), we find it no surprise that the populations were discovered in June and early October. The waters were of course seasonally astatic, and included two granitic tanks, a pool in a dry stream channel (Eng *et al.* 1990), and what we suspect is a ditch along the railroad given its undescribed habitat 1.6 km south of Glamis. The only other shard of information concerning the California habitat of *S. texanus* is that the two tanks were turned green by algae.

Our knowledge of the biology of this streptocephalid comes from populations in other portions of its distribution, which extends eastward through Arizona (where it is also uncommon) and into the Great Plains (where it is common), then northward to Wyoming and Montana. *S. texanus* has been collected in water ranging from 13-37°C. It will tolerate the latter temperature for awhile, but will not survive at 10°C for more than 5 days (Prophet 1963c). The chemistry of the soup in which it swims seems to depend upon the state in which it resides. For example, in Kansas, Prophet (1963c) reported a range of pH from 4.7-9.5 (extremes which seem questionable), and alkalinities of 10-270 ppm (mean of 96 ppm; borderline low alkalinity). TDS (calculated from conductivity) averaged 177 ppm, or what we classify as low dissolved solids. By contrast, Horne (1967), working in southeastern Wyoming, recorded pH values of 7.5-8.5, alkalinities of 60-542 ppm, and TDS (from conductivity) of 73-16,455 ppm, the latter rising from 9,500 ppm over a three-day period because of evaporation. That's a lot of TDS! We suspect California habitats are moderate both in alkalinity and TDS. Our reasoning follows from the fact that summer rain is often of the cloudburst type, and, in this vegetation-sparse land, the rush of water will flush the tanks and washes, leaving behind pools of relatively fresh water. The other reason is that *Thamnocephalus platyurus*, a common co-inhabitant with streptocephalids elsewhere, and a resident of moderately alkaline water, was taken with *S. texanus* in two of its California locations.

If there are heat-loving adventurers amongst our readers who routinely follow reports of Colorado Desert weather, they might head for the hills and washes 11 days after a good downpour, for that is the time *Streptocephalus texanus* requires to hatch as a nauplius and grow to sexual maturity...at least in a laboratory at 20°C (Prophet 1963b). Let us know what you find, and supply a habitat description and water sample if possible.

Prophet's interest in the procreative details of anostracans that fight for space with Kansas wheat, led to the only information available concerning the reproductive potential of *S. texanus*. When a female first becomes mature, her initial clutch contains fewer than 25 cysts. Over a reproductive period of 11-27 days, females assemble 3-5 clutches with 3-654 cysts per clutch, resulting in the production of an average of 650 cysts, with the record being 1,635. That's a lot of cysts for an animal which hangs around for only 3-4 weeks, but perhaps not surprising inasmuch as the average cyst is only 0.21 mm in diameter (Hill & Shepard in press).

Thamnocephalus platyurus

(Map 5.11, p. 127)

The scientific handle for this animal means "shrub-headed flat-tail". The first part of the generic name comes from the highly divided frontal appendage on the male's head (Fig. 7.3, p.142), and the latter from the fusion of its cercopods with the telson to form a paddle-like posterior end (Fig. 7.1, p.140), both traits peculiar to this creature. In California, *Thamnocephalus platyurus* dwells in playas, a roadside ditch, a borrow pit, a tank, and several unspecified man-made places (Eng *et al.* 1990; Simovich & Fugate 1992) perhaps including stock ponds and road-side ditches which accounted for 90% of its residences in Arizona (Belk 1977a). Given its ability to live in non-natural pools, innumerable of which have been constructed throughout its distribution from Wyoming to Missouri to central Mexico, humans have obviously been responsible for a significant increase in the populations of *T. platyurus* (Belk 1977a).

The basins that house *Thamnocephalus platyurus* are located in the Mojave and Colorado Deserts at elevations of 1,235 m down to 65 m below sea level. These sites may fill in winter as well as summer and early fall. But because cysts will not hatch at water temperatures below about 17°, or at 32°C or above (Prophet 1963b; Belk 1977a), our "shrub-headed flat-tail" fairy shrimp is restricted to seasonally astatic pools, normally formed from mid-May to Mid-October, in Imperial, Riverside, San Bernardino, and San Diego counties. In these places it has been found twice with *Streptocephalus texanus*. It may occur with *Branchinecta mackini* also, since the cysts of both species have been removed together from several playas. Cysts of *T. platyurus* and *B. lindahli* are also present in the soil of one playa, but because they hatch at different temperatures, these two creatures would not swim together.

Except for a tank formed in a granitic outcrop and whose water clarity was reduced by algae, the habitats of *Thamnocephalus platyurus* are typically clay-bottomed and highly turbid. We also know from a California Academy of Sciences collection label that on September 12, 1955, 28°C and a pH of 7.5 were recorded as individuals of this species were snatched from the muddy waters of Bicycle Dry Lake on the Fort Irwin Military Reservation in San Bernardino County. Leaping forward a decade in time, Bob Brown scooped *T.*

platyurus from a 20x30-m borrow pit which he described as "not alkaline", along I-10, 40 km west of Blythe in Riverside County. This Arizona State University graduate student's observation was entirely feasible, for we note from information collected outside of California that *T. platyurus* is a species of low to moderate alkalinity (mean about 165 ppm) and TDS (mean of 320 ppm, from conductivity) (Horne 1967; Prophet 1963c; Belk unpubl.).

Hillyard and Vinegar (1972) collected adults from pools in Arizona and New Mexico whose temperatures reached 36.5°C and sometimes hovered near 35°C for much of the afternoon. From work in the laboratory, they noted that the animal tolerates temperatures as high as 38-40°C for at least an hour or two, but they died within 20 minutes at 44°C. Belk (1977a) determined a one-hour LD/50 of 41°C, and, at the other extreme of its temperature range, Prophet (1963a) observed that none survived 5 days at 10°C. The total of these facts shows that *T. platyurus* not only "loves" warm water but tolerates the highest temperatures of any North American anostracan. They appear to deal with about the widest pH range as well (4.7-9.2; Belk 1977b; Horne 1967; Prophet 1963c) if all data are to be believed.

The typical cyst is 0.27-0.30 mm in diameter (Hill & Shepard in press; Belk 1977a). This size, Denton says, is large for rainpool species, but because females of *T. platyurus* are more massive, and possess more spacious ovisacs than other anostracans on a length-for-length basis, they are able to carry as many big cysts as they do. For example, the ovisac of a 22.1-mm female contained 633. Of the other species studied which had individuals approximating this length, only females of *S. dorothae* carried more cysts (846); but remember, hers are perhaps the smallest amongst fairy shrimps. In any event, once expelled and dried, cysts begin to yield nauplii as early as 6 hours after wetting (Prophet 1963a) if temperatures are between 15-35°C, but they certainly hatch best from 20-25°C (Belk 1977a). How long it takes to reach maturity, and what the potential fecundity might be, are unknown, as are so many facets of this animal's life. In fact, this creature is so wonderfully strange in structure, and so tolerant of desert temperatures, it might well serve as a model for a number of biological questions worth asking about desert species. So, who will ask, then seek to solve them?

Fairy shrimps of cool- to warm-water pools which are great to impressive in dissolved solids, predictable, and temporary or permanent

Branchinecta campestris

(Map 5.12, p. 128; Fig. 5.1, p. 74)

Branchinecta campestris has been stumbled upon only once in California, the location being Soda Lake, 593 m in elevation, on the Carrizo Plain of San Luis Obispo County. The discoverer, biologist Larry Serpa of The Nature Conservancy, only said of his encounter that he ventured 6 m from shore (Belk & Serpa 1992). We use the word stumbled because of Clyde's close up and personal experience with Soda Lake's shore several years earlier. Under the supposed guidance of Robert Brown (who was without hip boots that day), Clyde waded out onto what had the appearance of an ice-covered bottom. You're right, it couldn't have been, and wasn't, ice. Rather, it was a thick crust of precipitated salts, and, in spite of his big feet, the crust didn't long support Clyde's 190 pounds. As he crunched through the salt and into the soft black ooze below, the stumbling began. In trying to pull one foot out, he pushed the other further into the quick-sand-like muck. When thigh-deep, his stumbling and progress decreased as panic increased. Yet somehow, "for the sake of science", and with "friend" Bob laughing in the background, he swept the water within arm's length for anostracans. The story's end was not Clyde's end, as you can tell by the prose in this book, but although the lake finally released him, it offered no anostracans as solace for its cruel joke.

In addition to *Branchinecta campestris*, Larry collected many brine shrimps in this very salty sump on April 20, 1991. Clyde's inability to sieve *Artemia* from the water was probably explained by the January date of his encounter, a time too early in the season for *Artemia*'s hatch to have yet occurred, but why *B. campestris* did not appear in his net goes unexplained.

Most of what is known about *Branchinecta campestris* and its abodes comes from research by Edmund Broch (1969) of Washington State University, and from a few tidbits of information supplied by James Lynch of the University of Washington (and *B. lynchi* fame) in his description of the species (Lynch 1960). From these sources we note, in the arid lands east of Washington's Cascades, *B. campestris* occurs in either seasonally or perennially astatic alkaline-saline waters at elevations from 335-730 m. This real estate lays claim to 9.5-10.0 pH readings, and possesses minimal turbidity because of high TDS (about 1,000-21,000 ppm). Around 95% of the major ions present are Na^+, Mg^{++}, and $SO4^=$ (Anderson 1958; Broch 1969). Recognizing that magnesium sulfate is what we call Epsom salts, the anostracans that spend their lives in this cathartic elixir must be very relaxed indeed! We wonder if they are equally serene in two Nebraska pools where Mg^{++} went unevaluated but HCO_3^- and $CO_3^=$ predominated at the expense of $SO_4^=$ (McCarraher 1970). We also wonder what the ionic proportions of these substances are in Soda Lake.

In Washington, Broch noted that a seasonally astatic habitat called Penley Lake alternated between standing water and frozen slush and ice throughout February. It wasn't until March 2, in 4°C water with a TDS of 1,080 ppm (from mOsm/L), that metanauplii of *B. campestris* appeared in large numbers. Broch (1969) intimates that water with a low TDS and a low temperature constitutes the hatching stimulus for its relatively large cysts (0.30-0.35 mm in diameter, Lynch 1960; 0.26 mm, Hill & Shepard in press). Broch also writes that individuals were mature about a month after hatching; the smallest female, 12 mm long, carried two cysts in her ovisac. By April 6, and at 10°C and about 15,000 ppm TDS, nauplii of *A. franciscana* made their debut. The population of *B. campestris* decreased in size during the three weeks of coexistence of the two species. By the time they disappeared (April 27), TDS equaled about 18,900 ppm and the temperature had reached 19°C. These data certainly parallel those of Lynch, who made all his Washington collections between late March and mid-June at water temperatures from 9-20°C. He did come across a Wyoming population on August 5, but this later date may be explained by its much higher locale (2,057 m) near Rawlins.

Broch concluded that the two species are able to divide common habitat on a seasonal basis because *B. campestris* is restricted to the cooler, lower-salinity phase, while *Artemia* carries on in warmer water and higher salt concentrations. Note that the upper limit of the "lower-salinity phase" in Brock's study is higher in dissolved solids than the typical habitat of any anostracan other than *Artemia*.

Also keep the foregoing facts in mind as you ponder what the yearly life cycle of *Branchinecta campestris* might be in central California. Regarding hatching temperatures, Clyde's experience does not help, for in his haste to extract his body from the mud of Soda Lake, measuring anything was far from his mind. He can say with assuredness though that the water was not icy cold. However, winter or spring rains and their runoff probably create a surface layer of dilute cool water that may activate the hatching process when it floods cysts lying in the desiccated shore of this seasonally astatic lake. Whatever the hatching clue might be, all we really know is that when collected on April 20 both anostracan species were mature, water in Soda Lake was 20°C, and both species swam together in a bucket of the brew for several days thereafter (Belk & Serpa 1992).

In his desire to show what it was about the physiology of *B. campestris* and *A. franciscana* that allowed them to divide a pool's tenure between them, Brock (1969) compared the total salt concentration of blood of *B. campestris* with that of their pool environment a number of times over the season. By so doing, he determined that individuals regulate hyperosmotically at lower concentrations of environmental TDS up to about 9,600 ppm (from mOsm/L). As their medium becomes further concentrated, the level of salts in their blood conforms to that of the environment. They tolerate this up to 21,000-25,500 ppm (from mOsm/L). Brock determined these latter figures in the laboratory by noting the concentrations at which all experimental animals died within 24 hours. That the level actually tolerated might be somewhat lower is suggested by the fact that he collected no individuals in concentrations greater than about 18,900 ppm TDS. Still, what is ecologically important here is that *B. campestris* can live in waters of greater TDS than any North American anostracan other than *Artemia franciscana* and *A. monica*. You will remember that the ability of *Artemia* to regulate its blood hypoosmotically allows it the freedom of swimming unmolested (by invertebrates) in extraordinarily concentrated brines.

Most of the time *B. campestris* swims alone, but not uncommonly it occurs with *Artemia franciscana*, as in Soda Lake. Given their preference for alkaline water, no one should be surprised that *Branchinecta mackini* and *B. lindahli* have also been recorded in the same pool at the same time as *B. campestris*.

Artemia franciscana

(Map 5.12, p. 128)

Most kids who read comic books, or anyone interested in the aquatic creatures sold in pet shops, know of "sea monkeys". Buy a packet of "eggs" (cysts), add a pinch of these to some salty chloride-laden water (sea water does just fine), and presto, instant life! "Instant" means be patient for a day or two, at which time tiny nauplius larvae of the brine shrimp *Artemia franciscana* will appear, swimming jerkily, before your very eyes. As they mature, and males begin to chase females, you will see them looping through the water, perhaps suggesting a monkey swinging from tree branches, and thus, we suppose, their name.

Throughout this book you have seen us refer to anostracan species with both their generic and specific names – with an exception, and that is *Artemia*. For this beast, sometimes only the generic name is used. Until "recently" much of the literature referred to these creatures as *Artemia salina*, or frequently merely as *Artemia*. The reason is simple; the explanation could be long and involved. Suffice it to say that *Artemia* dwells in a great array of highly concentrated chemical habitats almost always high in Cl^- (Cole & Brown 1967), and a host of physiological differences has developed among populations to deal with these and other environmental exigencies (e.g., Bowen *et al.* 1988). However, little anatomical variation has appeared even among those that are now accepted as distinct species. So, for example, it is all but impossible to distinguish structurally between the two California species *A. franciscana* and *A. monica*. In order to make distinctions between populations, one must inquire into the sexual compatibility of their members (do they mate and produce fertile offspring?), sexual preferences (do they reproduce without males, by producing cysts, or by giving life birth?), genetic similarity (or lack of same), and their tolerance of brines of different chemical compositions. Obviously none of these chores is accomplished in a few minutes under optical magnification, nor by those unschooled in such matters – like your authors!

Artemia, then, is a complex of species, incipient species, physiological races, call them what you will. Some of the intricate matters concerning population differences have been worked out by the likes of Sarane Bowen, a professor at CSU San Francisco and world-expert on the subject. But what species or population was utilized in many of the works published over the years is conjectural by her and other experts, and unknown to the rest of us. Now you know "the rest of the story".

Thanks to Sarane and her coworkers (e.g., Bowen *et al.* 1985) we are reasonably sure that California populations of *Artemia*, except the one living in Mono Lake, are *Artemia franciscana*. This species was originally described from specimens collected in a saltern (salt-evaporating pond) near Redwood City on the shores of San Francisco Bay. There are various salterns around the Bay, and *A. franciscana* occurs in all. Its presence has also been noted at Monterey and San Diego bays' saltworks. Whether these populations are natural, or were introduced to benefit the process of evaporation in salt extraction (see p. 8 in the section on "What good are fairy shrimps?"), is not known. Because *Artemia* is restricted to highly saline waters, its distribution in inland California is spotty, limited to approximately the central third of the state, and from near sea level to 1,495 m. In the Mojave Desert, most playa lakes are high in alkali minerals but low in chloride and are thus unsuitable for *Artemia*. However, in a few playas with elevated chloride, there resides *A. franciscana*. Populations are known from Koehn Dry Lake in Kern County, and from South Panamint Dry Lake, Owens Lake, and Deep Springs Lake in Inyo County. In the arid southern half of the Central Valley, our saline friend has shown up in Contra Costa County, near Livermore in Alameda County, on the Kesterson NWR in Merced County, and close to Lemoore (Kings County), the latter site appearing to be excavated to collect saline run-off. In the Central Coast Mountains Region, at its interface with the southern Central Valley, *Artemia franciscana* swims in Soda Lake, in a number of pools in run-off channels that empty into the lake, and in several sag ponds along the San Andreas Fault about 30 km to the southeast in San Luis Obispo County and just over the border in Kern County.

All sites just mentioned are seasonally or perennially astatic hypersaline playas, lakes, and pools, or human-constructed sumps or salterns. Natural habitats among these fill with winter and spring rains; the sumps and salterns are undoubtedly flooded by rain, or whenever economic reality dictates. Although the animals' briny bath may be full, cysts do not hatch until temperature reaches 9-10°C (Broch 1969; Relyea 1937); the optimal range is 15-30°C (Bowen *et al.* 1984). This means that in some of the smaller bodies of water which heat up hurriedly, *Artemia* has been collected as early as mid-January; in larger basins, and at higher elevations, its presence is delayed. Collections from these larger sites have been so spotty that we do not know when individuals first appeared and when they disappeared, but animals have been taken as late as the end of July. No problem; just because summer means high temperatures doesn't mean *A. franciscana* can't "hack it", for this hardy animal is known to tolerate at least 37°C (Galen 1969). Because evaporation at this number of degrees is great, so may be the salinity of what began as already high-TDS water, but no problem here either for this anostracan can even handle saturated brines.

In California, this amazing creature has been removed from natural brines of about 1.0-4.9 times the concentration of sea water, namely 34,914-172,000 ppm of dissolved material (Eng *et al.* 1990), the latter being enough to make all multicellular life, except *Artemia* and the brine fly, gag! In coastal salterns the milieu is, of course, some concentration of sea water and, therefore, high in Na^+ and Cl^- and low in alkalinity (HCO_3^- and $CO_3^=$). Little information is available concerning the chemical makeup of its inland California habitats, although from what is known Cl^- dominates (6,420-34,000 ppm), and alkalinity is a minor player (74-1,307 ppm. pH ranges from 7.4-9.1 (Eng *et al.* 1990). We remind you that at TDS levels much above 3,000 ppm, clay particles precipitate to yield clear, though possibly tea-colored, water, a description applicable to California's habitats harboring *Artemia franciscana*.

How adults of *Artemia* deal with such wide osmotic and ionic variations, and extreme levels of salt, is a story told in the classic papers by Croghan (1958a,b,c,d,e; see p. 18 in section on "Water, salts, and liquid wastes: their regulation"). Obviously, nauplii face challenges similar to those of adults, and thus have the same physiological abilities (Russler & Mangos 1978; Conte 1984). Suffice it to say here that all life stages of *Artemia* are hyperosmotic regulators at lower environmental salt concentrations, an ability which allows them to acclimate slowly to solutions with TDS of only 8% that of sea water (2,600 ppm; Croghan 1958b) even though they do not reproduce in them. Then, with greater capability than any other multicellular species except perhaps the brine fly, individuals can hypoosmotically regulate their body fluids so ably that they can dwell in unbelievably concentrated brines – perhaps as high as 330,000 ppm (almost 9.5 times the concentration of sea water; Bowen *et al.* 1984), a figure twice that in our field data, but one which must commonly occur in the final aquatic stages of salterns.

Artemia presents special difficulties in describing or interpreting its biology. Because its populations live in, and have become adapted to, a variety of conditions which are so wide and extreme, it behooves us to know not only from which population the studied batch of organisms comes, but what their environmental background has been. Seldom is much of this known, although if they are raised from cysts in the lab, a simple and common practice, at least conditions under which they grow up can be prescribed and described. In any event, consider the comments that follow to be generalizations, because they are accumulated from laboratory and field, and from a mix of populations often facing quite different environmental realities.

We have mentioned that cysts begin to hatch around 10°C. But we have not mentioned that those cysts are the smallest produced by California anostracans, averaging 17.9 mm (minimum 12.1, maximum 22.6 mm; Hill & Shepard in press). At around 15°, three days of wetting are necessary before nauplii appear. At the comfortable temperature of 20°C, nauplii emerge in two days, while they can be hurried from their cysts in one at 30°C (Galen 1969). Bowen *et al.* (1984) describe populations in San Francisco Bay salterns as hatching best at 15-30°C while those from Fallon, Nevada, hatch optimally between 10-20°C, a difference that makes ecological sense (described below), and illustrates the fact that the biology of this animal cannot be detailed with a few average measurements.

In a parallel Mediterranean situation, Browne (1993) noted that "*Artemia tunisiana* tolerates cold quite well and produces mainly cysts, so it is well adapted to conditions found in ephemeral inland lakes, which are usually filled with water during only the colder winter months ". Browne goes on to say that forms giving live birth and tolerating warm water are more suited to salterns which are maintained for much of the year. *Artemia franciscana*, hatched and reared in the laboratory from San Francisco cysts, apparently has a phyllopod in both camps. To oversimplify the complex work and sometimes seemingly contradictory findings of Berthélémy-Okazaki and Hedgecock (1987), at temperatures of 16-22°C and photoperiods of 12 hours or less of light, 68-99% of females produce cysts (the remainder give birth to live nauplii), but only 10% do so when days are long or light is continuous. Ah ha, photoperiod is very important, but its influence is lessened by higher temperatures, in which case 50% of females produce cysts irrespective of day length. To show you how complicated things can get, we'll add the following interesting information then move on to another subject. Under 9 hours of light (short photoperiod) and 19-23°C, an average of 67% of females produced live young in their first clutch. However, hidden within this figure is the fact that if they matured rapidly (15-18 days), more than 85% of females had live births, but less than 50% did so if maturation was delayed (20-27 days). In their second and successive clutches, only 15-35% released live young; the remaining percentages, of course, belonged to cyst producers. As you poke through these details, you will see they make sense ecologically. By initially generating a preponderance of live young, the population gets off to a fast start. But, as the season advances and the habitat shrinks, possibly soon to evaporate to oblivion, the situation demands that females get on with cyst production!

In their paper, Berthélémy-Okazaki and Hedgecock (1987) show in graph form that females mature in 15-32 days when temperatures approximate 20°C and the brine is 30,000 ppm. Weisz (1946) reported 32 days for the attainment of maturity at this temperature and salinity, but only 22 days at 115,000 ppm, suggesting that the time to attainment of *Artemia*'s sex life is inversely dependent on the salt concentration of the environment in which its lot is cast. But then along comes Gilchrist (1960) who claims that the extent to which growth is determined by salinity varies with sex, and we would add probably with the source of cysts as well.

Once mature, how big can *A. franciscana* become and just how long can it live? Relyea (1937) said that adult males from the Great Salt Lake grow to 8-10 mm in length, while females measure in at 10-12 mm; that's pretty small compared to most anostracans! Browne and Salle (1984) reported that the mean maximum life-span of two California populations was 92 days (13 weeks). What the "normal" average might be is undoubtedly lost in the "noise" of all the variation that exists.

Browne (1980) confided that an *Artemia* female produces a clutch every 4-6 days, and a total of 10-19 clutches (maximum of 25) over her life-span. Given that each clutch contains from 78-111 cysts (the record of 300 seems a terrible load for an animal of *Artemia*'s size), total fecundity per female could approximate 1,500-2,000 potential offspring. In places like the Great Salt Lake, there may be so many hemoglobin-laden *Artemia* crammed together that they turn the water red. In such a circumstance, if each female churned out even a portion of the above number of cysts that when extruded from the ovisac float on the high-density saline water (Bowen *et al.* 1984) and get blown to shore, it is no wonder that, during the early days of the *Artemia*-cyst industry, shovels were used to collect these little jewels from wind-rows at water's edge. By the way, related to this thought is a neat bit of trivia. Given there are about 330,000 cysts per gram (9.25 million per ounce; Hill 1995), can you imagine how many there are in a shovel full? In a ton? In the 2,200 tons now harvested annually (Williams 1995; see also p. 8 in "What good are fairy shrimps?")? That number must approach the national debt!

Anyhow, all good things must come to an end, and Relyea (1937) describes an end to the yearly reproductive escapades of Great Salt Lake adults when they die as temperatures drop below 6°C in the fall.

In California, *Artemia franciscana* has been seen in the same place and at the same time with only one other anostracan – and only once. Given its briny living standards, that fact is not surprising. The one species was *Branchinecta campestris*, and that one place was Soda Lake in San Luis Obispo County. The fact that these two phyllopodous philanderers have been netted together there only once is not particularly surprising either, because Soda Lake is apparently not oft collected. To review the elaborate details of their co-occurrence, refer to the section on *B. campestris* (pp. 109-111).

Artemia monica

(Map 5.12, p. 128)

Artemia monica is a California endemic found only in one place, Mono Lake in Mono County. That sounds pretty restrictive, and so it is, yet we have stated that *Linderiella santarosae* is the California-endemic anostracan most limited in distribution even though it is found in several pools. The difference, of course, lies in land area covered. Mono Lake, even though smaller than it was in the forties because of water diversion from its basin by the City of Los Angeles, is still some 25 times greater in surface area than the entire tract of pools in which *L. santarosae* dwells.

Certainly the contents of this oldest lake in North America (500,000 years; Lajoie 1968) began as fresh water, but with the continual addition of small amounts of salts carried to it in run-off, and the fact that over much of Mono Lake's life the only way water left was via evaporation, slowly, very slowly, its dissolved materials rose in concentration. Somewhere in time, after it became sufficiently saline, some cysts were introduced, most probably from a population of *Artemia franciscana.* As the water continued to concentrate, and the saline character of the lake became unique, so did the biology of its population of *Artemia* (Bowen *et al.* 1984, 1985).

About 50 m deep, Mono Lake contains such a large volume of water that fluctuations in its physical and chemical nature are minimized. Thus, the population that evolved into *Artemia monica* has not had to deal with the environmental extremes faced by other *Artemia* stocks. Yearly, water temperatures throughout the lake's depth range from 4-24°C (Lenz 1980). In the days when Mark Twain took a boat ride on its surface, TDS was probably around 50,000 ppm. When David Mason was doing the first intensive aquatic study of the lake in the mid-sixties, he found TDS of its clear waters to be 76,000 ppm, Cl^- was 17,500 ppm, and pH stood at 9.7 (Mason 1967). By 1988, TDS had risen to 93,600 ppm and Cl^- had reached 19,500 ppm (David Herbst pers. comm.). These figures are certainly not out of the ordinary for *Artemia* habitats. So what's the big deal? It turns out that the alkalinity recorded at Mono Lake is far and away greater than anything known from California (19,500 ppm in Mason's day, 36,700 ppm in 1988), or anywhere for that matter except Jesse Lake in those old sand hills of Nebraska.

One reason for the uniqueness of *Artemia monica*, then, is that it must live in brines which have a high ratio of alkalinity to chloride. Given this reality, the species cannot survive in the salt solutions that support *A. franciscana.* The reverse is also true, that is, *A. franciscana* dies when subjected to *A. monica*'s highly alkaline water. Obviously the physiologies of these two, as blueprinted by their genetics, have become quite different.

Even though the ionic composition of water in Mono Lake differs so considerably from the variations on the theme of those inhabited by *A. franciscana*, we doubt you will be surprised to read here that the Mono Lake brine shrimp, being an *Artemia*, can regulate its blood concentration hypo-osmotically over quite a range (at least from 50,000-146,000 ppm TDS). Below 50,000 ppm, males show signs of regulatory stress. From 146,000-189,000 ppm, still "a breeze" for *A. franciscana*, both sexes of *A. monica*, males particularly, exhibit signs of regulatory loss, verified by an increased number of deaths (Herbst & Dana 1980). Experiments aimed at studying hyperosmotic regulatory abilities of *Artemia monica* have not been undertaken. However, given the above comments that males show signs of regulatory stress below 50,000 ppm TDS, Mono Lake brine shrimps apparently do not possess this skill.

The cyst of *A. monica* falls within the same size range as that of *A. franciscana* (mean of 0.19 mm, Hill & Shepard in press). But that's about where the similarity ends. Unlike those of the latter, *A. monica*'s cysts sink when released from the ovisac, do not require a period of desiccation, but do need 1-3 months of cold-water incubation before hatching, in March, at an optimal temperature of 5°C (Bowen *et al.* 1984). Gravid females begin to appear in May which suggests that about two months are required to attain maturity during the low temperatures of spring. When reared at 20°C (which approximates summer surface temperatures), only 30-40 days are needed. Females produce live young throughout May, but switch to cyst production in June). The summer population is usually smaller than the spring one, but the actual size depends on food supply and salinity (Dana & Lenz 1986). Individuals have been seen plying Mono Lake's water throughout the year but their numbers are severely reduced in winter (Lenz 1980). Even though Mason (1963) measured shrimps from 7.9-11.1 mm in length (similar to *A. franciscana*), and clutch size has been determined to vary directly with animal length and inversely with salinity, from data at hand it appears that *A. monica* produces about half the number of offspring per clutch (in the range of 40-65) as does *A. franciscana* (Dana & Lenz 1986). No one has calculated *A. monica's* fecundity, however, we suspect that females have the potential to churn out clutches until their genetically allotted time runs out (about 65 days; Dana and Lenz 1986), since they live in a permanent habitat, or until they serve as a tasty treat in the diet of the myriad of breeding and migratory birds that spend time plying the salty surface of Mono Lake (Herbst & Dana 1980).

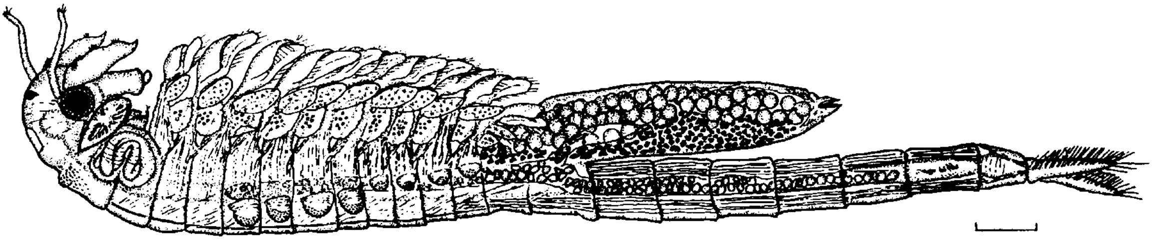
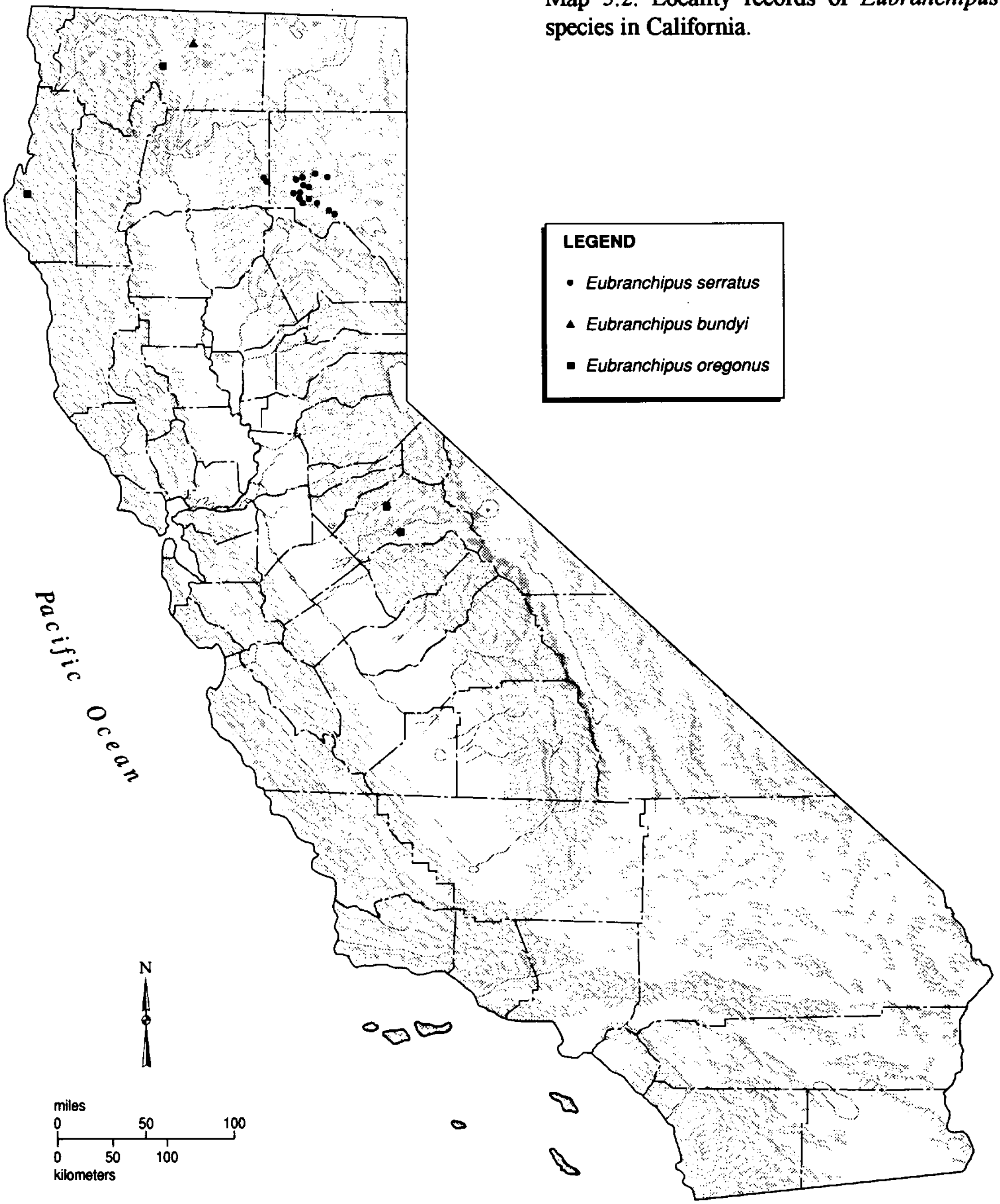


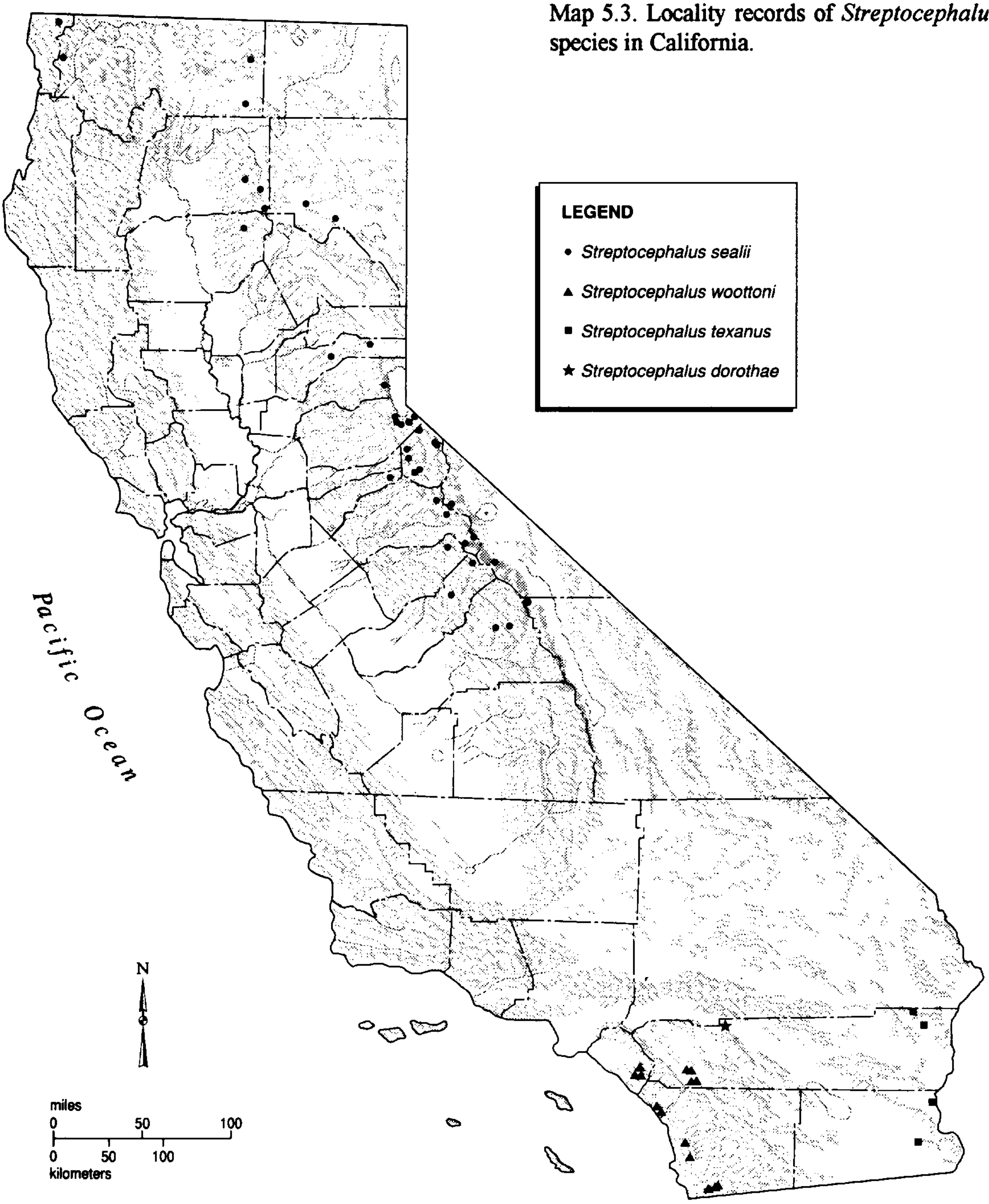
Fig. 5.3. Female of *Branchinecta lindahli* from Lynch (1964); reprinted courtesy of *The American Midland Naturalist* (scale = 1 mm).

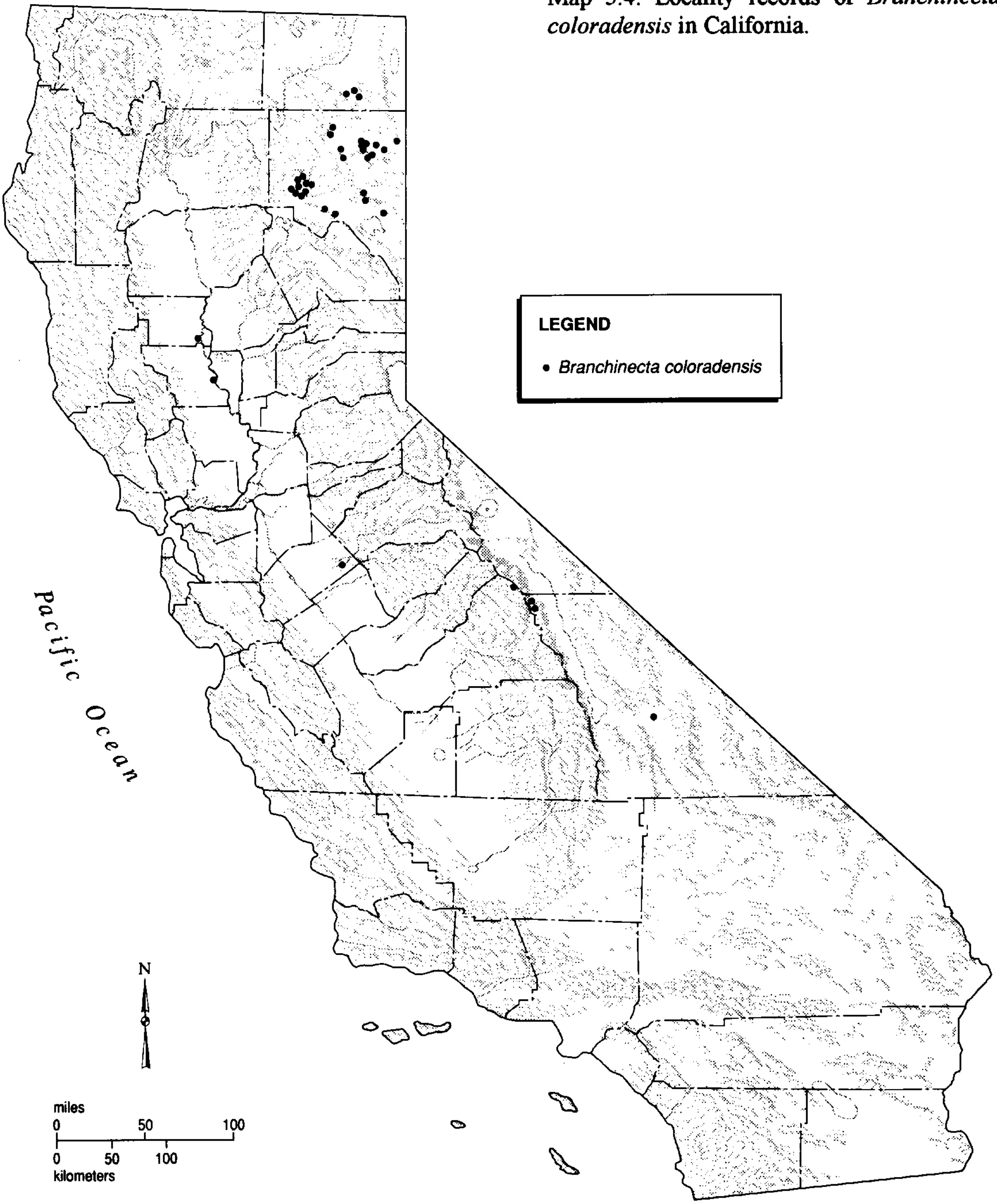
Map 5.1. Counties of California.

Map 5.2. Locality records of *Eubranchipus* species in California.



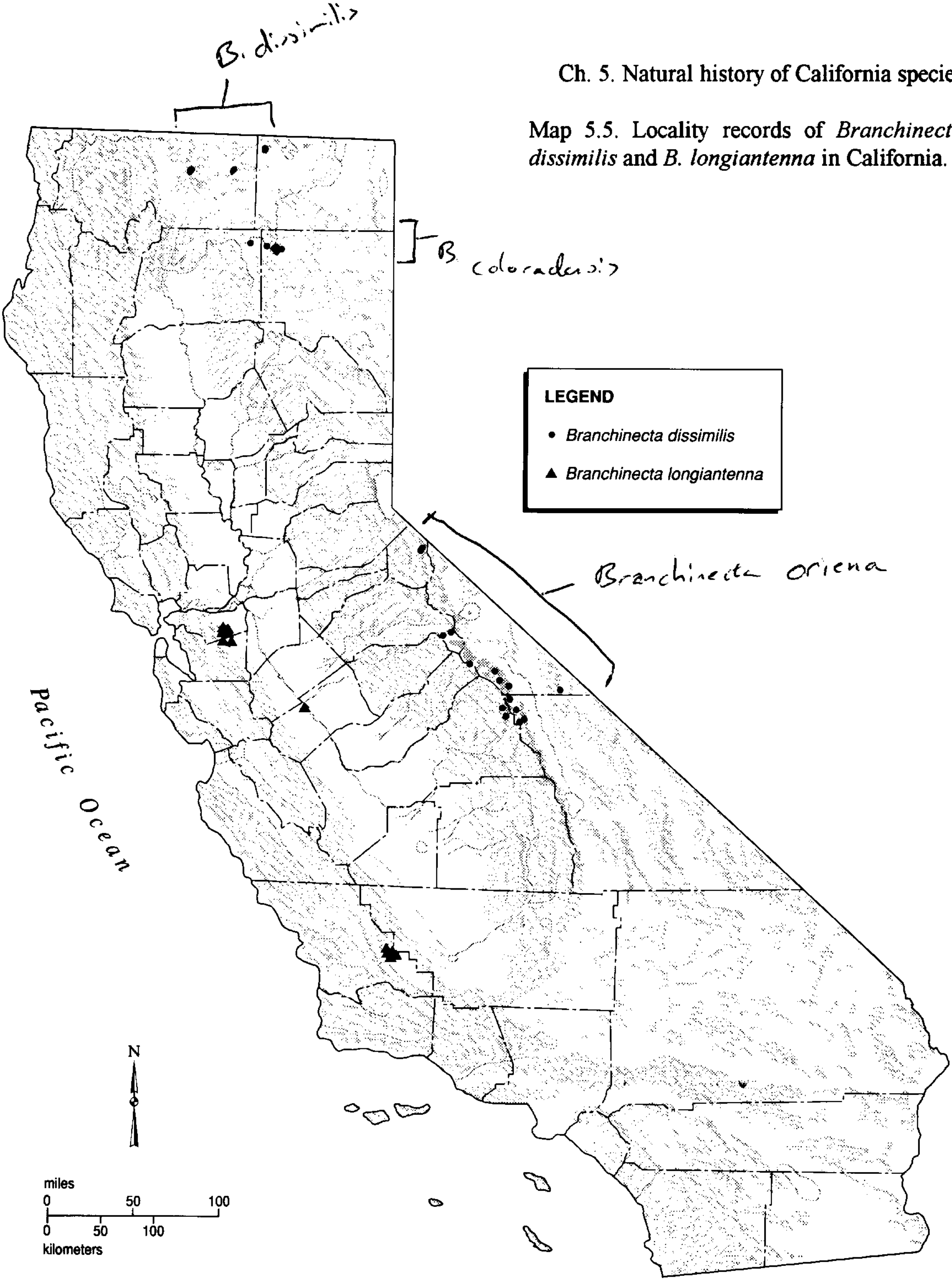
Map 5.3. Locality records of *Streptocephalus* species in California.

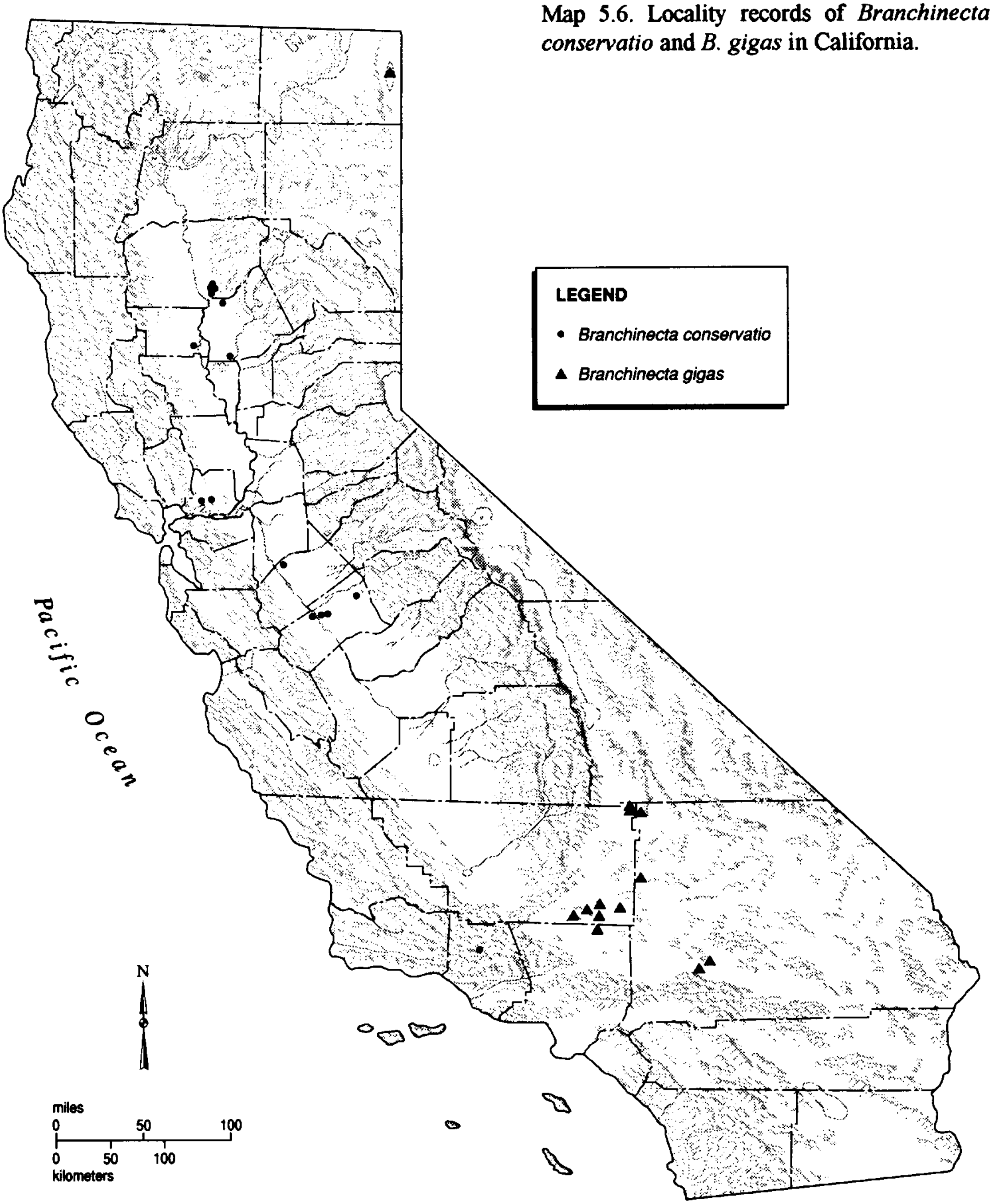




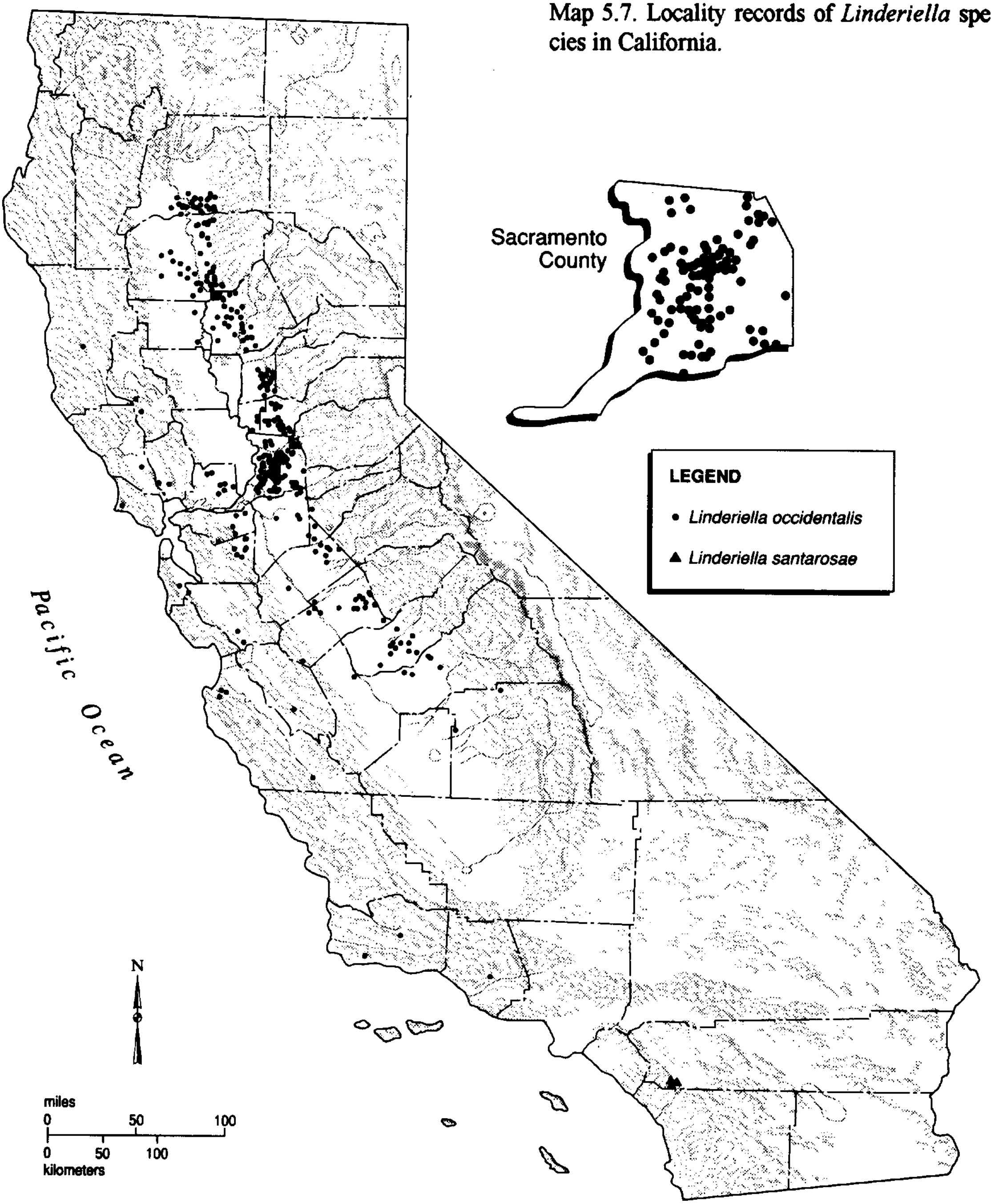
Map 5.4. Locality records of *Branchinecta coloradensis* in California.

Map 5.5. Locality records of *Branchinecta dissimilis* and *B. longiantenna* in California.

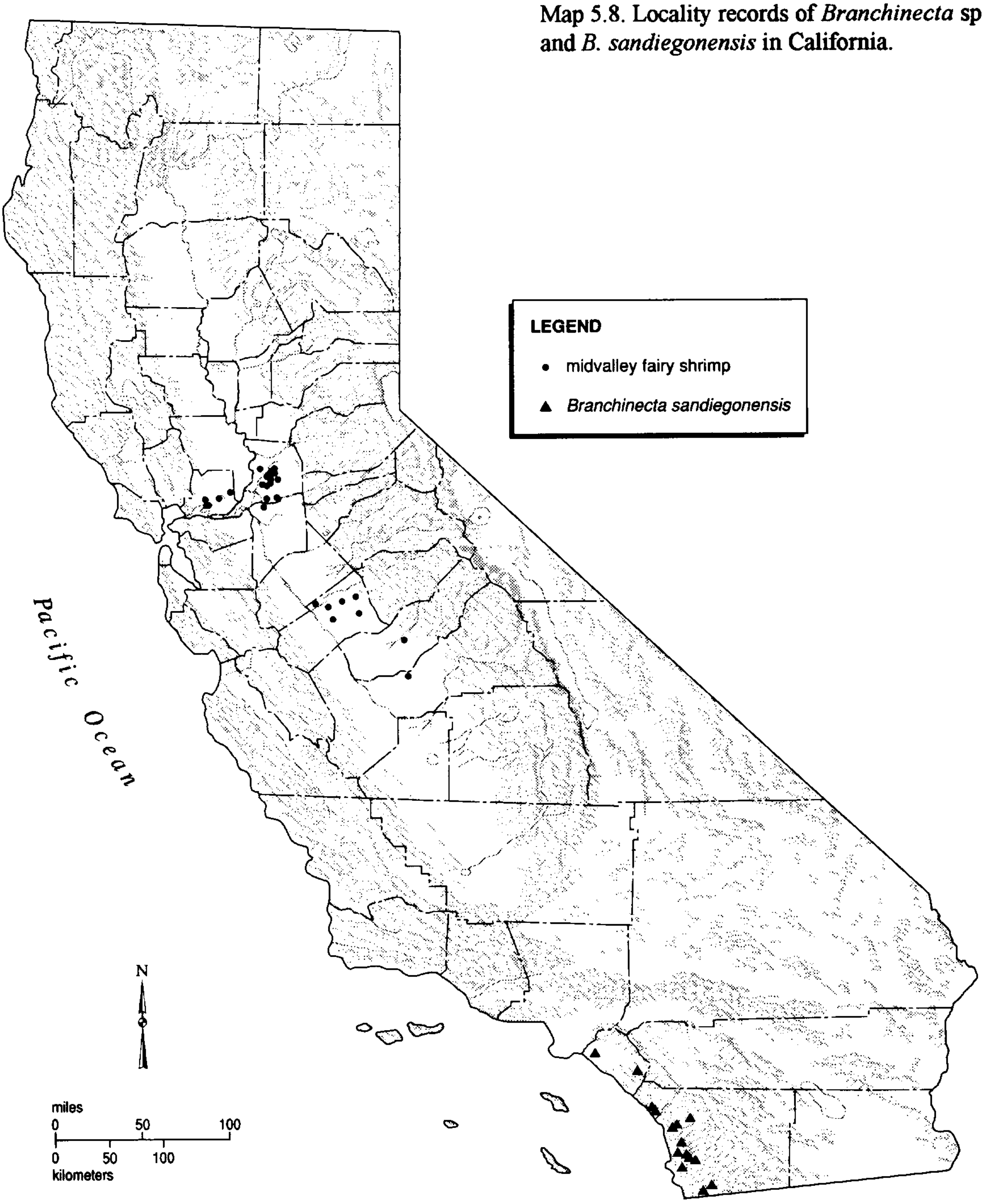




Map 5.6. Locality records of *Branchinecta conservatio* and *B. gigas* in California.

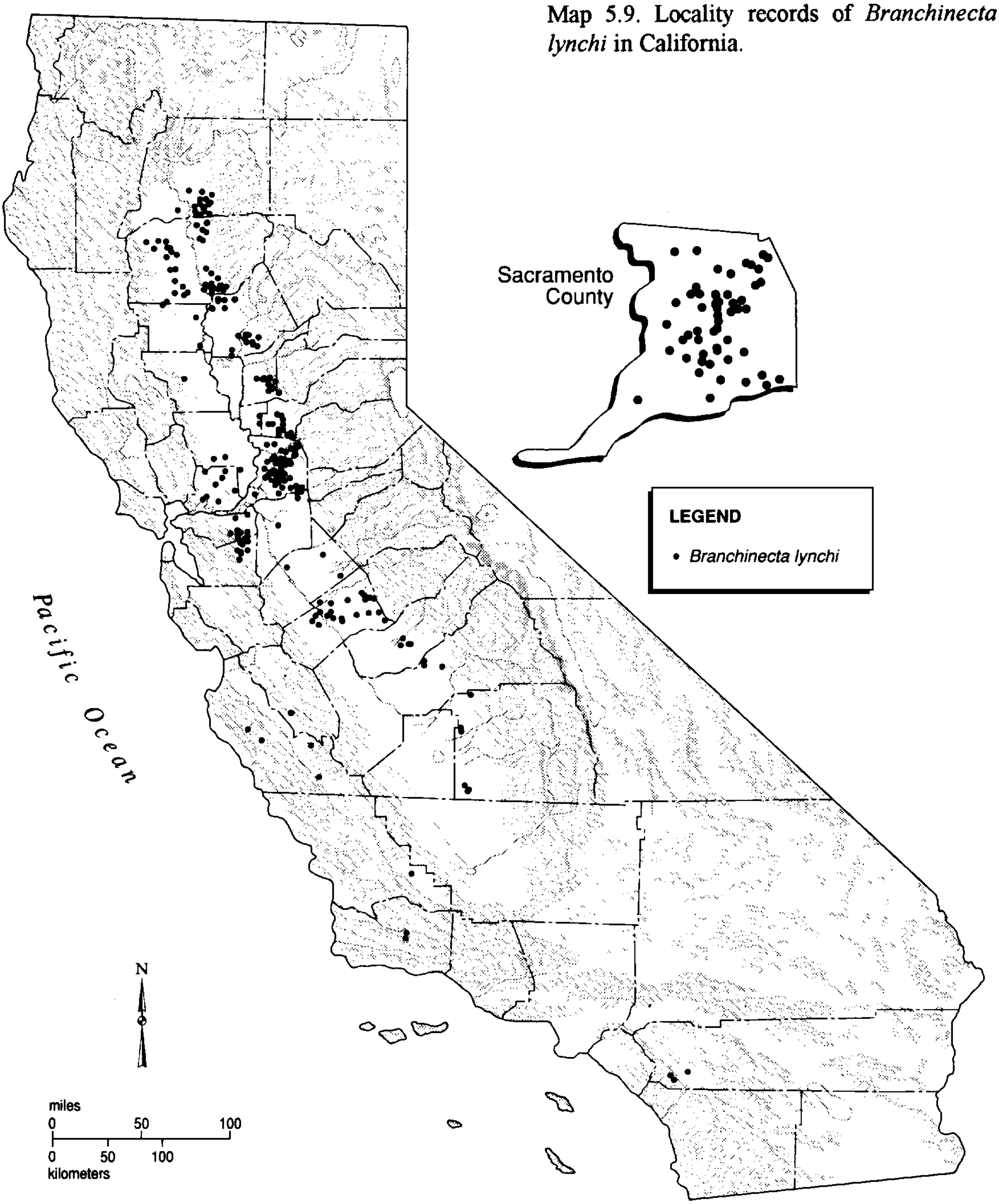


Map 5.7. Locality records of *Linderiella* species in California.

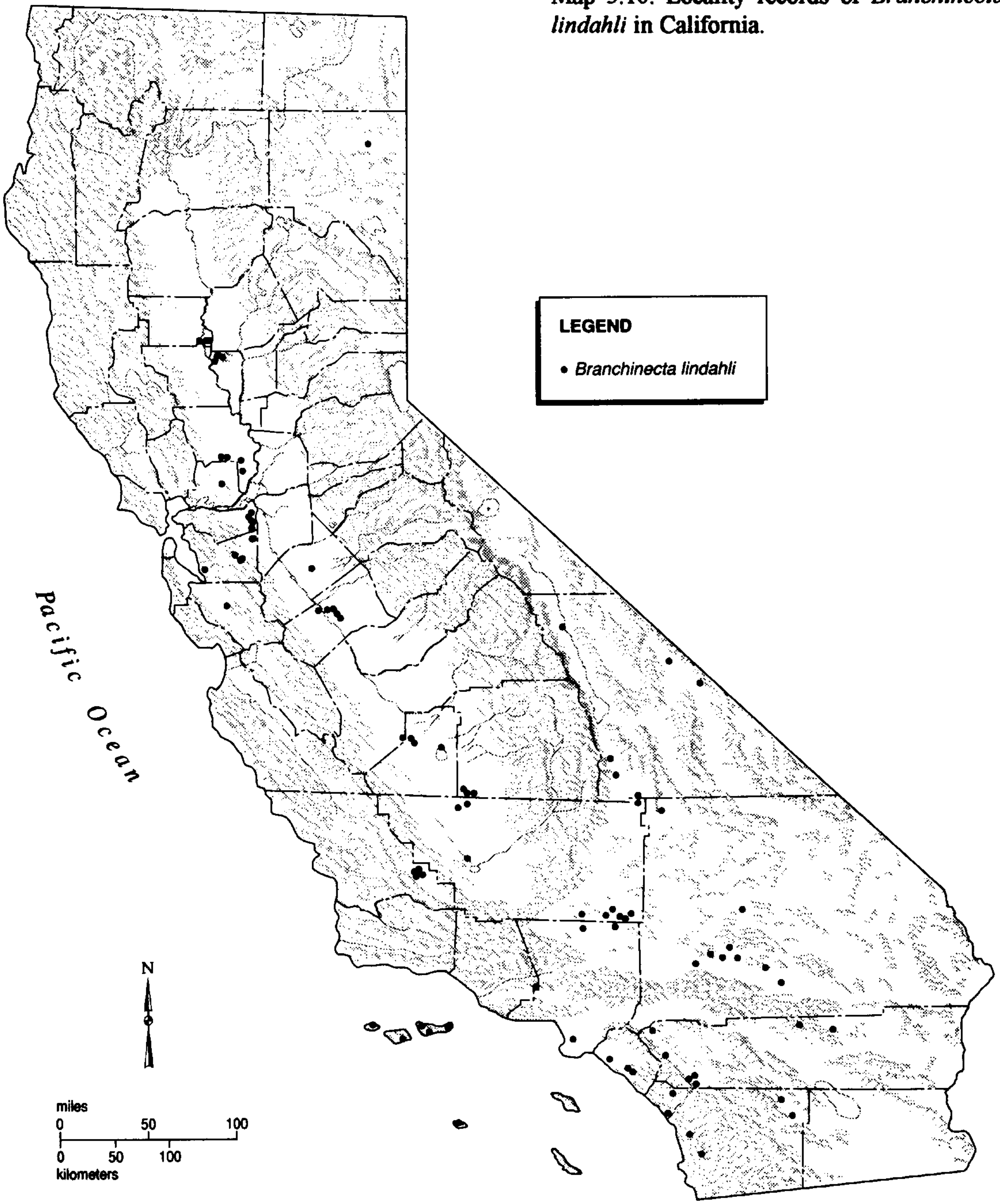


Map 5.8. Locality records of *Branchinecta* sp. and *B. sandiegonensis* in California.

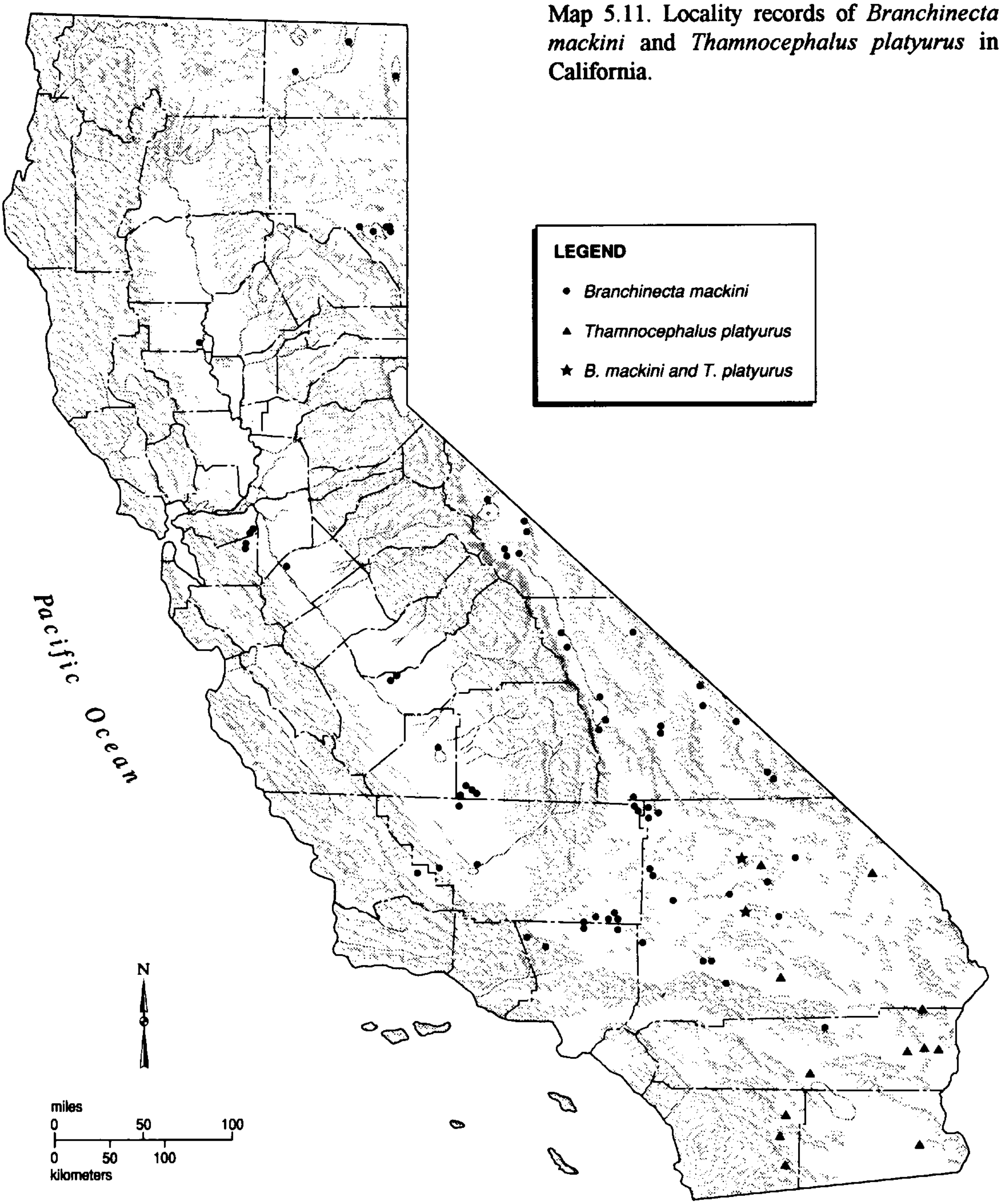
Map 5.9. Locality records of *Branchinecta lynchi* in California.



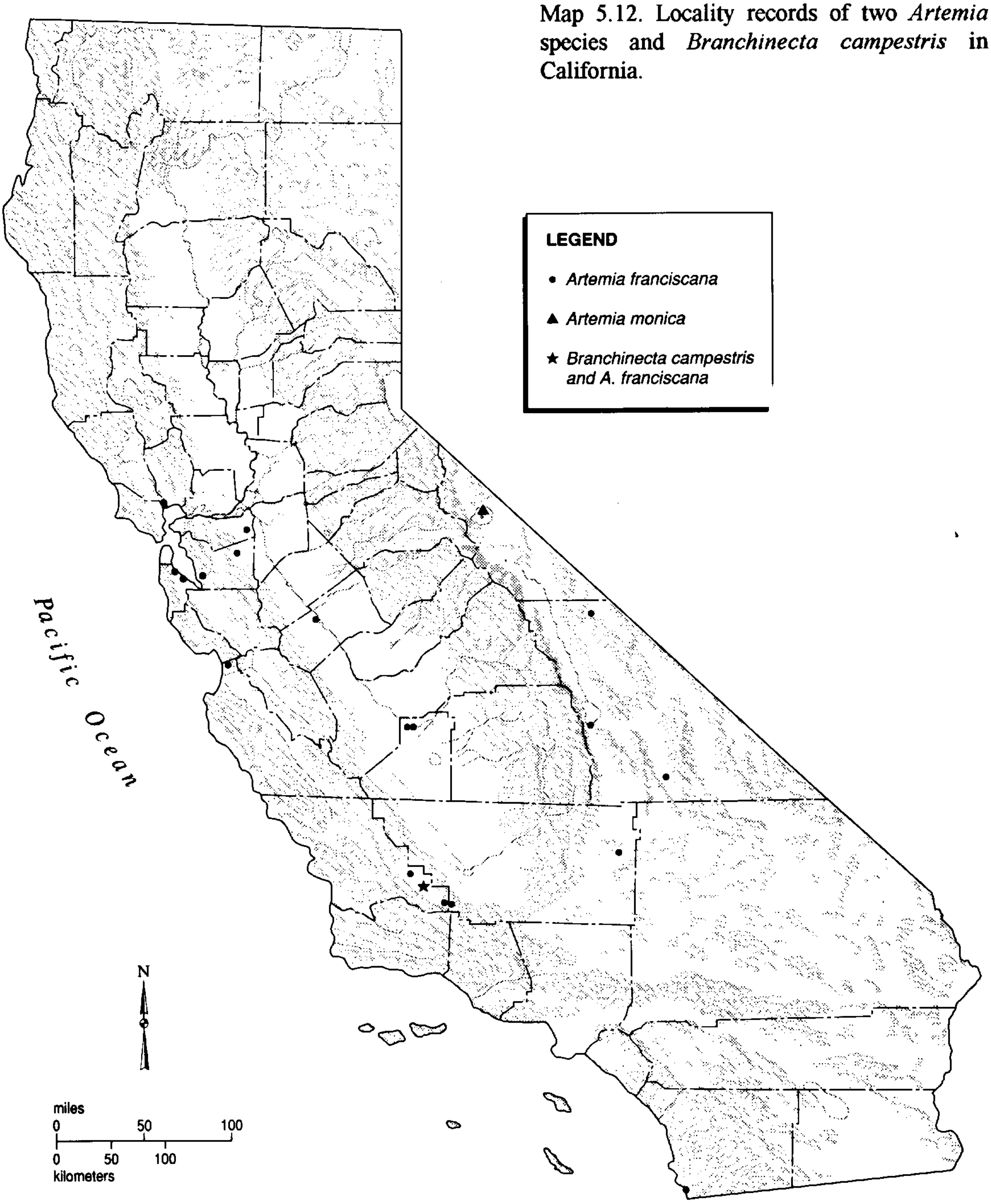
Map 5.10. Locality records of *Branchinecta lindahli* in California.



Map 5.11. Locality records of *Branchinecta mackini* and *Thamnocephalus platyurus* in California.



Map 5.12. Locality records of two *Artemia* species and *Branchinecta campestris* in California.



Chapter 6

STATUS, INCLUDING ENDANGERMENT, AND CONSERVATION

The degree of threat facing any particular fairy shrimp species is directly related to the extent of its range and desirability of its habitat for conversion to human uses that are destructive to seasonal wetlands. Widespread species which live in high mountain pools or periodically inundated basins in the most inhospitable reaches of desert landscapes are the fortunate ones. They tend to enjoy the obscurity and security of never making it onto the list of threatened or endangered species. Cases in point are a number of California's rare, though not endemic, fairy shrimps and include *Branchinecta campestris*, *B. gigas*, *Eubranchipus bundyi*, *E. oregonus*, *Streptocephalus dorothae*, and *S. texanus*. On the other hand, *Branchinecta conservatio*, *Branchinecta longiantenna*, *Branchinecta sandiegonensis*, and *Streptocephalus woottoni*, which have limited ranges within land forms highly desirable for agriculture and urban development, hold the dubious distinction of having their names emblazoned on the U.S. Fish and Wildlife Service's roster of endangered animals. The larger range and broader ecological scope of *Branchinecta lynchi* resulted in it being assigned to the threatened category. Strong political opposition kept *Artemia monica* off the Federal Endangered Species List long enough for a resolution of the water needs of its habitat to be worked out, and delayed the listing of *Branchinecta sandiegonensis* until February of 1997 (Federal Register 1997).

The intrigue swirling around *Artemia monica* and its habitat is interesting indeed. The story began in the forties with the initial diversions of water to Los Angeles from the supplies that would normally have maintained the species' only home, Mono Lake. The result was a gradual lowering of the lake's level and, at its extreme, an approximate doubling of its salt content. For a number of reasons, including the fact that increasing salinity began to reduce the reproductive rate of *A. monica*, the Federal Government designated Mono Basin a National Scenic Area, and the courts ordered the rewatering of Mono Lake's inlet streams, and thus the lake itself. Now that the future looks better for Mono Lake and its inhabitants, pursuing endangered status for *Artemia monica* has been put on hold.

With regard to *Branchinecta sandiegonensis* and its living sites, careful studies of old maps revealed that by the mid-1980s over 97% of vernal-pool habitat in San Diego County had been destroyed by development (Bauder 1986). With its range restricted to coastal mesas of San Diego County and small sections of Orange County and northern Baja California, Mexico, it was clear that *B. sandiegonensis* was in serious trouble, thus its Federal listing as endangered. Survival of this species depends on the outcome of actions, large and small, of agencies and individuals. The largest is the U. S. Fish and Wildlife Service's proposed San Diego National Wildlife Refuge. A high-priority goal of this proposal is to "protect the remaining vernal pool habitat". A smaller action is the relocation of soils from a vernal pool on an Albertson's Supermarket construction site to the safety of a basin created on the campus of Mt. Woodson School in Ramona, California. These efforts were spearheaded by Alisha Pentis, a Mt. Woodson School student and Science Club member, with the aid of her environmental-activist parents. Thanks to those involved, this reconstructed vernal pool will continue to provide hands-on learning experiences for students at the school and, we hope, remain a continuing home for a once doomed population of *B. sandiegonensis*.

We use the word "hope" because building a basin and filling it with tap water is one thing, making it work long-term is another. A pool is truly a complex place, and humans know and understand few of those complexities! Although some pools made for purposes of mitigation seem to have functioned for a few years, there are many which have ultimately failed. One case in point was spread across several pages of the July 10, 1995 edition of the *L.A. Times* (Miller 1995). The article noted that CalTrans threw nearly a million dollars at creating an 18-acre wetland near the southern California town of Moorepark. After a time, they found that sediment build-up would eliminate the wetland in 20 years. Their scientist in charge, Paul Caron, was quoted as saying "Like most biologists in the state and nation, I firmly believe that creating wetlands should be a last-ditch alternative. A lot of people seem to think it's easy to do. But it is extremely detailed and complex." The problem for society and the future, though, lies in his comment that "Our obligation to this project is essentially over.... We've satisfied our mitigation requirements". Our shorthand for such remarks is that knowledgeable individuals are concerned about long-term outcomes, while agencies, businesses, governments, and landowners all too often involve themselves with short-term solutions that suffice only to relieve their responsibilities if not their consciences.

A final important thought is that a pool is not an entity unto itself. Substantiating evidence is gained from experiences, particularly on the Bernard Biological Field Station of The Claremont Colleges. One pool created for *Branchinecta mackini* lost its alkali chemicals after about five years, and, as a result, the population ceased to exist. Other pools seemed to suffice for *Streptocephalus woottoni* and *Branchinecta lindahli* as long as plentiful and sequential precipitation put run-off water in their basins. During a time of insufficient rain, tap water was added to maintain the pools; it killed the fairy shrimps. Particularly in the Central Valley, where California Vernal Pools are unique because of their endemic plants, we now know the flora will **not** survive unless **native** bees which pollinate those specific plants are found on immediately adjacent land. The reason for the latter truth is that, unlike honeybees, these bees fly only short distances. Suffice it to say, that constructing a basin which merely impounds water probably provides few of the necessities, let alone amenities, required by the bevy of organisms inhabiting specific life-giving pools.

Returning to the real world of real pools, The Nature Conservancy provides protected habitat for three of the five Federally-listed fairy shrimps, all California species. The type locality for *Branchinecta conservatio* is the large Olcott Pond, a vernal pool on the Jepson Prairie Preserve. Additional populations swim in protected habitats on the Vina Plains Preserve. *Branchinecta lynchi* may also be found living on the latter preserve, but in separate, typically smaller, basins. In addition, *B. lynchi* dwells unmolested, except by normal ecological pressures, in pools at the Conservancy's Santa Rosa Plateau Preserve, and possibly on the Carrizo Plain Preserve as well. Basins in the latter swatch of land also give protection to one of California's rarest fairy shrimps, *Branchinecta longiantenna*. But the rarest of them all, *Linderiella santarosae*, is saved from being listed as an endangered species because its entire range is contained within The Nature Conservancy's Santa Rosa Plateau Preserve.

The same three federally listed species that find sanctuary on The Nature Conservancy lands are also found in vernal pools at a number of National Wildlife Refuges. These include Kesterson NWR for *B. longiantenna*; Sacramento NWR, San Luis NWR, Kesterson NWR, and Arena Plains NWR for *B. conservatio*; and all the above refuges, in addition to the Pixley NWR, for *B. lynchi*.

The only listed fairy shrimps not yet found on lands managed to save natural habitats, and thus the species, are *Branchinecta sandiegonensis* and *Streptocephalus woottoni*. Such a situation puts these species at greater risk than the others currently receiving federal protection. In what is potentially a helpful circumstance, both *B. sandiegonensis* and *S. woottoni* are now known from sites at Camp Pendleton, a U.S. Marine Corps facility in San Diego County. And if the San Diego NWR comes on line, further habitat protection will be realized.

Well-managed ranch land generally supports good fairy shrimp habitat. Loss of range land to "higher development" of course constitutes a loss of pools and their fairy shrimp inhabitants. In addition to development, invasive species often endanger native wildlife, including fairy shrimps. Foreign annual grasses, and even native vegetation, threaten vernal pool habitats by ultimately choking them with accumulated plant litter if it is not harvested or removed by herbivores. Barry (undated) presents photographic evidence supporting the role of grazing in protecting vernal pools from invasive weeds and native vegetation. In Germany, army tanks have been documented performing the role of reducing vegies and maintaining open water necessary for the support of some anostracans (Hössler *et al.* 1995). And guess what? Never to be outdone, California too has its tanks maintaining fairy shrimp habitat...on the Camp Pendleton Marine Corps Base near Oceanside in San Diego County.

Only time and public support will determine whether anostracans will continue to live scattered broadly across the California landscape, or if one day they will be relegated only to nature reserves, cyst banks, museum collections, and pictures in books like the one in which you are presently absorbed.

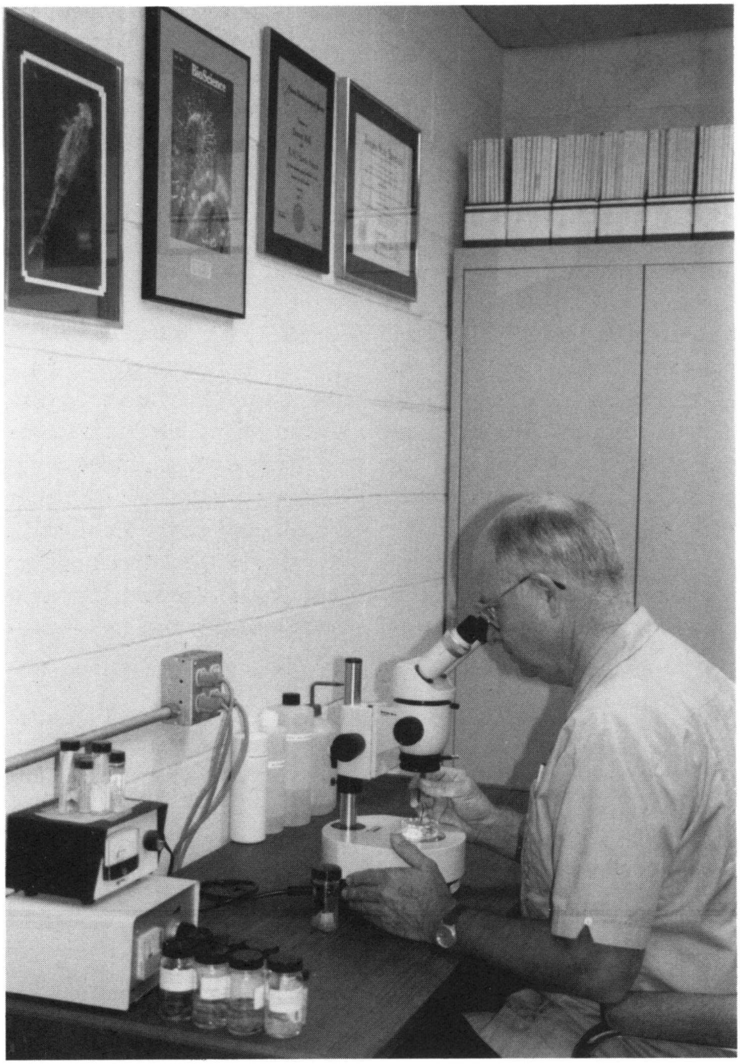


Fig. 7.0. Denton identifying a fairy shrimp.

Chapter 7

HOW TO KNOW THE CALIFORNIA FAIRY SHRIMPS

Introduction

At one point or another we all want to pin a name on what is before us. In order to do so, that is to identify a particular organism, biologists "key it out". A KEY is constructed so that you may work your way through a series of choices, each with only two alternatives. Our key for the fairy shrimps of California is designed to be used only with mature animals. Females show the best indicator of maturity because their brood pouches are conspicuously filled with brownish-shelled cysts. However, the key is based on male characters because only with mature males can identification be made with confidence. Luckily, both sexes reach maturity at the same time, so if you see a female carrying cysts, you know the males are mature. Checking female traits is desirable, and will increase accuracy in a few cases, but one cannot normally identify a species utilizing only female characteristics.

Be alert to the fact that some collections may be a mixture of species, and perhaps generations also. Different species of fairy shrimps may hatch at different times under different stimuli, and maturation rates may vary as well. Not only that, as the water level of a pool recedes, cysts, caught in the desiccating ring of mud, may hatch should the pool refill, thus providing a second generation (cohort) to swim with the remainder of the previous population(s). The result is that while you usually have but one mature species in your collection, at times there may be more than one. Males and females of the same generation will be approximately the same size. However, adult size, usually 15-30 mm, may vary with environmental conditions. It's that old adage "you are what's in your genes"...as modified by environment.

There are three ways to find the meaning of terms and location of parts mentioned in the key. One is to check the Figure(s) referred to in the key where you first encounter the unfamiliar item. The second is to look in this book's Glossary for technical terms. The third applies to words of "standard usage" and involves joy-reading in your favorite dictionary.

Drawings for the key were constructed to satisfy not only a real taxonomist (Denton), but also several who consider themselves novices at such an art-form (Clyde, and our artist Ina Rae Lengyel). Denton then field-tested our product at a number of workshops. Student "feed-back" was really helpful in working out rough spots.

When examining a preserved fairy shrimp you will often see what appear to be two lines around the periphery of its surfaces. Preservation causes the body wall to separate from its cuticle (exoskeleton) so we have faithfully represented this appearance in several of the drawings, but do realize that if you view a living specimen, you will see only one line.

Friendly advice has it that you should NOT attempt to take short-cuts with the key. Begin at the beginning, for that is the way it was designed to be used! Make a choice between the alternatives in the first couplet (1a or 1b). If, when you arrive at a distant couplet and decide you need to go back to where you came from and review your options, the number and letter in parenthesis to the right of the couplet number tells you "where to go". This format is continued throughout. When you are fully familiar with the key you may occasionally want to match your material with one of the drawings and then work backwards, checking to be sure your specimen has all of the characters itemized. As a final comment, you may wonder about the meaning of the name(s) and date immediately following each scientific name. This is typical scientific format identifying the scientist(s) who described the species and the year in which the author(s) perpetrated the deed.

Key

1 **a.** Cercopods fused to sides of telson and lateral abdominal ridges (Fig. 7.1A) **2**

b. Cercopods not fused to sides of telson or lateral abdominal ridges; cercopods attached only to posterior border of telson (Figs. 7.1B, 7.2A,B) **3**

2(1a) **a.** Branch 1MD of frontal appendage (see "frontal appendage" in Glossary) conical with a distinct spine on its medially directed terminus; branch 2D with three subbranches (Fig. 7.3)
Thamnocephalus platyurus **Packard, 1879**

Note: Only one other species of *Thamnocephalus* is known from North America, *T. mexicanus*, the Mexican beavertail fairy shrimp. Populations of *T. mexicanus* occur in southern Arizona (Belk 1977a). Branch 1MD of *T. mexicanus* is flat, broad, and leaf-like; branch 2D has four or five subbranches, the proximal one being very short and small (see Belk & Pereira 1982).

3(1b) **a.** Cercopods long tapering cones, each with a row of short plumose setae extending most of its length on the ventrolateral surface, and with much longer plumose setae extending from distal end for only about half the distance back to telson on dorsomedial surface (Fig. 7.1B); antennae of female as long as antennae of male (Fig. 4.1); largest species known, adults may reach 150 mm in total length; frontal view of male head in Fig. 7.20
Branchinecta gigas **Lynch, 1937**

b. Cercopods not as above **4**

4(3b) **a.** Distal (second) segment of antenna shifted to ventrolateral position and largely replaced by a distal outgrowth which forms a large folded tube-like limb (peduncle) ending in a cheliform structure (hand) (Fig. 7.4, 7.5, 7.6, 7.7, 7.8)...................... **5**

b. Distal (second) segment of antenna extends ventrally from distal end of basal (first) segment (Figs. 7.10, 7.11, 7.12, 7.20)... **8**

5(4a) **a.** Cercopods of adult male with plumose setae located proximally along both medial and lateral edges and with spines located along both edges distally (Fig. 7.2A,C); shoulder on lateral side of distal tooth less than one-third height of distal tooth (Fig. 7.7) (in Eng, Belk, & Eriksen 1990, fig. 5a is a lateral view, not medial as stated)
Streptocephalus sealii **Ryder, 1879**

b. Cercopods of adult male with plumose setae along entire lengths of both medial and lateral edges **6**

6(5b) **a.** Distal end of spur on thumb shaped similar to a human foot when viewed in profile; finger with a subterminal swollen part lacking spines or processes (Fig. 7.5)
Streptocephalus dorothae **Mackin, 1942**

Note: *Streptocephalus mackini*, the Chihuahua fairy shrimp, differs from *S. dorothae* only in having a slender spine on the lateral surface of the subterminal swollen part of the finger. *S. mackini* occurs in Arizona (Belk 1977a) and may one day be found in California.

b. Spur on thumb tapering to a point (Figs. 7.6, 7.7, 7.8); finger terminating variously
.... **7**

7(6b) **a.** Reflexed end of finger terminating smoothly without a spine, process, or subterminal lateral lamella; distal edge of proximal tooth with a slight to prominent triangular projection; shoulder on lateral side of distal tooth about half as high as distal tooth (Fig. 7.8) (in Eng, Belk, & Eriksen, 1990, fig. 5b is a lateral view, not medial as stated)
Streptocephalus woottoni **Eng, Belk, & Eriksen, 1990**

b. Reflexed end of finger with a subterminal lateral lamella which possesses a projecting lobe; no lateral shoulder on distal tooth (Fig. 7.6)
Streptocephalus texanus **Packard, 1871**

8(4b) **a.** Distal segment of antenna flattened into a wide, roughly triangular blade with apex directed medially (Fig. 7.11) **9**

b. Distal segment of antenna not as above **10**

9(8a) **a.** Occurring in Mono Lake
***Artemia monica* Verrill, 1869**

b. Occurring elsewhere; probably
***Artemia franciscana* Kellogg, 1906**

Note: The genus *Artemia* encompasses a complex of sibling species with no morphological characters useful in separating the North American species. Biochemical characters must be used to establish identity with certainty for any individuals not collected from Mono Lake, or another site where identity has been properly determined – see Browne and Bowen (1991).

10(8b) **a.** Antennal appendages present (Figs. 7.9, 7.10, 7.12, 7.13, 7.14).......... **11**

b. Antennal appendages absent.......... **15**

11(10a) **a.** Antennal appendage rigid and pyramidal, with spines on its relatively flat medial surface (Figs. 7.9, 7.10).......... **12**

b. Antennal appendage flexible and lamelliform, with finger-like processes along its edges (Figs. 7.12, 7.13, 7.14).......... **13**

12(11a) **a.** Tip of antennal appendage relatively straight, with spines on medial surface often extending to tip (Fig. 7.9)
***Linderiella occidentalis* (Dobbs, 1923)**

b. Tip of antennal appendage clearly curled laterally; spines absent from curled tip (Fig. 7.10)
***Linderiella santarosae* Thiéry & Fugate, 1994**

Note: *Linderiella santarosae*, the Santa Rosa Plateau fairy shrimp, is known only from the Santa Rosa Plateau in Riverside County.

13(11b) **a.** Labrum with a knob-like protuberance at anterior end projecting between flanking outgrowths on bases of antennae (Fig. 7.12)
Eubranchipus bundyi **Forbes, 1876**

b. Labrum without a knob-like protuberance **14**

14(13b) **a.** Antennal appendage does not extend beyond distal end of basal segment of antenna, triangular in outline with finger-like processes along both edges of distal half; distal segment of antenna with a short, knobby medially directed process near proximal end (Fig. 7.13)
Eubranchipus oregonus **Creaser, 1930**

b. Antennal appendage longer than basal segment of antenna; shape as in Fig. 7.14 with finger-like processes along both edges of distal two-thirds; a group of about 7 near center of lateral edge much longer than others. Distal segment of antenna with a medially directed process near its proximal end; this process about half as long as distal segment (Fig. 7.14)
Eubranchipus serratus **Forbes, 1876**

15(10b) **a.** Pulvillus (see note below) on medial surface of antenna near proximal end; an apophysis may or may not be present in posteromedial position near proximal end of antenna (Figs. 7.15, 7.19, 7.23, 7.24, 7.25, 7.26) **16**

b. No pulvillus on antenna; basal segment of antenna with an apophysis in posteromedial position near proximal end (Fig. 7.16) **17**

Note: The pulvillus is a mound-like area covered with minute cuticular spinules. It appears as a cloudy or milky patch which is most easily viewed using substage lighting. Removing all the soft tissue and viewing just the exoskeleton may make the pulvillus easier to see. Removal can be accomplished by placing the severed head in a 10% solution of a commercial sodium hypochlorite bleach such as Clorox®.

16(15a) **a.** Basal segment of antenna with a large, conspicuous, spiny bulge near center of medial side, and a small, round pulvillus near proximal end on anteromedial surface; older adult males with an apophysis located posteromedially on basal segment of antenna; apophysis not present in young adult males (Fig. 7.15A)
Branchinecta coloradensis **Packard, 1874**

b. Basal segment of antenna without a large, conspicuous, spiny bulge; males never have an apophysis near proximal end of basal segment of antenna **18**

17(15b) **a.** Antennules of female longer than her antennae; brood pouch lacks outpocketings. Compare end of antenna of male with Fig. 7.16A
Branchinecta mackini **Dexter, 1956**

b. Antennules of female equal to or shorter than her antennae; brood pouch with conical outpocketings in midlateral position (Fig. 7.17); these outpocketings not found in any other branchinectid. Compare end of antenna of male with Fig. 7.16B
Branchinecta campestris **Lynch, 1960**

Note: Males of these two species are morphologically very similar; compare the distal ends of their antennae for specific differences using Fig. 7.16A,B.

18(16b) **a.** Many prominent spines covering more than half of medial surface of basal segment of antenna (Fig. 7.19A,B) **19**

b. Few to no spines on medial surface of basal segment of antenna (Figs. 7.15B, 7.23, 7.24, 7.25, 7.26) **20**

19(18a) **a.** Antennae long enough to reach genital segments; basal segment with an oval pulvillus near proximal end, a band of prominent spines along medial surface from pulvillus to near distal end, and a large patch of low wart-like mounds covering medial surface at distal end (Fig. 7.19A)
Branchinecta longiantenna **Eng, Belk, & Eriksen, 1990**

b. Antennae not long enough to reach genital segments; basal segment with a small pulvillus near proximal end, a band of spines from near center of medial surface to distal end (Fig. 7.19B), and no wart-like mounds
Branchinecta dissimilis **Lynch, 1972**

20(18b) **a.** Basal segment of antenna with a small elongate pulvillus located near proximal end, a small ridge-like outgrowth located near anterior edge of medial surface just distal to pulvillus, and a small, variably developed, mound-like bulge on anteromedial side of basal segment just distal to middle (Fig. 7.15B). Female with dorsolateral processes on thoracic segment 3 (Fig. 7.18B), unlike similar looking female in 23a
Branchinecta lynchi **Eng, Belk, & Eriksen, 1990**

b. Basal segment of antenna with a large, elongate, oval pulvillus near proximal end; the only other outgrowths being small spines which occasionally develop near middle of medial surface, these usually absent (Figs. 7.23, 7.24, 7.25, 7.26). **USE CAUTION AS THE NEXT FOUR SPECIES CAN BE CONFUSED WITH EACH OTHER UNLESS SPECIAL CARE IS EXERCISED** **21**

21(20b) **a.** Distal segment of antenna with only one hump extending above half the total height of its medially bent end (Fig. 7.21A,B) **22**

b. Distal segment of antenna with two unequal humps extending above half the total height of its medially bent end (Fig. 7.21C,D) **23**

22(21a) **a.** Distal segment of antenna increases in width up to level at which end bends medially (Figs. 7.21A, 7.23); female with two dorsolateral conical processes on each side of thoracic segments 3 and 5-8 (Fig. 7.22A)
Branchinecta sandiegonensis **Fugate, 1993**

b. Distal segment of antenna constricted near level at which end bends medially (Figs. 7.21B, 7.24); female with only one dorsolateral conical process on each side of a variable number of thoracic segments (Fig. 7.22B)
Branchinecta lindahli **Packard, 1883**

23(21b) **a.** Distal segment of antenna with a large anterior hump and a small posterior hump on distal edge of its medially turned end (Figs. 7.21C, 7.25). Female lacks dorsolateral processes on thoracic segment 3 (Fig. 7.18A), unlike similar looking female in 20a
midvalley fairy shrimp (Belk & Fugate in review)

b. Distal segment of antenna with a small anterior hump and a large posterior hump on distal edge of its medially turned end (Figs. 7.21D, 7.26).
Branchinecta conservatio **Eng, Belk, & Eriksen, 1990**

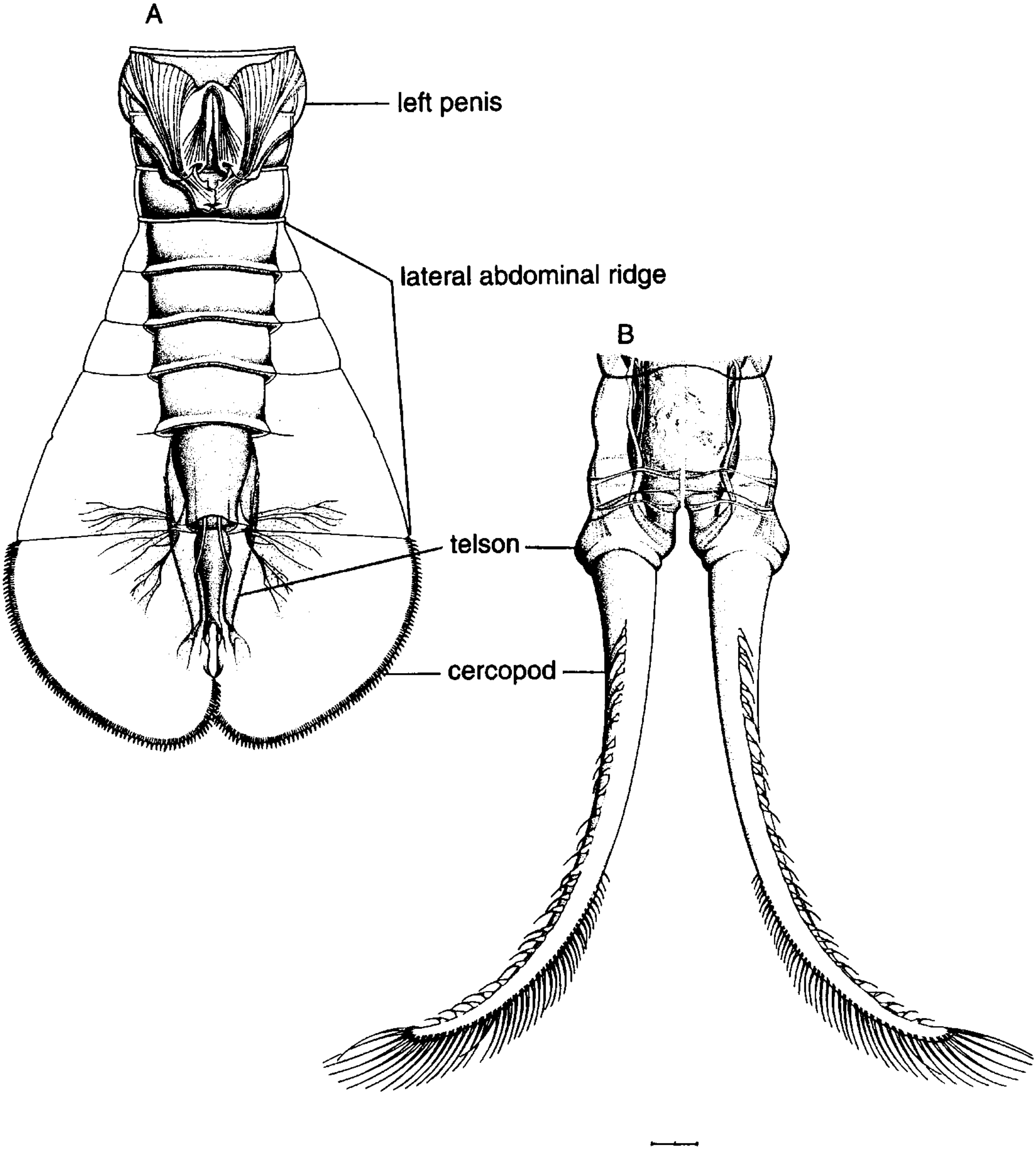


Fig. 7.1. **A.** *Thamnocephalus platyurus*, ventral view of genital segments, abdomen, and cercopods of a male. **B.** *Branchinecta gigas*, ventral view of telson and cercopods. Enlarged view of setae in Fig. 7.27 p. 166. Scale = 1 mm.

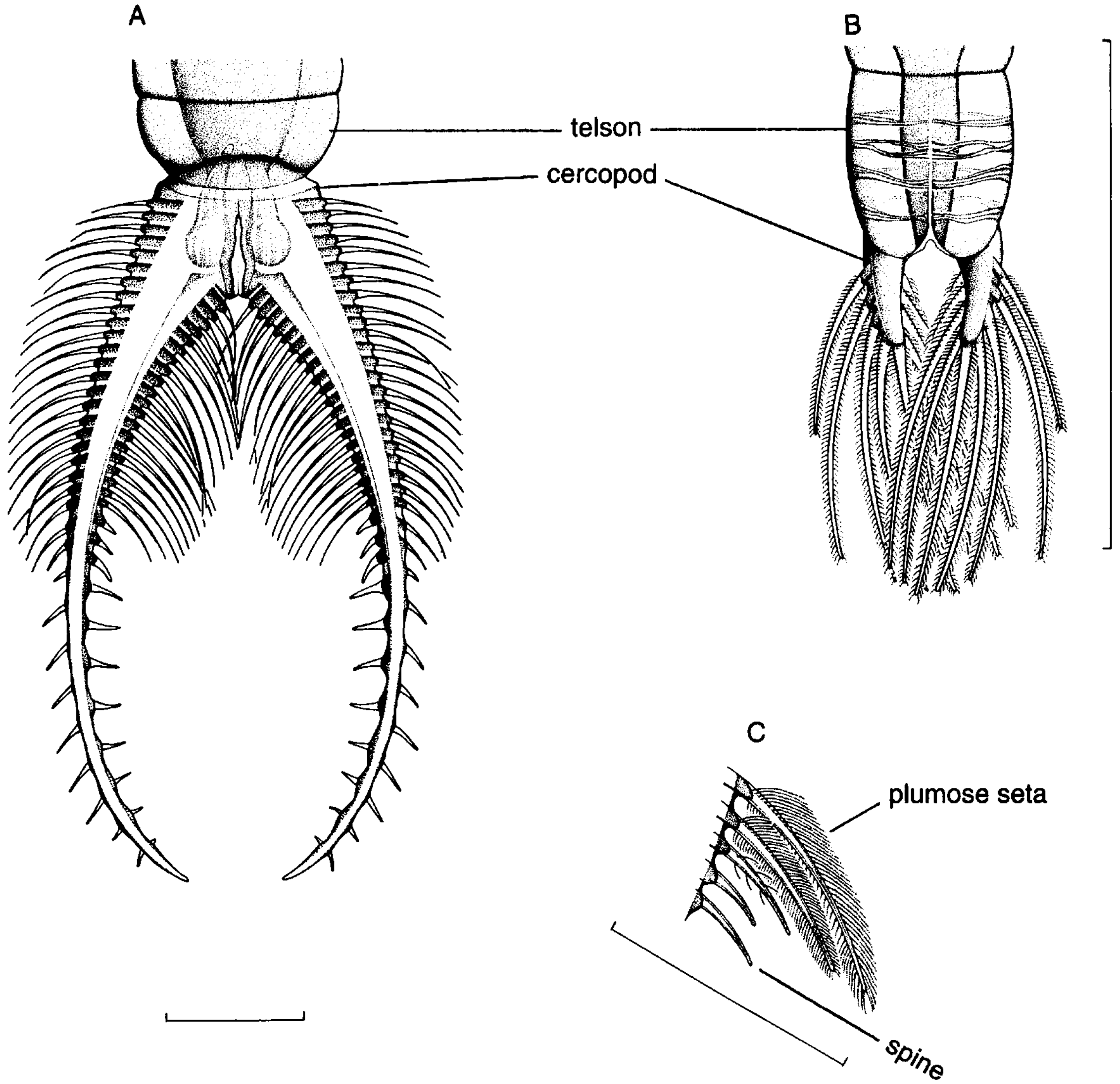


Fig. 7.2. **A.** *Streptocephalus sealii*, telson and cercopods of adult male. **B.** *Artemia monica*, telson and cercopods. **C.** Enlarged view of the region on the cercopod of *S. sealii* where fringing plumose setae and spines meet. Scale = 1 mm.

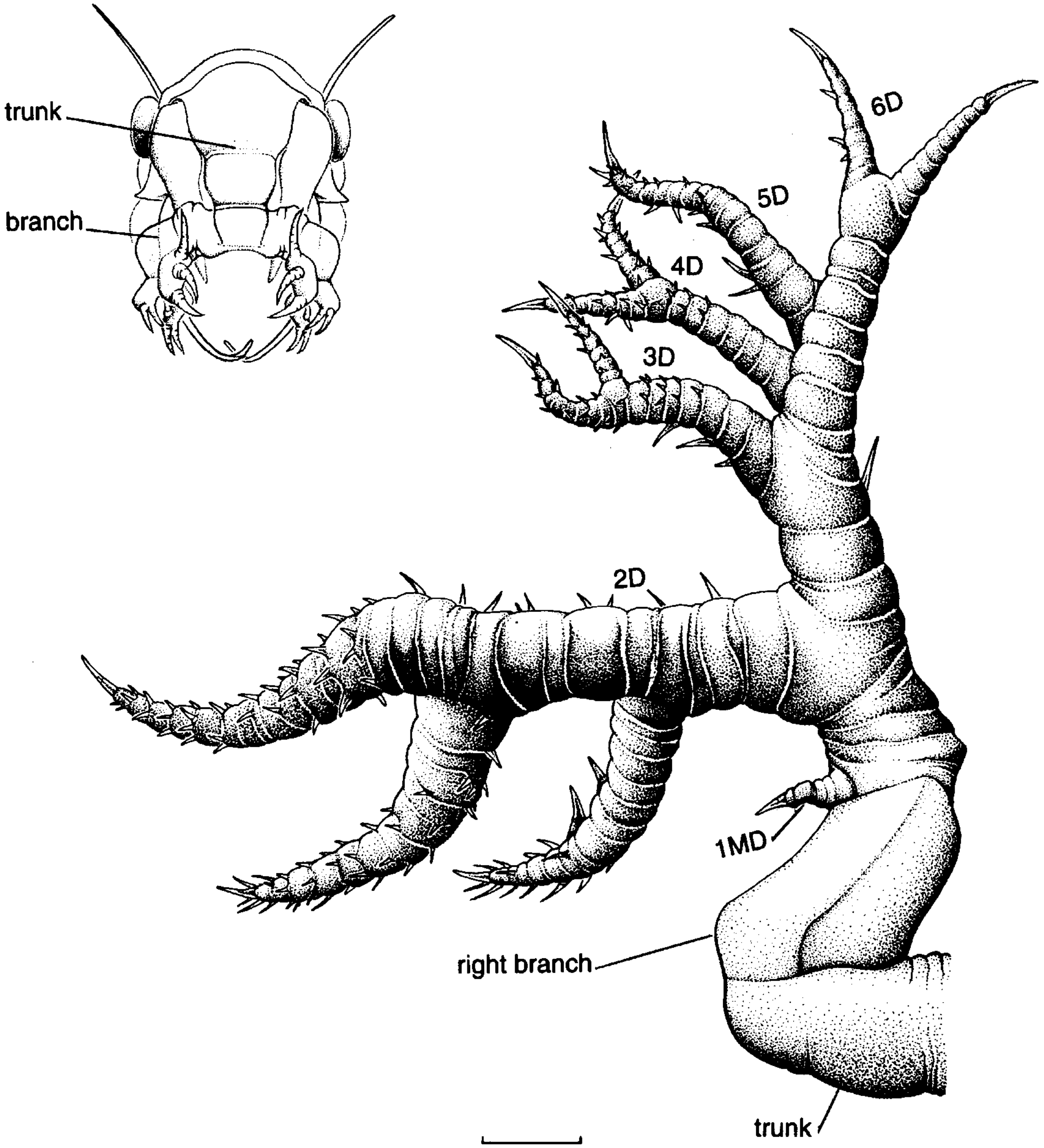


Fig. 7.3. *Thamnocephalus platyurus*, lateral view of the trunk and right main branch of the frontal appendage, branches extend from dorsal surface. The insert shows how the frontal appendage is situated on the male's head. Scale = 1 mm.

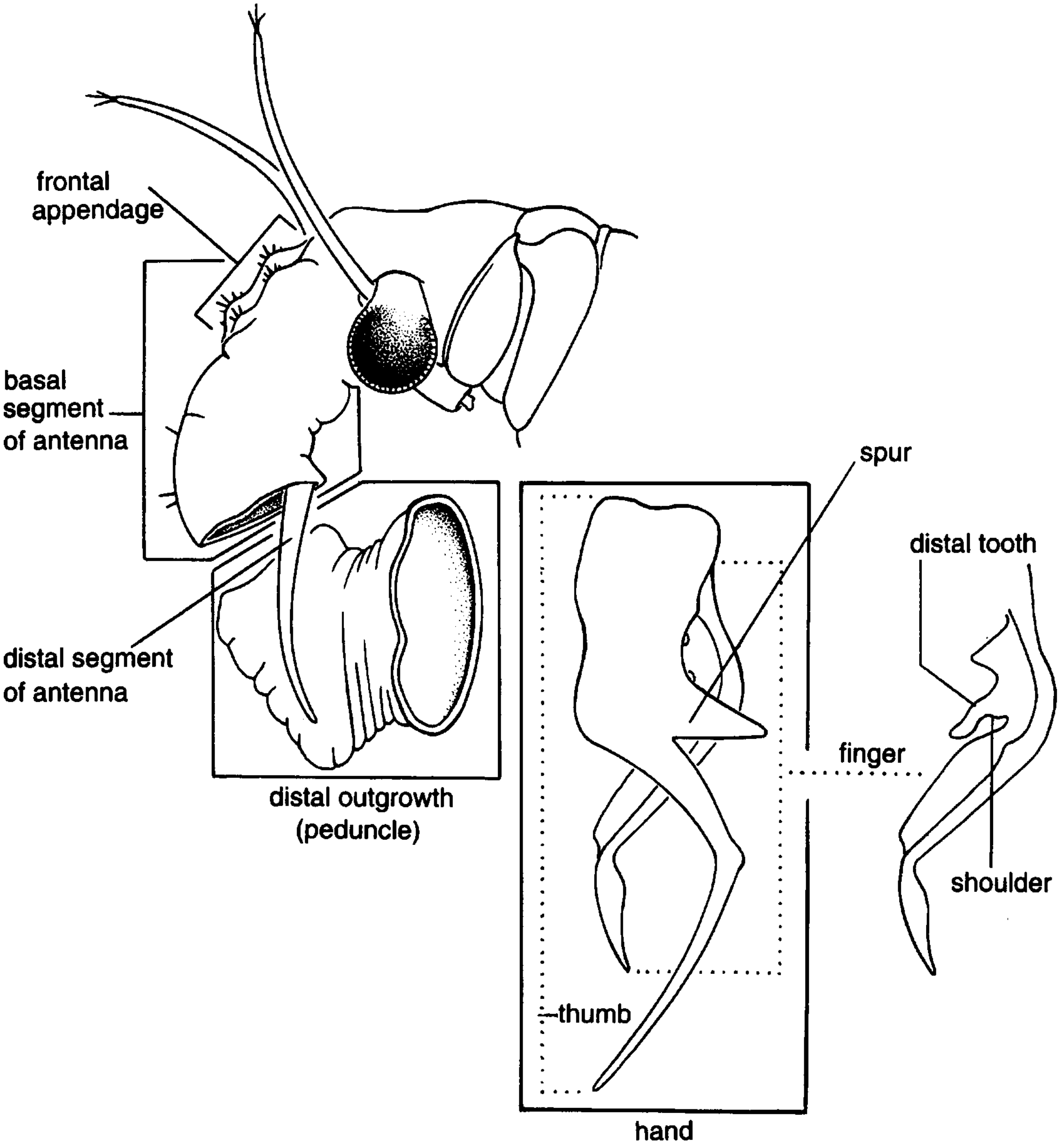


Fig. 7.4. Schematic of *Streptocephalus sealii* showing head and antennal structures of males in the genus *Streptocephalus*; drawn in lateral view. For the intact view, see Fig. 7.7 p. 146.

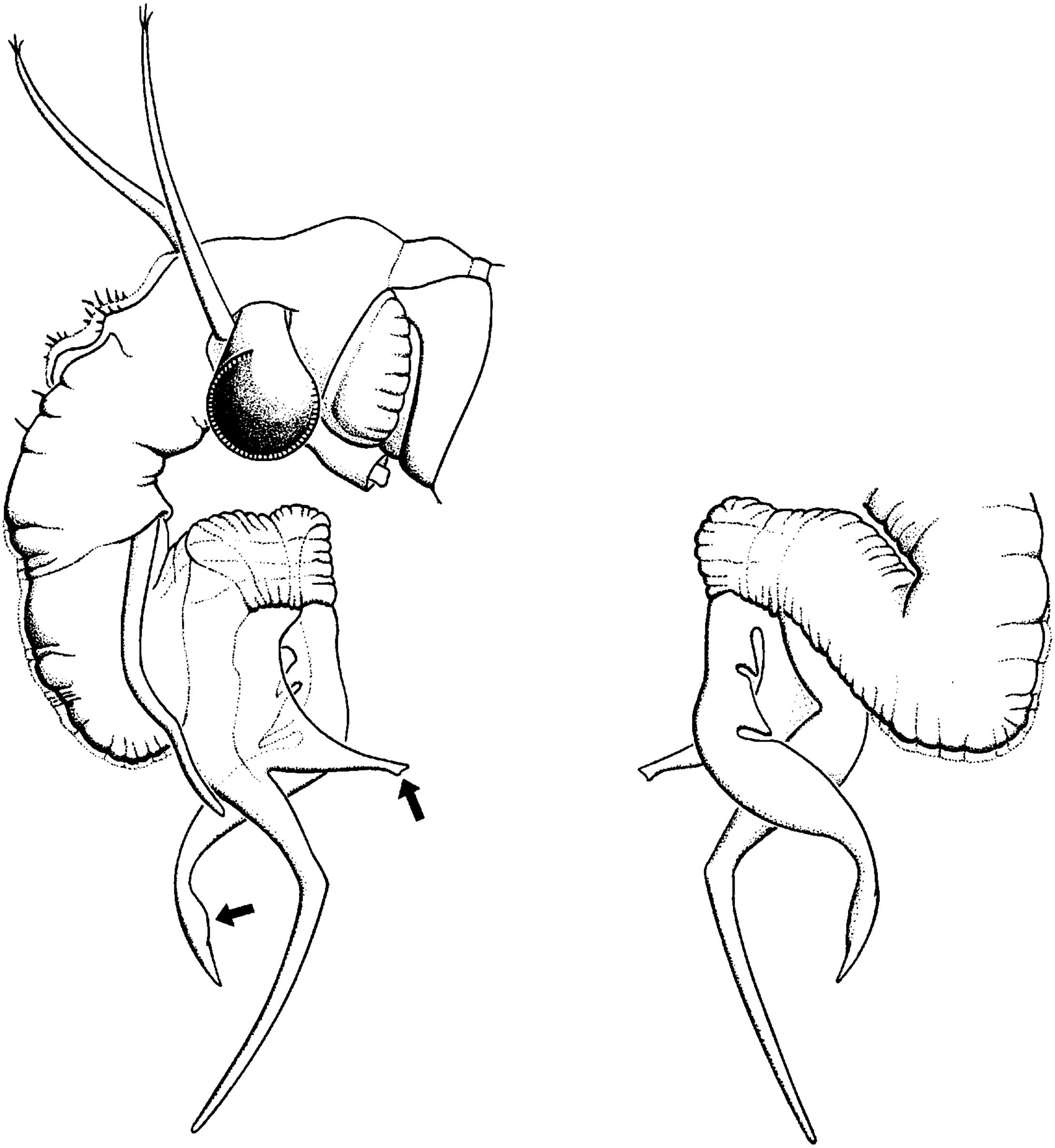


Fig. 7.5. *Streptocephalus dorothae*, lateral view of male's head, and medial view of distal outgrowth and hand. Check Fig. 7.4 for names of structures.

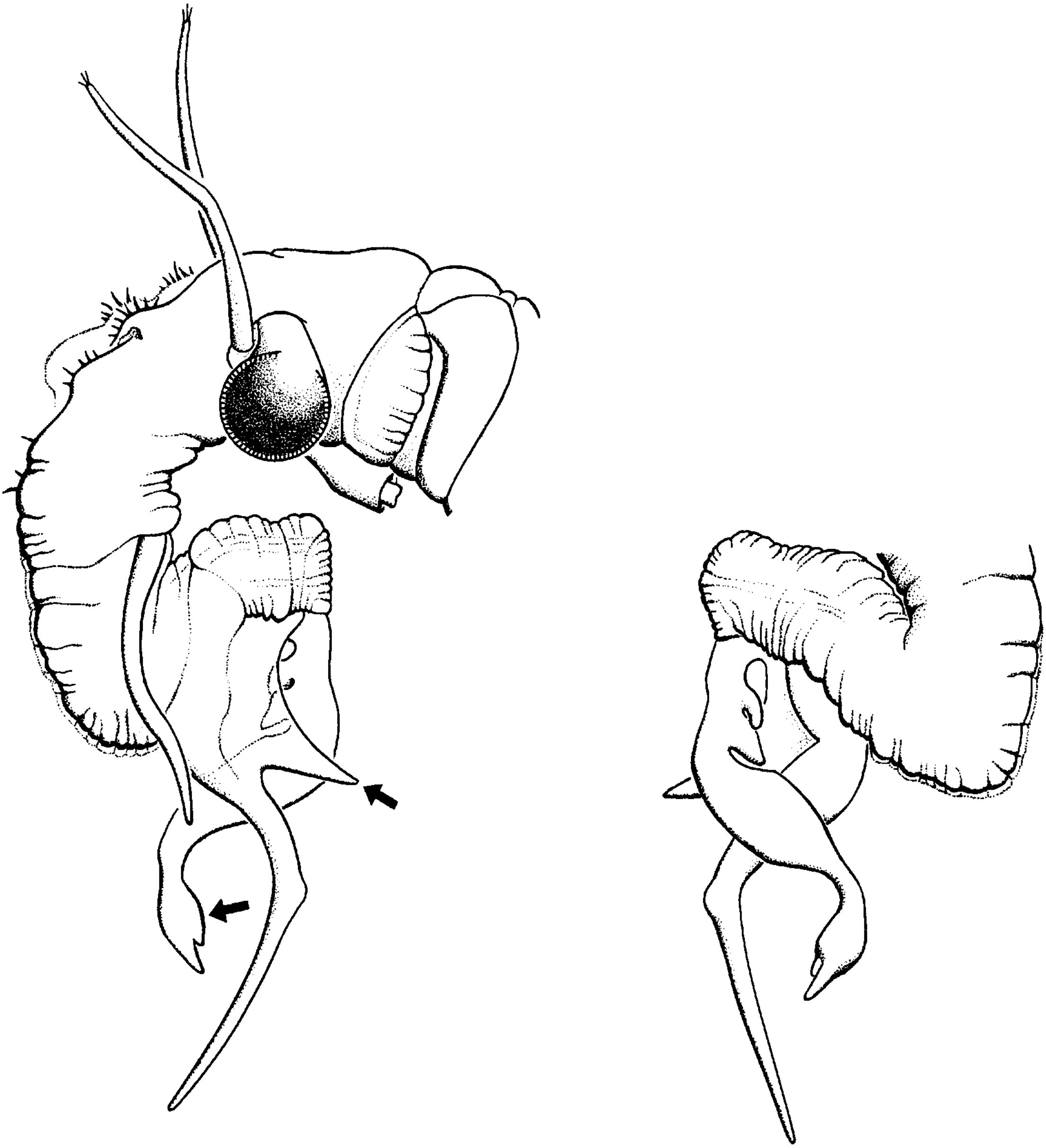


Fig. 7.6. *Streptocephalus texanus*, lateral view of male's head, and medial view of distal outgrowth and hand. Check Fig. 7.4 for names of structures.

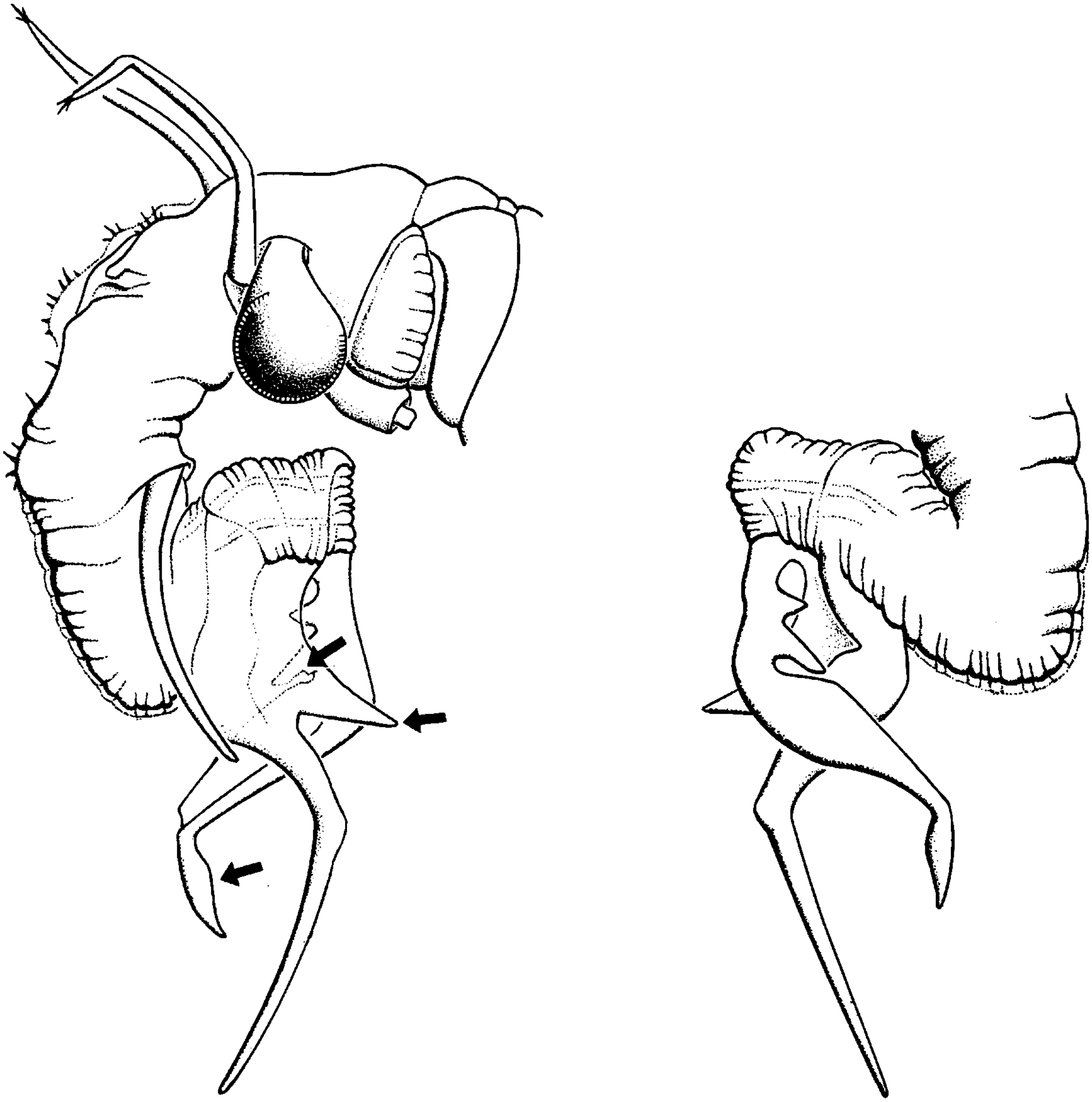


Fig. 7.7. *Streptocephalus sealii*, lateral view of male's head, and medial view of distal outgrowth. Check Fig. 7.4 for names of structures.

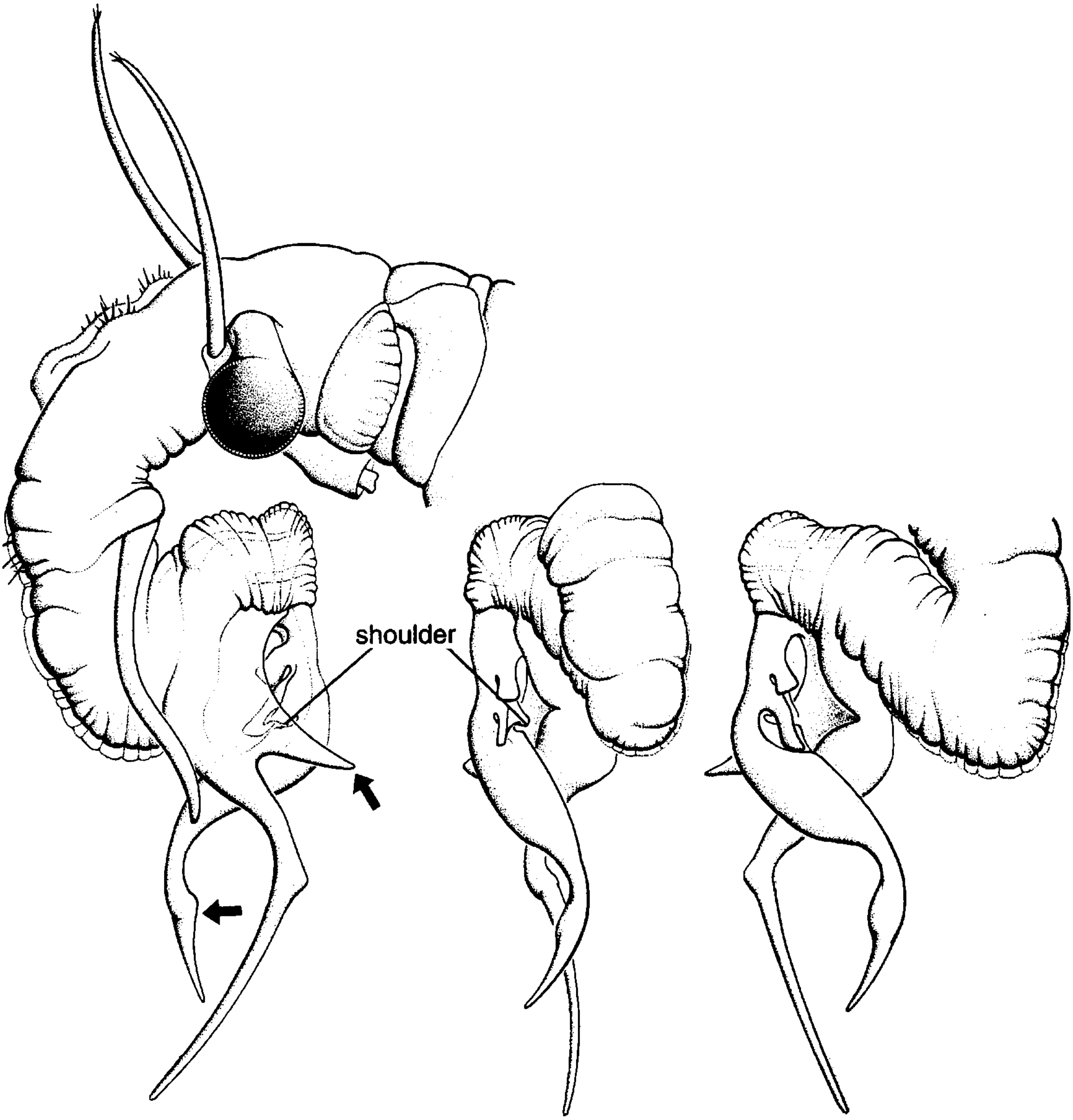


Fig. 7.8. *Streptocephalus woottoni*, lateral view of male's head, and dorsomedial and medial views of distal outgrowth and hand. Check Fig. 7.4 for names of structures.

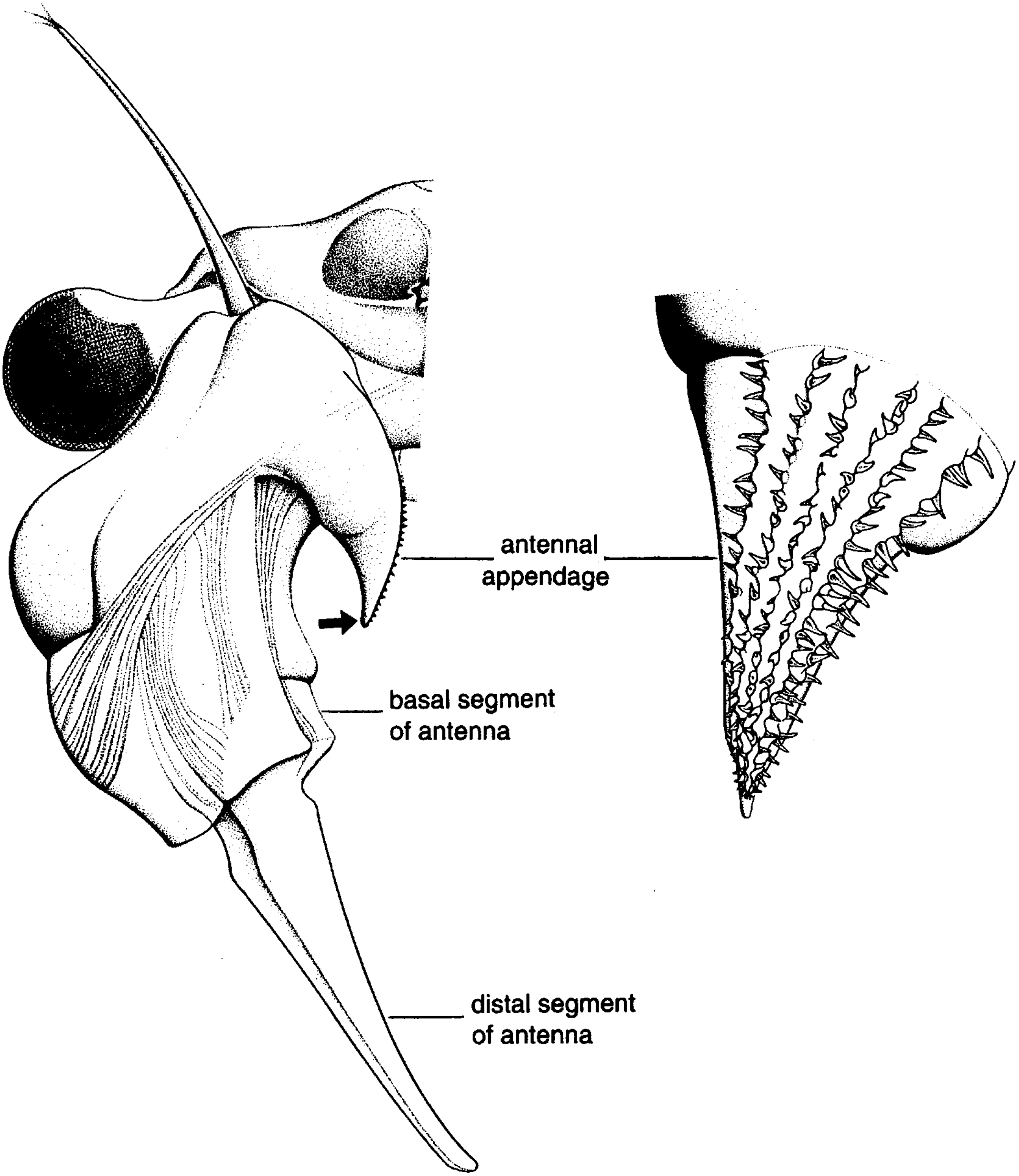


Fig. 7.9. *Linderiella occidentalis*, frontal view of male's head (right half, for view of intact head see next page), and enlarged view of medial surface of the antennal appendage.

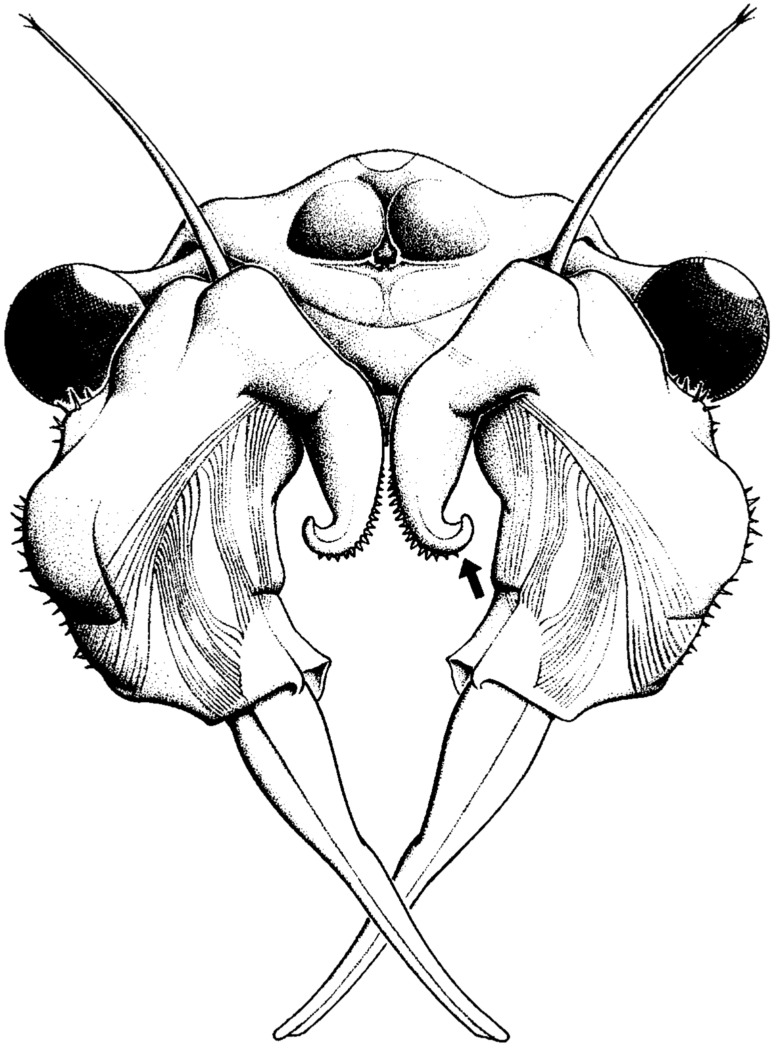


Fig. 7.10. *Linderiella santarosae*, frontal view of male's head.

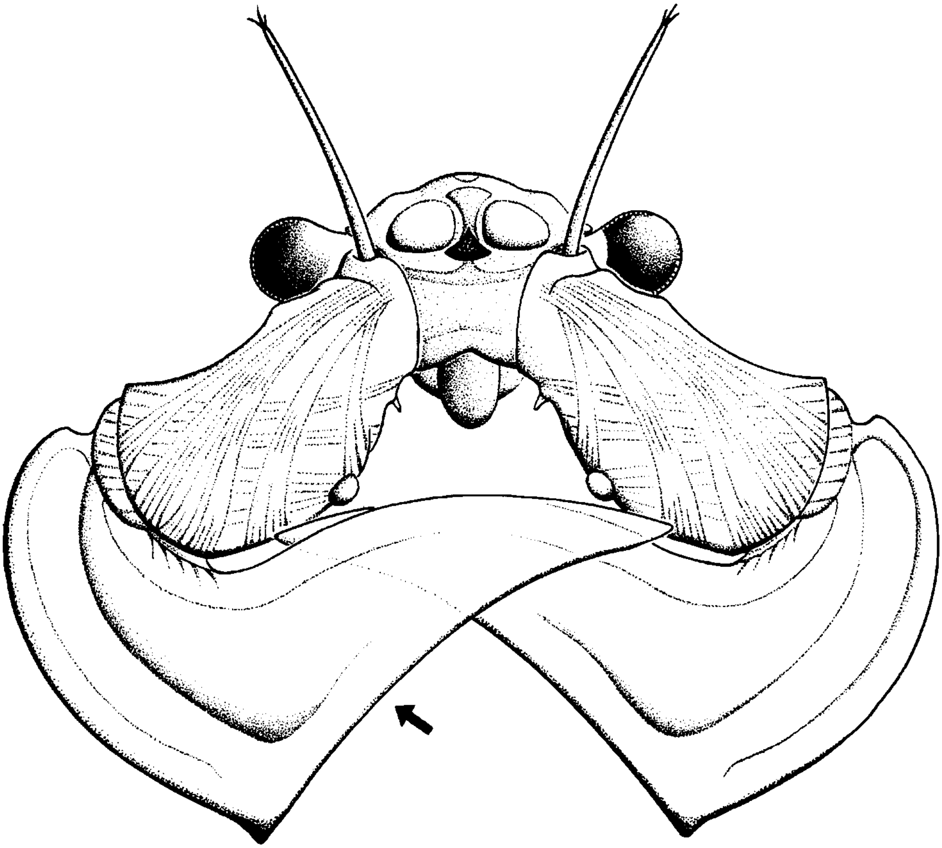


Fig. 7.11. *Artemia monica*, frontal view of male's head showing the triangular medial extension of the distal segment of the antennae common to all members of the genus *Artemia*.

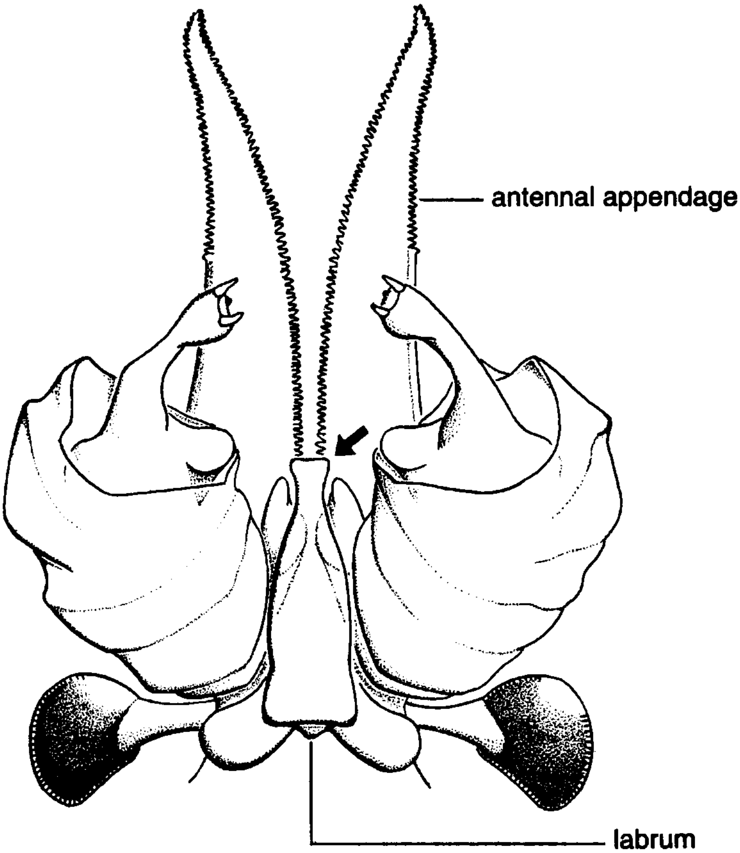


Fig. 7.12. *Eubranchipus bundyi*, ventral view of male's head with antennal appendages unrolled and extended, and view of labrum showing its unique anteriorly placed knob-like extension.

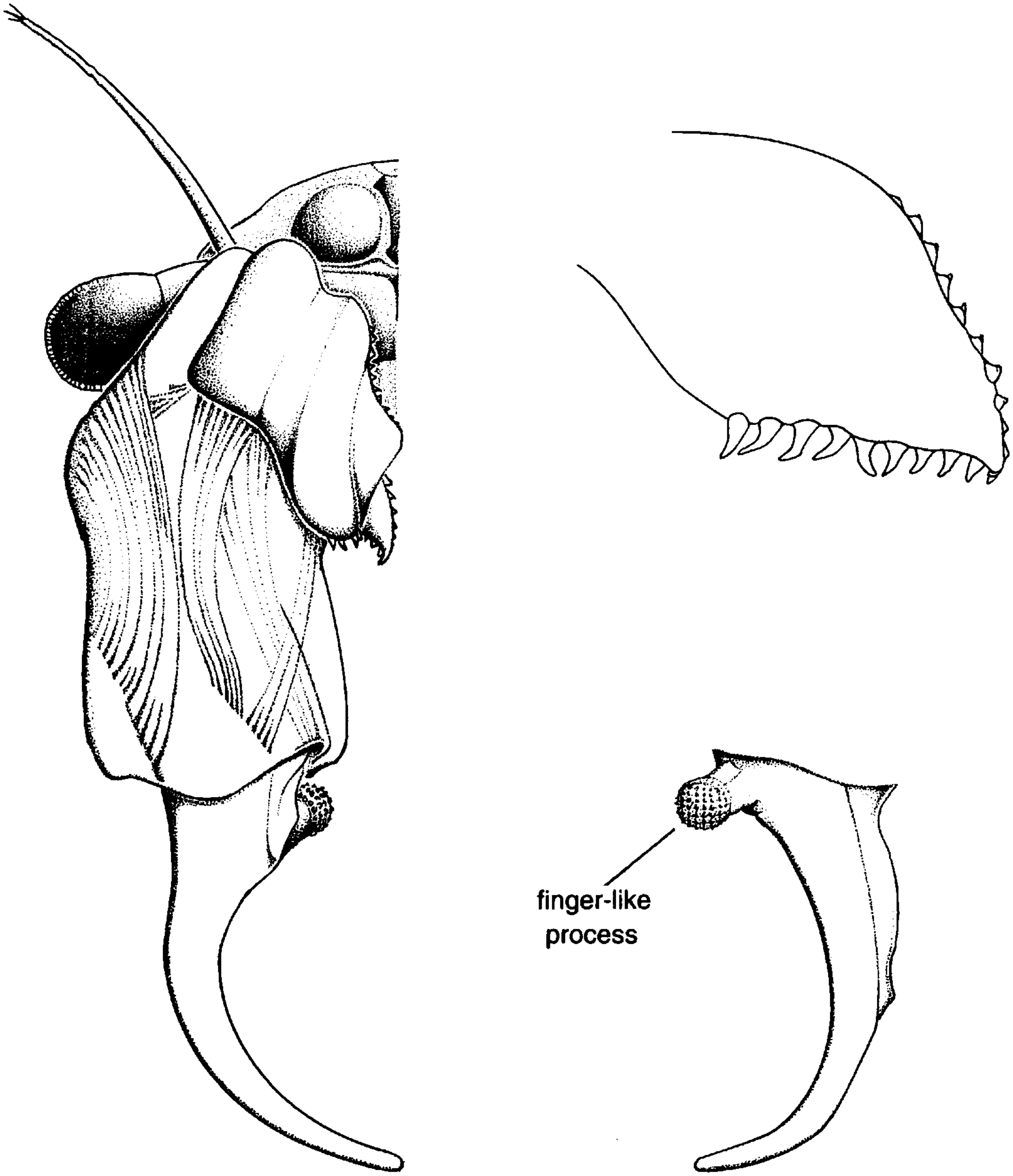


Fig. 7.13. *Eubranchipus oregonus*, frontal view of male's head (right half) with antennal appendage partially folded, posterior view of distal segment of antenna, and dorsal view of right antennal appendage unrolled and extended.

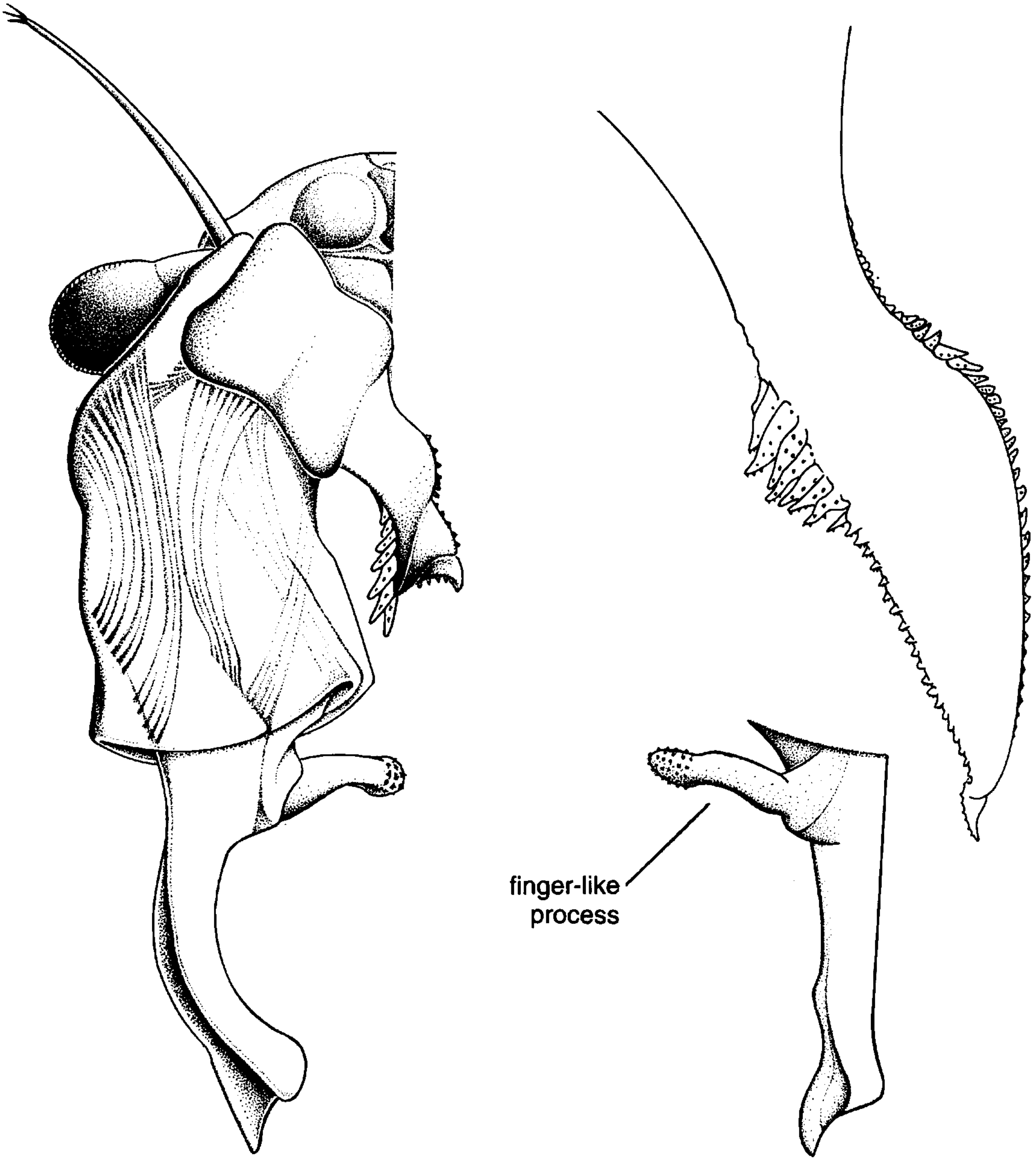


Fig. 7.14. *Eubranchipus serratus*, frontal view of male's head (right half) with antennal appendage partially rolled, posterior view of distal segment of antenna, and dorsal view of right antennal appendage unrolled and extended.

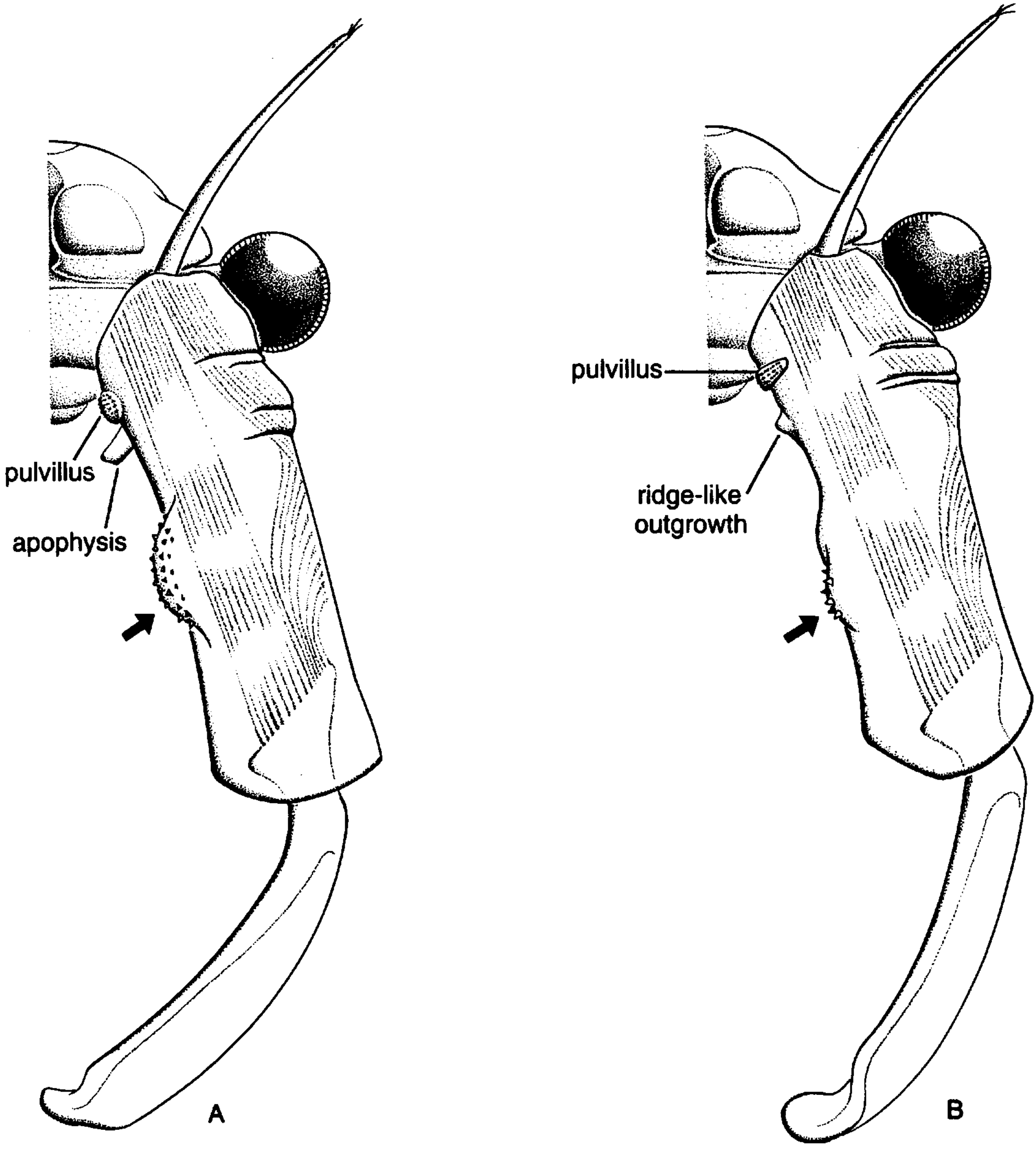


Fig. 7.15. **A.** *Branchinecta coloradensis*, frontal view of male's head (left half). **B.** *Branchinecta lynchi*, frontal view of male's head (left half).

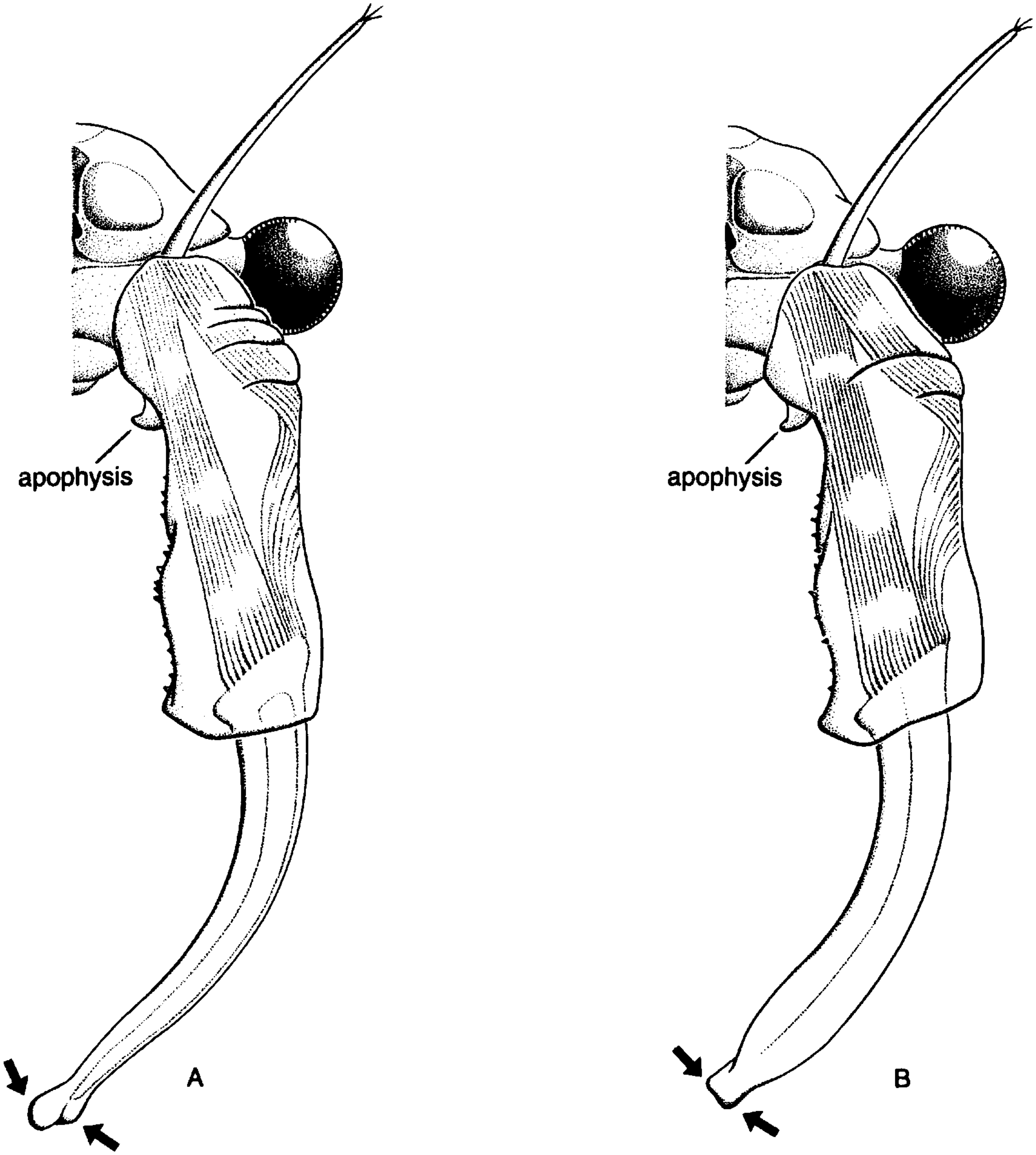


Fig. 7.16. **A.** *Branchinecta mackini*, frontal view of male's head (left half). **B.** *Branchinecta campestris*, frontal view of male's head (left half).

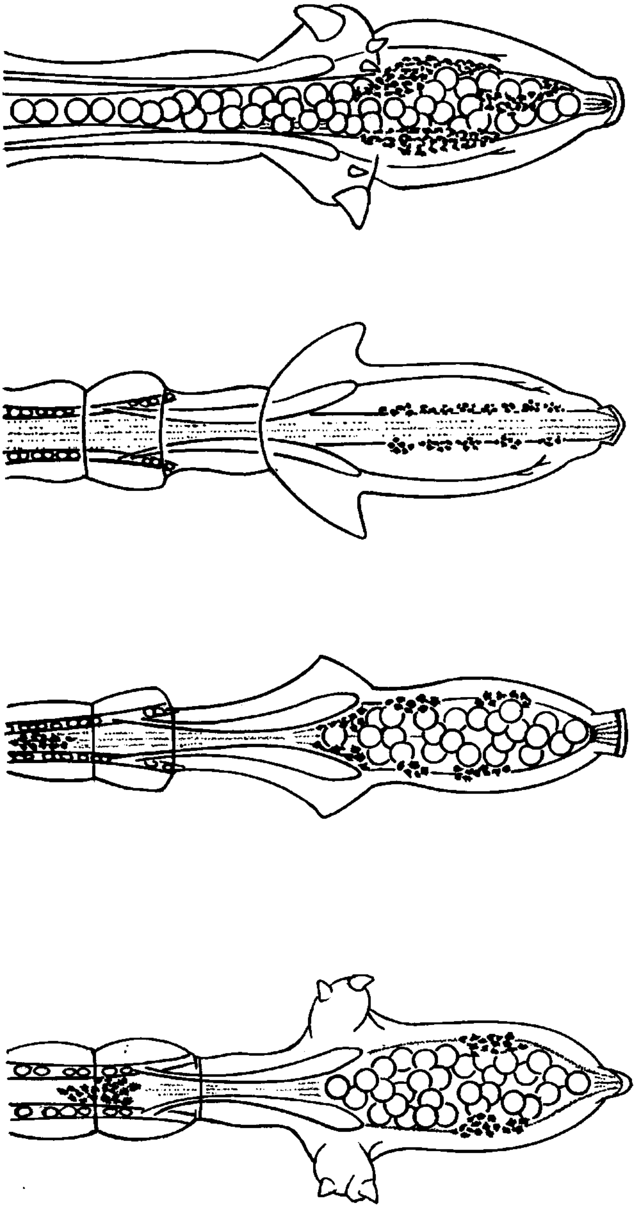


Fig. 7.17. Ventral views of brood pouches of *Branchinecta campestris* showing some of the variety of conical outpocketings found uniquely in females of this species; redrawn from Lynch (1960).

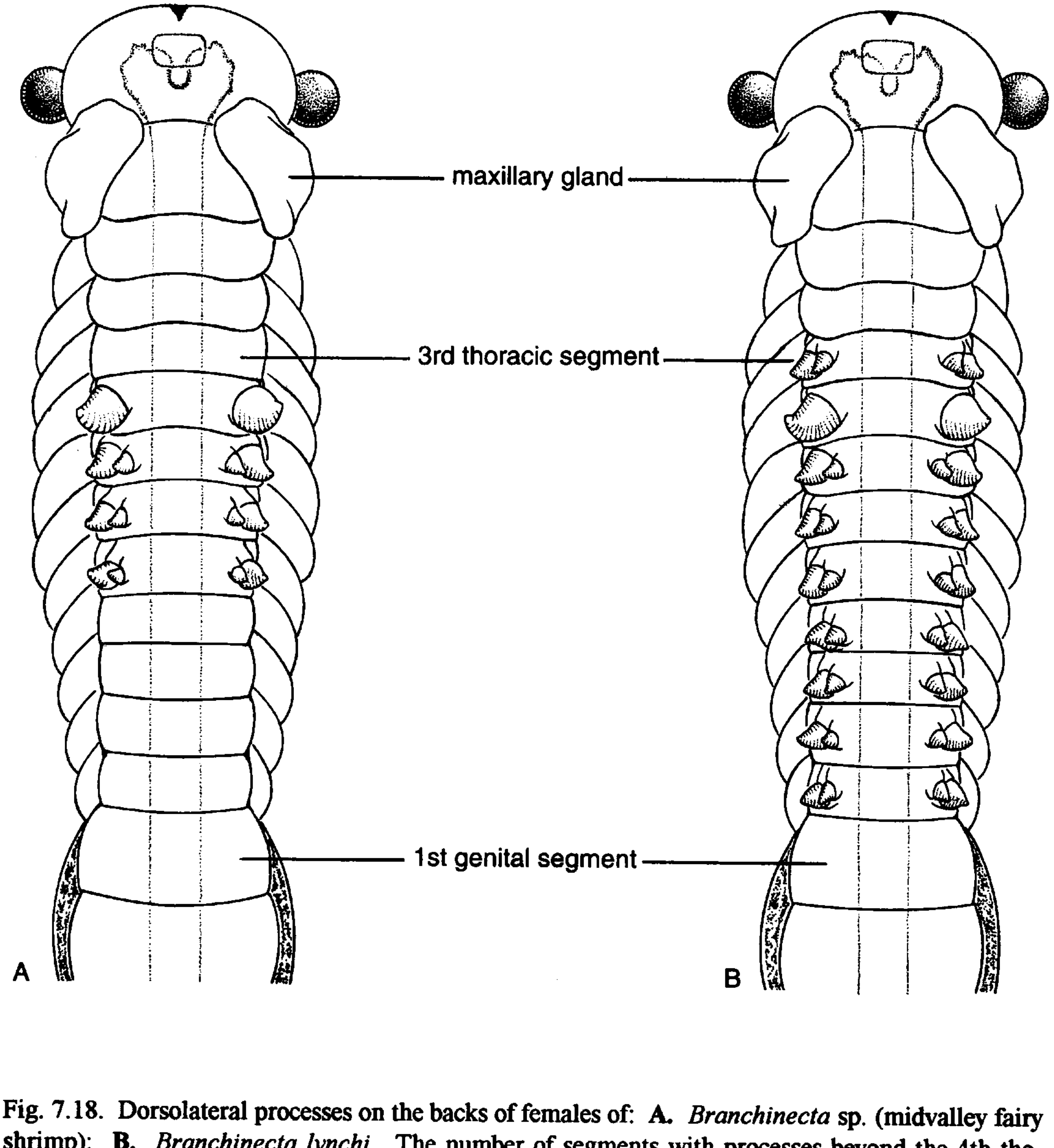


Fig. 7.18. Dorsolateral processes on the backs of females of: **A.** *Branchinecta* sp. (midvalley fairy shrimp); **B.** *Branchinecta lynchi*. The number of segments with processes beyond the 4th thoracic segment is variable in both species.

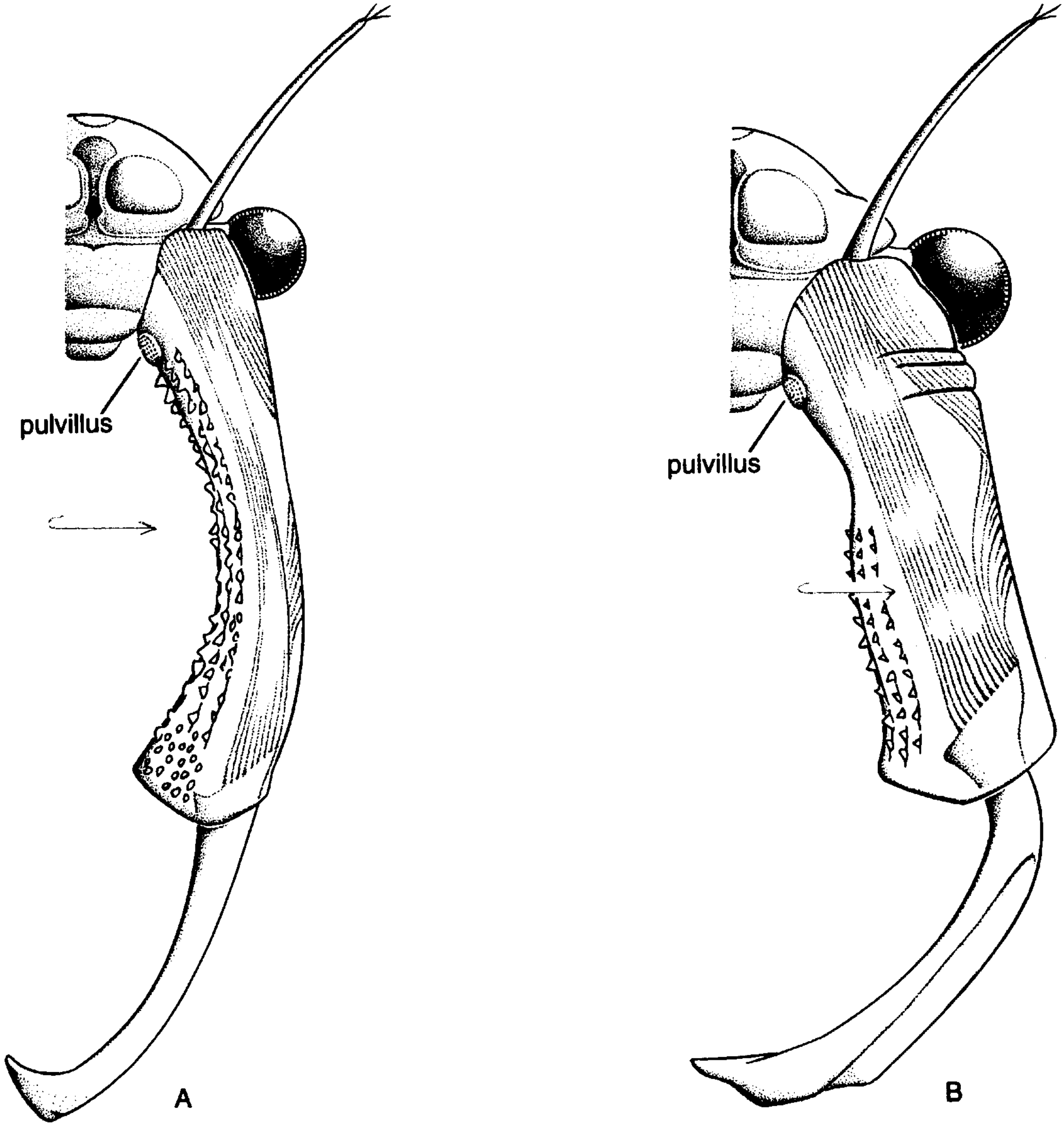


Fig. 7.19. **A.** *Branchinecta longiantenna*, frontal view of male's head (left half).
B. *Branchinecta dissimilis*, frontal view of male's head (left half). Antennae slightly rotated to expose more of the medial surface as indicated by arrows with a curled shaft.

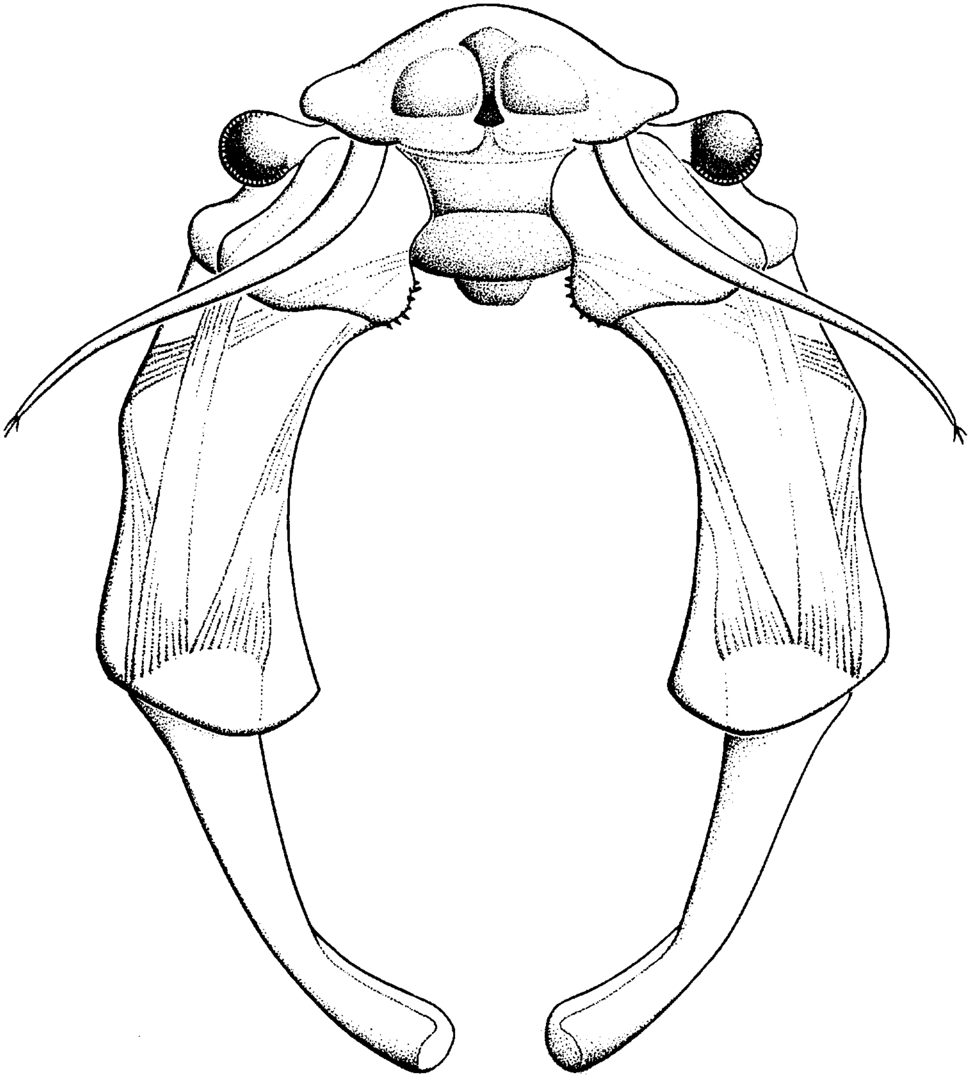


Fig. 7.20. *Branchinecta gigas*, frontal view of male's head. For side views of the whole body of both sexes, see Fig. 4.1 p. 73.

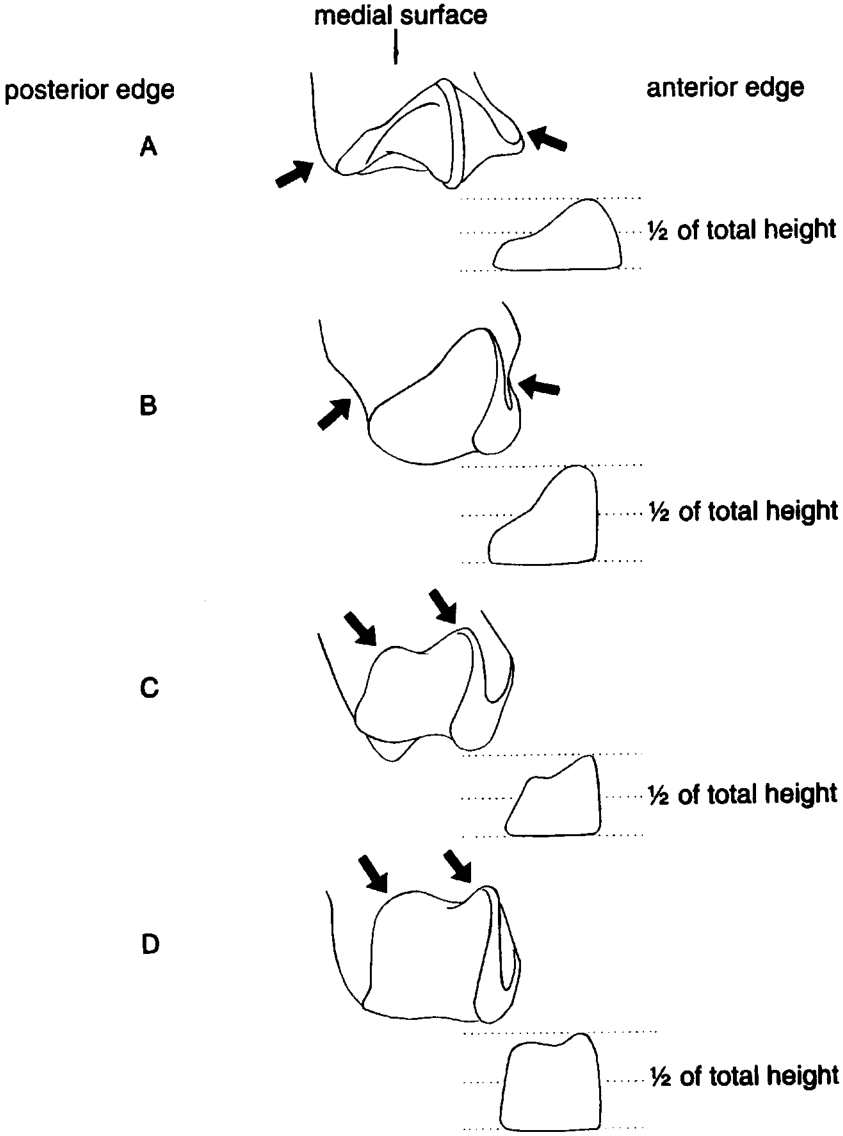


Fig. 7.21. Schematic comparing features at the distal ends of the second antennae of four species of *Branchinecta*. Outline drawings at right show which species have one or two humps above half the total height of the medially bent end. **A.** *Branchinecta sandiegonensis*, **B.** *B. lindahli*, **C.** *B.* sp. midvalley fairy shrimp, and **D.** *B. conservatio*.

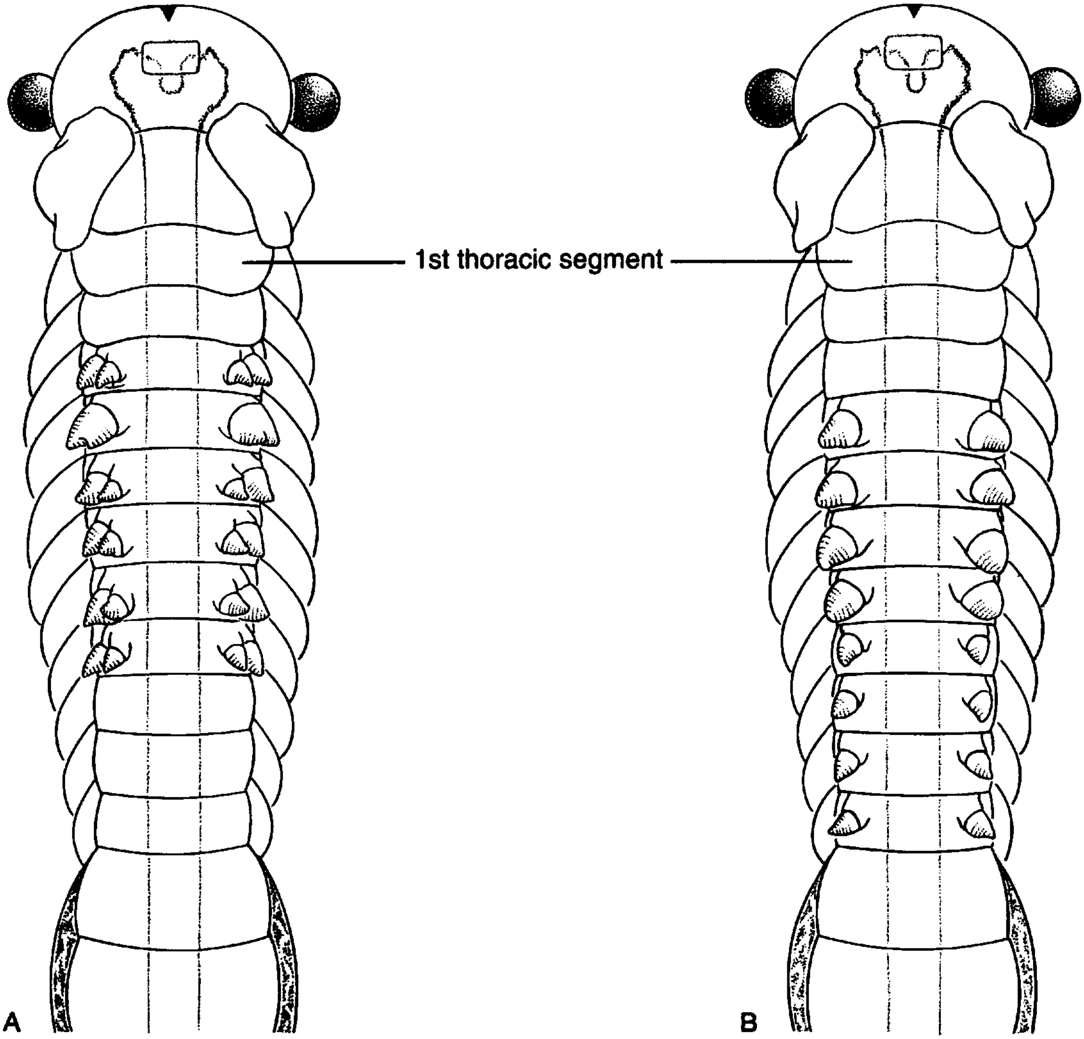


Fig. 7.22. Dorsolateral processes on the thorax of females of: **A.** *Branchinecta sandiegonensis*, and **B.** *Branchinecta lindahli*. The number of segments with processes is variable in both species.

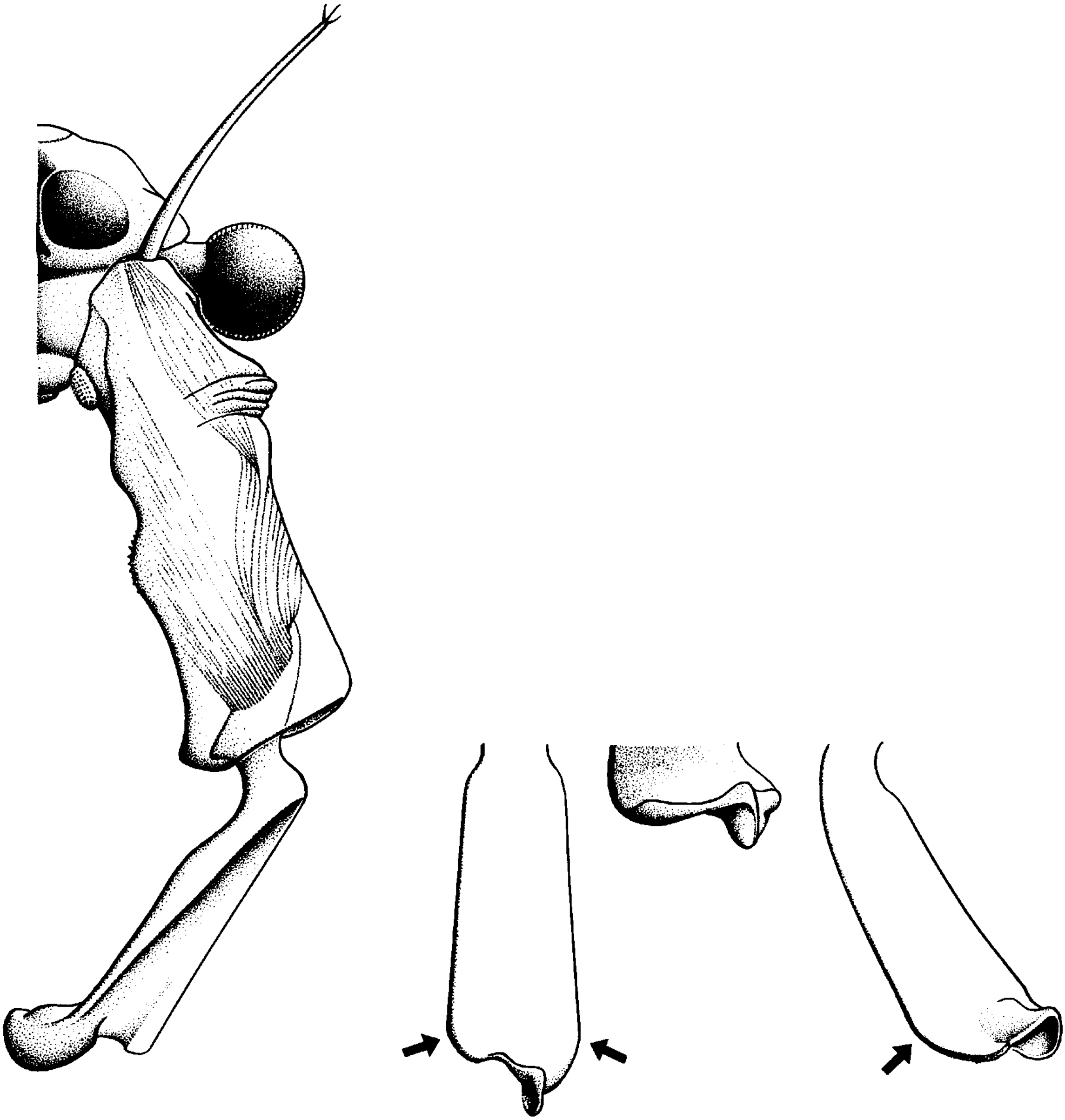


Fig. 7.23. *Branchinecta sandiegonensis*, frontal view of male's head (left half). Views of distal segment of second antenna from left to right: medial, tip in medioventral view, and posteromedial.

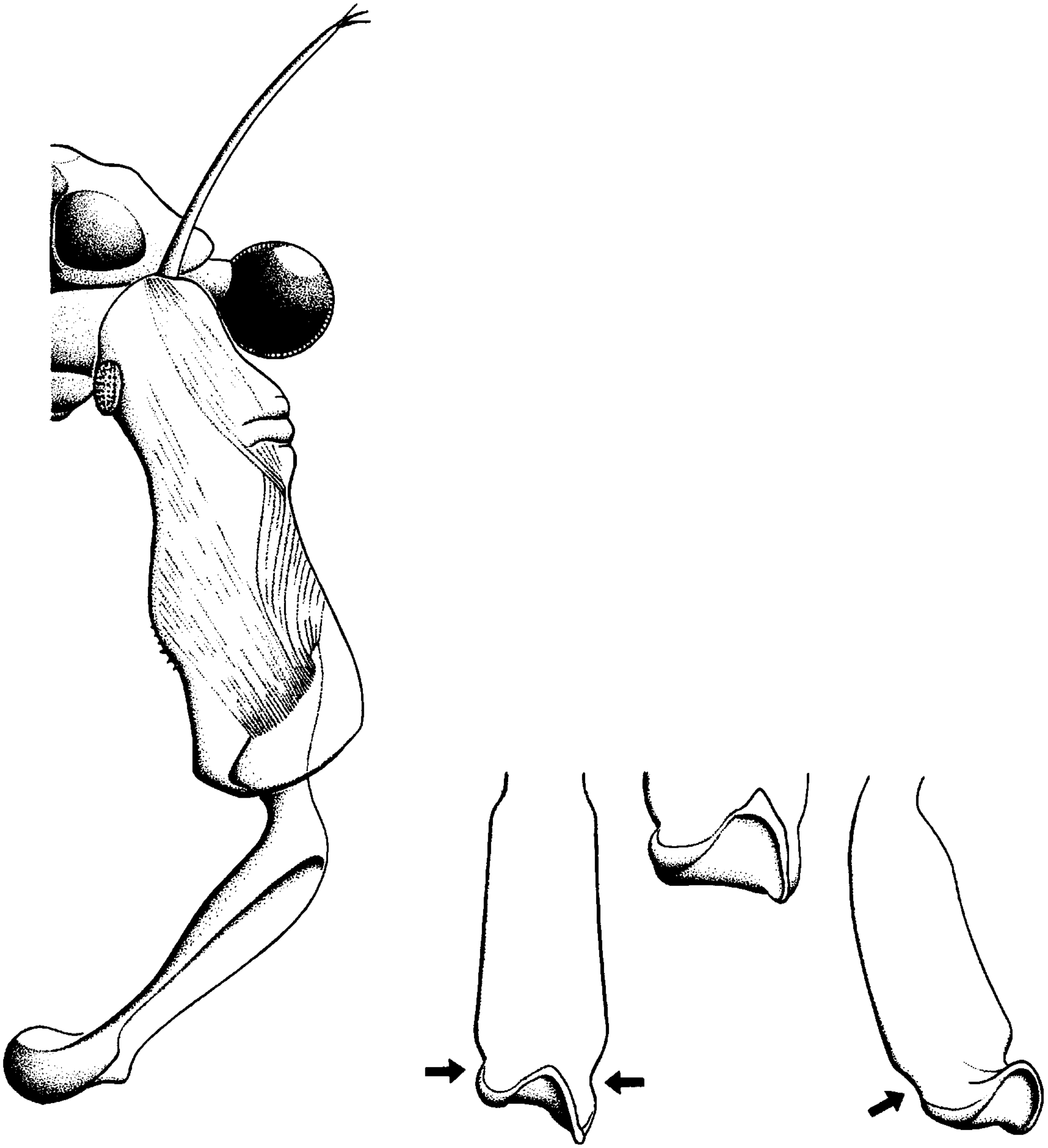


Fig. 7.24. *Branchinecta lindahli*, frontal view of male's head (left half). Views of distal segment of second antenna from left to right: medial, tip in medioventral view, and posteromedial.

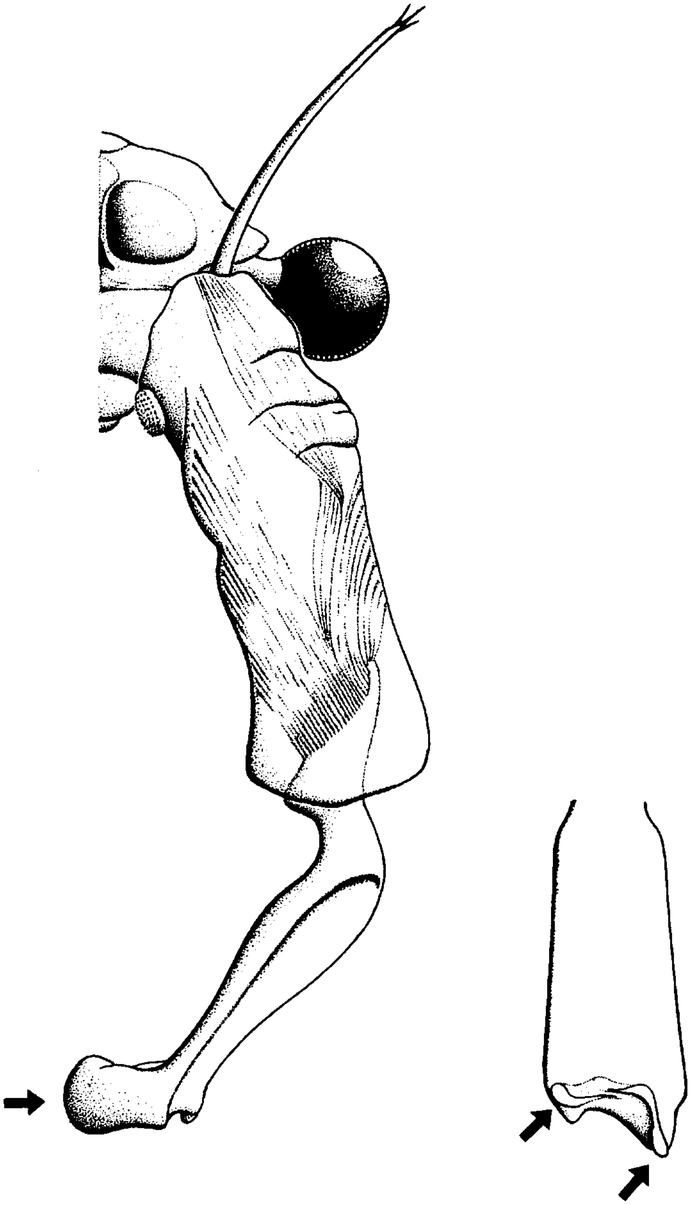


Fig. 7.25. *Branchinecta* sp. (midvalley fairy shrimp), frontal view of male's head (left half) and medial view of distal segment of second antenna. For view of medially bent tip, see Fig. 7.21C p. 160.

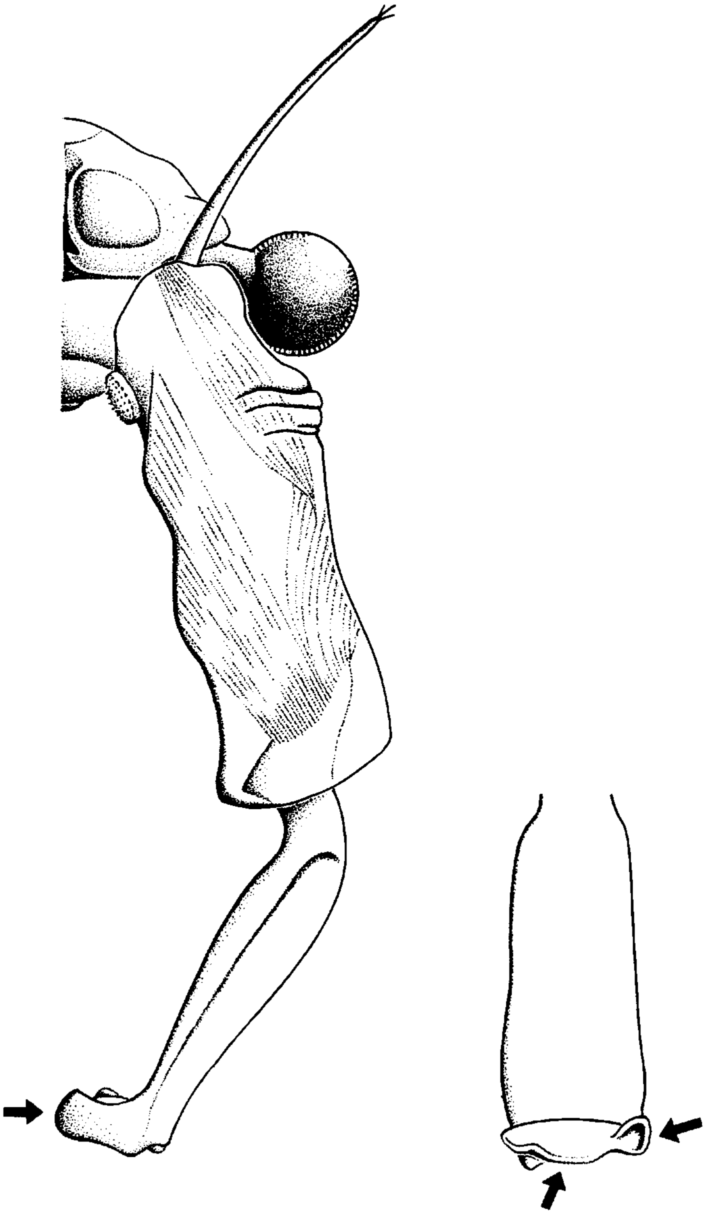


Fig. 7.26. *Branchinecta conservatio*, frontal view of male's head (left half) and medial view of distal segment of second antenna. For view of medially bent tip, see Fig. 7.21D p. 160.

Fig. 7.27. Short seta from the ventral surface and long seta from the medial surface of the cercopod of *Branchinecta gigas* (see Fig. 7.1 p. 140) (scale = 1 mm).

Appendix 1

Glossary

This glossary contains technical terms used in our book. If certain words are not located here, don't fret, they can be found in your favorite dictionary. An excellent source of definitions for terms used in ecology, evolution, and systematics is Lincoln *et al.* (1982).

abdomen: Body region posterior to the two fused genital segments; consists of 7 segments including the telson as the seventh and last segment (Figs. 1.2, 1.3). Many works incorrectly consider the genital segments as part of the abdomen; see Walossek (1993) for discussion.

aestival: Refers to aquatic habitats which, though they contain water all year, freeze completely during winter.

alkalinity: The measure, in ppm (parts per million), of the buffering capacity of water, or the amount of substances in water which can combine with, and therefore neutralize, acids. These materials are usually bicarbonate, carbonate, and hydroxide ions, but may include borates and silicates.

anostracan: A fairy shrimp; a member of the crustacean order Anostraca. Fairy shrimps that live in highly saline waters are often called brine shrimps.

antenna (pl. antennae): One member of the second pair of anterior appendages of the head. In male anostracans, they are typically two-jointed and function as claspers enabling the male to hold onto the female during mating (Figs. 1.2, 1.3). Syn: second antenna.

antennal appendage: A comparatively large outgrowth from the anteromedial surface near the proximal end of the basal joint of the antenna in males of some anostracan species (Figs. 7.9, 7.10, 7.12, 7.13, 7.14).

antennule: One member of the first pair of anterior appendages of the head. They are uniramous structures that are unjointed though they may appear superficially segmented. They may be tipped with sensory setae (Figs. 1.2, 1.3). Syn: first antenna.

anterior: A word denoting relative position, indicating that the structure referred to is placed closer to the front of the animal than another structure, or is situated on or toward the front; the fairy shrimp's head is at the anterior end of its body.

apophysis: In *Branchinecta*, an outgrowth projecting from the surface of the antenna near the proximal end of the basal segment (Figs. 7.15, 7.16).

astatic: As applied to a type of pool, refers to pools with unstable water levels.

biramous: Having two branches; for example, the fairy shrimp's swimming appendage, or phyllopod.

branchiopod: As a structure, a leg having a gill on it. Syn: phyllopod, thoracopod (Figs. 1.2, 1.3, 3.1). As a name, any member of the crustacean class Branchiopoda.

brood pouch: A sack-like structure extending from the ventral surface of the genital segments of female anostracans. It contains the ovisac, lateral pouches, and shell glands. In the past, it was often inappropriately referred to as the ovisac (Fig. 1.3).

cercopod: One of a pair of terminal appendages that articulate with the telson. The cercopods function as stabilizers and enhance the rudder-like function of the abdomen (Figs. 7.1, 7.2). Syn: caudal ramus, furcal ramus.

cheliform: Having a pincer-like shape.

clutch: A batch of cysts contained in the ovisac.

conductivity: A measure of the ability of water to conduct electricity, quantified in µmhos. This measure is directly related to the dissolved material (salinity) in the water.

cyst: A shell-covered dormant embryo. The "resting egg" expelled from the ovisac of a female anostracan. The stage of the life cycle adapted to survive unfavorable environmental conditions and nonaquatic phases of ephemeral pools; it also functions as a dispersal stage. Syn: resting egg, dormant egg (Fig. 3.2).

distal: Situated away from the midline of the body, or along an appendage away from its point of attachment to the body.

dorsal: A word denoting relative position, indicating that the structure referred to is placed on or toward the animal's back; in normal swimming the fairy shrimp is upside-down, its back faces the bottom of the pool.

endemic: Native to, and restricted to, a particular geographic region.

fecundity: Total cyst production during the life of a female.

finger: A term used for the ventral branch of the cheliform part of the distal outgrowth of the antennae on members of the genus *Streptocephalus* (Fig. 7.4)

frontal appendage: Median outgrowth from the front of the head (Fig. 7.3); formed during embryonic development by fusion of the right and left antennal appendages. Belk & Pereira (1982) proposed a method of labeling the branches which we follow in this work. Branches or other outgrowths of each right or left arm (primary branch of the frontal appendage) are assigned consecutive numbers starting with the most proximal branch or outgrowth. In addition to the number, a letter designates the insertion of the outgrowth. For example, if the first branch inserts on the medial side of the arm, it will be designated 1M. If the second is on the dorsal side of the arm, it will be labeled 2D. A third branch on the ventrolateral side would be 3VL.

frontal view: Looking in the face of the fairy shrimp. Syn: anterior view.

genital segments: Two fused body segments from the ventral surface of which arise the penes or brood pouch; they are the last two thoracic segments. In the species found in California, these are post-cephalic body segments 12 and 13 (Figs. 1.2, 1.3). Many works incorrectly consider the genital segments as part of the abdomen; see Walossek (1993) for discussion.

head: Anterior most region of the body (Figs. 1.2, 1.3). The head is formed by coalescence of 5 segments. It is superficially subdivided dorsally by a transverse mandibular groove. The head includes the stalked compound eyes, antennules, antennae, mandibles, maxillules, and maxillae.

hemolymph: Fluid filling body spaces (hemocoel) of arthropods. Analogous to blood and lymph of vertebrates in distributing nutrients etc.

hyperosmotic: Adjective meaning that the concentration of dissolved materials in body fluids is greater than in the surrounding aquatic medium. Syn: hypertonic.

hypo-osmotic: Adjective meaning that the concentration of dissolved materials in body fluids is less than in the surrounding aquatic medium. Syn: hypotonic.

ionic: An atom or group of atoms existing in a charged form (e.g., K^+, $HCO3^-$).

iso-osmotic: Adjective meaning that the concentration of dissolved materials in body fluids is equal to that in the surrounding aquatic medium. Syn: isotonic, isosmotic.

labrum: Upper lip; a large, puffy lobe covering the mouth and mandibles; attached anterior to the mouth (Figs. 1.2, 1.3, 7.12).

lamelliform: Thin and sheet-like in shape.

lateral: A word denoting relative position, indicating that the structure referred to is placed on or toward the side.

lateral abdominal ridge: In *Thamnocephalus*, a thin, plate-like, midlateral projection of the body wall emerging on abdominal segment one and increasing in width until it ends at the posterior edge of abdominal segment 6 (Fig. 7.1).

lateral pouch: A sack-like enlargement of each oviduct just in front of the ovisac. Mature, infertile eggs are stored here before being moved into the ovisac (Fig. 1.3). Passage from the lateral pouch into the ovisac is controlled by a "shutter" which is a mixture of cellular and fibrous components (Criel 1980). Syn: lateral oviducal pouch.

LD/50: A comparative laboratory measure of the conditions (e.g., temperature) at which 50% of the experimental organisms survive and 50% die by the end of a particular period of time (e.g., one hour, one day, etc.). This is a non-ecological measure because such conditions can probably not be tolerated long-term.

life cycle: For an individual, it is the sequence of events from its origin as a zygote to its death. At a more general level, it may be thought of as the stages an organism passes through between the production of gametes by one generation to the production of gametes by the next generation.

longevity: Number of days of life (birth to death).

low critical-level of oxygen: The level of dissolved oxygen in the habitat below which the organism cannot get enough O_2 to maintain metabolism and so dies.

maturity: For an anostracan female, when her first clutch appears in the brood pouch.

maxilla: (pl. maxillae): The second of two pairs of accessory mouth parts posterior to the mandibles. They lie between the maxillules and the first phyllopods (swimming appendages); 5th paired appendage of the head. Syn: second maxilla.

maxillule: First of two pairs of accessory mouth parts that lie between the mandibles and maxillae; 4th paired appendage of the head. Syn: first maxilla.

medial: A word denoting relative position, indicating that the structure referred to is placed closer to, toward, or in the midline of the body.

metanauplius: (pl. metanauplii): Postnaupliar crustacean larva distinguished from a nauplius by increasing addition of body segments and appendages, and more adult-like development of the appendages (Fig. 2.2).

µmho: A unit of measure of conductivity (the ability of water to conduct an electrical current). Because conductance is the inverse of resistance, the measure for which is the ohm, the unit for conductivity is dubbed the mho. A µmho = 0.001 mho.

nauplius: (pl. nauplii): The first larval stage of a crustacean. Its body consists only of a head and the telson. At this stage of development the head possesses only 3 pairs of appendages (antennules, antennae, and mandibles) and a single median eye called the nauplius eye (Fig. 2.2).

osmoconformer: An organism which is unable to regulate the dissolved material content of its blood and thus conforms to the osmotic concentration of its aquatic medium.

osmotic concentration: Concentration of dissolved materials in a solution (e.g., blood, water).

oviparous: Adjective for reproduction involving fertilized eggs that complete their development and hatch outside the body of the parent; egg-laying. This is the typical method used by fairy shrimps.

ovisac: A single, expandable, sack-like structure located centrally within the brood pouch (Fig. 1.3). Left and right lateral pouches and ducts of the shell glands attach to it. The ovisac receives semen during copulation. It functions as the site of fertilization, site of early embryonic development (in *Artemia*, some fertilized eggs may develop all the way to the nauplius larval stage), and site for application of shells to fertilized eggs thus completing their transformation into cysts. Cysts are expelled from the ovisac through a posterior gonopore. In *Artemia*, nauplii also leave via the posterior gonopore during ovoviviparous reproduction.

ovoviviparous: Adjective for reproduction involving fertilized eggs that complete development and hatch within the mother in a specialized parental structure such as the ovisac of anostracans. Members of the genus *Artemia* are the only anostracans able to use this method of reproduction.

phyllopod: As a structure, one of a pair of basically biramous and flattened, leaf-like, swimming appendages on the ventral surface of a thoracic segment. Syn: branchiopod, thoracopod (Figs. 1.2, 1.3, 3.1). As a common name, used for members of the three large branchiopod orders: Anostraca, Conchostraca, and Notostraca. This use derives from the formal grouping of these three taxa into a single taxon, Phyllopoda, by the 19th century biologist G. O. Sars, a grouping no longer considered taxonomically valid.

posterior: A word denoting relative position, indicating that the structure referred to is placed closer to, or is situated on or toward the rear of the animal; the cercopods are at the posterior end of the fairy shrimp's body.

proximal: A word denoting relative position, indicating that the structure referred to is situated toward the point of attachment.

pulvillus (pl. pulvilli): In some species of *Branchinecta*, a mound-like area covered with minute cuticular (exoskeletal) spinules, and found near the proximal end of the basal segment of the antennae (Figs. 7.15, 7.19, 7.23, 7.24, 7.25, 7.26, and couplet 15 p. 137). A scanning electron micrograph may be seen in Fugate (1993; fig. 10a).

saltern: An artificial diked basin where salt water is evaporated by the sun leaving only the minerals.

subterminal lateral lamella: In *Streptocephalus*, a ventrally directed sheet-like expansion of the ventrolateral surface of the finger (Fig. 7.6). The anterior edge of the lateral lamella terminates just back of the tip of the finger, thus subterminal. A scanning electron micrograph may be seen in Maeda-Martinez *et al.* 1995a; fig. 13c).

TDS (total dissolved solids): A measure, in ppm, of the amount of dissolved material in water.

telson: Last body segment; its anterior region is the growth zone which buds off the postcephalic segments during development from nauplius larva to adult. A terminal pair of cercopods extends posteriorly from this segment in adults (Figs. 1.2, 1.3, 7.1, 7.2).

thorax: The postcephalic region of the body composed of the leg-bearing segments, 11 in California species, and the two fused genital segments (Figs. 1.2, 1.3). Many works incorrectly consider the genital segments as part of the abdomen; see Walossek (1993) for discussion.

trunk: Region of body posterior to the head. The adult anostracan trunk consists of two main divisions, thorax and abdomen (Figs. 1.2, 1.3).

turbidity: A measure of the amount of suspended particles (e.g., clay) in water. When these are abundant, the water is opaque and said to be "muddy" or highly turbid.

ventral: A word denoting relative position, indicating that the structure referred to is placed closer to, or is situated on or toward, the leg-bearing surface of the fairy shrimp's body; in normal swimming the legs are directed upward toward the surface of the pool.

Fig. Ap. 1.1. Clyde collecting fairy shrimps.

Appendix 2

Collecting, Preservation, and Storage

If you were to see Denton and Clyde collecting fairy shrimps, you would note they carry dip nets while wading around in pools, playas, or muddy stock tanks. That's about all there is to it folks; so get yourself a net, perhaps some hip boots (no problem if you are also a fly fisherperson), wade on in, and net away! Well, OK, that description is a bit oversimplified, but you get the idea.

Certainly **dip-netting** is the most common means of collecting fairy shrimps. The standard instrument has a wooden handle about 1.3 m long. To this is anchored a metal ring, usually 25 cm in diameter, that supports a bag about 25 cm deep. The bag's cotton or nylon fabric has a 1-2 mm mesh size. Of course dimensions of any of these features can be altered to satisfy specific collecting needs. For example, a much finer netting must be utilized when collecting larvae; a longer handle can be employed for reaching to greater distances, and when "mucking up" a pool by wading is undesirable. If the site is a puddle, a small aquarium net is probably best. Once entrapped, shrimps can be lifted out with fingers, though this is best done with blunt forceps, or the contained materials can be emptied into a pan or jar of water for observation.

Seldom can you stride up to a pool, spot an anostracan or two, and casually reach out and dip them up, for fairy shrimps, like other animals, utilize escape movements when threatened, including by you. Those escape movements may have already removed them from the immediate vicinity by the time you reach pool's edge, for they probably see you before you see them. Admittedly, some species are less flighty than others, so you may dip in and come up satisfied, but at other times you may go wanting. If that's the case, don't leave yet, for "over there" similar actions could result in a passel of wriggling shrimps in your net.

After spending some time with anostracans, you will become more familiar with their habits, and will be better able to judge where in their habitat individuals have gone to escape, or where they are more likely to spend their time.

For example, a number of species do not just cruise the pool, at least in daytime. Rather, they may "hang out" around vegetation where shade offers cooler water, the plants provide protection, and where concentration of small animal foods (e.g., protozoans and rotifers) will undoubtedly be greater. If the habitat is not homogeneous in temperature, then the cooler water lies deeper; so at the warmer times of day, fairy shrimps may congregate in bottom waters. Of course bottom water would also be the favored place for those which include scraping in their feeding activities. Additionally, remember that fertilized females of some species retreat to the depths of the pool, while the males cruise nearer the surface. The point is, to be fully successful in your collecting activities, you must sample the various portions of the habitat, particularly near the bottom and near and amongst vegetation.

Merely dipping a net into a pool is usually not a very effective way to catch fairy shrimps. Typically, the net is "swept" back and forth through the water at any desired depth, an action which entraps whatever does not or has not removed itself from harm's way. Sweeping back and forth several times very close to a particular piece of the bottom will stir up some of the bottom materials and possibly some fairy shrimps, thus the return sweeps will capture those individuals that were rousted out. Of course, if you sweep too close to a detritus-covered bottom, a massive amount of debris may appear in your net and you will never find the organisms that are included amongst it.

As in driving a nail or playing the violin, practice is the key to developing a successful netting technique! And though you might say "don't make a simple procedure more complex than it is", we suspect you will find our comments pretty close to the mark. We illustrate this truth with a real-life drama described by Richard Hill. Richard's first sweeps in a pool on the Modoc Plateau were unsuccessful, so he began gazing into the water to see what could be seen. After awhile, individuals of what turned out to be *Branchinecta coloradensis* began emerging from among mats of vegetation covering the bottom. When he tried to net them, they darted downward and disappeared once more. After a good deal of patience, and practice, Richard became a rather adept fairy shrimp stalker! During his next outing, he directed several colleagues to rest their nets on the bottom of the pool and sweep rapidly upward when the shrimps made their debut. After awhile, Richard had collected a number of individuals, while his friends, lacking practice, and thus technique, had few amongst them.

A different technique, possibly also useful for collecting anostracans with *B. coloradensis*-like behaviors, was sometimes practiced by Clyde in Mojave Desert playa lakes. Playas are so muddy that you and the fairy shrimps will not see each other. However, sweeping a net back and forth through these milk-shake-like universes may result in amassing fewer shrimps than hoped. Why? Perhaps the species living in such places sense you coming via the waves sent out from your advancing legs and net, and take advantage of the official fairy shrimp escape behavior. Clyde often had greater success by walking in reverse while sweeping the net back and forth over the path just traversed, for his passage scared up the animals that the sweeping net then sieved out. Once collected, fairy shrimps may be transported in a bucket of habitat water if the animals are not too crowded, or placed in small containers with tight-fitting lids and preserved in 70-95% alcohol.

A collecting technique that has rather recently come into favor is **dry sampling**. The method involves taking soil from a dry pool bed, and sorting out any anostracan cysts that might be present. The amassed cysts are then either identified from their surface ornamentations (a job for specialists), or hatched, with the hatchlings being raised until maturity allows identification. This method offers several advantages. One is that a particular pool does not have to be sampled within the narrow time frame when animals are large enough for the collector to note their presence, and mature enough to distinguish the species. Also, because the pool is dry and the aquatic vegetation dead, the habitat will not be torn up by a collector moving through it. A disadvantage is that cysts have been found even where no pools exist; that is, their agents of distribution have been successful, but the habitat is inhospitable. Also, just because a cyst is found in a pool basin does not mean that the larval or adult organism can actually survive there.

How does one sample dry soil? Employing a hand trowel to remove the top inch or so of sediment will do the trick, but it is not at all quantitative. Clyde and his students designed a simple device that covers a certain surface area and takes a known volume of the top inch of compact sediments. Hardware stores sell various sizes of hole saws for use with hand drills and drill presses. We merely welded a T-shaped, foot-long handle made from water pipe to the back of the cup of a hole saw. The handle allowed us to rotate the saw into sediments near the lowest portion of the basin and lift out a 25-mm-thick core. Volume of the sample is determined by the diameter of the hole saw used. Our collections were stored in plastic sandwich bags until analyzed. Analysis involves placing a sample in a shallow tray, adding water, waiting for the hard soil to crumble, then washing the material in a sieve with a mesh size (about 0.15 mm) that will catch all cysts. The sieve is then placed in a pan with a water level that barely covers the screen. The items caught by the screen are scanned with the aid of a dissecting microscope, and the cysts amongst them are removed with a pipette. Depending on the information desired, the different types of cysts can be counted and their numbers related to the volume of, or surface area covered by, the sampler.

Keeping in mind some of the pros and cons of the methods we have mentioned, it's now up to you to choose the one that best meets the purpose for sampling your puddle, pool, or playa. By the way, remember, four California species are listed as endangered and one as threatened, and a permit from the USFWS is required to collect or disturb them.

If you do not yet have all the collecting gear you need, the following is an abbreviated list of **sources for supplies:** BioQuip Products, 17803 LaSalle Ave., Gardena, CA 90248; Carolina Biological Supply Co., 2700 York Road, Burlington, NC 27215; The Biology Store, 275 Pauma Place, Escondido, CA 92029; Ward's Natural Science, P.O. Box 5010, San Luis Obispo, CA 93403; your local aquarium shop; your local hardware store.

If you are into making collections of animals for future reference or study, they will require preservation. All that is needed are some bottles with tightly fitting lids and a supply of 70% isopropyl or ethyl alcohol. To avoid having specimens contort into odd shapes when they succumb, it is best to slowly relax them by adding small amounts of alcohol to the water in the collecting bottles. Starting the process with CO_2 is even better for it will anesthetizes your captives. A handy source of this gas is a bottle of club soda; add it slowly and in small amounts. Once the animals are immobile, transfer them to fresh preservative for long-term storage because the body fluids, plus water adhering to their surfaces, may dilute the 70% alcohol to such an extent that the shrimps will soon become "mush".

Careful labeling and record keeping are a very important part of collecting. So write on good quality cotton fiber paper, using alcohol-stable ink or pencil, at least the date, the name of the individual who scooped the creatures from their aquatic world, and, as precisely as possible, the location of your collection. Place this label in the storage bottle with your specimens. The collection will be even more valuable if you are able to describe the pool and its setting (see Chapter 4 for ideas), and make environmental measures (e.g., temperature, TDS)! Such information can be recorded in a notebook coded with a reference number, and this number should be inscribed on the label you place in the collection bottle as well. In addition, Denton typically takes one or more photographs of each collecting site as an acknowledgment that "a picture is worth a thousand words" of habitat description. It also may be a source of information for data not recorded, as well as help in jogging the memory about the place at a later date. Don't forget to record the reference number on the picture(s)!

Store your collections in a safe, cool, place, preferably in the dark. And, remember to check the bottles periodically to guard against having your specimens destroyed by drying. Alcohol, like Houdini, is an escape artist from even the tightest lid.

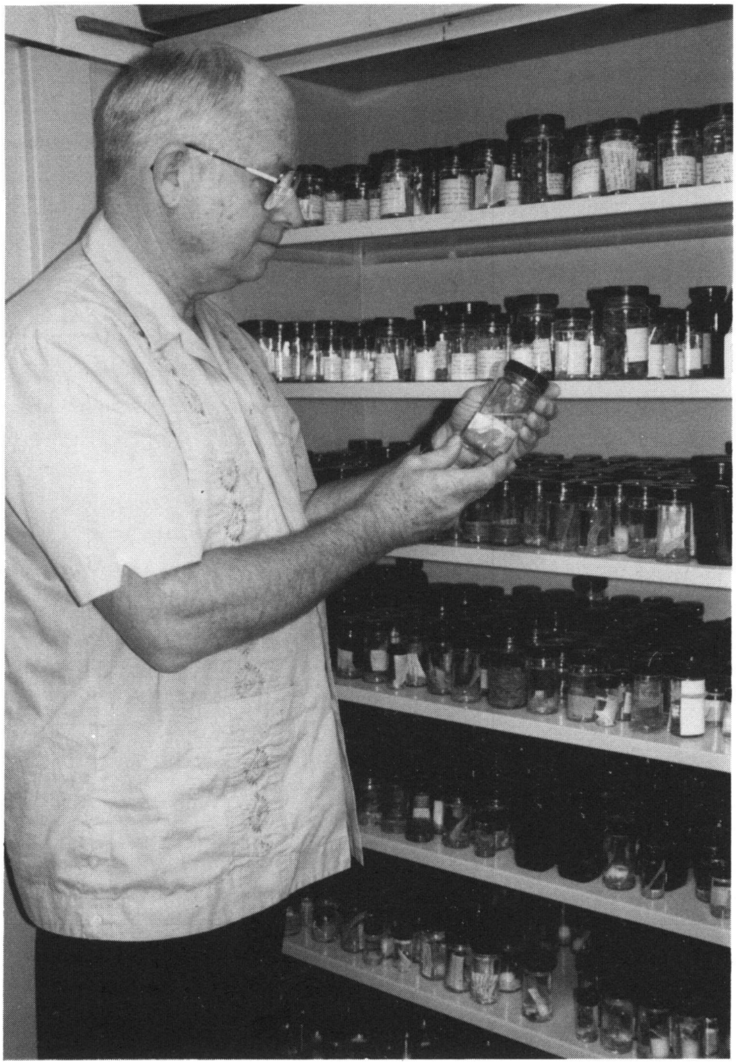


Fig. Ap. 2.1. Denton tending his fairy shrimp collection.

Appendix 3

Hatching and Rearing

Back in the bowels of this book we noted that if one takes dry soil samples from a pool basin, preferably at its deepest point, one can then "just add water and stir". In a day or two nauplii appear if their cysts are present. O.K., so they won't always appear, but you get the idea.

If your desire is to hatch and rear fairy shrimps the hi-tech way, you should get some guidance from Brendonck *et al.* (1990) and Maeda-Martinez *et al.* (1995c). If you merely want to see what an anostracan is like, buy some *Artemia* cysts at the local aquarium shop and follow directions on the container. Should you wish to find out what's in your favorite pool, or gather together sufficient animals for a study of behavior or some other biological phenomenon, then several low-tech approaches are available.

Most any broad and shallow container can serve as a hatching and rearing vessel, but it needs to be compatible with your project and available space. Plastic kiddy wading pools, perhaps 1.0-1.5 m in diameter, serve well outside. Once a thin layer of soil is added, nature is allowed to take its course. When rains come, and conditions are suitable, hatching happens. Obviously, if this method is chosen you are not in control of temperature, timing, or other conditions.

In the kitchen, basement, or lab, "aquaria" holding 1-2 gallons of fluid work fine. They are small enough to move easily from place to place or temperature to temperature as desired or necessary. Spread a thin layer of soil on the aquarium bottom, then add distilled, deionized, or rain water. Remember, most pools initially fill from rain, snow-melt, or flash-floods, sources **low** in TDS. However, salts may leach from soils to ultimately make the water salty, a situation which commonly turns off hatching. Tap water is usually unsatisfactory, either because it has high TDS, or because it contains chlorine or chloramine, disinfectants which may inhibit hatching or kill emerging nauplii.

As you have read time and again in Chapter 5, temperature is an important environmental cue for coaxing larvae from their dormant state. You can guess what temperatures might need to be approximated given the sample's origin. Try incubation at about 3-5°C if it came from the mountains or high desert. If from California grasslands, 10° is a good level at which to start. Should it be a Mojave Desert sample, you might try anywhere from 5-25°C, for cysts of both winter and summer species may be in your soil, and these of course hatch at different temperatures. To play it safe, containers placed at about 5, 10, and 25°C will give you the greatest chance of coaxing forth some larvae.

If you have an aquarium aerator, prudence says use it to keep oxygen at elevated levels. Remember, hatching is a highly energetic process, so emerging larvae need considerable O_2.

Growth is rapid, particularly if you raise (slowly) the temperature after hatching, so a continuous food supply is necessary. Powdered yeast and powdered aquarium-fish food both seem to do the job. Do **not** add too much, for an unused excess will decay, putrefy the water, and quite likely kill your developing shrimps.

Just a word to temper unabashed optimism for success. Although the above procedures will result in hatching cysts and growing larvae of many, if not most, fairy shrimps, individuals of a few species have either not yet been coaxed from their cysts, emerged only grudgingly, or no attempt has been made to get them out and rear them. Should you end up with difficult-to-hatch cysts, we wish you well in finding a simple recipe that cajoles larvae into making their debut. Go for it!

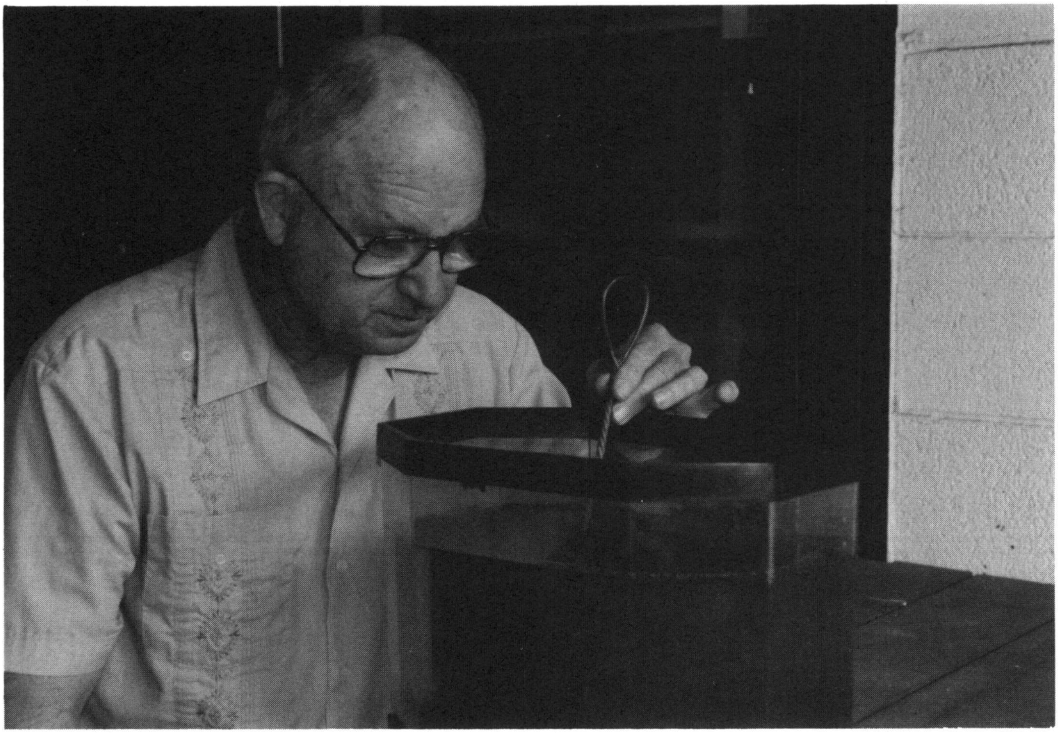


Fig. Ap. 3.1. Denton checking a culture of *Artemia franciscana*.

Appendix 4

Classification of Fairy Shrimps and Some of Their Arthropod Relatives

Taxonomy is the science of naming species. Classification is the attempt to place these species into ever larger groupings that demonstrate phylogenetic relatedness. Because new information is constantly appearing, there is often an on-going reshuffling in and of these larger categories – a reshuffling that sometimes creates disagreement among specialists (fairy shrimps and their relatives are not immune to this scenario). Although some scientist may have published different names or groupings at one time or another, we use Belk and Brtek's (1995) classification of the Anostraca, with the addition of two newly described genera (Brendonck 1995; Hamer & Brendonck 1995). For Conchostraca, we follow Martin and Belk (1988) and Sassaman (1995). The two genera of Notostraca are well accepted, but the species need considerable reevaluation. For those of you with geographical interests, we have indicated where on this small world of ours these "Large Branchiopods" dwell. The additional categories included are highly selected, and are offered only to give you an idea of where the other arthropods mentioned in this book "fit" into the scheme of things, at least as portrayed by Ruppert and Barnes (1994). Taxa are listed in alphabetical order.

Phylum: Arthropoda

- Sub-phylum: Crustacea
  - Class: Branchiopoda
    - Order: Anostraca
      - Family: Artemiidae
        - Genus: *Artemia* (Eurasia, the Americas, Africa, Australia)
      - Family: Branchinectidae
        - Genus: *Branchinecta* (Eurasia, the Americas, Antarctica)
      - Family: Branchipodidae
        - Genus: *Branchipus* (Europe, Africa, Pakistan)
        - Genus: *Branchipodopsis* (Africa, Asia, Armenia)
        - Genus: *Metabranchipus* (Somalia)
        - Genus: *Parartemia* (Australia)
        - Genus: *Pumilibranchipus* (Namibia)
        - Genus: *Rhinobranchipus* (South Africa)
        - Genus: *Tanymastigites* (North Africa)
        - Genus: *Tanymastix* (Europe, North Africa)

Family: Chirocephalidae
Genus: *Artemiopsis* (Russia, U.S.A. [Alaska], Canada)
Genus: *Branchinectella* (Eurasia, North Africa)
Genus: *Chirocephalus* (Eurasia, North Africa)
Genus: *Eubranchipus* (Eurasia, Japan, North America)
Genus: *Phallocryptus* (Argentina)
Family: Linderiellidae
Genus: *Dexteria* (U.S.A. [Florida])
Genus: *Linderiella* (France, Spain, Morocco, U.S.A. [California])
Family: Polyartemiidae
Genus: *Polyartemia* (arctic & subarctic Eurasia)
Genus: *Polyartemiella* (arctic & subarctic North America, Russia)
Family: Streptocephalidae
Genus: *Streptocephalus* (Africa, North America, Eurasia, Australia)
Family: Thamnocephalidae
Genus: *Branchinella* (Australia, Eurasia, Japan, Africa, U.S.A., Paraguay)
Genus: *Dendrocephalus* (South America, Costa Rica)
Genus: *Thamnocephalus* (U.S.A., Mexico, Venezuela)
Order: Conchostraca = Diplostraca (Martin & Davis 2001)
Sub-order: Laevicaudata
Family: Lynceidae
Genus: *Lynceus* (Eurasia, Africa, Japan, the Americas, Australia)
Genus: *Lynceiopsis* (Africa)
Genus: *Paralimnetis* (South America, Mexico, U.S.A. [Texas])
Sub-order: Spinicaudata
Family: Cyclestheriidae
Genus: *Cyclestheria* (tropical and subtropical regions of all continents except Antarctica)
Genus: *Paracyclestheria* (China [Yunnan Province])
Family: Cyzicidae
Genus: *Caenestheria* (Eurasia, Africa, Australia)
Genus: *Cyzicus* (Eurasia, Africa, the Americas, Australia)
Genus: *Eocyzicus* (Eurasia, Africa, North America)
Family: Leptestheriidae
Genus: *Eoleptestheria* (Eurasia, Africa)
Genus: *Leptestheria* (Eurasia, Africa, the Americas)
Genus: *Leptestheriella* (India)
Genus: *Maghrebestheria* (Morocco)
Genus: *Sewellestheria* (India)

Family: Limnadiidae
    Genus: *Eulimnadia* (Eurasia, Africa, the Americas, Australia)
    Genus: *Imnadia* (Europe)
    Genus: *Limnadia* (Eurasia, Africa, the Americas, Australia)
    Genus: *Limnadiopsis* (Australia)
    Genus: *Limnadiopsium* (Australia)
    Genus: *Metalimnadia* (South America)
Order: Notostraca
  Family: Triopsidae
    Genus: *Lepidurus* (Eurasia, Africa, the Americas, Australia)
    Genus: *Triops* (Eurasia, Africa, the Americas, Australia)

The following list of arthropod relatives is highly selected

- Sub-phylum: Crustacea (included again for clarity)
  - Class: Branchiopoda
    - Order: "Cladocera" (water fleas) [for current classification see Fryer 1987]
  - Class: Cirripedia (barnacles)
  - Class: Malacostraca
    - Order: Isopoda (sowbugs, pillbugs, roly-polys)
    - Order: Decapoda (shrimps, lobsters, crabs)
- Sub-phylum: Uniramia
  - Class: Chilopoda (centipedes)
  - Class: Insecta (insects)
- Sub-phylum: Chelicerata
  - Class: Arachnida
    - Order: Scorpiones (scorpions)
    - Order: Araneae (spiders)

Last Minute News — Fairy Shrimp Science Swims On

And Now There Are 25 Species Found in California

With ice still on the pools in March of 1998, Christopher Rogers captured an unnamed fairy shrimp in Modoc Co., California. He found the same species in Utah also. The animal turned out to be a new species first discovered in Oregon by Dr. Michael Fugate. Michael and Christopher are working on a co-authored description of this new form they call the winter fairy shrimp.

Early in 1999, Christopher Rogers called Denton to report that the distal segments of the antennae of *Branchinecta dissimilis* he collected in Modoc Co. looked very different from what we were calling *B. dissimilis*. When these two workers got together and examined Lynch's type material borrowed from the Smithsonian, they discovered that they were dealing with two species differing only in the morphology of the distal segment of the antenna. The specimens from Modoc Co. proved to be *B. dissimilis*. Those taken in the mountains from Alpine Co. south to Fresno and Inyo counties are a new species. Denton and Christopher are working on a description of this new anostracan they are calling the mountain fairy shrimp. Use this information as you read about *Branchinecta dissimilis* on pages 87-88 and look at its distribution on Map 5.5, page 121. The dots in Shasta and Lassen counties on Map 5.5 are incorrect and should be ignored. The key will identify both *B. dissimilis* and the mountain fairy shrimp as *B. dissimilis*. So far, *B. dissimilis* is known in California only from Modoc Co.

Branchinecta lynchi *Now Found in Oregon*

Brent Helm collected *Branchinecta lynchi* near Medford, Jackson County, Oregon in 1998. The area is a vernal pool landscape similar to the Central Valley of California.

Branchinecta mackini *Not Found East of the Continental Divide*

Detailed comparative studies by Denton revealed that populations east of the Continental Divide that were being called *B. mackini* are in fact an unrecognized new species. Dr. James Lynch, of *B. lynchi* fame, observed that there was something different about the eastern populations when he was ask to look at specimens from Alberta and Saskatchewan by Dr. Richard Hartland-Rowe (1965). Lynch suggested to Hartland-Rowe that the specimens appeared to him to be a distinct subspecies. Richard passed on taking up the challenge of testing this hypothesis and proposing a new subspecies name. Denton studied specimens from British Columbia to Baja California, and from Alberta, Wyoming, and Minnesota. The results are in a nearly completed manuscript naming the eastern alkali fairy shrimp in honor of Canadian naturalist and friend Ken Reading.

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Table of conversion factors

1 μm = 1/1,000 mm

1 mm = 0.04 inches

1 cm = 10 mm

1 m = 39.37 inches

1 km = 0.62 miles

1 ha = 2.47 acres

1 mg/L = 1 ppm

1 L = 1.06 quarts

μmhos/cm (conductivity) x 0.65 ≈ ppm TDS

mOsm/L (salinity) x 50 ≈ μmhos/cm (conductivity)

mOsm/L (salinity) x 32.5 ≈ ppm TDS

Cover Pictures

Front Cover:

Upper right. This female *Linderiella occidentalis* is ready to mate; note the cluster of eggs in her left lateral pouch and the enlarged shell glands filling most of her brood pouch. Check Fig. 1.3, p. 3 if you need help in finding these structures. Also, compare her red eyes with the black eyes of the fairy shrimps in the picture below. Photo by Larry Serpa.

Lower left. Explore the internal anatomy of both males and females in this shot of *Branchinecta longiantenna.* Figures 1.2 and 1.3 (pp. 2 & 3) are available to aid in your discovery. Note the exceptionally long antennae on the male; these are the stimulus for the name of this species. Photo by Larry Serpa.

Back Cover:

Upper right. Look closely at the many beautiful colors in this male of *Eubranchipus serratus.* His cercopods just brush the cyst filled brood pouch of a female *E. serratus* in the lower corner of the picture. The two small red animals are copepods. Photo by Richard Hill.

Lower right. This female *Streptocephalus woottoni* is practicing the alternate feeding method of scraping. She has her back toward the water's surface which is upside down for a fairy shrimp. Note the dark blue-green color associated with her reproductive structures. You may read about the limited information we have concerning such color development in the section on "Color" in Chapter 2 (pp. 27-30). Photo by Larry Serpa.

Upper left. Your authors posing beside a created temporary pool at the Bernard Biological Field Station of The Claremont Colleges. Photo by Clyde with the aid of a shutter-release timer, and a lot of running back and forth.

About the Authors

Denton Belk is a native of Texas and lives in San Antonio. For his M.A. (University of Texas at Austin) he studied ecology of the clam shrimp *Eulimnadia antlei*. He earned a Ph.D. from Arizona State University for work on the zoogeography of Arizona fairy shrimps and a key to North American species. Denton is chair of the Inland Water Crustacean Specialists Group, Species Survival Commission of IUCN, the International Union for the Conservation of Nature; Adjunct Professor of Biology, Our Lady of the Lake University of San Antonio; and Research Associate, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution. Denton belongs to 8 professional societies, and published over 50 technical papers, primarily on crustacean biology and taxonomy, and authored or coauthored descriptions for 15 species of fairy shrimps (4 from California), and 5 species of clam shrimps.

Clyde Eriksen is a native of southern California, where he resides in winter, but retreats to his Montana mountain cabin in summer. He received his M.S. from the University of Illinois in zoology, physiology, and entomology, and his Ph.D. in zoology and botany at the University of Michigan. Clyde recently retired from The Claremont Colleges where he was Director of the Bernard Biological Field Station, and Professor of Biology for more that 25 years. Clyde has reviewed for 12 technical journals, and belonged to 5 professional organizations. He is known for the chapter, Aquatic Insect Respiration (with V. Resh and G. Lamberti), in Merritt and Cummins' "An Introduction to the Aquatic Insects of North America". Clyde works with government agencies on conservation issues and published over 40 papers on invertebrate physiology, fisheries, water quality, ecology, and land management.

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