

Order Odonata

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Chapter Outline

Introduction	355	Odonata: Suborders	364
Limitations	356	Odonata: Zygoptera: Superfamilies	364
Terminology and Morphology	356	Odonata: Anisoptera: Superfamilies	364
Glossary	356	Odonata: Anisoptera: Cordulegastroidea: Families	364
Material Preparation and Preservation	363	Acknowledgments	364
Keys to Odonata	363	References	365

INTRODUCTION

Odonata, commonly known as damselflies and dragonflies, is one of the most ancient orders of Pterygota. It is comprised of cosmopolitan, hemimetabolous insects that are ubiquitous in most aquatic environments (including several brackish and terrestrial habitats). Due to their relatively big size and beauty, these insects have received adequate taxonomical attention, and currently there are approximately 6,000 identified species (Dijkstra et al., 2013). Another 1,000 to 1,500 species are expected to exist worldwide (Kalkman et al., 2008).

Although considered as a monophyletic group (e.g., Davis et al., 2011), the position of extant Odonata relative to Ephemeroptera and Neoptera and the validity of Paleoptera as a natural taxon are still debated (Hovmöller et al., 2002; Rehn, 2008; Odgen & Whiting, 2003). The higher relationships within the order, including the composition and relationships among superfamilies, is controversial and not fully resolved (see Bybee et al., 2008; Rehn, 2008; Trueman, 2007). For practical reasons, we follow the latest classification scheme (Dijkstra et al., 2013) which considers that: (1) Zygoptera is comprised of four superfamilies (Lestoidea, Platystictoidea, Calopterygoidea, and Coenagrionoidea); (2) Anisozygoptera

includes only the superfamily Epiophlebioidea; and (3) Anisoptera is composed of five superfamilies (Aeshnoidea, Petaluroidea, Gomphoidea, Cordulegastroidea, and Libelluloidea). Except for Epiophlebioidea, all these superfamilies are represented in the Neotropical region. A detailed discussion of the phylogenetic of the order and the composition and systematics of the superfamily can be found in Suhling et al. (2015). Additional information is treated under each superfamily chapter.

The Neotropical region, with 1,768 species presently described (Neiss & Hamada, 2014), has the richest fauna of Odonata worldwide. Many new species and previously unknown immature stages are being described, but still, the larvae of only about 75% genera and 40% of the species are known (Garrison et al., 2006, 2010; von Ellenrieder, 2009). In the period of 2004–2009, 93 species and 11 genera, and the larval stage of 90 species were described (von Ellenrieder, 2009). Zygoptera is represented in this region by 10 families, 108 genera, and 974 species, while Anisoptera includes 9 families, 102 genera, and 794 species (Fleck, 2011; Fleck & El Adouzi, 2013; Neiss & Hamada, 2014).

Zygoptera has a very high level of endemism. Indeed, 89 of the 103 genera of the group are endemic to the Neotropical region. Additionally, two families

(Dictyrididae and Polythoridae) and many coenagrionid genera are also endemic.

Anisoptera also shows a high endemicity, with about 64% of the 59 currently described genera being endemic to the Neotropics, with the remarkable endemicity of Neopetaliidae in the subantarctic forests of southern South America, represented by the monotypic genus *Neopetalia*.

The traditional regionalization based on Wallace (1876) extends the Neotropical region from Mexico to central Argentina. Up to date classifications do not include Chile and part of Mexico and Argentina in this region (e.g., Morrone, 2014); but for practical reasons in the use of the keys, which are mainly oriented to Central and South American scientists and readers, we include here all the fauna of Argentina, Chile and Mexico, and will also refer to this area as the Neotropical region in a wide sense.

LIMITATIONS

In the recent years the publication of several keys for adults (e.g., Förster, 2001; Trapero & Naranjo, 2004; Lencioni, 2005, 2006) have made it easier to identify odonate taxa, especially generic keys for Anisoptera and Zygoptera of the New World (Garrison et al., 2006, 2010), but determination at the species level is still difficult and the Odonata literature is widely dispersed.

For the immature stages, there are several keys at the regional or country level: Amazonas (Neiss & Hamada, 2014), Brazil (Costa et al., 2004), Costa Rica (Ramírez, 2010), Mexico (Novelo-Gutiérrez, 1997) and Patagonia (Muzón et al., 2014). One particular problem is that larval descriptions are mainly based on the ultimate stadium, and the identification of early stages is almost impossible without rearing specimens, a difficult task for many seasonal and fast water species (Neiss & Hamada, 2014).

Given that only about 75% of the genera have been described and many descriptions are too brief or out of date, the keys presented in this book must be used with caution. The degree of knowledge for each family is described in their respective odonate chapters.

TERMINOLOGY AND MORPHOLOGY

Odonatologists have used the term larva(e) for the immature post-egg stages since the end of the 19th century (cf. Tillyard, 1917). Recently, some authors have advocated use of the term naiad for Odonata (Bybee et al., 2015); however, others disagreed (Muzón & Lozano, 2016; Rédei & Štys, 2016; Sahlén et al., 2016). In this chapter, the most widely used term larva is adopted, following the terminology proposed by Corbet (2002). Larvae of Odonata are mostly aquatic and active predators. They inhabit many different kinds of environments, and their morphology varies according to where they live. Details of Odonata's biology

and morphology are discussed in Volume I (Thorp & Rogers, 2015) of this series.

Here we present a glossary which is fundamental for the correct understanding of the terminology used in the keys. Some structures are especially important for identifying larvae, including the head and its parts (e.g., antennae, labium, labial palps), abdominal spines or tubercles, caudal appendages, and anal pyramid, among others.

Glossary

Abdominal projections: Mainly in Anisoptera, larvae bear lateral spines and/or dorsal hooks, used as defense devices against predators like fishes. Their presence, size, and shape are useful for diagnostic purposes.

Anal pyramid: Epiproct and paraprocts are scaliform in Anisoptera (Fig. 14.2), resulting together with the cerci in a five-parts pyramid. At the base of this complex is the anus. Combination of contraction of rectal muscles and the anal pyramid are responsible for the “jet propulsion” of anisopterous larvae.

Caudal appendages: Also referred as caudal lamella, because of their nonappendicular origin. The epiproct and paraprocts are greatly enlarged in Zygoptera (Figs. 14.3, 4, 10, 11, 13) resulting in the dorsal (= epiproct) and lateral (= paraprocts) caudal appendages/lamellae. Dorsal and lateral appendages are quite similar in the same larva (differing mainly in chaetotaxy of dorsal and ventral margins), but they exhibit a wide range of differences among taxa. Caudal appendages give useful diagnostic characters, including shape, presence/absence and location of nodus, color pattern, tracheation pattern and chaetotaxy (i.e., series of spines/setae on dorsal and ventral margins). Corbet (1999), based on Tillyard (1917), gives a classification distinguishing different types, from which we use the following: (1) **saccoid or triquetral** (referred to as saccoid in this book): inflated, sac-shaped, sometimes with three carinae (e.g., Platystictidae, Fig. 14.11, most Megapodagrionidae, Fig. 14.4); (2) **triquetral:** composed of three lamellae, that in posterior view are T-shaped (e.g., Calopterygidae, Fig. 14.10, some Megapodagrionidae); and (3) **lamellate:** flattened, usually ovoid or lanceolate (dorsal one usually held in the vertical plane) (e.g., Coenagrionidae, Fig. 14.15, Lestidae, Fig. 14.13).

Caudal appendages nodus: Structure present at one margin of greatly enlarged caudal appendages in the Zygoptera, usually as a small cleft, that continues as a transversal line that divides the caudal appendage in a basal and a distal part; the distal one is less sclerotized (e.g., Fig. 14.6.27, 37). Usually the spines at the lamella's margin are reduced or absent distal to the nodus. In some species the nodus is slightly evident, and it is only indicated by a change in the stoutness of the marginal setae.



FIGURE 14.1 Gomphoidea, *Ebegomphus* sp., larval habitus, dorsal view.

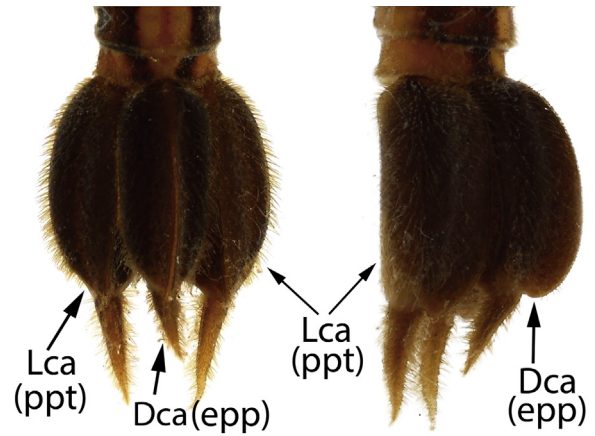


FIGURE 14.4 Calopterygoidea, *Paraphlebia zoe* Selys in Hagen, 1861. Larval caudal appendages, dorsal (left) and lateral (right) view. *Dca*, dorsal caudal appendages; *epp*, epiproct; *Lca*, lateral caudal appendages; *ppt*, paraprocts.

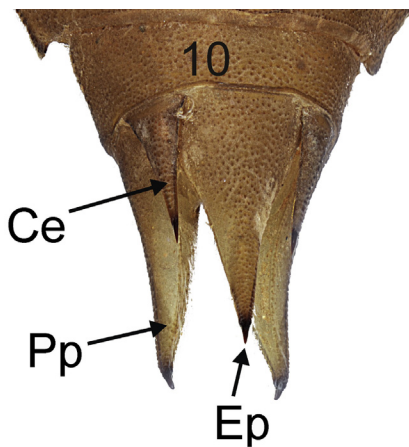


FIGURE 14.2 Gomphoidea, *Ophiogomphus susbehcha* Vogt & Smith, 1993. Larval abdominal segments 9–10. 10, abdominal segment 10; *Ce*, cercus; *Ep*, epiproct; *Pp*, Paraproct. Pictures courtesy of Rodolfo Novelo-Gutierrez.



FIGURE 14.5 Platystictioidea, *Palaemnema brasiliensis* Machado, 2009. Larval prementum, dorsal view. *C*, prementum cleft; *Lp*, labial palp. Black line indicates maximum width.

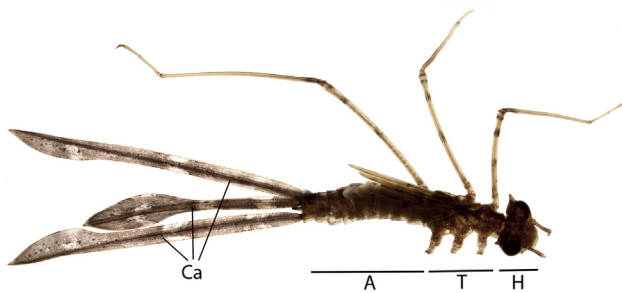


FIGURE 14.3 Calopterygoidea, *Megapodagrion megalopus* (Selys, 1862), larval habitus, dorsal view. *A*, abdomen; *Ca*, caudal appendages; *H*, head; *T*, thorax. Original pictures by Neiss & Hamada (2014).



FIGURE 14.6 Platystictioidea, *Palaemnema brasiliensis*. Larval labial palp dorsal view. *Eh*, end hook; *Mh*, movable hook. Original pictures by Neiss & Hamada (2014).



FIGURE 14.7 Coenagrionoidea, *Paraphlebia zoe*. Larva; prementum, dorsal view. Black line indicates maximum width.

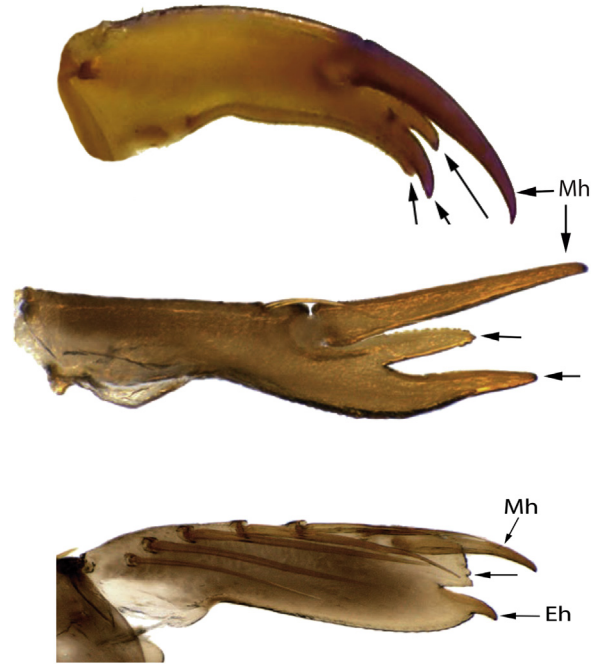


FIGURE 14.9 Coenagrionoidea, *Paraphlebia zoe* (above); *Argia* sp. (middle); *Psaironeura* sp. (below). Larval labial palps. Arrows indicate hooks. Eh, end hook; Mh, movable hook. Original pictures by Neiss & Hamada (2014).

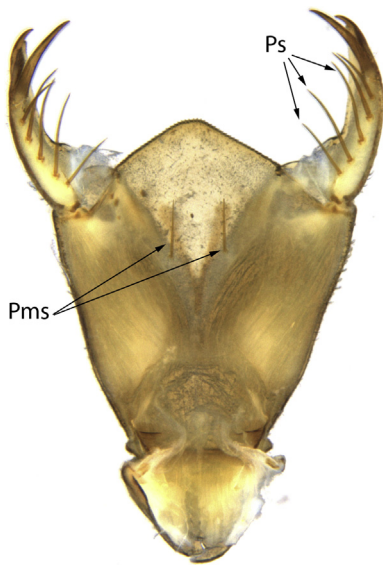


FIGURE 14.8 Coenagrionoidea, *Forcepsioneura sancta* (Hagen in Selys, 1860). Larva; prementum, dorsal view. Pms, premental setae; Ps, palpal setae.



FIGURE 14.10 Calopterygoidea, *Hetaerina americana* (Fabricius, 1798). Larva lateral caudal appendage, dorsal (left) and posterior (right) view.



FIGURE 14.11 Platystictioidea, *Palaemnema brasiliensis*. Larval lateral caudal appendage, lateral (above) and dorsal (below) views.



FIGURE 14.12 Calopterygoidea, *Rimanella arcana* (Needham, 1933). Larval caudal appendages, dorsal view.

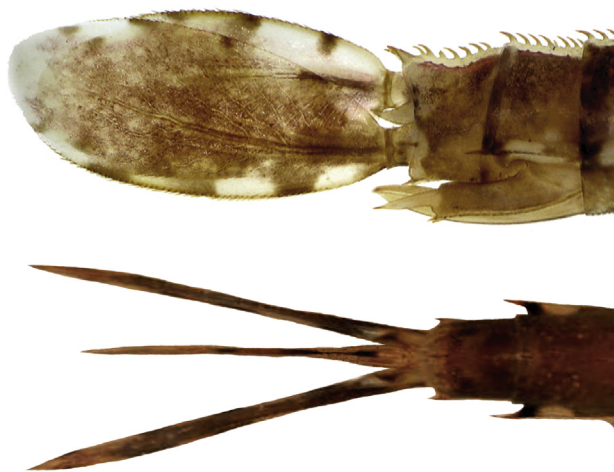


FIGURE 14.13 Lestoidea, *Perilestes attenuatus* Selys, 1886. Larval caudal appendage, lateral (above) and dorsal (below) view. Original pictures by Neiss & Hamada (2014).



FIGURE 14.14 Calopterygoidea, *Hetaerina* sp. larval habitus, dorsal view. Original pictures by Neiss & Hamada (2014).



FIGURE 14.15 Coenagrionoidea, *Psaironeura tenuissima* (Selys, 1886) larval habitus, dorsal view. Original pictures by Neiss & Hamada (2014).

Cerci: They are the 11th abdominal segment appendages. They are unsegmented, small, and little informative, except in several Coenagrionidae genera (e.g., *Enallagma*).

End hook: Hook present at the inner-distal margin of labial palp, usually well developed (e.g., most Coenagrionidae and Megapodagrionidae, Fig. 14.9), sometimes reduced (e.g., Austropetalidae), curved (e.g., most Coenagrionidae, Fig. 14.9), or straight (e.g., *Gynacantha*, *Staurophlebia*).

Labial palp: Modified raptorial palp (Figs. 14.5–9) which are very mobile and usually with an end hook and a movable hook (see in this glossary). These are highly variable in shape and relative size with the distal margin sometimes greatly lobulated (e.g., *Lestes*), with end hook and small teeth (e.g., *Psaironeura*, Fig. 14.9), or bare (e.g., *Triacanthagyna*). The inner margin may be crenulated or with small teeth (e.g., *Roppaneura*) or

bare (e.g., *Bromelagrion*), with (e.g., *Forcepsioneura*, *Psaironeura*, Figs. 14.8–9) or without palpal setae (e.g., *Palaemnema*, *Paraphlebia*, Fig. 14.6, 9) close to its outer margin.

Labium: The prehensile labium of Odonata larvae is unique due to its extendable capacity. It is integrated by a post and a prementum (Figs. 14.5, 7, 8, 27, 29) and two labial palps. The labial palp ends in a movable hook. In a resting position, the labium can reach posteriorly a different pair of coxae, or even abdominal S1 in some Lestidae. There are different labium types:



FIGURE 14.16 Lestoidea, *Perilestes solutus* Williamson & Williamson, 1924. Larval prementum, dorsal view. C, prementum cleft. Original pictures by Neiss & Hamada (2014).



FIGURE 14.17 Lestoidea, *Lestes* sp. larval prementum, dorsal view. Original pictures by Neiss & Hamada (2014).

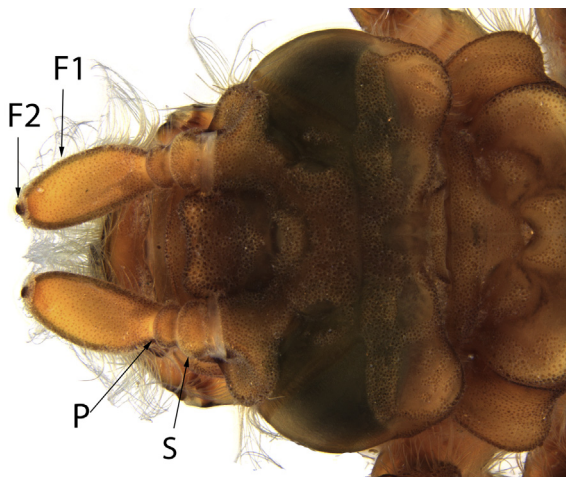


FIGURE 14.18 Gomphoidea, *Praeviosgomphus proprius* Belle, 1995. Larval head, dorsal view. S, scape; F1–2, flagellomeres 1–2; P, pedicel.

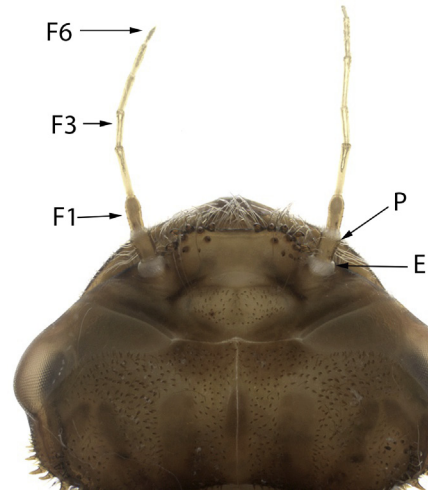


FIGURE 14.19 Cordulegastroidea, Cordullidae sp. Larval head dorsal view. E, scape F1–6, flagellomeres 1–6; P, pedicel.



FIGURE 14.20 *Phyllopetalia apollo* Selys, 1878. Detail of larval head, dorsal view. F1–3, flagellomeres 1–3.



FIGURE 14.21 Petaluroidea, *Phenes raptor* Rambur, 1842. Larval leg. Arrows indicate tibial spines.

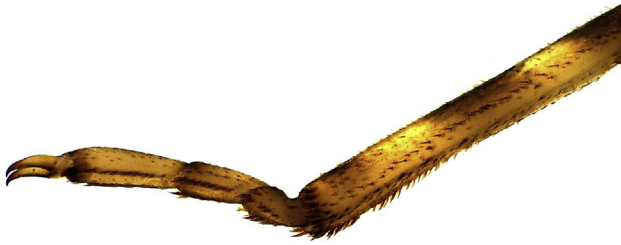


FIGURE 14.22 Aeshnoidea, *Rhionaeshna* sp. Larval tibia and tarsus.



FIGURE 14.25 Cordulegastroidea, *Cordulegaster diadema* Selys, 1868. Larval labial palp, inner view. *Mh*, movable hook.



FIGURE 14.23 Aeshnoidea, *Rhionaeshna* sp. Larval head, lateral view. *Lp*, labial palp.

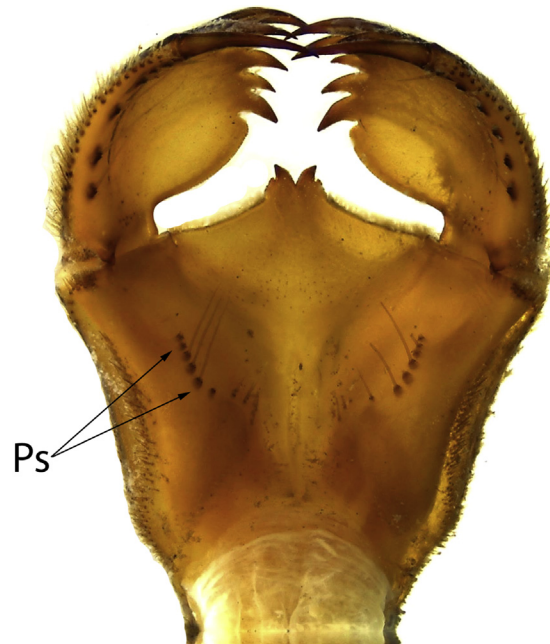


FIGURE 14.26 Cordulegastroidea, *Cordulegaster diadema*. Larval prementum, dorsal view. *Ps*, premental setae



FIGURE 14.24 Libelluloidea, *Riella villosa* (Rambur, 1842). Larval head, lateral view. *Lp*, labial palp.

broad and flat (e.g., most Zygoptera as in Figs. 14.7–8; and in Aeshnidae Fig. 14.23), extremely long, petiolated and scoop-shaped (Lestidae, Fig. 14.17), and short and scoop-shaped (e.g., Libellulidae and Cordulegastroidea, Figs. 14.24, 27, 29) (Corbet, 1999). Besides these general distinctions, there is a great variation depending on feeding preferences or behavior. According to these preferences there are variations on the number and size of prementum and palpal setae, and different types of structures at the prementum anterior



FIGURE 14.27 Cordulegastroidea, *Neopetalia punctata* (Hagen in Selys, 1854). Larval prementum, dorsal view. Arrow indicates anterior margin with a cleft and dentiform median process

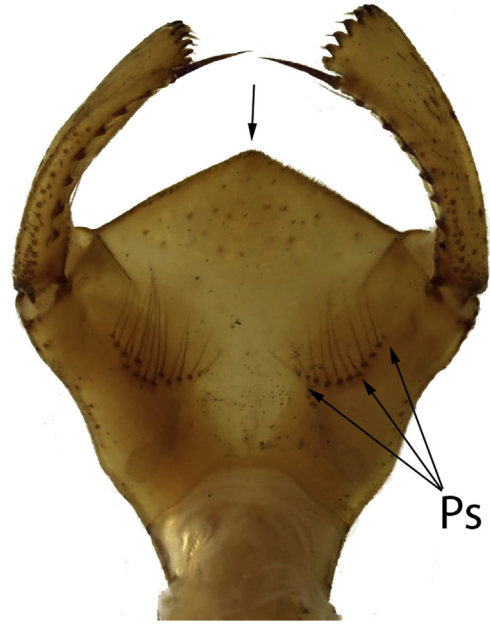


FIGURE 14.29 Libelluloidea, *Rialla villosa*. Larval prementum, dorsal view. Ps, premental setae. Arrow indicates absence of cleft and tooth-like median process



FIGURE 14.28 Libelluloidea, *Rialla villosa*. Labial palp.

margin (ligula) and palps' inner and distal margins (e.g., setae, spines, hooks, and crenulations).

Ligula: Anterior margin of prementum, with variable development and shape across the order. The ligula can

be more or less triangular (Figs. 14.8, 29), convex, more or less rounded (Figs. 14.5, 7), with tooth-like median process (Fig. 14.26), and with (Figs. 14.5, 7) or without (Figs. 14.8, 29) a medial cleft.

Movable hook: Long, slightly curved hook (Figs. 14.6, 9, 25) developed at the outer distal margin of labial palp and articulated with it. The hook can be variable in length from about half to more than one and a half times the length of labial palp, and be bare or with raptorial setae (e.g., Lestidae).

Palpal setae: Setae developed close to the outer margin of labial palp. They vary in number and size (e.g., *Forcepsioneura*, *Psaironeura*, *Rialla*, Figs. 14.8, 9, 28) or can be absent (e.g., *Palaemnema*, *Paraphlebia*, Figs. 14.6, 9).

Prementum: Distal part of Odonata labium (e.g., Figs. 14.5, 7, 27) which bears the labial palps. It can be very long and slender (e.g., Lestidae, Fig. 14.17), more or less triangular (e.g., *Forcepsioneura*, Fig. 14.8), quadrangular (e.g., *Paraphlebia*, Fig. 14.7, Aeshnidae), etc. It bears (when present) premental setae on its dorsal surface. Its anterior margin is also known as ligula, may bear a prementum median cleft.

Prementum median cleft: Cleft present in the middle of labium distal margin. It can be absent (e.g., some Libellulidae, Coenagrionidae, Figs. 14.8, 29) or well developed (e.g., *Palaemnema*, *Paraphlebia*, *Perilestes*, Figs. 14.5, 7, 16).

TABLE 14.1 Genera of Coenagrionidae Previously Included Within Protoneuridae and Pseudostigmatidae

Genus	Protoneuridae	Pseudostigmatidae
<i>Amazonaura</i>	X	
<i>Anomisma</i>		X
<i>Drepanoneura</i>	X	
<i>Epipleoneura</i>	X	
<i>Epipotoneura</i>	X	
<i>Forcepsioneura</i>	X	
<i>Idioneura</i>	X	
<i>Junix</i>	X	
<i>Lamproneura</i>	X	
<i>Mecistogaster</i>		X
<i>Megaloprepus</i>		X
<i>Microstigma</i>		X
<i>Neoneura</i>	X	
<i>Peristicta</i>	X	
<i>Phasmoneura</i>	X	
<i>Proneura</i>	X	
<i>Protoneura</i>	X	
<i>Psaironeura</i>	X	
<i>Pseudostigma</i>		X
<i>Roppaneura</i>	X	

Premental setae: Setae developed at the dorsal surface of prementum. These vary in number and size (e.g., *Forcepsioneura*, *Cordulegaster*, *Rialla* Figs. 14.8, 26, 29), or can be absent (e.g., *Perilestes*, *Neopetalia*, Figs. 14.16, 27) (Table 14.1).

S1–9: Abbreviation for abdominal segments 1–9.

MATERIAL PREPARATION AND PRESERVATION

In Volume I (Thorp & Rogers, 2015) of this series, specimen preparation and preservation are discussed and to some extent, also in the odonate chapters of the present volume.

KEYS TO ODONATA

Superfamilies with low diversity and poorly represented in the Neotropical region (1–2 genera) do not require a separate chapter and a key of their own, therefore, they are included in the keys presented in this chapter.

Platystictioidea includes only one family, Platystictidae, distributed in the Oriental and Neotropical regions, where it has one genus (*Palaemema*) and 43 species (Garrison et al., 2006). It is distributed in central and northern South America, but a few species enter North America (Garrison et al., 2006). The larva of six species are known, with all living in fast current streams with rocky bottom (Novelo-Gutiérrez and González-Soriano, 1986; Novelo-Gutiérrez, 2003; Neiss & Hamada, 2016).

Cordulegastroidea is a relatively small taxon, containing three families: Chlorogomphidae, Cordulegastridae, and Neopetaliidae, but only the last two are recorded in the Neotropical region. Cordulegastridae is a Holarctic family represented by 45 species in three genera. One genus (*Cordulegaster*) and 10 species are recorded in the New World, but only one enters Central America and is present from Mexico to Costa Rica. Larvae are characterized by

living in forested streams where they bury themselves in soft sandy substrate (Garrison et al., 2006). Neopetaliidae is a monotypic family, endemic to the subantarctic forest of southern Argentina and Chile, with a wider distributional range in Chile than in Argentina (Muzón et al., 2014). The larva of *Neopetalia punctata* has been described (Carle & Louton, 1994), and it inhabits small streams within *Nothofagus* forests, burrowing shallowly in their muddy bottom (Carle & Louton, 1994).

Petaluroidea includes only the family Petaluridae which consist of very large dragonflies. It includes five genera and 11 species and has a transpacific distribution pattern, being present in Australia, New Zealand, North America and southern South America (Garrison et al., 2006). *Phenes raptor* is the only representative of the family in South America; it inhabits the subantarctic forest of southern Argentina and Chile (Muzón et al., 2014). Larvae of this species was described by Schmidt (1941) and Needham & Bullock (1943), they have terrestrial habits, being found in the moist forest ground and seepages (Garrison & Muzón, 1995). The biology of this species is well documented by Baird (2013).

Odonata: Suborders

- 1 Abdomen slender (Fig. 14.3, 15), ending in three large caudal appendages of variable shape (Figs. 14.3, 4, 10, 11, 15) **Zygoptera** [p. 364]
- 1' Abdomen robust (Fig. 14.1), ending in an anal pyramid (epiproct plus paraprocts) (Fig. 14.2) **Anisoptera** [p. 364]

Odonata: Zygoptera: Superfamilies

- 1 Prementum not distinctly widened on its basal half (Figs. 14.7, 8), labial palp with end hook and one or more additional teeth (Fig. 14.9), caudal appendages variable 2
- 1' Prementum distinctly widened on its basal half (Fig. 14.5), labial palp with only one robust and truncated tooth (end hook) (Fig. 14.6), caudal appendages saccoid (Fig. 14.11) Platystictioidea, one genus: *Palaemnema*
- 2(1) Caudal appendages lamellate, held nearly vertically (Figs. 14.13, 15), prementum cleft present (Lestoidea, Fig. 14.16) or entire (Coenagrionoidea, Fig. 14.8), labium may be petiolate and elongate, extending beyond metacoxae (Fig. 14.17) or may be normally developed 3
- 2' Caudal appendages triquetral (Fig. 14.10), saccoid (Figs. 14.4, 11) or greatly modified (Fig. 14.12), longer (Fig. 14.3) or shorter than body (Fig. 14.14). Prementum cleft, labium not elongate **Calopterygoidea** (Chapter 14.4, p. 499)
- 3(2) Prementum cleft, labium normal (Fig. 14.16) or petiolate and elongate, extending beyond metacoxae (Fig. 14.17) **Lestoidea** (Chapter 14.5, p. 469)
- 3' Prementum entire, labium normal (Fig. 14.8) **Coenagrionoidea** (Chapter 14.6, p. 475)

Odonata: Anisoptera: Superfamilies

- 1 Antennae with scape, pedicel, and 3–6 flagellomeres, the first < half antenna length (Figs. 14.19, 20) 2
- 1' Antennae with scape, pedicel, and two flagellomeres, the second reduced or vestigial, the first > half antenna length (Fig. 14.18) **Gomphoidea** (Chapter 14.2, p. 377)
- 2(1) Tibiae usually without robust apical spines (Fig. 14.22), if present (*Hypopetalia pestilens*), labial palp with several tooth on its inner margin (Fig. 14.14); body usually not robust and big; rarely terrestrial 3
- 2' Tibiae with robust apical spines for digging (Fig. 14.21); labial palp without tooth on its inner margin; body very robust length to >45 mm; terrestrial and aquatic **Petaluroidea**, Petaluridae, one species: *Phenes raptor* Rambur, 1842 [Patagonia]
- 3(2) Prementum spatulate, labial palp at rest covering anterior part of head (Fig. 14.24) 4
- 3' Prementum flat, labial palp not covering anterior part of head at rest (Fig. 14.23) **Aeshnoidea** (Chapter 14.1, p. 367)
- 4(3) Labial palpi with long and irregular teeth (Fig. 14.25), distal margin of prementum with a cleft and dentiform median process (Figs. 14.26, 27) **Cordulegastroidea** [p. 364]
- 4' Labial palps variable, usually without long and irregular teeth (Fig. 14.28); prementum distal margin entire and not dentiform (Fig. 14.29) **Libelluloidea** (Chapter 14.3, p. 399)

Odonata: Anisoptera: Cordulegastroidea: Families

- 1 Prementum and palpi without setae (Fig. 14.27) Neopetaliidae, one species: *Neopetalia punctata* (Hagen in Selys, 1854) [Patagonia]
- 1' Prementum and palpi with setae (Figs. 14.25, 26) Cordulegastridae, one genus; *Cordulegaster* [Costa Rica. Holarctic]

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