

INTRODUCTION

Dragonflies and damselflies make up the insect order Odonata.

They are found worldwide, except for Antarctica. Most treatments recognize three suborders within the Odonata. The names of these groups derive from the relative shapes of the fore- and hindwings. The dragonflies belong to the suborder Anisoptera, the hindwings of which are broader than the forewings. The damselflies, suborder Zygoptera, have fore- and hindwings of the same shape. The members of a third suborder, the Anisozygoptera, are often called “living fossils” and can be recognized by a mix of the characters seen in the Anisoptera and Zygoptera. This group contains only two extant species, both restricted to East Asia. In most parts of the world the term “dragonfly” refers to members of any of the three suborders, but in North America the term usually refers specifically to members of the Anisoptera. In this book I will refer to dragonflies and damselflies collectively as Odonata or odonates.

Because odonates are remarkably distinctive in appearance, and unique in many other aspects of their biology, they are seldom mistaken for other insects. Some 5,500 species are known worldwide, just 433 of them in North America north of Mexico. Odonata, especially in the tropics, is one of the larger aquatic insect orders, giving its members, wherever they occur, an ecologically important role in aquatic ecosystems. (Other insects that spend a substantial period of their life in the water include mayflies, order Ephemeroptera, and stoneflies, order Plecoptera.)

The Odonata represent one of the most primitive living insect groups. The earliest fossil odonates are some 250 million years old. Members of the order Protodonata, the probable ancestors of Odonata, lived more than 300 million years ago, and some had wingspans greater than 71 cm (2 feet)! The closest living relatives of the Odonata are the mayflies. Odonates exhibit many primitive features, including the inability to fold their wings flat and fanlike over the abdomen, a trait they share with the mayflies. The wings have dense venation, and each

wing is fully functional and independently movable. The robust thorax is strikingly skewed, forcing the legs forward and the wings backward.

Even the most casual observer must appreciate the phenomenal agility that odonates display in flight. Throughout human history they seem to have spawned not only interest but also fear. Their large size and fast, buzzing flight are the basis for such names as “devil’s darning needles” and “horse stingers.” Although some of the larger dragonflies can pinch a finger placed in the mouthparts, odonates do not normally bite humans. These names may have originated in part from occasional instances in which a female dragonfly mistakes the leg of a wader or river rafter for a plant when laying her eggs. Though I have never experienced this firsthand, those that have confirm that having a dragonfly attempt to lay eggs in you is painful!

Not only are odonates among the most beautiful of insects, they are also beneficial. Both dragonflies and damselflies are voracious predators, both as aquatic larvae and as adults, and one of their main prey items is mosquitoes.

Habitats and Zoogeography of the South-Central United States

The south-central United States, as defined herein, includes Texas and its four surrounding states. The area covered is approximately 1.2 million km², of which 695,000 km² are in Texas. The region encompasses ten biotic provinces (Fig. 1). The Mississippi River forms the eastern boundary of the region (which means that the few parishes of Louisiana that lie east of the Mississippi are not covered), and the Apachian and Navahonian biotic provinces bound the western edge.

A considerable amount of work has been done on the distribution of vegetation types in Texas (Bray 1901, 1905; Carter 1931; Tharp 1926, 1939), Louisiana (Viosca 1933; Holland 1944), Arkansas (Turner 1935; Stroud & Hanson 1981), and Oklahoma (Ortenburger 1928a,b; Bruner 1931). There is a tremendous variety in the environments available

2 INTRODUCTION

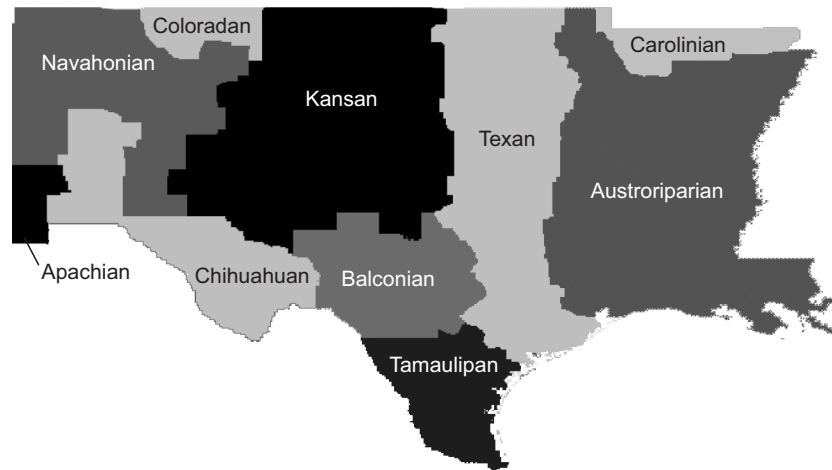


Fig. 1. The ten natural biotic provinces of the south-central United States (modified from Blair 1950, Dice 1943, Blair & Hubbell 1938).

for plant and animal communities, which are determined largely by climatic conditions and topography. A north-south line passing through central Oklahoma and Texas divides our region into areas of moisture sufficiency and moisture deficiency (Blair 1950), thus dictating plant and animal distributions in the region. Cope (1880) recognized three major biotas in Texas: a Sonoran fauna, an Austroriparian fauna, and a Neotropical fauna. I recognize a further division into ten distinct regional biotic provinces, as outlined by Blair and Hubbell (1938), Dice (1943), and Blair (1950), and as shown in Fig. 1. These provinces, which differ in topography, annual temperature range, vegetation, soil type, geology, and climate, have been given the names Apachian, Austroriparian, Balconian, Carolinian, Chihuahuan, Coloradan, Kansan, Navahonian, Tamaulipan, and Texan. The provinces are useful in detailing the distribution of Odonata, biologically vs. politically, within our region, as you will see in the individual species accounts.

Mean annual precipitation ranges from 147 cm/yr in the moist eastern parts of the region, such as New Orleans, to less than 25 cm/yr in the arid western areas, such as El Paso. Most of the precipitation falls during the months of March to May. Temperature is also an important factor in dictating the distribution of plant and animal communities, and ranges from an annual average of 22.8° C (73.4° F) in subtropical Brownsville, Texas, to 12° C (53° F) in the Texas pan-

handle, resulting in a shorter growing season in the latter. Major vegetation types include eastern pines and hardwoods, central prairies and grasslands, western semidesert areas, and western montane forests. Elevation ranges from sea level along the coastal areas to 4,011 m (Wheeler Peak, Taos County, New Mexico) in the Carson National Forest. The major watersheds in the region (Fig. 2) drain in an eastward or southeastward direction, and nearly all of them enter or approach the Austroriparian province. These stream systems provide important dispersal routes for the westward distribution of species of the Austroriparian province into the more arid, treeless environments (Blair 1950).

The Austroriparian province, as defined by Dice (1943), encompasses the Gulf coastal plain from extreme east Texas to the Atlantic Ocean. This biotic region's western boundary is demarcated by the availability of moisture. The typical vegetation types include longleaf pine (*Pinus palustris*) and loblolly pine (*P. taeda*) and hardwood forests variously consisting of sweetgum (*Liquidambar styraciflua*), post oak (*Quercus stellata*), and blackjack oak (*Q. marilandica*). The lowland hardwood forests of the southeastern portion of this province are typically characterized by magnolia (*Magnolia grandiflora*), tupelo (*Nyssa sylvatica*), and water oak (*Q. nigra*) in addition to those trees mentioned above. Other plants typical of this region include Spanish moss (*Tillandsia usneoides*) and palmetto (*Sabal minor*).

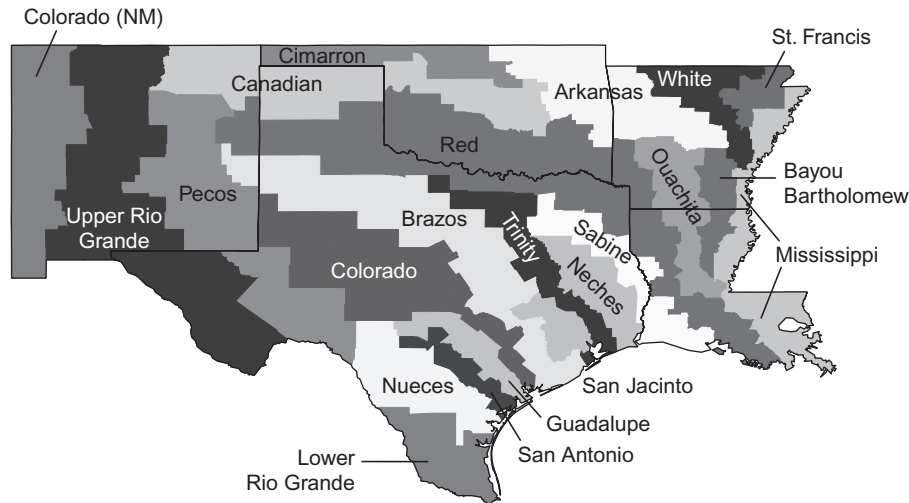


Fig. 2. The natural watersheds of the south-central United States.

The Texan biotic province constitutes a broad ecotone between the forests of the Austroriparian province in the eastern portion of this region and the western grasslands. The Balcones Escarpment forms an abrupt boundary to the west, otherwise delineated by a line based on soil type. This area was once characterized by tall-grass prairies supported by clay soils, but cultivation of much of the area has led to sandy soils characterized by combination oak-hickory forests, dominated usually by post and blackjack oaks and hickory (*Carya texana*). Thornthwaite (1948) classified this province as having a moist, humid climate, but receiving little water beyond that required for growth. The drainage pattern of the Texan province is an important biogeographical feature (Blair 1950). The Red and Trinity rivers, along with their tributaries, drain the northern part of this province. Both of these rivers enter the Austroriparian province before emptying into the Gulf. The southern portion of this province is drained largely by the Brazos, Colorado, San Marcos, and Guadalupe rivers.

One of the unique features in this province is the Arbuckle Mountains in south-central Oklahoma, just north of the Red River. This area is dominated by granite and travertine limestone geologic formations. One of the most prominent of these formations is in Turner Falls Park near Davis, Murray County, Oklahoma. Within the park, there is a 25 m waterfall on Honey Creek.

For the Kansan province, I follow Blair (1950), who delineated the province differently than did Dice (1943). Dice limited the province, excluding the Permian redbeds, while Blair included the areas north of the Edwards Plateau and south of the Red River. The province is characterized by a mixture of eastern forest species and western grassland species. Notable exceptions to the monotonous prairies of this province are Palo Duro Canyon State Park and Caprock Canyon State Park, which have been characterized as relict habitats. Moisture decreases from east to west in this province, and Thornthwaite (1948) considered the region moisture-deficient.

The Balconian biotic province is defined by the Edwards Plateau of Texas and derives its name from the Balcones fault zone that forms its southern and eastern boundaries (Blair 1950). It is characterized by scrub forests of juniper (*Juniperus* spp.) and oaks (*Quercus* spp.), including stunted live oak (*Q. virginiana*).

Farther south, the Tamaulipan province extends from southern Texas into eastern Mexico. This semiarid region is dominated by mesquite (*Prosopis glandulosa*), *Acacia* spp., *Mimosa* spp., and prickly pear cactus (*Opuntia* spp.). Thornthwaite (1948) noted a marked deficiency of moisture for plant growth, though some growth occurs year round. This province is drained in the north largely by the Nueces River and its tributaries, and is poorly drained in the southern portion by minor tributaries.

4 INTRODUCTION

ies of the Rio Grande. In the Brownsville region, to the south, the province becomes subtropical.

The Chihuahuan province includes the Trans-Pecos area of Texas, excluding the Guadalupe Mountains. It extends southward into the Mexican states of Chihuahua and Coahuila and is drained largely by the Rio Grande. This biotic province is more diverse in physiographic features than all others in the region (Blair 1950). The climate in this area is arid and moisture-deficient (Thornthwaite 1948), and the vegetation is variable, but basin areas up to 1,500 m in elevation include grasses, desert shrubs, and creosote bush (*Larrea tridentata*). Streams in this area are usually small and intermittent; those that are permanent are usually spring-fed. The various mountains, including the Chisos and Davis ranges, show a vertical zonation of plant communities, with elevations above 1,500 m dominated by Emory oak (*Quercus emoryi*) and cedars (*Juniperus* spp.).

The Navahonian province includes most of New Mexico and barely enters the northern edge of western Texas (Culberson County) at the southern extension of the Guadalupe Mountains. A vertical zonation in elevation similar to that of the Chihuahuan province characterizes this area. Trees dominant at elevations above 2,500 m include various pines (*Pinus* spp.), oaks (*Quercus* spp.), and Douglas Fir (*Pseudotsuga menziesii*).

Small portions of the Carolinian (northern Arkansas), Coloradan (northwestern New Mexico), and Apachian (southwestern New Mexico) provinces are also found within the region covered by this book. These peripheral provinces are home to several odonates whose ranges barely extend into the south-central United States.

Life History of Odonata

As is true of any living organism, reproduction is a critical stage in the life cycle of odonates. It may take an individual adult anywhere from a day to several weeks, depending on the species, temperature, availability of food, and other environmental factors, to become sexually mature. Upon maturity, the male will, in most species, patrol a territory he has established over and around water. The male will search for females in this territory, and will defend it against other males of his species and occa-

sionally males of other species. At some point a receptive female looking for suitable egg-laying areas is seized by the male. This capture usually takes place in midair, the male flying over the female and grabbing her head and thorax with his legs. In damselflies, the male grasps the female's prothorax (the segment of the thorax behind the head) with the clasping structures at the tip of his abdomen (this is the **tandem position**).

In dragonflies he grasps her head, and in aged females of some larger species (darners) the resulting damage to the eyes is often noticeable. The male will then curl his abdomen around so that sperm can be transferred from the genital pore on the ventral side of his segment 9 to the accessory genitalia located on the ventral side of his segment 2. This usually happens quickly, and the male then straightens his abdomen so that the receptive female can curl her abdomen around, such that her genital opening on the ventral side of segment 8 is in contact with his accessory genitalia on segment 2. It is not unusual to see odonates in this **wheel position**. They may remain in this position, usually protected within vegetation, for minutes or hours, depending on the species. Still others copulate while in flight. (A number of the color photos in this book are of mating pairs.) Females will mate more than once, and in at least some species, males are known to remove the sperm from previous males before mating.

Egg-laying

Female damselflies, petaltails, and darners all lay their rod-shaped eggs using a specialized structure called the **ovipositor**. They use the bladelike structures of their ovipositor to make slits in the soft tissues of plant stems, where they then lay their eggs. These eggs may be laid above, at, or below the water line. In other odonate families the eggs are generally more round in shape and often have a gelatinous covering. These eggs are laid in or near water or in an area that will fill with water. Female Spiketails employ a specialized ovipositor in sewing-machine fashion to deposit eggs in the substrate of shallow streams. The eggs will generally hatch in about a week. Eggs laid in temporary pools, however, will hatch more quickly, whereas others may be delayed for months. The male may continue to grasp the female (in the tandem position) while she lays eggs, or he may release her, but he will remain hovering

or perched nearby to guard against intruding males. Females of some species of damselflies will actually submerge themselves underwater for an hour or more while ovipositing. Regardless of whether a female descends underwater or not, she, and often the male, are vulnerable to predation by fishes, frogs, birds, spiders, and other insects during this time.

Larvae

Dragonfly and damselfly larvae (also called nymphs or naiads), although most common in ponds, marshes, lakes, and streams, have exploited a wide range of permanent and temporary aquatic habitats, including brackish pools and estuarine habitats. Some larvae survive in moist substrates under rocks and in otherwise dry streambeds or ponds. When the larvae hatch from the eggs, they look very little

like the adults they will eventually become (see Fig. 3). They are voracious predators, feeding on worms, small crustaceans, mosquito larvae, and other insects, and the larvae of larger odonate species may even take small fish and amphibians. They capture their prey by extending their lower lip (the **labium**), which is equipped with two movable toothed palps. The labium, which may reach one-third of the larva's body length, extends at lightning-fast speed. Because the larvae are generally shades of green and brown, they blend in well with their environment. Many are cylindrical in shape, but others are dorsoventrally flattened. The larvae of some species grow by molting their exoskeleton 7–18 times over a period of a few (typically 11–13) months to several years or more. Their wing pads will become more and more evident as they grow in size and approach adulthood (see Fig. 3).



a



b



c



d

Fig. 3. Odonata larvae: (A) Great Spreadwing (*Archilestes grandis*); (B) Common Green Darner (*Anax junius*); (C)

Blue Dasher (*Pachydiplax longipennis*); (D) Skimmer (Libellulidae).

Damselfly larvae have three leaflike gills at the tip of the abdomen. Although the gills are used in respiration, they are also used like fins for swimming. Larvae have the ability to regenerate these gills, at least in part. Damselfly larvae also have the ability to absorb oxygen through the wall of their rectum. Dragonfly larvae lack the terminal gills and absorb oxygen through internal rectal gills instead.

Adults

An odonate larva will typically climb out of the water onto an emergent piece of vegetation, bridge pylon, or similar structure to begin its adult emergence. Some species are known to walk considerable horizontal distances (30 m) and heights (10 m) from the body of water in which they developed. Emergence generally occurs at night or in the early morning, under the cover of darkness. Clubtails and damselflies, however, often emerge during the day. A split develops along the dorsal side of the head and thorax as the larval skin dries. The adult will then start to pull itself free from the old larval exoskeleton, or *exuviae* (see photo 48f). This process may take some time, since the legs have to harden before it can pull itself completely free. Once it has done so, it will remain hanging from its perch until its wings have been inflated (via the veins) and the body has begun to harden. This newly emerged, or *teneral*, adult will not have the bright vibrant colors of its mature counterpart; the wings will appear cloudy or have a shimmer to them, and the tenerals are vulnerable during this time of limited mobility. Although they can fly, almost immediately, they usually do so only when disturbed. It may take several days or more than a week before sexual maturity is reached. During this time most odonates remain away from the water. Males usually mature more quickly than females and make their way back to suitable egg-laying habitats, where they set up territories and wait for females.

Odonates of a number of species are *crepuscular*: they feed actively at dusk. Occasionally, a dragonfly or damselfly will come to a light at night, but most of these are individuals roosting nearby and not actively flying. Odonates of some species, however, like the shadowdragons, may actually be nocturnal.

Dragonflies typically have no reason to fly great distances, but because they are accomplished gliders, they are quite capable of sustained flight, in

some cases even across oceans, on the wings of prevailing wind currents.

Seasonality of Odonata in the South-Central United States

The flight season of most species of Odonata in this region extends from the spring through the summer months, and occasionally persists into the fall. The onset and duration of emergence, however, are both variable. Many species of temperate origin (e.g., Attenuated Bluet, Springtime Darner, Harlequin Darner, Banner Clubtail, Twin-spotted Spiketail, Stream Cruiser, Blue Corporal) have early (March–May) and explosive emergences in this area and then soon disappear. In the southern portions of the region, the year-round temperatures, averaging 23° C (73° F), and the subtropical climate allow several species to fly year round. Fifteen species (including Familiar Bluet, Fragile Forktail, Common Green Darner, Eastern Pondhawk) have been encountered as adults in every month. Other species (Fine-lined Emerald and Blue-faced Meadowhawk) are seen flying only later in the year. Because of the latitudinal gradient in temperature seen in the region, emergence occurs one to several weeks later in the more northern areas than in the subtropical southern areas.

Damselflies generally emerge as soon as temperatures permit in the spring, and continue to emerge throughout much of the summer. This results in a heterogeneous age structure, often allowing more than one generation per year. Many of the smaller pond damsels, for example forktails, have multiple (two or three) generations per year. The larger pond damsels, the spreadwings, and the broad-winged damsels generally require a full year for development.

Many dragonflies differ from damselflies in having an obligate larval diapause (a required period of arrested development), followed by a synchronous spring or early-summer emergence. This pattern results in a homogeneous age structure and a sudden disappearance later in the summer or fall. Most species require at least a year to develop, and some, for example spiketails, require longer (several years). A more or less typical adult lifespan, barring predation or other calamity, might be three months.

Development time is generally longer for those species restricted to running-water situations than it

is for those found in ponds or lakes. A general seasonal progression, with the peak months in June and July, as seen for the entire south-central United States, was observed by Bick (1957) in Louisiana. Species present early in the year (January–February) were also generally present later in the year (November–December).

Conservation

Odonates play a major beneficial role as predators of mosquitoes and other biting insects, both as adults and as immatures. The larvae also form an important link in food chains for fish and other aquatic vertebrates. Historically, the Odonata have not been acknowledged as good indicators of water quality, but numerous authors (Castella 1987; Dolny & Asmera 1989; Bulankova 1997; Chovanec & Raab 1997) have recognized that capacity in this group recently. Schmidt (1985) presented a convenient working scheme for the rapid evaluation and characterization of aquatic habitats.

The most recent estimates (Dunkle 1995) are that about 15% of the dragonfly species and 6% of the damselfly species in North America have limited or restricted geographic ranges and may be at risk of extinction. Areas of particularly high endemism in the United States include the New England coast, Florida, the central Gulf of Mexico coast, and the Pacific Coast. A few species, the Oklahoma and Ozark Clubtails and the Texas Emerald, for example, are endemic to smaller regions within the south-central United States. Those species living in streams, rivers, and other flowing-water habitats are at greatest risk.

Sewage and other organic wastes run off into streams and promote bacterial growth that depletes the oxygen content of the water and in turn stresses or kills odonate larvae. Fertilizer runoff from agricultural fields leads to eutrophication, promoting algal growth that may lead to blooms removing oxygen from the system and preventing sunlight from penetrating the water. Pesticide runoff also kills larvae. Those species of Odonata living in ponds and lakes are generally at less risk. In fact, human activities resulting in the construction of new ponds, lakes, borrow pits, and even stock tanks may provide some Odonata with a new habitat, lacking competition, to colonize. Other human activities,

however, such as allowing livestock access to these areas, can severely impact these pond species.

The single most important factor in the conservation of Odonata is the protection of land and aquatic habitats. The efforts needed for the protection of these resources vary with the type of habitat. Removing the surrounding vegetation from streams by mowing will completely alter the composition of the water, effectively removing some species. A buffer zone of vegetation on either side of a stream (generally, at least 30 m is recommended) helps to prevent erosion. Construction of dams poses a real challenge to stream species. In all of Texas there is now only one natural lake (Caddo Lake), which indicates just how prevalent dams are in the state. The numerous manmade reservoirs may provide habitat for those few species that can breed in lakes, but they deprive other odonates of habitat. Rivers are seldom protected from human impact and disturbances, but groups in areas like the Big Thicket National Preserve in east Texas are working hard to secure these areas by purchasing riparian lands and creating corridors between their preserve units.

For some species, especially those living in more arid conditions, a small area of suitable habitat may be all that is needed for their continued existence. For most species, however, larger areas of suitable habitat are necessary. This is where a good network of local, state, and national parks is so important. Though such areas provide protected habitats for odonates, on the whole they protect relatively little land. Private groups like the Nature Conservancy are crucial for securing and protecting land. Time is of the essence, for whereas observations have shown some species expanding their ranges because of global warming, many others are left to compete for fewer habitats of poorer quality.

Collecting odonates on these protected lands requires special permission and often a scientific collecting permit. I have found that land stewards or agencies in charge of these protected areas generally have no problem with the collection of the voucher specimens needed to ensure proper documentation and identification. Often they encourage this practice in order to ensure that the fauna of the lands they manage and protect are properly documented. In Texas, like most other states, scientific collecting permits are required for any state park property or preserve, and are administered through a central agency (Texas Parks and Wildlife). Because National

8 INTRODUCTION

Parks administer their own scientific collecting permits, each park must be contacted separately. In my experience the need for a scientific collecting permit in National Forests varies from state to state, despite the fact that they are all federally maintained. Some states require a fishing license if one is to collect insects on these or other lands. City and municipal parks may also be protected, and you should contact the appropriate administering agency in these areas to inquire about collecting. Before issuing a scientific collecting permit, the administering agency will require a proposal of the research being conducted, and will mandate the depositing of vouchers (specimens accessioned or numbered) in a legitimate and publicly accessible collection.

In addition to the preservation and management of natural habitats, the creation of new habitats, especially ponds, can play an important role in conservation. An artificial pond, especially one in an arid area, that has an assortment of aquatic vegetation and a lush riparian zone protected from livestock will provide productive breeding habitats for many species. Although many Odonata can coexist with fish in such ponds (as long as there is plenty of vegetation to hide in), the presence of fish will prevent some species from persisting in the habitat.

We still have a lot to learn about the specific microhabitat requirements of our individual Odonata species. Although many species are at risk, others (for example Great Spreadwing, Double-striped Bluet, Widow Skimmer, and Swift Setwing), seem to be expanding their ranges. It is unclear in most instances if the expansion of these species is at the expense of others. We need more refined methods of population estimation, ones that rely on exuvial and larval counts rather than adult counts, if we are to begin getting at these questions. Collection and photography of individuals will also play a critical roll in filling gaps in our knowledge and understanding of species distributions.

Both larvae and adults are recreationally important; fly fishermen have patterned tied flies after them, and the terrestrial adults are observed and studied by layman and scientists because of their colors, flying ability, and curious habits. Odonates have also served for centuries as favorite subjects of poets, naturalists, artists, and collectors. Particularly during this time of growing interest in the group, we should be vigilant in our attempts to conserve aquatic habitats. The British Dragonfly Society has published two pamphlets dealing with dragonflies

and ponds (*Dig a Pond for Dragonflies* and *Managing Habitats for Dragonflies*). Both are available at their website, <http://www.dragonflysoc.org.uk>.

Studying Odonata

Because many of the more common species can be seen almost anywhere, even far from water, it is easy to begin studying odonates. And because they breed in water, any relatively nonpolluted body of water will provide a good opportunity to observe them. Many are large enough to be observed and identified readily with a good pair of close-focusing binoculars. But it is important to remember that not all species (particularly many damselflies) can be reliably identified without capture and closer examination. A small magnifying glass or jeweler's loupe can be useful for this kind of scrutiny in the field, and reversing a pair of binoculars will often work in a pinch.

Remember that, in addition to observing the physical appearance of an odonate, you should note the habitat, season, and observed behavior. (How and where does it perch? Does it spend most of its time perched or in flight?). Consideration of these characteristics jointly may yield a more confident identification. There are also certain physical features you will want to make careful notes or photographs of as well. The color of the eyes and front of the head, the pattern of thoracic stripes, the wing color or pattern, including the appearance of the pterostigma (colored cell at the tip of the wing), and the color pattern of the abdomen are useful identifying marks.

It may become necessary to capture an odonate, so as to examine it more closely in the hand. All you need if you are to capture one is an aerial net and a fair amount of hand-eye coordination. The best way to handle an odonate is to pinch its wings together above its back, so that they stand straight up. They are generally unharmed by the experience and can be released to carry on their activities after you have studied them.

At some point you may choose to expand your interests to the collection of odonates. Collecting small numbers of most odonates will have no harmful impact on their populations. Like other insects, they have a high reproductive potential. Most states do not require a collecting permit, so long as you are not collecting in state, federal, or, in some cases,

municipal parks and preserves. Making a permanent collection can be rewarding and will allow you to develop a greater appreciation for these insects. Unfortunately, unlike some other insects, such as beetles and butterflies, odonates do not hold their brilliant colors after death. The best way to preserve these colors is to immerse the odonate in acetone for 12–24 hours and then allow it to dry. This will fix the colors to some degree and will remove many of the fatty acids in the body that can discolor the specimen. Specimens for scientific study are generally placed in clear cellophane or polypropylene envelopes with a 3' × 5' card recording the locality and other data pertinent to the collection of the specimen.

With the increase in popularity of odonates, regional newsletters and societies are appearing, and in 1999 an active and informative international email discussion group was created. The International Odonata Research Institute (IORI) has a fairly complete assortment of field guides and books on Odonata for sale. There are currently two international dragonfly societies (the Worldwide Dragonfly Association and the International Odonatological Foundation, *Societas Internationalis Odonatologica*) that publish biannual and quarterly journals, respectively. Another society, the Dragonfly Society of the Americas, produces a quarterly newsletter and an occasional journal. Anyone interested in Odonata in North America will find the small yearly dues for this society well worth the price. A full list of these societies with their contact information is given at the back of the book in the Bibliography.

Photographing Odonata

It probably won't be long after you have started observing odonates that you will want to begin photographing them. Given their beauty, this is a natural extension of one's interest. Most of the photographs in this book were taken with a 35 mm SLR (single-lens reflex) camera and a 100 or 180 mm macro lens. Damselflies, not as easily disturbed, are generally easier to photograph, and if they do fly off, they generally don't fly far. Dragonflies, however, present a number of challenges. The longer the focal length of the lens, the greater the working distance you will have. A 180–200 mm macro lens or a close-focusing 300 mm telephoto lens equipped with a teleconverter will allow you to frame an odonate in

your camera without having to get so close. Extension tubes can also be used with your macro lens to increase magnification and or working distance. There is a trade-off, however: these longer lenses generally require the use of a tripod to prevent a blurred image. A tripod can be useful or even critical in the field, but it is also another piece of equipment that can brush up against vegetation, perhaps scaring your subject away, and another thing to carry.

There are many films on the market and I find that photographers are generally committed to a favorite brand. Film speeds (ISO) are an indication of the film's sensitivity to light. The higher the ISO the more sensitive to light the film is, but also the grainier it is. I prefer Fuji films because of their saturated colors, which produce a vivid image. I use 50 or 100 ISO film, both of which work well on sunny days. With the advent of high-resolution SLR digital cameras, film may be less of an issue in the near future. A few of the photographs in this book were taken with a digital SLR, which I now use exclusively. The light sensitivity of the chip in the camera allows you to shoot at speeds as high as 400 and 800 ISO without the grain you would expect from film.

I often employ a macro ring flash and one or two slaved off-camera flashes. An electronic flash dedicated to your camera body with TTL (through-the-lens) metering can be useful in close-up photography, both as direct lighting and fill-flash. Using flash as direct lighting will allow you greater depth of field and eliminate blurring from camera shake, because you can shoot at a higher shutter speed, but some criticize the non-natural lighting that may result. It is also necessary to make sure that the background you are shooting against is not too distant, so that your resulting photo does not have a black background and appear as though it were taken at night.

When photographing odonates, it is important to make sure that your line of sight is completely perpendicular to the body surface you are photographing, so that the entire individual is in sharp focus. With large dragonflies, it is easy to have one end of the body—the head, say—in focus, but have the other end, the tip of the abdomen, a complete blur. Many cameras come with a depth-of-field preview feature, which is helpful in placing the complete insect in the focal plane. Another important criterion is the background. You may not always be able to choose this, but the better photographs have contrasting backgrounds (blue sky, green vegeta-

tion) that aren't too busy and distracting. Finally, be sure that in addition to your camera equipment, to take along a healthy dose of patience. Odonate photography can be rewarding, but it is not without frustrations!

External Anatomy of Adult Odonata

My purpose here is to introduce briefly the terminology I use in this field guide when describing adult odonates. Table 1 summarizes some of the major differences between adult dragonflies and adult damselflies; Figs. 4, 5, and 6 illustrate the particulars of odonate anatomy; and the Glossary furnishes definitions of most of the technical terms used in the figures and text.

Head

The large **compound eyes** are the most distinctive feature on an odonate's head. They make up the largest portion of the head, particularly in dragonflies. These eyes, composed of many small facets (ommatidia) fused together, secure odonates as dominant aerial predators and some of the most acrobatic and skillful fliers in the animal world.

The eye color is often one of the most distinctive features of an odonate. In many the dorsal color of the eyes will differ from their ventral color, the dorsal surface usually darker. Unless stated otherwise, when eye color is given in the species accounts, I am referring to the dorsal surface of the eye. Odonates see a wide spectrum of colors that includes not only the spectrum visible to us but also ultraviolet and

polarized light. This explains why some female odonates try to oviposit on a shiny asphalt road or car hood. They are presumably mistaking the horizontally polarized reflection of these structures with that of water. In addition to their huge compound eyes, odonates have three **ocelli**, or simple eyes used for light detection, on top of the head. They also have a small pair of antennae.

Thorax

The thorax comprises three segments (pro-, meso- and meta-), each bearing a pair of legs. The first segment, the **prothorax**, is so reduced as to appear almost necklike, and articulates with the fused **mesothorax** and **metathorax**. The wings attach to the mesothorax and metathorax, which are much larger than the prothorax and sometimes jointly referred to as the **pterothorax**, because they are involved with wing function. Stripes are often visible on the pterothorax, and terms have been applied to them (starting anteriorly, the mid-dorsal, antehumeral, humeral, anterior lateral, and posterior lateral).

Wings

As just mentioned, two pairs of wings attach to the last two thoracic segments. The wings are made up of numerous **veins** enclosing **cells**. The arrangement of the veins and cells is often useful in identifying odonates. For that reason many of these, too, have been accorded specific terms. One need not become an expert on wing venation to identify most Odonata, but it is helpful to learn some of the general terminology used in this guide. I use the tra-

TABLE 1. DISTINGUISHING CHARACTERISTICS OF DAMSELFLIES AND DRAGONFLIES

<i>Damselflies (Zygoptera)</i>	<i>Dragonflies (Anisoptera)</i>
Of slighter build, and generally weaker fliers	Of robust build, and strong fliers
All wings similar in shape	Hindwings broader basally than forewings
Wings held closed or nearly so over the abdomen when at rest (except the spreadwings)	Wings held horizontally outward from the body when at rest
Eyes separated by at least their width	Eyes touching or at least not separated by their width
Males with two pairs of caudal appendages	Males with a pair of superior caudal appendages and a single inferior caudal appendage
Females with functional ovipositors	True ovipositor lacking or reduced in females (except the darners and petaltails)

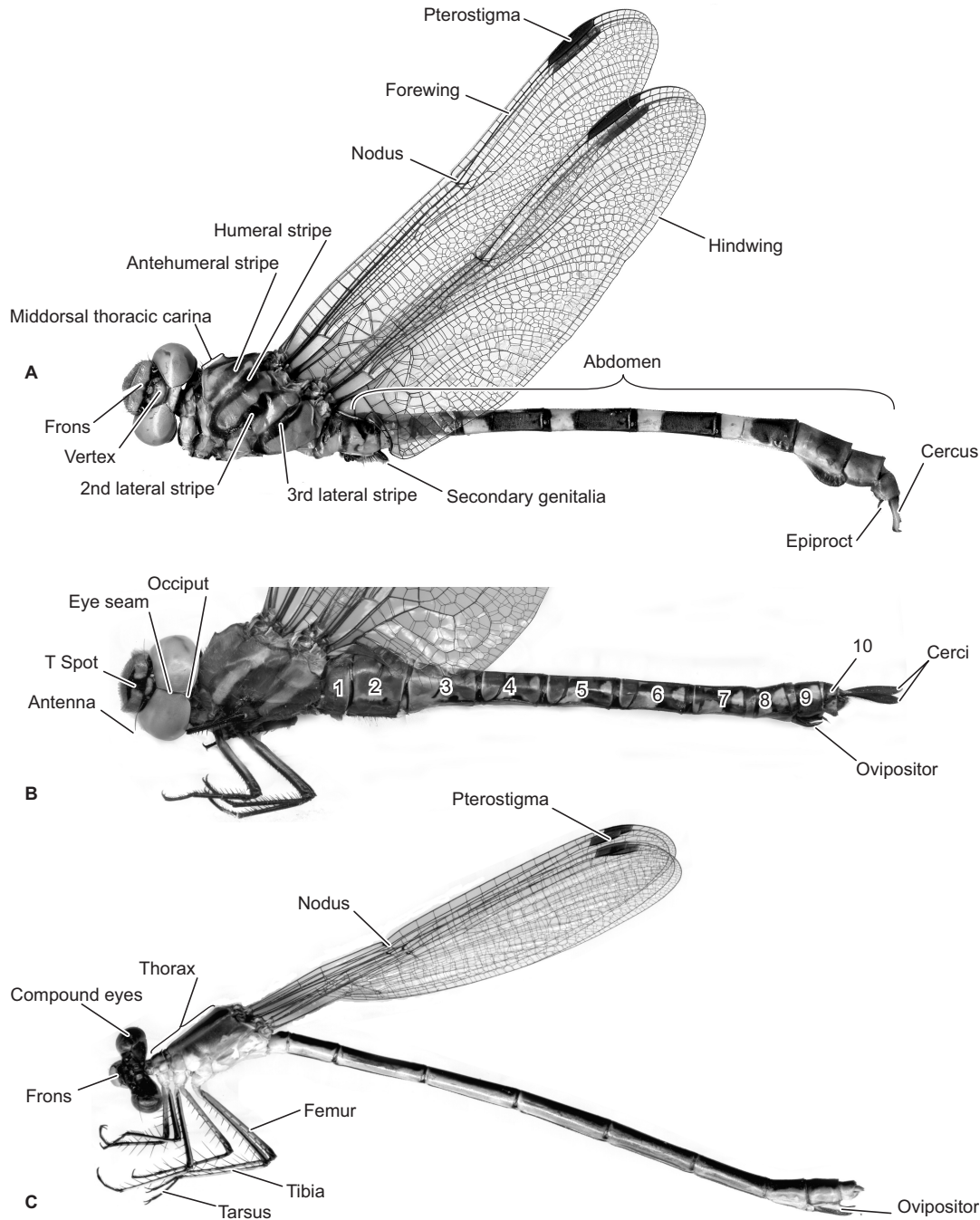


Fig. 4. Odonata adults, showing structures important in identification: (A) Four-striped Leaftail (*Phyllogomphoides*

stigmatus), male; (B) Blue-eyed Darner (*Aeshna multicolor*), female; (C) Elegant Spreadwing (*Lestes inaequalis*), female.

12 INTRODUCTION

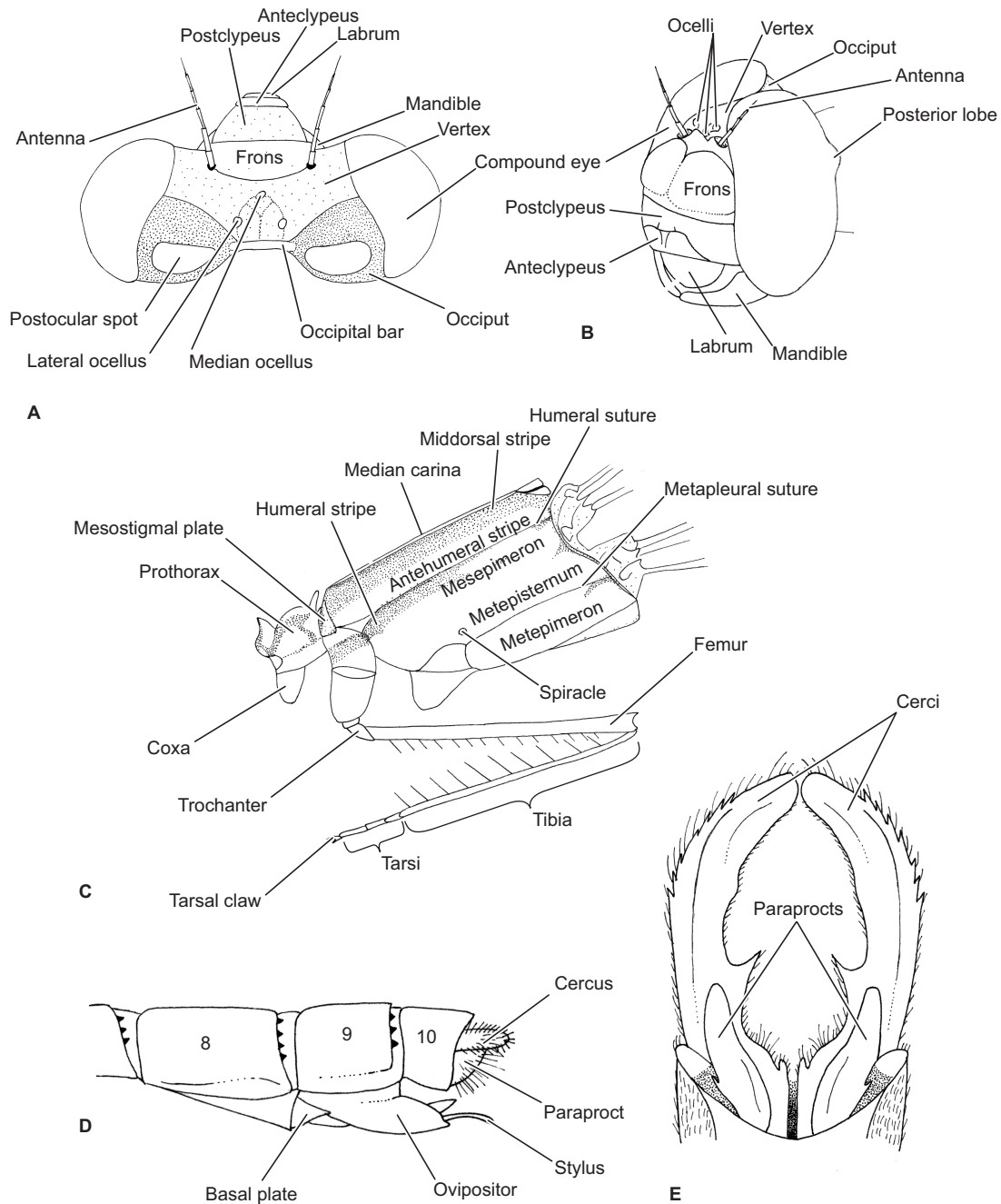


Fig. 5. Further structures important in odonate identification: (A) head of damselfly, dorsal view; (B) head of baskettail (*Epitheca*); (C) thorax of Variable Dancer (*Argia fumipennis*), lateral view; (D) posterior

abdominal segments of female Swamp Spreadwing (*Lestes vigilax*), lateral view; (E) terminal abdominal segments of male Great Spreadwing (*Archilestes grandis*), ventral view.

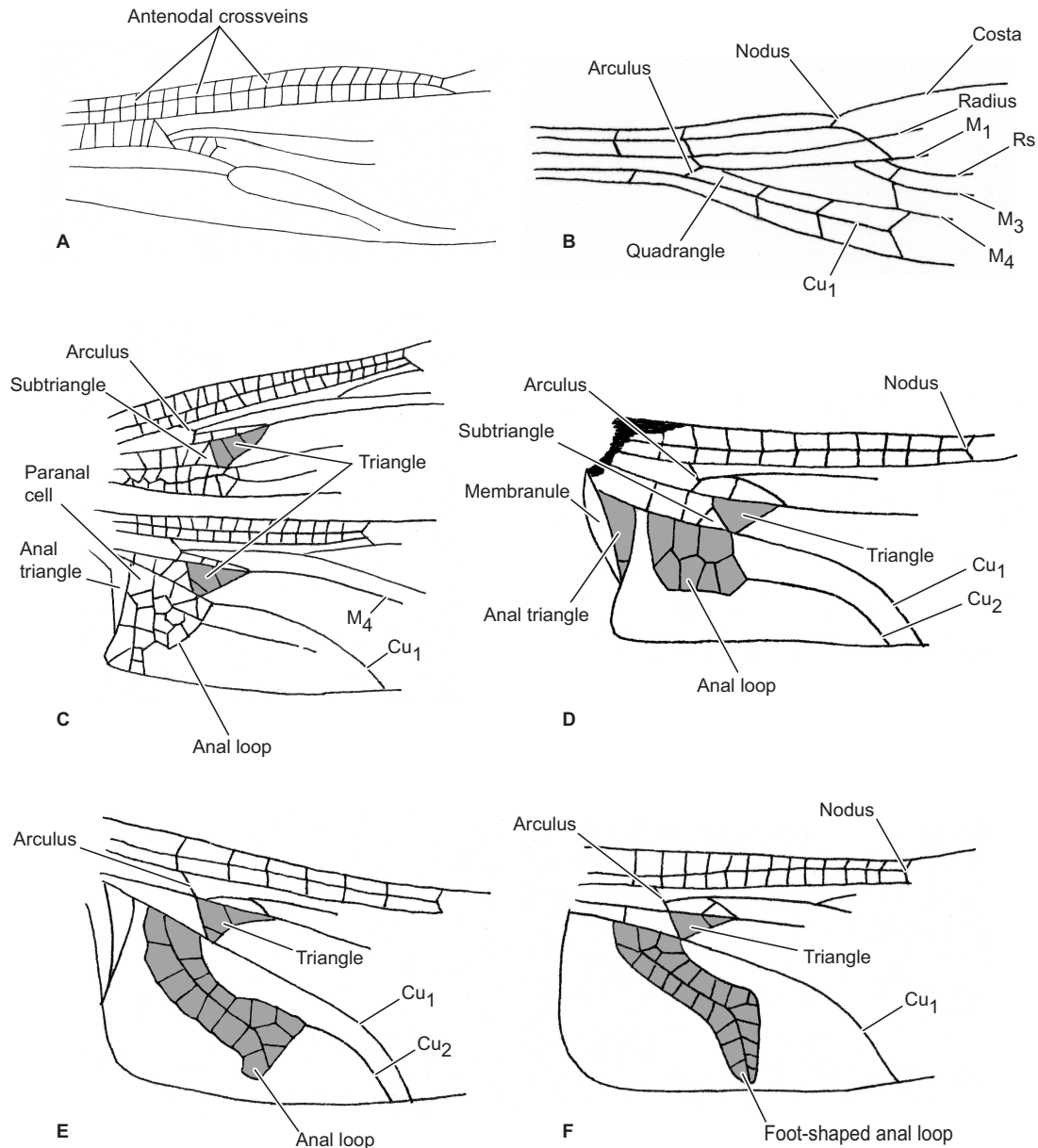


Fig. 6. Wing details in Odonata: (A) forewing of broad-winged damselfly (Calopterygidae); (B) basal hindwing of Orange-striped Threadtail (*Protoneura cara*); (C) basal area of wings of Springtime Darner (*Basiaeschna*

janata); (D) basal hindwing of river cruiser (*Macromia*); (E) basal hindwing of baskettail (*Epithea*); (F) basal hindwing of skimmer (Libellulidae).

ditional Comstock-Needham system of naming veins here, but there are several alternative systems of nomenclature. A detailed comparison of these terms is given in Carle (1982). The strong anterior-most vein in each wing is called the **costa**. The costa is slightly notched toward the middle of its length at a region termed the **nodus**. The **ptero-stigma** (sometimes called the stigma) is a colored area at the tip of the wing along the costal margin. In dragonflies, there is a loop of veins near the base of the hindwing called the **anal loop**. These veins present different shapes in different families. There are also areas of cells in the fore- and hindwings that make up **triangles**, **supertriangles**, and **subtriangles**. In dragonflies the configuration of these cells is useful in distinguishing among the different families.

Abdomen

The abdomen, elongated in all odonates, comprises ten **segments**, the first and last of which are reduced and often hard to see. The color pattern on these segments is often useful in making field identifications, especially with many of the damselflies. (In some cases, especially the clubtail dragonflies, the terminal segments will be dilated into a clublike structure.) Females typically have slightly broader abdomens than males, and in damselflies, darners, and petaltails an **ovipositor** (a bladelike egg-laying structure) is evident ventrally on the female's segment 9. Those dragonflies lacking an obvious ovipositor have a **subgenital plate (vulvar lamina)** originating ventrally from segment 8 and extending to segment 9. It is often notched at its middle. A pair of **cerci** (sing. **cercus**), extending terminally, is usually visible, though in most groups these are reduced in the female.

Males have secondary, or accessory, genitalia, lo-

cated ventrally on segments 2 and 3. In damselflies, the cerci are enlarged and form a dorsal pair of claspers. Below these is a pair of **paraprocts**. Together with the cerci, these structures form the caudal appendages, and are used for grasping the female during mating. In dragonflies, the paraprocts are reduced, and a single **epiproct** is located below the enlarged cerci.

Coloration

The beautiful and varied coloration of odonates is a significant factor in their appeal. In odonates, most of the colors seen result from pigment rather than from structural artifacts of the body. But the bright-blue color so characteristic of many damselflies is a result not of pigment, but rather of the scattering of light by tiny refractive granules located in epidermal cells; and the metallic coloration seen in many emerald dragonflies is also a result of the insects' surface structure. In many odonates a **pruinescence**, or waxy blue-white covering, will develop with age, and as noted above, the newly emerged, or teneral, adult will not have the vibrant colors of its mature counterpart.

In many cases, coloration is an important and useful tool for making field identification, but it is important to recognize some of the difficulties of using color. Odonates of many species are sexually dimorphic in this respect; the males and females differ in coloration. Moreover, many species of damselflies and darners are known to change colors with temperature; individuals will often become darker in color when exposed to cooler temperatures. This is important to remember when observing odonates on a cool early morning. Several species of pond damsels, such as Springwater Dancer, also become darker while in copulation.

A GUIDE TO THE SPECIES ACCOUNTS

The species accounts in this book treat 85 species of damselflies and 178 species of dragonflies, all occurring in the south-central United States. These 263 Odonata species are distributed among ten families and 69

genera. Two of the ten families, the pond damsels (Coenagrionidae, 66 spp.) and the skimmers (Libellulidae, 81 spp.), account for 56% of our total species and six of our 69 genera (*Lestes*, 10 spp.; *Ischnura*, 12 spp.; *Gomphus*, 12 spp.; *Libellula*, 17 spp.; *Argia*, 22 spp.; and *Enallagma*, 23 spp.) number ten

KEY TO THE FAMILIES OF SOUTH-CENTRAL ODONATA

1. Fore- and hindwings similar in size and shape, having quadrangles instead of triangles and subtriangles; eyes well separated on top of the head, by more than their own width	Damselflies (Suborder Zygoptera, p. 19)	2
1'. Fore- and hindwings not similar in size and shape, the hindwing considerably wider basally, each wing having a triangle and a subtriangle; eyes meeting middorsally on top of the head, or, if separated, then by less than their width	Dragonflies (Suborder Anisoptera, p. 149)	5
2(1). Numerous antenodal crossveins; postnodal crossveins not in line with veins posterior to them	Broad-winged Damsels (Family Calopterygidae, p. 21)	
2'. Only 2 antenodal crossveins; postnodal crossveins in line with veins posterior to them		3
3(2'). Veins M_3 and Rs arise nearer to the arculus than to the nodus	Spreadwings (Family Lestidae, p. 29)	
3'. Veins M_3 and Rs (see Fig. 6) arise nearer to the nodus than to the arculus		4
4(3'). Anal vein absent or greatly reduced; Cu_2 absent or at most only 1 cell long	Threadtails (Family Protoneuridae, p. 46)	
4'. Anal vein and Cu_2 not absent or reduced	Pond Damsels (Family Coenagrionidae, p. 52)	
5(1'). Eyes widely separated on top of the head		6
5'. Eyes touching or only narrowly separated on top of the head		7
6(5). Pterostigma at least 1/4 the distance from nodus to wing apex; body color gray and black; front margin of labium with a median cleft	Petal tails (Family Petaluridae, p. 151)	

KEY TO THE FAMILIES OF SOUTH-CENTRAL ODONATA (*cont.*)

6'. Pterostigma not more than 1/6 the distance from nodus to wing apex; body color yellow or green with black (if gray, then total length less than 70 mm); front margin of labium without a median cleft	Clubtails (Family Gomphidae, p. 176)
7(5'). Eyes narrowly touching or barely separated on top of the head	Spiketails (Family Cordulegastridae, p. 215)
7'. Eyes broadly touching on top of the head	8
8(7'). Triangles in fore- and hindwings similar in shape	Darners (Family Aeshnidae, p. 153)
8'. Triangles in fore- and hindwings dissimilar	9
9(8'). Anal loop generally foot-shaped, with well-developed toe; no tubercle on rear margin of each compound eye	Skimmers (Family Libellulidae, p. 240)
9'. Anal loop either foot-shaped, but with little development of the toe, or circular and not foot-shaped; generally a tubercle on rear margin of each compound eye	Emeralds & Cruisers (Family Corduliidae, p. 218)

or more species each and collectively account for 38% of the total species.

Family and generic accounts introduce the respective groups and include keys to genera and species. Keep in mind that in many cases information given in these sections is restricted to what is applicable to the odonates of the south-central United States fauna. Species accounts include illustrations and photographs that will allow you to identify odonates in the region. I have intentionally cropped many of the photographs in an attempt to better show specific characters. This is especially true in the dragonflies, where in some areas I have cropped out one set of wings (especially when they were clear), to reveal more detail on the thorax and abdomen. Families are organized phylogenetically (along lines of their relationships), but for ease in accessing family members, the genera and species are arranged alphabetically by scientific name.

Individual species accounts consist of the following information: (1) common (English) name, taken from Paulson and Dunkle (1996) and updated when necessary at <http://www.ups.edu/biology/museum/NADragons.html>, (2) scientific name, as the species

is known throughout the world, (3) identifying numbers for figures, photos, and tables illustrating or characterizing the species, (4) measurements, including total length, length of the abdomen, and length of the hindwing, (5) lists of the regional biotic provinces and watersheds where the species is known to occur (see Figs. 1 and 2, in the Introduction), (6) the species' general distribution, (7) flight season within the region (state abbreviations are given in parentheses; early and late dates are reported from the literature and museum collections; in some cases, where specimens and data are scarce, only one date may be known for our region), (8) a description of the species, emphasizing tips on identification, (9) notes on similar species encountered in our region, with details on their differences, (10) a brief description of the species' preferred habitats, (11) a discussion of behavior and other matters, and (12) a selection of the relevant literature pertaining to the species (all sources cited in text are given in the Bibliography). Accompanying each species account is a map of the species' distribution within our region (updated through June 2002).

Figs. 7 through 32, falling at various points

throughout the text, present comparisons of certain body parts among related species, to assist in making identifications. Color photographs of living specimens of virtually all species treated, in many cases two or more photos per species, are gathered

in a single section of the text, easily located; all 452 of them are referred to in the species accounts.

The preceding key will often be useful in initiating the task of identifying a specimen in hand. Similar keys are presented throughout the text.