THE LARVA OF NEOPETALIA PUNCTATA AND ESTABLISHMENT OF AUSTROPETALIIDAE FAM. NOV. (ODONATA)

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Abstract.—The larva of Neopetalia punctata is described and the Neopetaliidae transferred to the Libelluloidea (sensu Carle 1986). The Austropetaliidae fam. nov. (type genus: Austropetalia Tillyard) is established for the remaining species formerly placed in Neopetaliidae, and Austropetaliidae fam. nov. placed within the Aeshnoidea (sensu Carle 1986). Keys to the superfamilies and families of Anisopteran adults and larvae are provided, and comments on biology and distribution are included.

Key Words: Odonata, Austropetaliidae, new family, Neopetaliidae, Aeshnoidea, Libelluloidea

While undertaking phylogenetic studies of the Anisoptera, the senior author became intrigued by several enigmatic characteristics attributed to the rare Neopetalia punctata Selvs. Adults were obtained from Carl Cook and the National Museum of Natural History, and study of these not only verified the unique splash plate and reduced ovipositor of the female, but revealed short but well-developed male tibial keels on all legs, chlorogomphid-like antefrons and clypeus, a cordulegastrid-like penis, and hamuli of a unique form. Although the wing spots, oblique pterostigmal brace, and general archaic morphology (e.g. compound eyes meeting at a point), suggested a close affinity with Phyllopetalia and its relatives, several additional characteristics seemed to suggest that its current placement was problematic. These included presence of a wide anal loop, configuration of the middorsal mesothorac-

During reorganization of unsorted Odonata larvae at the National Museum of Natural History, the junior author discovered a peculiar cordulegastrid-like larva with parallel wing pads and short terminalia. Further examination revealed a cordulegastrid-like labium except that there were only vestigial mental setae and only two small palpal setae. The specimen was in an unlabeled lot with several final instar Phyllopetalia larvae (known only from eastern Australia and southwestern South America). Because Cordulegastridae are not known to occur in the southern hemisphere a careful search was undertaken of all unbroken lots of Chilean larvae. Fortunately, a second cordulegastrid-like larva was found in a labeled lot of Phyllopetalia larvae from Dalcahue, Chile. These specimens were brought to the attention of the senior author and careful study revealed a large pointed epi-

ic carinae, flattened elongate male cerci, pointed male epiproct, and extensive hairiness of the thorax and abdomen.

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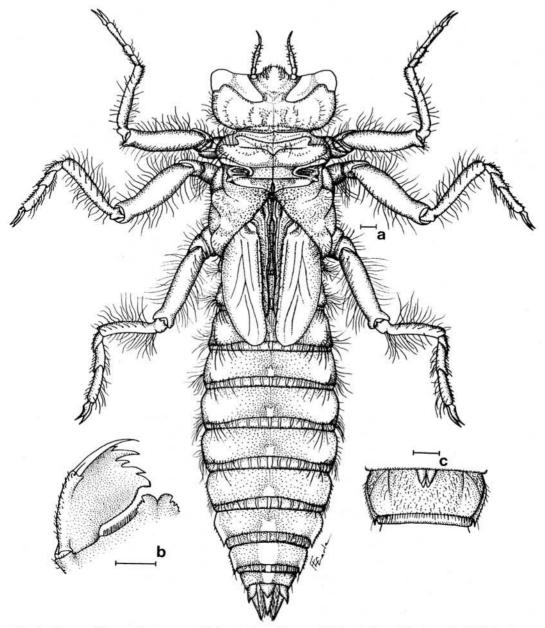


Fig. 1. Larva of *Neopetalia punctata*: (a) dorsal view of larva,—(b) dorsal view of ligula and left labial palp,—(c) ventral view of female sternum 9; scale bars equal 1mm.

proctal process, three cubital-anal crossveins, bridge crossvein near subnodus; oblique pterostigmal brace, and a well-developed anal loop, all reminiscent of the condition in adult *Neopetalia*. Known localities for *Neopetalia* were compiled and an expedition to Chile planned to collect and rear the unknown larva. During a onemonth expedition several individuals of the unknown larvae were collected throughout central Chile from the Andes west of Santiago south to Chiloe Island. One of the larvae was successfully reared and proved to be that of Neopetalia punctata.

The close relationship between Neopetalia and Cordulegaster was first recognized by Selvs (1854) who placed Petalia (now Neopetalia) and Thecaphora (now Zoraena) with Cordulegaster in his legion Cordulegaster. Chlorogomphus was recognized as the only genus in the legion Chlorogomphus. however, it was placed near the legion Cordulegaster. The establishment of the subgenus Phyllopetalia (Selvs 1857) within Petalia for two newly discovered Chilean aeshnoid species represented the first of many misplacements which would continue to the present day. Surprisingly, discovery of the female of Petalia (Selvs 1869) or the female of Phyllopetalia (Selvs 1878) did not precipitate taxonomic revision. The group was first reported from Australia by Tillyard (1906) with the discovery of "Petalia apollo Selvs" from the Blue Mountains of New South Wales. This species was later redescribed as Phyllopetalia patricia Tillyard (1909) with the discovery of its larva leading to the following conclusion: "The consequent conviction that Phyllopetalia was a true Aeschnine genus is, I trust, happily vindicated by the present paper, on the evidence of this truly remarkable nymphal form." Unfortunately, Tillyard's conclusions were extended to include the entire "Petalia-group of genera."

Description of the Larva of Neopetalia punctata (Selys) Fig. 1

Larval material.—Chile: Chiloe Province; Dalcahue, 2 &, seepage areas along mill stream, 21&22-X-69, O. S. Flint Jr.; Dalcahue, 11 &, 13 &, seepage area south of mill stream, 16&17-XII-92, F. L. Carle, A. Ugarte, and L. E. Pena; Ahoni, 13 &, 8 &, seepage streams ca. 0.5 km south of main road, 20-XII-92, F. L. Carle and A. Ugarte;—Osorno Province; Aguas Calientes, 3 &, 2 &, small seepage stream southwest of

camping area, 26-28-XII-92, F. L. Carle, A. Ugarte, and L. E. Pena;—Curico Province; Quebrada Honda "El Coigo," 2 &, spring seep on south side of Est. Potrero Grande, 3-I-93, F. L. Carle and A. Ugarte;—Santiago; Farellones, 1 &, small seepage stream along south side of R. Molina, 5-I-93, F. L. Carle.

Measurements.—Total length 35.0–38.0 mm, abdominal length 23.0–24.5 mm, abdominal width 8.0–8.5 mm, wing pads 7.0–7.5 mm, profemora 4.2–4.4 mm, mesofemora 5.0–5.2 mm, metafemora 6.0–6.2 mm, epiproct 2.0 mm, paraprocts 2.2 mm, cerci 1.1 mm.

Head.-Antefrons inflated, shelf margin rounded, dorsal surface with medial glabrous area and lateral setal patches of stout setae, setae longer anteromedially: lateral ocellar mounds covered with tuft of thin setae: posterior portion of head with lateral and six longitudinal lines of bristlelike setae; antennae with short stiff setae, antennae 6-segmented, third segment 2.2 times length of second segment; labrum and anteclypeus concealed by retracted labium, clypeal sulci with fringe of hairlike setae which seal dorsal edge of labial palps; ligula with glossal and paraglossal lobes, glossae represented by two large robust teeth with apices directed laterally and medially separated by a wide cleft, paraglossae each represented by low row of 4-5 small semifused denticles: ligular margin from paraglossae to base of palpi with fringe of fine short hair setae; prementum elongate, ca. 3 times as long as basal width; prementum with ventral and dorsolateral setae, but without dorsolateral row of stout setae; premental raptorial setae vestigial, with only 1-3 per side; labial palpi without dorsomedial raptorial setae, but external lateral setae longer anteriorly with longest setae isolated apically near base of end hook; end hook robust, longer than lateral margin of palpi; medial margin of palpi somewhat bilobate with 5-6 irregular teeth, 3 teeth of the upper lobe larger and sharp pointed, teeth of the lower lobe smaller, inclined inward, and with ventral tooth rounded apically; edges of large irregular teeth with minute crenulations; inner margin of palpi with ca. 30 small crenulations, these larger and denticlelike medially.

Thorax.—Epaulettes ca. 1.7 times as long as wide at midlength, separated from anterior margin of pronotum by wide notch, and with dorsal cluster of long hair setae; mesonotum with robust conical spine at base of spiracle; wing pads parallel, extended to abdominal segment 4; folded labium extended posteriorly to posterior margin of mesocoxae, paracoxal processes absent; metasternal anterior transverse sulci angulate, fused to medial sulci to form Y-shaped seam, medial sulci ca. 1.0 mm long; legs edged with long fine hair; tibiae apically and tarsi ventrally with stout setae.

Abdomen. - Terga 1-9 with posterior margins fringed with short hair setae and with large paired dorsolateral swellings, each swelling with cluster of long fine hair setae. swellings and associated hair setae largest on segments 2-5, smaller posteriorly, vestigial on 8 & 9, with hair tuft incorporated into posterior hair fringe; dorsum with posteromedial light spot on terga, ca. 1/3 length on anterior segments, and full length on tergum 9; ventral surface with short fine hair setae, hairs longest along lateral sternal sulci: sterna without anterolateral apodemes; lateral margins of abdomen with long hair setae, lateral setae short and stout on segments 8 & 9; segments 8 & 9 with lateral spines, that on segment 8 smaller, ca. 1/2 lateral margin of 8 including spine, that of 9 ca. 1/6 lateral margin of 9 including spine; progonapophyses ca. 1/2 length of sternum 9, metagonapophyses with apices at ca. 1/4 length of sternum 9; epiproct shorter than apical width of segment 10, apex down turned: male epiproctal tubercle large acuminate, extended to ca. 0.45 length of epiproct; cerci robust, somewhat blunt in male, ca. 1/2 length of paraprocts; paraprocts straight tipped, slightly longer than epiproct; proventriculus with four sclerotized

toothlike lobes, dorsal lobes extended into long narrow triangular tooth with apex inclined posteriorly, medial edge with 6-8 denticles, lateral edge with 3-5 denticles; ventral lobes shorter and wider, medial edge with 4-5 denticles, lateral edge inclined laterally with 4-5 denticles, posterior surface ca. 1.6 times as high as wide.

DISCUSSION

The accompanying key is based on the senior author's phylogenetic research of the Anisoptera and includes several new characters which are presented to allow their evaluation by other workers. The key is not intended to imply a definite anisopteran phylogeny, although the authors believe the ultimate goal should be the creation of natural or phylogenetic keys. The third couplet of the adult and larval keys results in the placement of Neopetalia in the Libelluloidea (sensu Carle 1982a, 1986), and the placement of remaining "Neopetallidae" within the Aeshnoidea. Therefore, Austropetaliidae fam. nov. (type genus Austropetalia Tillyard) is established to include Austropetalia, Phyllopetalia Selys, Hypopetalia McLachlan, and Archipetalia Tillvard. Adults and larvae of the new family are separated in the fourth couplet of both keys. It is also noted that austropetaliid secondary genitalia is unique among Aeshnoidea in that the anterior lamina is short and wide, being similar to that of Petaluridae.

Placement of Neopetalia within Libelluloidea is quite straightforward as several apparent apomorphies are shared between their larvae; these include prementum scooplike, labrum concealed by triangular labial palps, labial endhook distinctly shorter than palp, epiproct acuminate, and proventriculus bilaterally symmetrical with sclerotized lobes large-toothlike and edged with 2–8 teeth. Adult similarities include exophytic oviposition with the uniquely reduced ovipositor which retains the metagonapophyses. Furthermore, placement of Neopetalia within the non-cordulegastrid

Libelluloidea is supported by several apparent synapomorphies including the loss of paraglossal spines, inflation of lateral clypeal lobes, well-developed ocellar lobe, short wide pterostigmata, male with meso-and metatibial keels, and further reduction of the metagonapophyses. Apparent auta-pomorphies of the Cordulegastridae include: supplementary sector arising near bridge crossvein, male meso- and metatibiae with peglike spines, anterior hamuli erect foliate, and female progonopodites appressed into an elongate, gently-tapered, spadelike organ for placing eggs into soft stream bottoms.

A sister group relationship between Neopetalia and remaining non-cordulegastrid Libelluloidea is supported by the following apparent apomorphies of this latter group: loss of oblique pterostigmal brace, male tibial keels long (obsolete in Libellulinae), and ventral proventricular lobes with at least a dorsal or basal tooth in addition to the apical tooth. The autapomorphies of Neopetalia are amazing and include: wings with costal series of 4 reddish blotches, apical blotch divided by yellowish orange pterostigmata: abdominal terga 5-8 with ventroapical tufts of long black hair, body excessively hairy; anterior hamuli contiguous and L-shaped; female tergum 2 with "genital lobes"; female sternum 10 expanded into huge circular splash plate, with elongate curved cerci supporting its outer rim; larval antennae 6 segmented, third segment ca. as long as distal portion of antennae; larval premental setae vestigial; larva with lateral lobes of labium bilobate and ending in 5 or 6 irregular medial teeth; and larval lateral lobes with one dorsomedial setae each. These character distributions suggest that an isolated taxonomic position is warranted, and therefore Neopetaliidae is retained as a monotypic family.

BIOLOGY

Neopetalia larvae were only found in the silt-bottomed pools of small streams and

seepage areas. The largest number of larvae were found in seepage streams, that is, streams averaging less than 1/2 meter wide and less than 10 cm deep, with about a 1 to 10 gentle riffle to pool ratio, and fed by numerous small feeder springs. The smallest larvae found (ca. 2 mm), were living in the small pools formed by livestock tracks at the very edge of a seepage area. Isolated larvae were found in streams up to 2 m wide, but only near shore in quiet silt-bottomed eddies on the lee side of logs or rocks. Compared to holarctic Cordulegastridae the larval habitat of Neonetalia is most similar to that of Zorgena bilineata Carle, Larvae kept in rearing cages quickly worked their way into the substrate leaving only the compound eyes and apex of the terminalia above the surface of the substrate. Feeding was accomplished from ambush with only slight reorientations of the head employed. Small Ephemeroptera were the preferred prev: Plecoptera placed in the rearing cages were not taken. From the sizes of larva collected three years are required for larval development.

Adults are most often observed flying at from 5 to 15 m above spring seeps where they become most active following the passing of a cloud. After an extended period of sunshine the somewhat fluttery back and forth feeding flight would end as individuals drifted away to hang up high in the forest. In the morning and toward dusk both sexes patrol sunlit forest roads at 1-3 m, where the flight of the females in particular seems quite labored. In these behavioral traits Neopetalia shows uncanny similarities with the following account of chlorogomphid behavior from Fraser (1929), "Their habits ... differ markedly from those of Cordulegaster; their flight on the level is comparatively weak, being not more fast than the speed of a fast running man, they are however given to soaring and on occasions rise to hundreds of feet above the tree-tops . . . Males have frequently been observed resting on twigs of dead or leafless trees some hundred or more feet above ground-level. At other times, both sexes are given to patrolling mountain roads. . . ."

The series of four reddish blotches along the coastal margin is unique among the Libelluloidea and may represent a mimicry of the pattern found in the Austropetaliidae fam. nov. The pattern is quite consistent throughout the austropetaliids, the major variation being the lack of the postnodal blotch in red Phyllopetalia. In austropetaliids the female is always marked more conspicuously suggesting a warning coloration and indicating that the group may be distasteful. In Neopetalia the apical blotch is always missing, the extent of blotching between males and females is more equal. and the pterostigmata is bright vellowish orange centrally dividing the pterostigmatal reddish blotch in two. Mimicry in the Odonata is not limited to this group as the Polythorids (e.g. Polythore manua Bick and Bick) mimic noxious butterflies (JAL, pers. observation).

Oviposition was apparently observed on one occasion while the senior author crawled through the cavelike understory along a small stream. The female hovered momentarily close to the water surface, turned to face shore, and smacked the water surface with the apex of the abdomen, she then slowly rose while intermittently stopping and turning to navigate upward through the dense understory. This behavior along with the unusual ovipositor indicates that the female may build up a large cluster of eggs on the progonapophyses before beginning oviposition, the splash plate may be utilized to disperse this egg cluster.

The known geographical range of *Neopetalia* extends from about sea level near Ahoni, 43°2′ latitude to about 1800 m near Farellones, 33°20′ latitude. The known flight season is from October 18 to January 26. *Neopetalia* is not known to occur outside Chile. Although the range of *Neopetalia* is quite widespread, its larval habitat, like that of *Zoraena* and *Taeniogaster*, is very lo-

calized. The extremely restricted habitat requirements for Neopetalia were not expected owing to the lack of related species in the down stream environment. In North America Zoraena, Taeniogaster, Kalvntogaster, and Pangaeagaster occupy sequential zones of lotic systems from spring seeps to small rivers (cf. Carle 1982b). However, the restricted occurrence of Neopetalia may be secondary, being the result of establishment of either non-native Brown trout (Salmo trutta), Atlantic salmon (Salmo salar), or Rainbow trout (Oncorhynchus mykiss) in all of the drainages where Neopetalia was found. It is difficult to determine how serious fish predation would be on a burrower like Neopetalia, but it was very clear that populations of nonburrowers such as Allopetalia. Phyllopetalia, and Hypopetalia were much more abundant above impassable falls. Other threats to the ancient stream fauna of Chile include the pasturing of livestock in spring seeps, and the piping and channeling of springs and small streams for domestic use, livestock, and irrigation.

KEY TO THE SUPERFAMILIES AND FAMILIES OF ANISOPTERA ADULTS

- Labium with palpal end hook as long as ligula, ligula entire; postfrons with postocellar ridge; supratriangles similar in shape and with anterior side concave posteriorly; posterior hamuli engaging female sternum 9, apical hooks directed anteriorly; ovipositor reduced to fused progonacoxae and progonapophyses, metagonopodites at most represented by small sternal plates Gomphoidea Gomphidae
- Labium with palpal end hook shorter than ligula, ligula variable; postfrons without postocellar ridge; supratriangles either not similar in shape or with anterior side straight; posterior hamuli engaging female sternum 8, apical hooks directed posteriorly or medially; ovipositor complete or reduced, metagonopodites at least represented by small peglike structures
- Compound eyes widely separated dorsally, anterodorsal surface of occiput trapezoidal; pterostigmata concave posteriorly and longer than distance between costal braces; ligula with wide medial cleft; male epiproct typically di-

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	varicate, and cerci strongly expanded distally; ovipositor complete and strongly upturned		ca. 8 times width; male without small protibial keels and meso- and metatibial peglike	
	Petaluroidea Petaluridae		spines; anterior hamuli vestigial or elongate	
-	Compound eyes contiguous or approximate		and directed posteroventrally; progonopod-	
	dorsally, anterodorsal surface of occiput tri-		ites not appressed into elongate gently tapered	
	angular; pterostigmata not concave posteri-		spade	6
	orly, shorter than distance between costal	6.	Pterostigmal brace thickened and oblique;	
	braces; ligula with medial cleft variable; male		wings with costal series of 4 reddish blotches,	
	epiproct typically quadrate or triangular, and		apical blotch divided by yellowish orange	
	cerci not strongly expanded distally; ovipos-		pterostigmata; abdominal terga 5-8 with ven-	
	itor variable, not upturned		troapical tufts of long black hair; male tibial	
3.	Pterostigmal brace thickened and oblique; an-		keels ca. 1/3 length of protibiae and 1/4 length	
	terior lamina with elongate medial cleft, an-		of meso- and metatibiae; anterior hamuli con-	
	terior hamuli directed medially, posterior		tiguous and L-shaped; female sternum 10 ex-	
	hamuli vestigial; median process of male ab-		panded into huge circular splash plate	
	dominal segment 2 short L-shaped; oviposi-		Neopetaliid	Jae
	tor complete, suited for endophytic oviposi-	7	Pterostigmal brace vestigial; wings without	
	tion Aeshnoidea 4		costal series of 4 reddish blotches, apical blotch	
=	Pterostigmal brace obsolete, (present in Neo-		not divided by yellowish orange pterostig-	
	petalia); anterior lamina without elongate me-		mata; abdominal terga 5–8 without ventroap-	
	dial cleft, anterior hamuli directed postero-		ical tufts of long black hair; male tibial keels	
	ventrally or absent, posterior hamuli well		more than \(\frac{1}{3} \) length of protibiae and \(\frac{1}{3} \) length	
	developed; median process of male abdomi-		of meso- and metatibiae (obsolete in Libel-	
	nal segment 2 long J-shaped; ovipositor reduced, suited for exophytic oviposition		lulinae); anterior hamuli not contiguous or L-shaped; female sternum 10 without splash	
	Libelluloidea 5		From the first the second control of the second control of the second control of the second control of the second	7
1	Wings with costal series of 5–8 reddish blotch-	7	Ligula longer than wide and with apical cleft;	,
4.	es; compound eyes approximate or meeting	/.	labial palps with well developed movable end	
	at point dorsally; abdomen without dorsal or		hook and apical spine; sectors of the arculus	
	lateral carinae, 7 or 8 often with lateral ex-		separated basally; supratriangles slightly con-	
	pansions; wings without planates; fore wing		vex anteriorly; antenodal crossveins not	
	triangle with proximal side more than ½ an-		aligned, with two costal braces; subtriangular	
	terior side; penis laterally exposed, prepuce		interspace dilated basally; anterior hamuli	
	well developed, segment 4 pendulous with		elongate and directed anteroventrally	
	huge paired flagellae directed posteroventrally		Chlorogomphic	dae
	Austropetaliidae fam. nov.		Ligula wider than long and without apical cleft;	
_	Wings without costal series of 5-8 reddish		labial palps with vestigial movable end hook	
	blotches; compound eyes meeting along dor-		and apical spine; sectors of the arculus fused	
	sal seam; abdomen with dorsal and lateral		basally; supratriangles strongly convex ante-	
	carinae, without lateral expansions; wings with		riorly; antenodal crossveins mostly aligned or	
	planates; fore wing triangle with proximal side		with 3 or more costal braces; subtriangular	
	less than 1/2 anterior side; penis laterally con-		interspace not dilated basally; anterior hamuli	
	cealed, prepuce obsolete, segment 4 swablike		short and erect or obsolete	8
	without huge paired flagellae directed pos-	8.	Median space with crossveins; wings with 5	
	teroventrally Aeshnidae		or 6 cubital-anal crossveins; abdomen cylin-	
5.	Supplementary sector arising near bridge		drical, tergum 7 without well developed mid-	
	crossvein; paraglossal spines present; lateral		dorsal ridge Synthemistic	dae
	clypeal lobes not inflated; ocellar lobe absent;	$\rightarrow 1$	Median space without crossveins; wings with	
	pterostigmata parallel sided, length typically		1-4 cubital-anal crossveins; abdomen ex-	
	ca.8 times width; male protibiae with short		panded, at least on segments 7 and 8, tergum	
	apical keels and meso- and metatibiae with		7 with well developed middorsal ridge	9
	outer spines peglike; anterior hamuli large erect	9.	Anal loop typically elongate without midrib;	
	foliate; progonopodites appressed into elon-		proximal side of hind wing triangle distal to	
	gate gently tapered spade Cordulegstridae		arculus by ca. ½ length of arculus and with	
_	Supplementary sector not arising near bridge		sectors of arculus diverging basally; male	

without genital lobe; progonapophyses typically longer than sternum 9, metagonapophy-

ses rodlike Gomphomacromiidae stat. nov.

crossvein; paraglossal spines obsolete; lateral

clypeal lobes inflated; ocellar lobe present;

pterostigmata not parallel sided with length

- Anal loop rounded or elongate with midrib; proximal side of hind wing triangle at arculus or separated from it by ca. length of arculus; with sectors of arculus typically fused subbasally; male with genital lobe; progonapophyses shorter than sternum 9, metagonapophyses peglike
- - Anal loop bootlike with midrib; proximal side of hind wing triangle near arculus, separated by less than ½ length of arculus; with lateral abdominal carinae on at least two segments; tarsal claws with ventral tooth ca. ½ as long as claw tip; anterior hamuli vestigial

..... Libellulidae

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LARVAE

- Antennae 3- or 4-segmented, third segment more than ½ antennal length; second mandibular segment movable; mesotarsi 2-segmented; abdominal segments 4 or 5 to 6 with linear transverse muscles and anterolateral sternal apodemes; sclerotized proventricular lobes elongate-rasplike, with 8-20 scattered teeth Gomphoidea Gomphidae
- Antennae 6- to 8-segmented, third segment less than ½ antennal length; second mandibular segment not movable; mesotarsi 3-segmented; abdominal segments 4 and 5 with vestigial or phragmatic transverse abdominal muscles and without anterolateral apodemes; sclerotized proventricular lobes mound or toothlike, with 0-8 posteriorly clustered teeth
- Tibiae with apical burrowing hooks; terminalia forming dorsally directed vent; labial palps with robust dorsolateral spur at base of endhook; molar lobe with teeth; transverse abdominal muscles 4 and 5 vestigial; proventriculus with 8 sclerotized lobes each with 0-6 similar blunt teeth ... Petaluroidea Petaluridae
- Tibiae without apical burrowing hooks; terminalia not forming dorsally directed vent; labial palps without robust dorsolateral spur at base of endhook; molar lobe without teeth; transverse abdominal muscles 4 or 5 phragmatic or obsolete; proventriculus with 4 sclerotized lobes each with 2–8 sharp teeth, apical tooth largest
- Prementum flat, dorsal surface of labium without long premental and palpal setae, la-

- brum not concealed by triangular labial palps, labial endhook distinctly longer than palp; epiproct typically bifurcate apically; proventriculus radially symmetrical, sclerotized lobes small-lobelike with 8 or fewer clustered teeth
- Aeshnoidea 4
 Prementum scooplike, dorsal surface of labium typically with long premental and palpal setae, labrum concealed by triangular labial palps, labial endhook distinctly shorter than palp; epiproct acuminate; proventriculus bilaterally symmetrical, sclerotized lobes large-toothlike, edged with 2–8 teeth
- 4. Abdominal segments 1-10 with lateral lobes; prementum slightly widened distally; labrum widened distally to ca. width of prementum; ventrolateral occipital ridge massive; paraprocts shorter than ½ width of abdominal segment 9; femora dorsally excrescent; transverse abdominal muscles obsolete; body surface extensively granulate

Abdominal segments 3-9 at most with lateral spines; prementum greatly widened distally; labrum ca. ½ width of prementum; ventro-

teeth; ligula with glossal and paraglossal lobes; mesosternum without paracoxal lobes; metasternum with transverse sulci joined by medial sulcus; ventral proventricular sclerotized lobes without large subapical tooth, dorsal lobes without posteromedial edge strongly inclined laterally; sternum 6 without anterolateral apodemes

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 Labial palpi with stout regular medial teeth; ligula with distal margin entire; mesosternum with paracoxal lobes; metasternum with transverse sulci contiguous, medial sulcus obsolete; ventral proventricular sclerotized lobes with large subapical tooth, dorsal lobes with posteromedial edge strongly inclined laterally; sternum 6 with anterolateral apodemes

6. Labial palpi bilobate with 5-6 medial teeth; prementum with 4-6 vestigial setae; palpi with 1 short dorsomedial setae near base of palpal end hook; antennae 6-segmented, third segment more than twice length of second segment; antefrons moundlike; wing pads parallel; male epiproctal tubercle acuminate; vulvar lamina ca. 1/3 length of sternum 9 . . .

..... Neopetaliidae

- Labial palpi trilobate with ca. 9 medial teeth; prementum with 10-30 elongate setae; palpi with 5-8 elongate dorsomedial setae; antennae 7- or 8-segmented, third segment less than twice length of second segment; antefrons shelflike; wing pads typically divergent; male epiproctal tubercle truncate; vulvar lamina not ca. 1/3 length of sternum 9
- Wing pads with narrow indistinct anal loop;
 ventral proventricular lobes without basal or dorsal denticulations;
 vulvar lamina more than
 length of sternum 9 Cordulegastridae
- 8. Labial palpi without setae along medial margin; dorsal proventricular lobes not united by medial sclerotization; ventral proventricular lobes with posterior face ca. as wide as that of dorsal lobes; ventral proventricular lobes with teeth separated by more than width of posterior face of dorsal lobes

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- Labial palpi with setae along medial margin; dorsal proventricular lobes united by medial sclerotization; ventral proventricular lobes with posterior face less than ½ as wide as that of dorsal lobes; ventral proventricular lobes with teeth separated by less than width of posterior face of dorsal lobes
- Metasternum with transverse sulci fused at short seam; wing pads parallel; hind femur ca.
 1.8 times length of front femur; pronotum laterally shelflike, widest distally; abdominal setae short-appressed; abdomen ca. 2.0 times as long as wide ... Gomphomacromiidae stat. nov.
- Mesosternum with transverse tubercle; frontal shelf erect hornlike; legs typically more than twice as long as abdomen ... Macromiidae
- Mesosternum without transverse tubercle; frontal shelf not erect hornlike; legs less than twice as long as abdomen Libellulidae

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LITERATURE CITED

- Carle, F. L. 1982a. A contribution to the knowledge of the Odonata. Ph.D. thesis, Virginia Polytechnic Institute & State University, Blacksburg, Virginia.
- . 1982b. A new Zoraena (Odonata: Cordule-gastridae) from Eastern North America, with a key to the adult Cordulegastridae of America. Annals of the Entomological Society of America 76(1): 61-68.
- 1986. The classification, phylogeny, and biogeography of the Gomphidae (Anisoptera), I. Classification. Odonatologica 15(3): 275–326.
- Fraser, F. C. 1929. A revision of the Fissilabioidea (Cordulegasteridae, Petaliidae, and Petaluridae) (Order Odonata) Part I. Cordulegasteridae. Memoirs of the Indian Museum 9: 69-167.
- Selys Longchamps, E. de. 1854. Synopsis des gomphines. Bulletins de l'Academie Royale des Sciences de Belgique 21: 23-114.
- 1857. Monographie des gomphines. Brussels and Leipzig, Nuguart; Paris, Roret. 460 pp.
- 1869. Secondes additions au synopsis des gomphines. Bulletins de l'Academie Royale de Belgique 28: 168-208.
- . 1878. Quatriemes additions au synopsis des gomphines. Bulletins de l'Academie Royale des Sciences de Belgique 46: 408-471, 658-698.
- Tillyard, R. J. 1906. New Australian species of the family Aeschnidae. Proceedings of the Linnean Society of New South Wales 31: 722.
- 1909. Notes on a new species of Phyllopetalia; with descriptions of nymph and imago. Proceedings of the Linnean Society of New South Wales 34: 697–709.