

Phylogenetic affinities of Petaluridae and basal Anisoptera families (Insecta: Odonata)

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Abstract

The petalurid genus *Phenes* has a larval proventriculus with only four dental folds. This genus is considered as the sister group of remaining Petaluridae and placed in the Pheninae **subfam. nov.** Two possible phylogenies of the Petaluridae are proposed and diagnoses of Tachopteryginae, Tanypteryginae, and Petalurinae are amended. The Petalurinae are split into Petalurini **tribe nov.** and Uropetalini **tribe nov.** The Petaluridae, Austropetaliidae and Aeshnidae are gathered in the new clade Siphonoprocta **taxon nov.** with Petaluridae sister taxa of (Aeshnidae + Austropetaliidae). The relative positions of the main basal clades Gomphida, Siphonoprocta and Cavilabiata are not solved. Within Cavilabiata the Cordulegastridae and Neopetaliidae are considered sister taxa and are gathered in the Cordulegastroidea **comb. nov.**, and the Chlorogomphidae are considered to represent the sister group of all remaining Cavilabiata or to represent the sister group of the Cordulegastroidea.

Key words: *Phenes*, *Tanypteryx*, *Tachopteryx*, *Uropetala*, *Petalura*, Siphonoprocta **taxon nov.**, Austropetaliidae, Aeshnidae, Chlorogomphidae, Neopetaliidae, Cordulegastridae, proventriculus, phylogeny, larva, Chile.

Zusammenfassung

Die Petaluriden-Gattung *Phenes* hat einen larvalen Proventriculus mit nur vier Zahnfalten. Diese Gattung wird als Schwestergruppe der übrigen Petaluridae angesehen und in die Subfamilie Pheninae **subfam. nov.** gestellt. Zwei mögliche Stammbäume der Petaluridae werden vorgeschlagen, und die Diagnosen der Tachopteryginae, Tanypteryginae und Petalurinae werden verbessert. Die Petalurinae werden in die beiden Tribus Petalurini **tribe nov.** und Uropetalini **tribe nov.** aufgespalten. Petaluridae, Austropetaliidae und Aeshnidae werden in dem neuen Stamm Siphonoprocta **taxon nov.** zusammengefasst, mit den Petaluridae als Schwestergruppe der (Aeshnidae + Austropetaliidae). Die Beziehungen zwischen den basalen Hauptstämmen Gomphida, Siphonoprocta und Cavilabiata bleiben vorerst ungelöst. Innerhalb der Cavilabiata werden die Cordulegastridae und Neopetaliidae als Schwestergruppen angesehen und in den Cordulegastroidea **comb. nov.** zusammengefasst, und die Chlorogomphidae sind entweder die Schwestergruppe aller anderen Cavilabiata oder die Schwestergruppe der Cordulegastroidea.

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1 Introduction

The family Petaluridae consists of a few relict modern species with only 11 species and five genera listed. Most of these species are distributed all around the Pacific, *Tanypteryx* (two species) is found in Japan and in Western USA and Canada, *Phenes* (one species) in Chile, *Petalura* (five

species) in Australia, and *Uropetala* (two species) in New Zealand. The genus *Tachopteryx* (one species) is the exception with an Atlantic distribution in eastern USA.

The distribution pattern of this family and a set of possible archaic characters and traits suggests a great antiquity for the group. Nevertheless, its phylogenetic position within the suborder Anisoptera is controversial, and the

basal phylogeny of the four main clades (Gomphoidea, Aeshnoidea, Petaluroidea and Libelluloidea), all rooted in the Jurassic, is still disputed (among others: PFAU 1991, LOHMANN 1996, CARLE 1995, NEL et al. 1998, BYBEE et al. 2008, FLECK et al. 2008, DUMONT et al. 2010).

The classification of Petaluridae is also controversial for the few published works using systematic reasoning (FRASER 1933, 1957; NEL et al. 1998). In the most recent one, the genus *Phenes* is placed within the Tachopterygidae although any characters are considered as autapomorphies of the Petalurinae.

This is illustrating the puzzling classification of the family. Consequently, every new element susceptible to contribute to the systematics and phylogeny of the Petaluridae should be mentioned. The larva of *Phenes* exhibits a unique organization of the proventriculus within the Petaluridae. This discovery represents the start point of revisional notes based on the adults of all genera and most of their larvae.

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2 Materials and methods

Material examined

Petalura gigantea: 1 ♂, 1 ♀, Australia, coll. Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS); *Petalura ingentissima*: 1 ultimate instar (=F-0) exuvia (external morphology), Australia (coll. BUTLER, United Kingdom); *Phenes raptor*: 1 ♂, 1 ♀, 1 F-0 larva, Chile (SMNS). 1 F-0 larva, Chile (coll. FLECK); *Tachopteryx thoreyi*: 1 ♂, 1 ♀, USA (SMNS). 1 penultimate instar (F-1), 1 F-3 larva, USA (coll. FLECK); *Tanypteryx hageni*: 1 ♂, USA (SMNS); 1 F-0 larva, USA (coll. FLECK); *Tanypteryx pryeri*: 1 ♂, 1 ♀, Japan (coll. FLECK); *Uropetala chiltoni*: 2 ♂♂, 1 ♀, New Zealand (SMNS).

Additional non-Petaluridae material, all F-0 larvae, all in coll. FLECK except *C. dyak* in coll. BUTLER: *Epiophlebia superstes*, Japan; *Archipetalia auriculata*, Tasmania; *Phyllopetalia* sp. 1 and sp. 2, Chile and Argentina; *Aeshna mixta*, France; *Boyeria irene*, France; *Onychogomphus forcipatus*, France; *Gomphus vulgatissimus*, France; *Neopetalia punctata*, Chile; *Cordulegaster boltonii*, France; *Anotogaster sieboldii*, Japan; *Chlorogomphus brunneus*, Japan; *Chlorogomphus risi*, Taiwan; *Chlorogomphus dyak*, Malaysia.

Methods

The works of TILLYARD (1921), WOLFE (1953), WINSTANLEY (1981) and ROWE (1987), and personal communication of G.

THEISCHINGER (Australia) have helped to get information on *Uropetala* larvae. Information on *Tanypteryx pryeri* larva and *T. hageni* female was taken from literature (ASAHINA & OKUMURA 1949, SUGIMURA et al. 2001, GARISSON et al. 2006).

Due to the state of preservation and the necessity to preserve rare collection material, no internal structures other than the mandibles and the proventriculus were investigated after careful dissection.

Drawings were made using stereomicroscopes Wild M3 and Leica MZ 12.5 with camera lucida. All the figures are original illustrations of the author, except Figs. 4, 14c–d, 15a and 16a, b.

The systematic analysis by 'hand and brain', following the principles of consequent phylogenetic systematics, was preferred to the so-called 'numerical cladistics'.

The wing terminology is that of BECHLY (1996) derived from RIEK & KUKALOVA-PECK (1984), vesica spermalis terminology is that of PFAU (2005), and the mandible terminology is that of WATSON (1956).

3 Results

The proventriculus (or gizzard) is an internal bulb-shaped structure of the alimentary canal making the junction between the foregut and the midgut. The part in contact with the lumen is essentially formed by longitudinal folds (generally 16, including Anisoptera), the totality or a part of them carrying denticles placed on a sclerotized excrescence (=dental folds). The proventriculus is of great importance in Odonata phylogeny and taxonomy. The number of dental folds does not change inside a given family or even inside a group of related families. Most of Zygoptera and Epiophlebioptera have a proventriculus with 16 dental folds and are therefore considered to represent the ground plan of Odonata. It is important to note that Anisoptera have also a proventriculus with 16 folds in their ground plan. These folds are particularly well visible in the families Petaluridae, Austropetaliidae and Aeshniidae, with four main folds wearing sclerotized plates with denticles (the 'dental folds'), four medium folds (wearing sclerotizations with denticles only in some Petaluridae), and eight minor folds (see, for example, Fig. 13a1, e1, f1). Within the Zygoptera, the family Amphipterygidae exhibits a unique proventriculus with 32 folds and the superfamily Lestinoidea (=Lestomorpha sensu BECHLY 1996) has eight dental folds (BECHLY 1996). Anisoptera exhibit only four dental folds except the Petaluridae that are known to have a remarkable proventriculus furnished with eight dental folds.

The proventriculus structure of *Phenes* was hitherto unknown. The proventriculus dissection of two *Phenes raptor* larvae (from different localities) clearly shows that this species presents only four dental folds (Fig. 13a, b). Thus, modern Petaluridae have four or eight dental folds. This remarkable result has consequences on the taxonomy and phylogeny of Petaluridae.

Phylogenetic consequence

The most recent works using morphological characters or morphological characters combined with molecular ones let the basal phylogeny of Anisoptera unsafe since nodes implying the main clades Gomphoidea, Aeshnoidea, Petaluroidea and Libelluloidea are not or insignificantly supported (REHN 2003, BYBEE et al. 2008); these works therefore will not be considered in this study. Recent phylogenies using molecular data are in conflict and propose different topologies for basal Anisoptera families (FLECK et al. 2008, CARLE et al. 2008, DUMONT et al. 2010). PFAU (1991), LOHMANN (1996) and CARLE (1995) do not consider the petalurids as the most inclusive group within Anisoptera. The different phylogenetic hypotheses of these authors have been invalidated by NEL et al. (1998). After BECHLY (1996) followed by NEL et al. (1998) the alleged eight dental fold proventriculus of Petaluridae represents a symplesiomorphy within the Anisoptera and constitutes the main argument to place the Petaluridae as sister group of all remaining Anisoptera (see below). The presence of only four dental folds in one representative of Petaluridae, gives distinctly less weight to the argument of these authors. Additionally, from a cladistic point of view, it is unjustified to consider an eight dental fold proventriculus as plesiomorphy, because in the outgroup taxa this number is 16 (ground plan of Zygoptera considered as monophyletic, and Epiophlebiptera). As this character does not exist in the ground plan of the outgroup taxa, it could be as well legitimately considered as a synapomorphy of the Petaluridae (CARLE 1995, LOHMANN 1996). Considering these facts, and considering *Phenes* as probable sister group of remaining modern Petaluridae because this genus possesses a set of plesiomorphic characters within the family (see below), I regard a proventriculus with four dental folds as belonging to the ground plan of Anisoptera (the parsimony implies only one change for the most advanced Petaluridae, this change being considered furthermore as an autapomorphy rather than a reversion to a hypothetical plesiomorphic state). The hypothesis of BECHLY (1996) and NEL et al. (1998) should be reexamined. In the case of an invalidation of this hypothesis and because other morphological studies are in conflict, it will be necessary to investigate new characters and to reinterpret other ones in order to try to clarify the internal phylogeny of Petaluridae as well as the position of Petaluridae within the Anisoptera.

Taxonomic consequence

As already mentioned above, the number of dental folds is extremely conserved for a given family or even for a group of related families, and except now the Petaluridae no other Epiproctophora family possesses a variable number of dental folds. The extraordinary peculiarity of *Phenes* regarding the proventriculus as well as a set

of other remarkable characters place the genus rather well apart from other modern petalurids, and allow to erect a new subfamily:

Pheninae subfam. nov.: Type genus: *Phenes* Rambur, 1842; type species: *Phenes raptor* Rambur, 1842; includes only the genus *Phenes*.

Diagnosis

Larva

(1) Antennae seven-segmented, straight, and only moderately thickened (Fig. 1). – Antennae distinctly more thickened in *Tachopteryx* and *Tanypteryx*, and distinctly horizontally curved (in dorsal view basally divergent and distally convergent) in *Petalura* and apparently also in *Uropetala*.

(2) Lateral ocelli covered each by a strong hemispheric and hairy excrescence, and dorso-lateral margins of the occiput, also furnished with rather well developed pubescent excrescences (Fig. 1).

(3) Pronotal shield with lateral margins trilobed (Fig. 1).

(4) Synthorax with a large conical spine near mesinfraepisternum (Fig. 1).

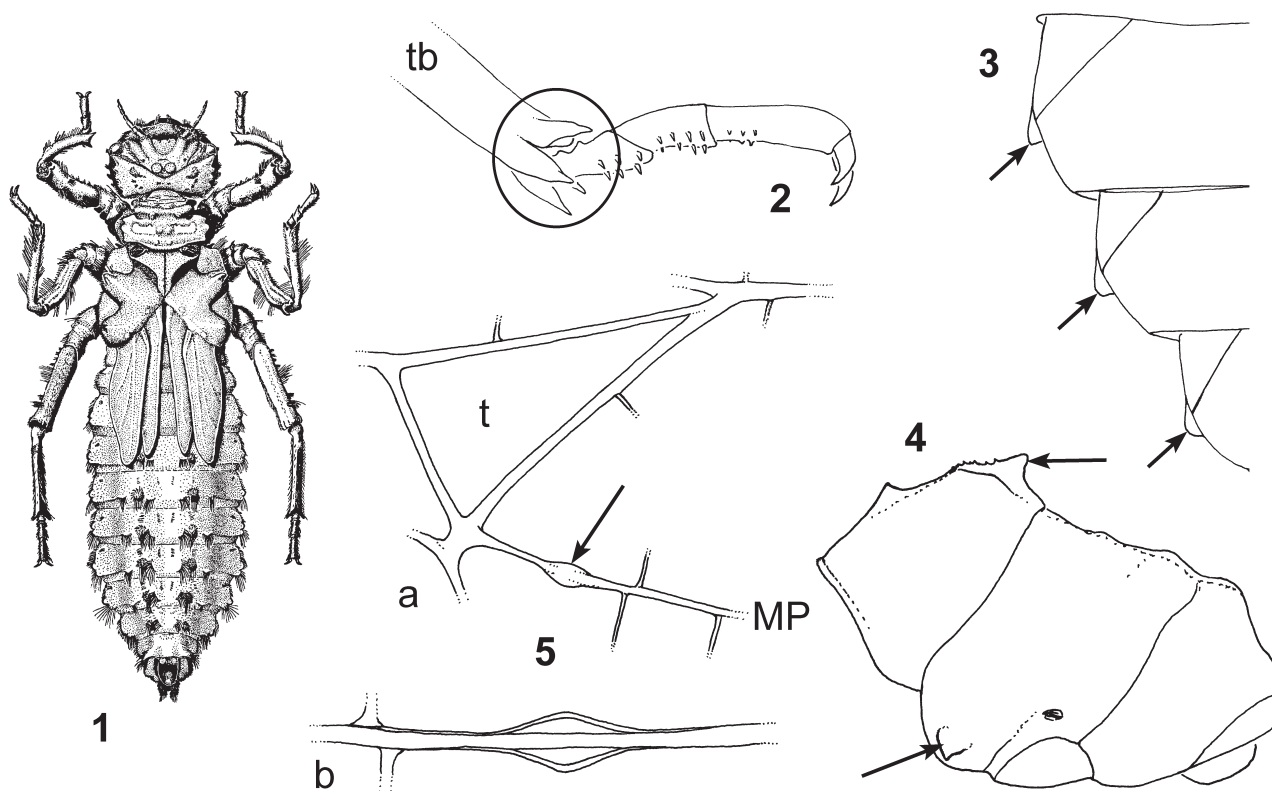
(5) Tibiae of all legs ending with four strong tibial spurs which are of approximately the same size (Figs. 1, 2). – In other Petaluridae one to three spurs are distinctly more reduced at least on the prothoracic and metathoracic legs.

(6) Distal margin of abdominal tergites with four pairs of symmetric brushes of setae well visible on S4–S8 or S4–S9 (=abdominal segments 4–8 or 4–9). One of this couple of brushes is placed on prominent cuticular tubercles ('Zottenhöcker') on S3–S9 (those of S3 small), and more laterally, another pair of brushes is placed on smaller tubercles on S3–S8 (those of S3 small) (Fig. 1). – This 'Zottenhöcker' arrangement is unique within the Petaluridae. Contra the opinion of NEL et al. (1998) the larva of *Tachopteryx* is deprived of 'Zottenhöcker', and other petalurid larvae do not possess 'Zottenhöcker', except maybe the Japanese *T. pryri* which could have a pair of low protuberances on S6–S9 (antagonist data published in WOLFE 1953 and SUGIMURA et al. 2001). Lastly, the larvae of *Petalura* do not present the typical paired medio-lateral brushes of long setae, and the larvae of *T. hageni* have particularly weakly developed brushes.

(7) Blunt and rather small lateral lobes present on S2–S9, homologous to the 'lateral spines' of other Anisoptera (those of S2 very small) (Figs. 1, 3).

(8) Anal pyramid with epiproct acute, and paraprocts ending as a ventral short blunt spine distal to siphon (Fig. 14a–d). – In other Petaluridae, the epiproct is not acute and appears in dorsal view broadly rounded or even somewhat truncated, and the paraprocts are ending abruptly at siphon.

(9) Proventriculus with four dental folds (Fig. 13a, b).



Figs. 1–5. *Phenes raptor*. – 1. Larva, habitus (modified from NEEDHAM & BULLOCK 1943). 2. Larva, mesothoracic leg, tarsus and apex of tibia (tibial spurs are encircled; tb = tibia). 3. Larva, right lateral margin of abdominal segments 6–8, ventral view (note the modest but distinct lateral expansions). 4. Adult, synthorax, left lateral view (modified from GARRISON et al. 2006; the arrows indicate the ventral conical spur and the dorsal antealar ridge). 5. Adult, left hindwing, ‘MP articulation’, localization on MP, a. ventral view, b. detail, dorsal view (t = discoidal triangle).

Adult

(10) Lateral clypeal lobes strongly developed and acute, and in frontal view clypeal lateral margins distinctly sigmoid (Fig. 16a). – In other Petaluridae, the lobes are generally distinctly less developed and not so strongly pointed. Only *Uropetala* has pointed and rather well developed clypeal lobes, they are nevertheless somewhat less strongly developed than those of *Phenes*, and the lateral margins are not sigmoid.

(11) Frons deprived of a supplementary large transverse carina placed between dorsal margin and clypeal margin (Fig. 16a). – A large medial transverse carina is present in other Petaluridae.

(12) Posterior side of occiput with a pair of small horns, and postocular lobes with some distinct blunt spines (Fig. 16b).

(13) Antealar ridge ending as a strong spur, and ventral part of mesepimeron developed as a strong cone (Fig. 4).

(14) MP just distal to discoidal triangle with a kind of articulation (Fig. 5). – This structure is also present in *T. pryori*, but distinctly less developed.

(15) Presence of a short postnodal pseudo-ScP.

(16) Distal side of pterostigma greatly shifted basally, consequently the pterostigma (relative to postnodal area) appears shorter than that of other modern petalurids. – *Tanypteryx* has also a short pterostigma and only slightly longer than that of *Phenes*, but contrary to this species it occupies a more distal position.

(17) Pterostigmal brace strongly separated from basal side of pterostigma.

(18) Synthorax, except for a small darkened humeral spot, nearly uniformly greenish to greyish-brown or yellowish-brown. – In other Petaluridae the synthorax presents well to rather well contrasting sombre and paler stripes.

(19) Unique shape of the strongly developed male anal appendages.

(20) Ovipositor not upwards curved, and except shorter styli, similar to that found in Austropetaliidae and Aeshnidae (Fig. 15a). – In other Petaluridae it is variously upturned.

4 Discussion

4.1 Systematic position of Pheninae subfam. nov.

FRASER (1933) splits the Petaluridae into two subfamilies: the Petalurinae including the genera *Petalura*, *Uropetala* and *Phenes*, and the Tachopteryginae including *Tachopteryx* and *Tanypteryx*. This author in 1957 moves *Tachopteryx* to the Petalurinae and consequently places the genus *Tanypteryx* into Tanypteryginae. The most recent comprehensive work dealing with the petalurids and partly inspired from BECHLY (1996) is that of NEL et al. (1998). These authors split the Petaluridae into Petalurinae and Tachopteryginae, this last subfamily being made by the tribes Tanypterygini and Tachopterygini. The latter includes the genera *Tachopteryx* and *Phenes*.

4.1.1 The Tachopteryginae sensu NEL et al. (1998), a critical view

NEL et al. (1998) proposed the following autapomorphies to define the Tachopteryginae: (1) distal accessory oblique vein suppressed (unique within Petalurida), and (2) the metaposternum on the venter of the adult metathorax more or less expanded and hairy ('ventral metathoracic tubercle'). For the genus *Phenes* these two characters are in conflict with two apomorphic characters defining the Petalurinae and considered by NEL et al. (1998) as convergences.

The character (1) is no longer unique within Petalurida since it is also present in *Eotanypteryx* Bechly, 2007 (from Brazil) and *Anglopetalura* Coram & Nel, 2009 (from Great Britain), species probably belonging to the petalurid fossil family Cretapetaluridae. The fact that the third closely related genus *Cretapetalura* presents two oblique veins, and the fact that five from a total of 13 genera (about 38 %) belonging to the Petalurida sensu NEL et al. (1998) do not possess a second oblique vein suggest that the character is rather variable within the Petalurida.

The oblique vein seems to be correlated to the presence of bulb located on the RP3/4. In *Petalura* and *Uropetala* the distal oblique vein originates from this bulb or a little distally (0–4 cells) (Fig. 6a), this variability being probably due the progress of a larval trachea originating from RP2 and joining the IR2 (not studied in this work due to inadequate state of preservation or maturation of larval tracheation). In *Phenes*, the bulb is well developed, the crossveins between RP2 and IR2 are straight proximal to the bulb, the first crossvein just distal to the bulb is distinctly arched and generally slightly stronger and slightly more curved and even very slightly more oblique than the following ones (Fig. 6b, structure also faintly visible on fig. 53 in GARRISON et al. 2006). Therefore the distal

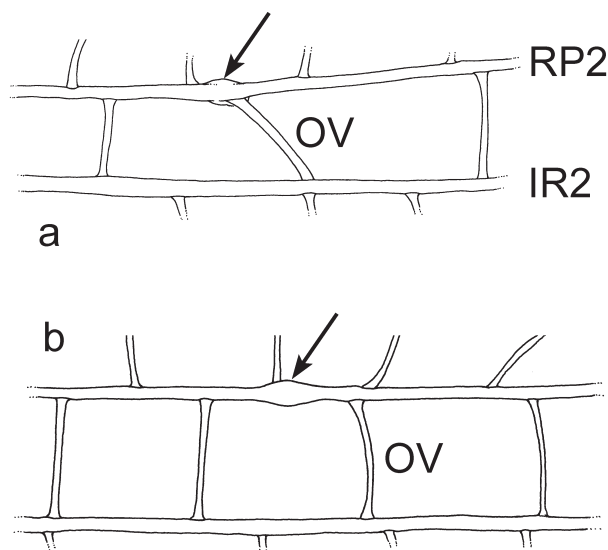


Fig. 6. Second oblique vein and 'RP2 bulb'. – **a.** *Uropetala chiltoni*, proximal part on the left, dorsal view. **b.** *Phenes raptor*, proximal part on the left, ventral view. – OV = distal oblique vein. – The arrows indicate the emplacement of the 'bulb'.

oblique vein in *Phenes* cannot be considered as completely lost, and the underlying mechanism "to build" a distal oblique vein considered as still present. The same phenomenon can be observed, in *Tachopteryx thoreyi* and *Tanypteryx pryeri*. For these species the bulb is always well visible, the curvature of the veins is sometimes less distinct than the ones observed in *Phenes*.

Within Petaluridae the character is not absolute for a given species and apparently somewhat variable from an individual to another one. From the studied material, the female *Uropetala* presents all oblique veins poorly indicated and one male has an indistinct proximal oblique vein in the forewings; the male *Petalura* presents an indistinct distal oblique vein in one forewing and in one hindwing and the female poorly indicated proximal oblique veins on the left wings; the male *T. pryeri* presents a well indicated distal oblique vein in one hindwing; more than 20 % of the individuals of *T. pryeri* from the set presented in SUGIMURA et al. (2001) have at least one wing with two oblique veins; the hindwing of *T. hageni* illustrated in GARRISON et al. (2006) presents two oblique veins. In the possibly closely related families Aeshnidae and Austropetaliidae (see below) a similar situation occurs: numerous Aeshnidae present two oblique veins, for example this characters can be considered as belonging to the genera *Neuraeschna* and *Gynacantha*; it is also very frequently found in numerous other genera at species level or at individual level. Within Austropetaliidae it seems that the genus *Hypopetalia* possesses two oblique veins, the proximal one being less

bent than the distal one. This character needs confirmation since only very few wings ($n=6$) have been checked, anyway it demonstrates the presence of two oblique veins inside the small family Austropetaliidae.

In conclusion and in concordance to the opinion of LOHMANN (1996), I consider the character (1) as atavistic and of low phylogenetic value (homoplastic), with a relative facility to be switched on or switched off for a given species and even for a given wing (reactivation of a latent potential).

The character (2) is also present in *Uropetala* with a development comparable to that of *Tachopteryx*. A ventral metathoracic tubercle represents therefore a possible symplesiomorphy of Petaluridae secondarily reversed in *Petalura*. Nevertheless, the polarization of the character is problematic since apparently found with variable development in the modern Petaluridae and unknown in the fossil stem groups Aktassiidae, Cretapetaluridae and Protolindeniidae. Therefore this character is of low phylogenetic value and like character (1) it should be removed from the Petaluridae phylogeny until fossil information allows a better polarization.

The characters of NEL et al. (1998) to define the Tanypterygini are dismissed and this subfamily is no longer supported.

4.1.2 The Tachopterygini sensu NEL et al. (1998), a critical view

NEL et al. (1998) proposed the following autapomorphies to define the Tachopterygini: (1) dull body colouration, convergent to *Petalura*; (2) hairy lateral tubercles ('Zottenhöcker') of the larval abdomen very distinct; (3) larva secondarily not burrowing gallery.

Tachopteryx thoreyi shows pale greyish or beige stripes alternating with blackish ones, the contrast between the stripes is strong (particularly evident in lateral view) except for the large antehumeral quadrangular stripes which are distinctly darkened. *Tanypteryx pryeri* has a semblable general colouration pattern and a strikingly similar thoracic colour pattern with large pale interpleural and metepimeral stripes and also the same noticeable darkened large antehumeral quadrangular stripes which can be considered as dull colour. The main difference between the species is the yellow to yellowish colour replacing the greyish one. Most of the species of *Petalura* are brownish to dark brown coloured with thin yellow or yellowish marking. As they do not have the plesiotypic black and lemon-yellow colours, already mentioned by NEL et al. (1998), they can be considered to harbour 'dull' colouration. *Uropetala* presents intermediate thoracic pattern with rather well developed pale antehumeral stripes and rather narrow

pale lateral stripes, the pale coloured areas on head, thorax and abdomen that contrast with the dark brown to blackish ground colouration is usually not bright lemon-yellow but pale yellowish or even whitish (except, apparently, mature specimen of *U. carovei*) and should be considered as a 'dull' colouration, additionally the end of the abdomen also has apparently brownish spots on black ground. Except *Tanypteryx hageni* with a plesiotypic black/lemon-yellow pattern of colouration, all other Petaluridae present deviant colouration in variable proportions. The colouration is highly variable within this family and no inference can be made with accuracy.

Alternative hypothesis conflicting with that of NEL et al. (1998) can also be evoked, for example, the strikingly similar thoracic pattern shared with *Tachopteryx* and *Tanypteryx* (*T. pryeri*) can be interpreted as apomorphic.

Contrary to all other Petaluridae, *Phenes* does not possess any thoracic stripes, and except a small lateral sombre spot, the thorax appears nearly uniformly brownish green to yellowish brown. The unique absence of well contrasting lateral stripes on thorax allows to think that *Phenes* is well separated from other living Petaluridae. Since the colours are variable within the Petaluridae and since the pattern of colouration is totally different between *Phenes* and *Tachopteryx* I interpret the superficial 'dull' colouration (pale greyish tendency in *Tachopteryx*, greenish brown or yellowish brown tendency in *Phenes*) as probable 'camouflage' convergence between the two genera.

For all these reasons I consider the character (1) as doubtful, and colouration pattern of low pertinence for the phylogeny of Petaluridae.

The character (2) is no longer valid since *Tachopteryx* definitively does not possess dorsal abdominal tubercles. The brushes of long setae are well developed but they are not placed on tubercles.

Gallery burrowing larvae of Petaluridae are apparently unique among Odonata, and the larval habits of fossil groups of Petalurida remain unknown. Therefore, the method of parsimony imposes to consider non-tunnelling larvae as a plesiomorphy, and the larvae of *Phenes* and *Tachopteryx* primitively unable to construct galleries. Moreover, the larvae of *Phenes* and *Tachopteryx* possess lateral abdominal extensions, a plesiomorphic condition apparently not seen in other Petaluridae, supporting the non-burrowing condition as plesiomorphic too. Consequently the character (3) is considered to be not an apomorphy acquired secondarily, but to be a plesiomorphy primitively present.

The characters of NEL et al. (1998) to define the Tanypterygini are dismissed and this tribe is no longer supported.

Remarks: The larva of *Phenes* I have captured in its natural environment was found in a small pool filled with a few millimetres water and containing a kind of dark liquid vegetal mud and abundant decayed vegetation including numerous short sticks of various diameters. After disturbance due to the collection of the pool material into a net, the larva, one of the largest among living Odonata, was only found after careful and systematic examination of the decayed material. First, the larva can stay minutes completely motionless, and secondly, it is remarkably similar to some of the small sticks present in its vicinity. This similitude is not only due to the same colour (the larva was partly covered by a layer of mud) and comparable shape and size of some decayed sticks, but also due to the comparable tactile feeling and consistence. So, that the first second in my hand I thought the larva was another old decayed piece of wood. The larva of *Tachopteryx* rather flattened and with distinct abdominal lateral extensions can be considered to have a leaf-mimicry camouflage, that of *Phenes* more cylindrical with rather small rounded abdominal lateral extensions and multitude dorsal rounded excrescences can be considered to have a decayed-stick-mimicry camouflage.

4.1.3 Position of the Pheninae

The subfamily Pheninae is regarded as the sister group of remaining Petaluridae because it possesses the following possible plesiomorphies:

(1) Larval proventriculus with four dental folds. – As I regard a four dental folds proventriculus belonging to the ground plan of Anisoptera, and in view of the remaining plesiomorphies encountered in *Phenes*, I consider the four dental fold of this genus as a plesiomorphy.

(2) Larval antennae seven-segmented, straight, and only moderately thickened. – The more thickened and hairy antennae of *Tachopteryx* and *Tanypteryx*, the horizontally curved antennae of *Petalura* and *Uropetala*, and the six-segmented antennae of *Tanypteryx* and *Uropetala* are all considered as derived states (see also chapter 4.2.1 below).

(3) Larval abdominal lateral lobes present and homologous to the ‘lateral spines’ of other Anisoptera and Epiophlebiptera. – Sympleiomorphy also present in *Tachopteryx*.

(4) Larval epiproct rather acute in dorsal view. – A pointed epiproct belongs to the groundplan of Anisoptera and Epiophlebiptera, it is secondarily more rounded in other Petaluridae, and truncated or bifid in the ground plan of (Austropetaliidae + Aeshnidae) (compare Fig. 14a–d, k–n and Fig. 14e, j).

(5) Paraprocts ending as a ventral spine distal to siphon. – In other Petaluridae the paraprocts are distinctly truncated at siphon and do not possess a ventral pointed

process, or only an extremely reduced remnant still faintly visible in *Tachopteryx*. The remarkable shape of the paraprocts observed in *Phenes* is nearly identical to that found in Austropetaliidae and Aeshnidae. It is considered to be homologous and represents a synapomorphy belonging to the ground plan of (Petaluridae + Austropetaliidae + Aeshnidae) (see below) (compare Fig. 14a–d, g–n and Fig. 14e, f).

(6) Larva primitively not burrowing galleries. – Sympleiomorphy also present in *Tachopteryx*.

(7) Pterostigmata relatively short. – Also present in *Tanypteryx*, but possibly reversal in this genera since several additional reversions are present in wing characters.

(8) Pterostigmal brace strongly separated from basal side of pterostigma. – The Protolindeniidae and Cretapetaluridae have also strongly separated brace from stigma; this character is therefore considered as sympleiomorphy and present in the ground plan of Petalurida, and secondarily reversed in most Petaluridae (see also NEL et al. 1998: 50).

(9) Adult frons, in frontal view, without a supplementary large transverse carina. – As a rather similar character is also present in Austropetaliidae and several Aeshnidae, including the basal genus *Gomphaeschna*, it cannot be ruled out that a transverse supplementary carina represents a synapomorphy of the clade (Petaluridae + Austropetaliidae + Aeshnidae) (see below), with a reversed state in *Phenes*.

(10) Female ovipositor not significantly up-turned, and except shorter styli, similar to the ovipositor found in many Austropetaliidae and Aeshnidae. – The ovipositor of *Tanypteryx*, *Uropetala* and *Petalura* is distinctly curved upwards, that of *Tachopteryx* represents an intermediate stage with solely a distal strong increase of the valves curvature (Fig. 15).

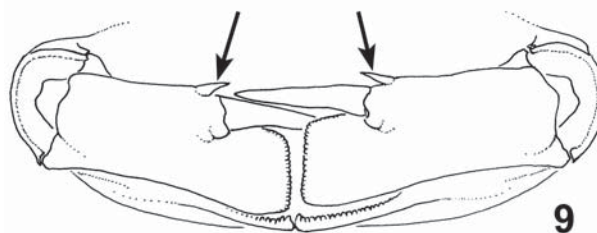
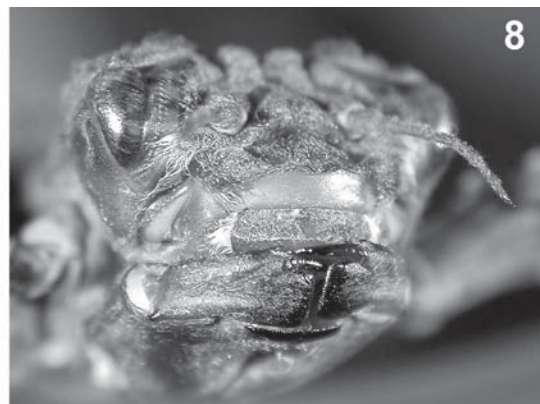
Remarks on the anal loop: Within the Petalurida, a posteriorly open anal loop is present in *Protolindenia*, *Anglopetalura*, *Aeshnogomphus*, *Aktassia*, *Phenes*, *Tanypteryx* and *Tachopteryx*. The anal loop is posteriorly zigzagged in *Mesuropetala*. It means that more than 50 % of known petalurid genera, from at least four independent groups, have a posteriorly ill defined or not defined anal loop (character unknown in *Pseudocymatophlebia*). It seems also that for a given genus, a non-negligible frequency of individuals possess an anal loop with opposite state: from the studied material, the *Petalura* male has the two anal loops distinctly closed, the *Uropetala* female has the left anal loop closed, and the right one nearly so; on the photographs on <http://www.dragonflies.org/petaluri.htm>, both of presented male and female *Tachopteryx* possess a posteriorly opened anal loop on one wing; one female *Phenes* in coll. FLECK has anal loops closed. The closure of the anal loop has no or low phylogenetic significance

within Petalurida, therefore this atavistic character is not considered in the present analysis to evaluate phylogenetic relationship between subfamilies, and is only used as diagnostic element for a given genus or a subfamily.

4.1.4 First hypothesis: monophyly of the groups having gallery burrowing larvae (Fig. 7)

Node 1, Petaluridae

Larvae with mask slightly concave (Figs. 8, 9) (convergent to some Zygoptera, to the gomphid genus *Archaeogomphus*, and to a lesser extent to some Gomphidae-Onychogomphini for which the concavity of the mask is less marked, see LEGRAND & FLECK 2005). Presence of a robust spine overlapping the base of the larval palpal moveable hook (Fig. 9) (contrary to the drawing given by FRASER 1957: fig. 45, the labial palps of *Petalura*, like all other Petaluridae, possess a robust spine surmounting the moveable hook; this probably led NEL et al. 1998 to mention erroneously its absence in *Petalura*). Larval tibiae with strong apical spurs (Fig. 2) (present and well developed in *Tachopteryx* and *Phenes*, contra the opinion of NEL et al. 1998). Larval paraprocts and epiproct forming a air respiratory siphon and bearing extremely dense alignment of thin, long and soft setae involved in the tightness and in the formation of the circular aperture (Fig. 14a–f). Adult head with bulged occiput. Pterostigmata strongly elongated, narrow with parallel anterior and posterior margin, and with their brace vein situated basal to mid-way between nodus and wing apex (except the forewing of numerous *Tanypteryx*). Male anal appendages strongly developed (convergent to several genera of Anisoptera). Ovipositor with styli shortened.



Figs. 8–9. *Phenes raptor*, larva. – 8. Head, fronto-lateral view (note the slightly concave mask and the relatively narrow antennae). 9. Labial palps, frontal view. – The arrows indicate the small and robust spines overlapping the moveable hooks.

Remarks: The Lower Cretaceous fossil genus *Argentinopetala* Petrusevicius & Nel, 2003, known only from a fragment of a wing apex, is considered as a Petaluridae incertae sedis. – The fossil genus *Nothomacromia* Carle, 1995, only known as larval stage, is considered as an Epiroctophora incertae sedis as long as the corresponding adult remains unknown.

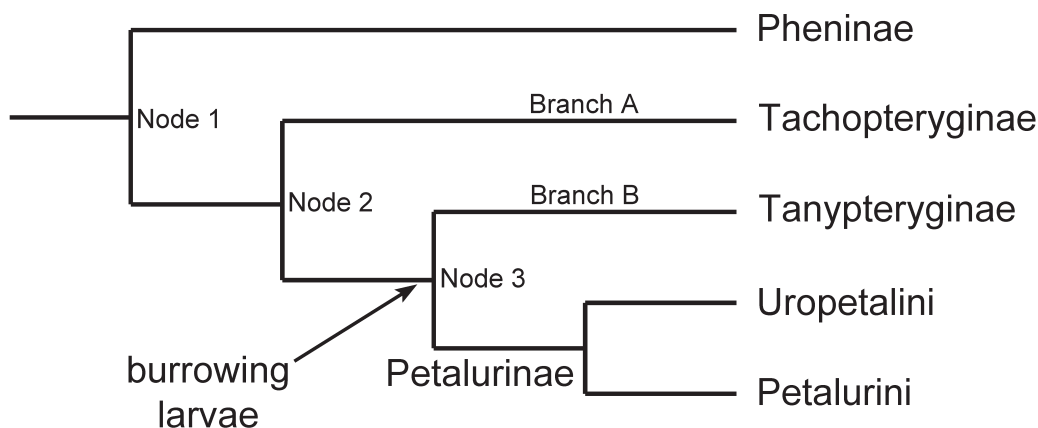


Fig. 7. Phylogenetic tree of recent Petaluridae, monophyly of the subfamilies with burrowing larvae. – For explanations see chapter 4.1.4.

Node 2

Larval proventriculus with eight dental folds (Fig. 13c, d). Larval antennae no more plesiotypically straight or moderately thickened. Larval epiproct rounded (Fig. 14e, f). Paraprocts truncated at siphon and therefore without distinct ventral tapered process (Fig. 14e, f). Pterostigmata elongated (somewhat secondarily reversed in *Tanypteryx* since pterostigmata are slightly distally shifted) with the brace vein and proximal side of pterostigma very close together or even at the same level. Adult frons, in frontal view, with a supplementary large transverse carina (Fig. 16c); this could be a plesiomorphy if this character belongs to the ground plan of (Petaluridae + Austropteliidae + Aeshnidae) (see below). Ovipositor variably but distinctly up-curved (Fig. 15b, c).

Additional possible apomorphies:

At least some larval tibial spurs reduced in the prothoracic and metathoracic legs. – This is a speculative apomorphy which appears as a cline within the family; it implies that four strong spurs per leg, acute and of approximately equal size, belong to the ground plan of Petaluridae; all the legs of *Phenes* and the posterior legs of *Tachopteryx* and *Tanypteryx* are built on this model. This putative apomorphy receives some support because the legs of *Tachopteryx* and *Tanypteryx* still present three or four strong spurs, acute and of about equal size, whereas those of *Petalura* and *Uropetala*, the most advanced Petaluridae, present only one or two obtuse strongly developed spurs.

Larval prothoracic leg with the spur occupying the external and anterior position reduced and distinctly proximally shifted on tibia (this spur apparently lost in *Petalura*). – A speculative apomorphy (see above).

Loss or strong reduction of the larval dorsal abdominal tubercles. – Again a speculative character, but as hairy dorsal tubercles are present in Austropteliidae, possibly also present even if reduced in *T. pryeri*, and also present (atavisms?) in some basal Aeshnidae like *Telephlebia*, they can belong to the ground plan of (Petaluridae + Austropteliidae + Aeshnidae) (see below).

Node 3

Larvae burrowing galleries. Larval lateral abdominal extensions lost. Larval dorso-lateral brushes of long setae at least less strongly developed. Larval paraprocts with process or remnant of process distal to siphon completely suppressed. Female ovipositor strongly up-curved (Fig. 15c).

Node 4, Petalurinae Needham, 1903
(sensu BECHLY 1996)

Type genus: *Petalura* Leach, 1815; type species: *Petalura gigantea* Leach, 1815; included genera: *Petalura* and *Uropetala* Selys, 1857.

Larvae burrowing complex galleries comprising adjacent excavations. Larval antennae divergent at base and distally convergent. All larval legs with the strongest spurs obtuse (putative apomorphy). Prothoracic leg showing a strong development of the inner spur and variable regression of other ones, and metathoracic leg showing a strong development of two spurs, one on each side of the tarsus, and a strong regression of other spurs (putative apomorphy). Posterior veins of the well enlarged cells bordering the MA making a long and not curved weak Mspl (that of *Petalura* somewhat slightly zigzagged, that of *Uropetala* rather straight; a kind of ill defined Mspl can occur in other Petaluridae but is distinctly more poorly defined than in Petalurinae: more zigzagged, shorter, and eventually curved). Pterostigmal brace strongly oblique and slightly separated from basal side of pterostigma (putative apomorphy). Adult male cerci foliate and enormously developed, wider than width of abdominal segment 10 in dorsal view.

Additional diagnostic character: Anal loop generally posteriorly open (character also present in Pheninae).

Remark on the wing length: NEL et al. (1998) indicate that Petalurinae have wings longer than 65 mm (forewing?). This character is not valid since most of the species belonging to this family do not have a wing length exceeding 65 mm, except *Petalura ingentissima*. The wing length of *Uropetala chiltoni* does not exceed 55 mm (forewing about 49–50 mm and hindwing about 47–48 mm in the studied material), and generally the forewing length of *U. carovei* and remaining *Petalura* species have the forewing length ranging from about 53 to less than 65 mm. The forewing length of *Phenes* falls into this last range (about 53–60 mm), and that of *Tachopteryx* overlaps it (about 50–55 mm). Lastly, that of *Tanypteryx pryeri* (42–49 mm) overlaps probably slightly that of *Uropetala chiltoni*.

Petalurini tribe nov.

Type species: *Petalura gigantea* Leach, 1815; included species: *Petalura gigantea*; *P. ingentissima* Tillyard, 1908; *P. hesperia* Watson, 1958; *P. litorea* Theischinger, 1999; and *P. pulcherrima* Tillyard, 1913 [with doubt, could be after THEISCHINGER (pers. comm.) a form of *P. gigantea*].

Larval antennae with the penultimate antennomere slightly enlarged and club-shaped, and with the ultimate antennomere with a distinct weaker diameter and pointed. Larval labial palp with distal margin ventrally largely rounded, correlated to a peculiar shape of the distal margin of the prementum which appears as a strong protuberant triangle with straight margins. Larval prothoracic leg with loss of two tibial spurs, and mesothoracic leg with loss of a tibial spur and loss or extreme reduction of another one. Larval abdomen with complete loss of the dorsal clumps of setae. Forewing discoidal triangle strongly

transversely elongated and costal margin shortened, correlated with an enlarged sub-discal triangle four- or five-celled (discal cell trapezine-like). Sombre ground colour of the adult generally largely brown.

Uropetalini **tribe nov.**

Type species: *Uropetala carovei* (White, 1846); included species: *U. carovei* and *U. chiltoni* Tillyard, 1921.

Possible unique organization of the larval tibial spurs (see WINSTANLEY 1981: fig. 4). Discoidal field beginning with three rows of cells in both pairs of wings. Presence of a distinct CuAb in the forewing, sometimes delimiting a small anal loop (putative apomorphy). The weak Msp1 apparently straighter than that of *Petalura*, especially in the hindwing. Unique shape of the male inferior appendage within Petaluridae: not strongly developed, triangular and with basal and apical teeth.

Branch A: Tachopteryginae Fraser, 1933 (sensu nov.)

Type genus: *Tachopteryx* Uhler in Selys, 1859; type species: *Tachopteryx thoreyi* (Hagen in Selys, 1857); includes only the genus *Tachopteryx*.

Proventriculus of ultimate or penultimate instars larvae with the mound-like excrescences of the dental folds bearing 6–19 small denticles each (Fig. 13c) (unique within Petaluridae, contra CARLE 1995). Larval antennae strongly thickened and hairy with the three first proximal segment of the flagellum very short and not longer than wide. Larval antennae basally convergent and distally divergent. Distal margin of the larval labial palps ventrally prolonged, making a rather acute angle with the ventral margin, correlated with a distinct ventral displacement of the distal part of the prementum. Rather flattened larval abdomen with well developed clumps of long blackish setae, not placed on tubercles, on S2–S9. Male hindwing with anal angle rather poorly developed. Adult general colour pattern greyish and blackish.

Additional diagnostic characters: Larva with lateral abdominal lateral extensions on S2–S9, those of S4–S9 spine-like and rather well developed (possible plesiomorphy). Pterostigmal brace aligned with basal side of pterostigma (character also present in Tanypteryginae). Anal loop generally posteriorly closed (character also present in Tanypteryginae).

Branch B: Tanypteryginae Fraser, 1957

Amended from NEL et al. (1998) as follows: Wing reduced in size, shorter than 50 mm (convergent to *Uropetala chiltoni*), and correlated with several further reductions and reversals (decreased number of cells; IR1 shorter and zigzagged; wing space between RP1 and RP2 not expended, with usually less than 8–9 rows of cells in *T. hageni* and less than 11–12 rows of cells in *T. pryori*; bridge space less narrowed). In the forewing the field between RP3/4

and MA is not so suddenly widened and generally also less widened than in other Petaluridae (reversal). The forewing veins RP3/4 and MA are not curved distally, and MA is not undulate (reversal). The distal side MAb of the hindwing discoidal triangle is slightly angled, correlated with the development of a weak convex secondary vein in the postdiscoidal area (an atavistic character apparently variable within the genus since absent, extremely reduced, or indistinct in several specimens presented in SUGIMURA et al. 2001). Larval antennae six-segmented (convergent to *Uropetala*). Adult 'ventral metathoracic tubercle' hypertrophied.

Additional diagnostic characters: Anal loop generally posteriorly closed (a variable character also present in Tachopteryginae). Pterostigmal brace aligned with basal side of pterostigma (character also present in Tachopteryginae).

4.1.5 Second hypothesis: polyphyly of the groups with gallery burrowing larvae (Fig. 10)

Node (Tachopteryginae + Tanypteryginae)

Similar organization of the larval tibial spurs with the antero-external spur of prothoracic legs and metathoracic legs distinctly reduced and distinctly shifted proximally. – As *Uropetala* seems to have also a quite similar organization, it cannot be ruled out that this condition represents a symplesiomorphy of the clade supported by the node 2 (first tree, Fig. 7); the evolution of these shortened and shifted spurs could have led to a kind of 'buttons' apparently somewhat better developed on *Uropetala* foreleg, and by further atrophy to their complete suppression in *Petalura*.

Larval antennae stouter and more hairy than in other Petaluridae. – The antennae of *Tachopteryx* are seven-segmented, proximally convergent and distally strongly divergent, furnished laterally by a dense fringe of very long and rather strong setae, enormously widened with the base of one antenna being as wide as the distance separating the antennae, and with the three first antennomeres of the flagellum remarkably short and not longer than wide. The antennae of *Tanypteryx* are differently built, they are six-segmented, straight, furnished laterally by a moderately dense fringe of shorter and thinner setae, only slightly more thickened than other non-Tachopteryginae Petaluridae with the base of one antenna being less than half as wide as the distance separating the antennae, and with the three first antennomeres of the flagellum 'normally' built, distinctly longer than wide. With so many differences, it could be possible that superficial resemblance hides parallel evolution, therefore the homology would demand confirmation.

Distal margin of larval prementum rather straight. – The character is possibly not homologous between the two

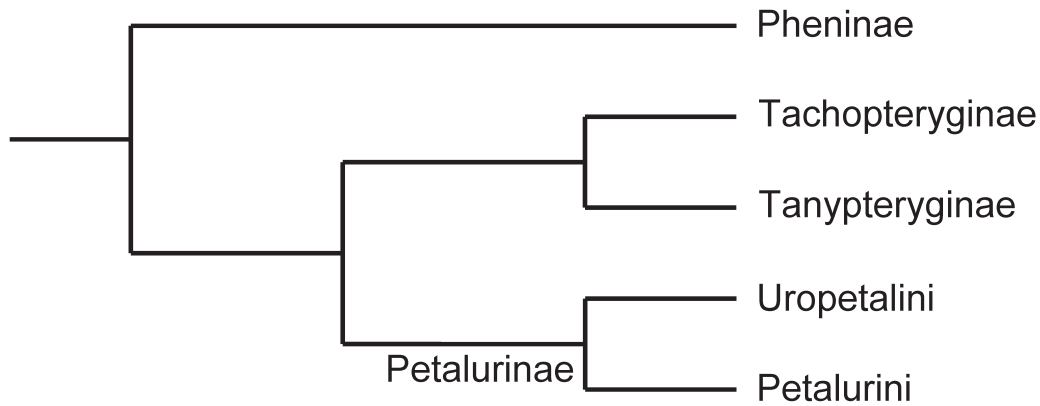


Fig. 10. Phylogenetic tree of recent Petaluridae, paraphyly of the subfamilies with burrowing larvae. – For explanations see chapter 4.1.5.

subfamilies because in *Tachopteryx* it is clearly due to the strong ventral development of the distal margin of the labial palps; the palps of *Tanypteryx* are shaped as those of *Phenes* or *Uropetala*, and contrary to *Tachopteryx*, the distal part of the prementum is not ventrally displaced.

Pterostigmal brace aligned with basal side of pterostigma. – Since some Aktassiidae – sister group of Petaluridae – have also aligned brace and basal side of pterostigma, the character is possibly subject to homoplasy.

4.1.6 Conclusion

The creation and the phylogenetic placement of the subfamily Pheninae seems to be justified in regard of the consistent set of apparently stable characters. PETRULEVICIUS & NEL (2003) have described the oldest true Petaluridae. This fossil is dated from the Early Cretaceous (about 120 Ma) and comes from the Atlantic side of Southern Patagonia. *Phenes* occurs also in Patagonia (Pacific side) and its placement as sister group of remaining living Petaluridae receives some support. Nevertheless this information should be taken with some prudence: the Aktassiidae are dated from the Late Jurassic (about 150 Ma) and reported until now exclusively from England and Germany to China; since Aktassiidae and Petaluridae are sister groups it follows that the origin of Petaluridae must be Eurasia (in the present state of knowledge; it must be kept in mind the existence of a 30 Ma gap), therefore nothing can be inferred with certainty in matter of biogeography.

The respective phylogenetic position of the Tachopteryginae and the Tanypteryginae is somewhat problematic, and the alternative hypotheses receive some support. I tend to consider the first hypothesis (tree 1, paraphyly of the Tachopteryginae and Tanypteryginae) more satisfying since I accord a great evolutionary weight to the unique and complex ability to dig galleries and since other characters like the ovipositor shape support well the clade,

contrarily to the second hypothesis (monophyly of the Tachopteryginae + Tanypteryginae) for which the characters are not entirely convincing.

4.2 Phylogenetic placement of Petaluridae within Anisoptera

As already indicated above, NEL et al. (1998) have first invalidated the already published hypotheses concerning the relative position of the four basal clades of Anisoptera, and in a second time proposed a new hypothesis. In the light of the results presented above and because of the finding of interesting or reinterpreted characters in other groups like Chlorogomphidae, their phylogenetic hypothesis must be reevaluated.

4.2.1 Critical view of the phylogenetic hypothesis of NEL et al. (1998)

I mainly follow the arguments of NEL. et al. (1998) invalidating the previously proposed hypotheses (HEIDEMANN & SEIDENBUSCH 1993, PFAU 1991, LOHMANN 1996, CARLE 1995), except for some important points presented by CARLE (1995) concerning the abdominal transverse muscles (see below) and the molar part of the larval mandible. I consider a moveable molar part of the larval mandible as a plesiomorphy belonging to the ground plan of Anisoptera, and not only primitively present in Gomphidae (according to CARLE 1995), but also primitively – and clearly – present in Epiophlebiidae and Chlorogomphidae (contra CARLE 1995).

NEL et al. (1998) listed the following alleged plesiomorphy uniquely retained in Petalurida, making this group the most basal branch of extant Anisoptera: (1) All the larval antennomeres are thick (non-filiform). – (2) Eight-folded [dental folds] proventriculus. – (3) Larvae incapable of

locomotion by jet propulsion, because the necessary abdominal muscles are primarily absent. Nevertheless water can be expelled from the rectal chamber by action of the rudimentary transverse muscle of segment 6. The absence of jet-propulsion-locomotion and of the transverse muscle 5 probably represents a unique plesiomorphy of Petalurida. A transverse muscle 5 belongs to the ground plan of all non-petalurid Anisoptera, while a transverse muscle 4 might represent an autapomorphy of Cavilabiata.

The antennae of *Phenes* and *Uropetala* can be considered as filiform even if they are somewhat thickened (see Figs. 1, 8). The last antennomere of *Petalura* is not at all thickened, and that of *Phenes* is not particularly thickened as well. The larvae of Zygoptera, Epiophlebiptera and Isophlebiptera, all sister groups of Anisoptera, have filiform antennae. The larvae unambiguously attributed to the Aeshnidiidae, the probable sister group of all remaining Cavilabiata, have apparently also filiform antennae. Other known fossil larvae like Nothomacromiidae are not attributed with certainty to any group for which the adult is known. The Gomphidae can be considered to have thickened antennae with an autapomorphic strong reduction of the apical fourth segment (secondarily reversed in some Onychogomphinae for which the terminal segment is greatly or even enormously widened). Larvae of Gomphaeschninae s. str. (Aeshnidae), *Palaeosynthemis*, *Archaeophya*, *Lathrocordulia* and *Austrophya* (all 'Corduliidae' s. lat.) have antennae about as thick or even thicker than those of *Phenes* and *Uropetala*, and to a lesser extent, the Cordulegastridae, some other Synthemistidae, and even some Libellulidae like *Diplacina* can be considered to have rather thickened antennae. Character (1) is somewhat variable within the Petaluridae, of uncertain polarity and subject to homoplasy, and should therefore be discarded from phylogenetic analyses. The variable development of the antennae is probably correlated to the mode of hunt of the larvae, privileging or not the sense of touch in detriment of the vision, or even to support and to rise up covering decaying mater before attacking prey.

As already mentioned above, character (2) is invalidated, and a proventriculus with four dental folds is considered belonging to the ground plan of Anisoptera.

Larvae of Petaluridae are incapable of locomotion by jet propulsion simply because they are semi-terrestrial. Semi-terrestrial larvae are not in the ground plan of Anisoptera, nor of Epiproctophora, nor of Odonata as affirmed also by NEL et al. (1998) themselves. Thus Petaluridae are secondarily semi-terrestrial, and also probably secondarily incapable of locomotion by jet propulsion, a completely useless function in their environment that led logically to a complete atrophy of useless muscles. The Zygoptera and Epiophlebiptera are not semi-terrestrial, do not possess any transversal abdominal muscle and are unable to jet propulsion. Contrary to these taxa sister groups of

Anisoptera, the presence in Petaluridae of a rudimentary transverse muscle of abdominal 6 exactly suggests a reversion due to semi-terrestrial habits. Thus character (3) can also be interpreted with the reverse polarity to that given by NEL et al. (1998). A same event has probably affected the Austropetaliidae that shows strong tendency to semi-terrestrial behaviour, and even could have had a fully terrestrial ancestor. For this family the absence of at least two transverse muscles (those of S5 and S6) is due to a secondary loss, since the close sister group Aeshnidae possesses well functional transverse muscles 5 and 6, which are considered homologous to those found in Gomphidae and some Cavilabiata. In accord with CARLE (1995), the evolution of transverse muscles is not certain, but it could be possible that those of the Gomphidae with their little specialized and little developed transverse muscles of S4, S5 and S6 represent the plesiomorphic state. This configuration explains easily a first evolution found in the Aeshnidae, leading to an unchanged plesiomorphic transverse elongate muscle of S6 and to a strongly specialized phragmatic muscle of S5, correlated to the loss of the transverse muscle of S4, and a second evolution found in the most derived Libelluloidea, leading to a rather unchanged plesiomorphic muscle of S6 and a strongly specialized phragmatic muscle of S4, correlated to the loss of the transverse muscle of S5.

The characters of NEL et al. (1998) are considered as unconvincing and the systematic position of Petaluridae put in question.

4.2.3 New phylogenetic hypothesis (Fig. 11)

It is not in the scope of this paper to propose a complete phylogeny of the Anisoptera (an extensive phylogeny will be published elsewhere, FLECK in prep.), the purpose being simply to try to clarify the position of the Petaluridae and the relative position of some basal groups.

Cordulegastroidea Tillyard & Fraser, 1940 **stat. nov.**
(sensu Selys, 1854)

The Cordulegastridae and Neopetaliidae are considered as sister groups based on the following synapomorphies:

(1) Unique shape of the distal margin of the larval prementum (Fig. 12). – Two apical strong, acute and divergent teeth flanked each laterally by a low rectangular tooth that could be itself cut by smaller irregular denticles is not found in any other Odonata and considered as unique synapomorphy.

(2) Distal larval palpal setae shortened, at least slightly displaced dorsally, close to the moveable hook and covering it (Fig. 12).

(3) Unique organization within Odonata of the larval proventriculus which has the ventral dental folds totally

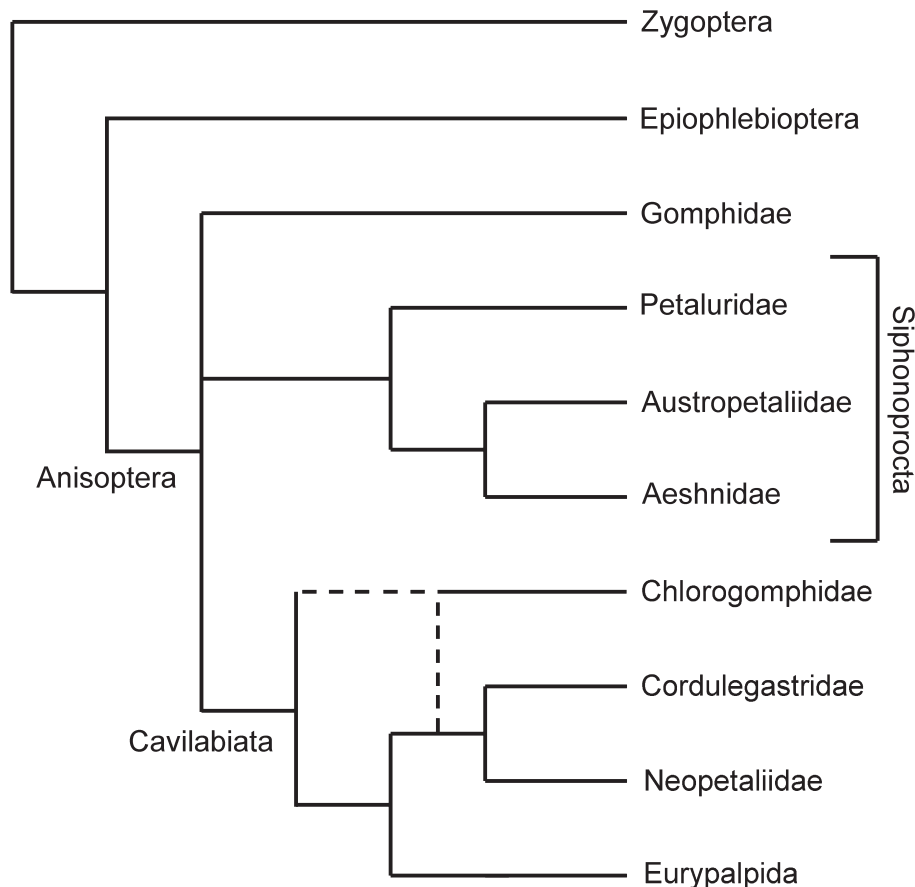


Fig. 11. Phylogenetic tree of recent Odonata.

deprived of denticles or tooth anterior to the tooth-like lobe (Fig. 13h). – In all other Cavilabiata, the presence of a moderately developed tooth or of denticles in the median part of the ventral dental folds is considered as a rest of the primitive rasp-like dentition.

(4) Apex of the tooth-like lobe of the ventral dental fold slightly anteriorly shifted (Fig. 13h). – Possibly correlated with the previous character.

(5) Exceptionally strongly pilose larvae. – The larvae of Cordulegastridae and Neopetaliidae have their body richly furnished with long pale hair-like setae, which are present in abundance on all abdominal segments except on the last one and the anal pyramid, on the lateral parts of thorax and wing pads, and on the legs. Within the Cavilabiata this abundance of hair-like setae surpasses the one of all other Cavilabiata (including the Chlorogomphidae), and more generally it is not frequently encountered in other Odonata (present also in some Gomphidae and some Petaluridae).

(6), (7) Remarkable general similarity of the male vesica spermalis, with the following apomorphies (see also

PEAU 2005): (6) V4 tongue very long, and (7) V4 posterior lobe bilobed, and rather well developed anterior lobe.

(8) Male tibial keel shortened. – Tibial keels are considered as belonging to the ground plan of Cavilabiata, or even possibly to that of Anisoptera since they are also present in Gomphidae. In *Neopetalia* the reduction is distinct, but not excessive, and the keels are still present in all legs, the reduction increasing toward the posterior legs. In Cordulegastridae the reduction affects also an antero-posterior gradient and the reduction is very strong. The keel is totally reduced in metathoracic legs, very short in mesothoracic legs (about $\frac{1}{10}$ to $\frac{1}{9}$ of the length of tibia) (at least present in the species of the *C. bidentata*-group, and *Anotogaster*), and rather short in the prothoracic legs (about $\frac{1}{6}$ to $\frac{1}{5}$ of the tibia length). The loss of the keel in the metathoracic legs and the reduction in the other legs can be explained by the fact that the unique arrangement of the autapomorphic peg-like setae (modified tumido-trichae) replaces the true tibial keels on meso- and metatibiae. At the base of the tibia the alignment of the peg-like setae is lateral, but after $\frac{1}{4}$ of its course, the homogenous

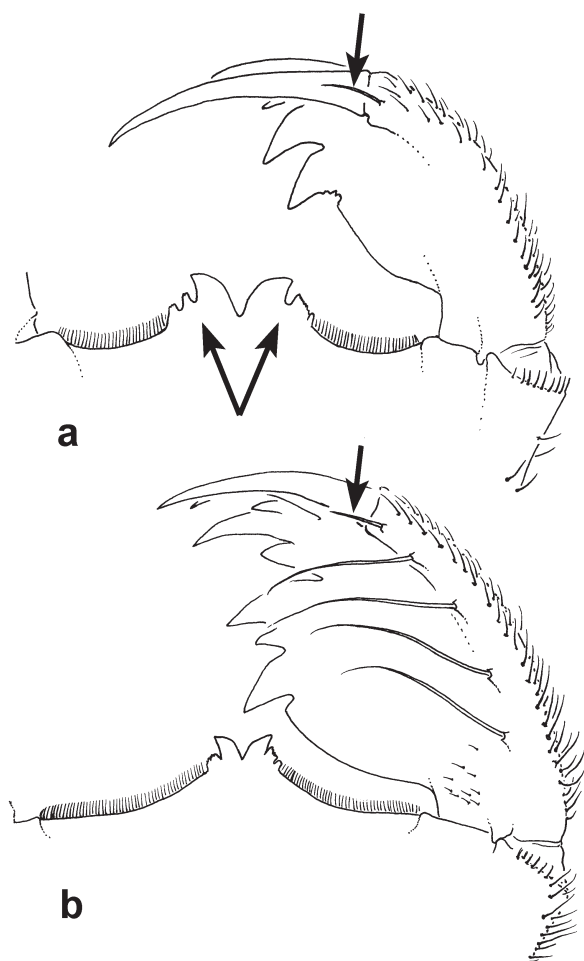


Fig. 12. Distal margin of prementum and right labial palp, dorsal view. – **a.** *Neopetalia punctata*. **b.** *Cordulegaster boltonii*. – The arrows indicate the unique shape of the distal margin of the prementum and the peculiar distal palpal seta.

alignment of setae is distinctly bent medially and replaces the tibial keel since it is occupying the same place and has the same height and width (formation of a plagiotibia). As such an arrangement is not present in females, the replacement of the true tibial keel by an analogous structure tends to be confirmed.

Beside these synapomorphies, it must be mentioned that the larvae of Cordulegastridae and Neopetaliidae are so strongly similar that it is difficult not to imagine a close relationship between these two families. It could be possible as well that *Neopetalia* is a 'true' Cordulegastridae, the adult being simply highly derived due to long isolation and regular reduction/expansion of the populations.

The following characters listed by CARLE (1995) and BECHLY (1996) are in favour of the paraphyly of Cordulegastroidea sensu nov.:

(1) Pterostigmata not parallel sided (distal side more oblique than basal side), and rather stout with length less than 8 times width.

(2) Anal loop at least elongated and enlarged, with more than five cells in the groundplan.

(3) Hindwing CuAa shortened, with fewer (1–6) posterior branches.

(4) Forewing nodus shifted distinctly distal to the middle of the wing.

(5) Adult compound eyes medio-dorsally even more approximated.

(6) Adult lateral clypeal lobes inflated.

(7) Adult intraocular lobe with at least a small posterior inflation.

(8) Males with true tibial keels that have at least $\frac{1}{3}$ length of the protibiae and $\frac{1}{5}$ length of the meso- and metatibiae.

(9) Adult glossal processes ("paraglossal spines") obsolete.

(10) Metagonapophyses of female ovipositor further reduced.

All these characters are considered unconvincing because of the following reasons:

Character (1): The modern Chlorogomphidae have parallel sided pterostigmata. Neopetaliidae must be considered to have also 'parallel sided pterostigmata' (among the 20 checked wings of *Neopetalia*, 'not parallel sided pterostigmata' were observed on only two wings). Numerous Eurypalpida Bechly, 1996 have also parallel sided pterostigmata. This implies that this character possibly does neither belong to the ground plan of Carinitibiata Bechly, 1996 nor Brachystigmata Bechly, 1996, or that it is greatly homoplastic. Short pterostigmata is a highly homoplastic character, it is present in most of Zygoptera, Epiophlebiidae, Henrotayidae, basal Stenophlebioptera like Liassostenophlebiidae or Prostenophlebiidae, Liassogomphidae, many Gomphidae, some Austropetaliidae and many Aeshnidae; it is reversed in some Libellulidae, furthermore some Cordulegastridae (*Neallogaster parvistigma*, *Anotogaster nipalensis*, *Cordulegaster diadema* among others) have rather short pterostigmata with the length less than 8 times width and not larger than those found in some Chlorogomphidae.

Character (2): More than five cells are very frequently found in the Cordulegastridae and some species like *C. maculata* or *C. diastatops* could have a rather large anal loop with frequently more than six cells, some specimens having even more than nine or ten cells. *Neopetalia*, exactly like most of Cordulegastridae, has rarely six cells in the anal loop and possesses generally only five cells, and even sometimes four cells. The character 'more than five cells in the anal loop' is not applicable for basal Carinitibiata.

Character (3) is extremely homoplastic within the Anisoptera and found in nearly all families, including the Cordulegastridae.

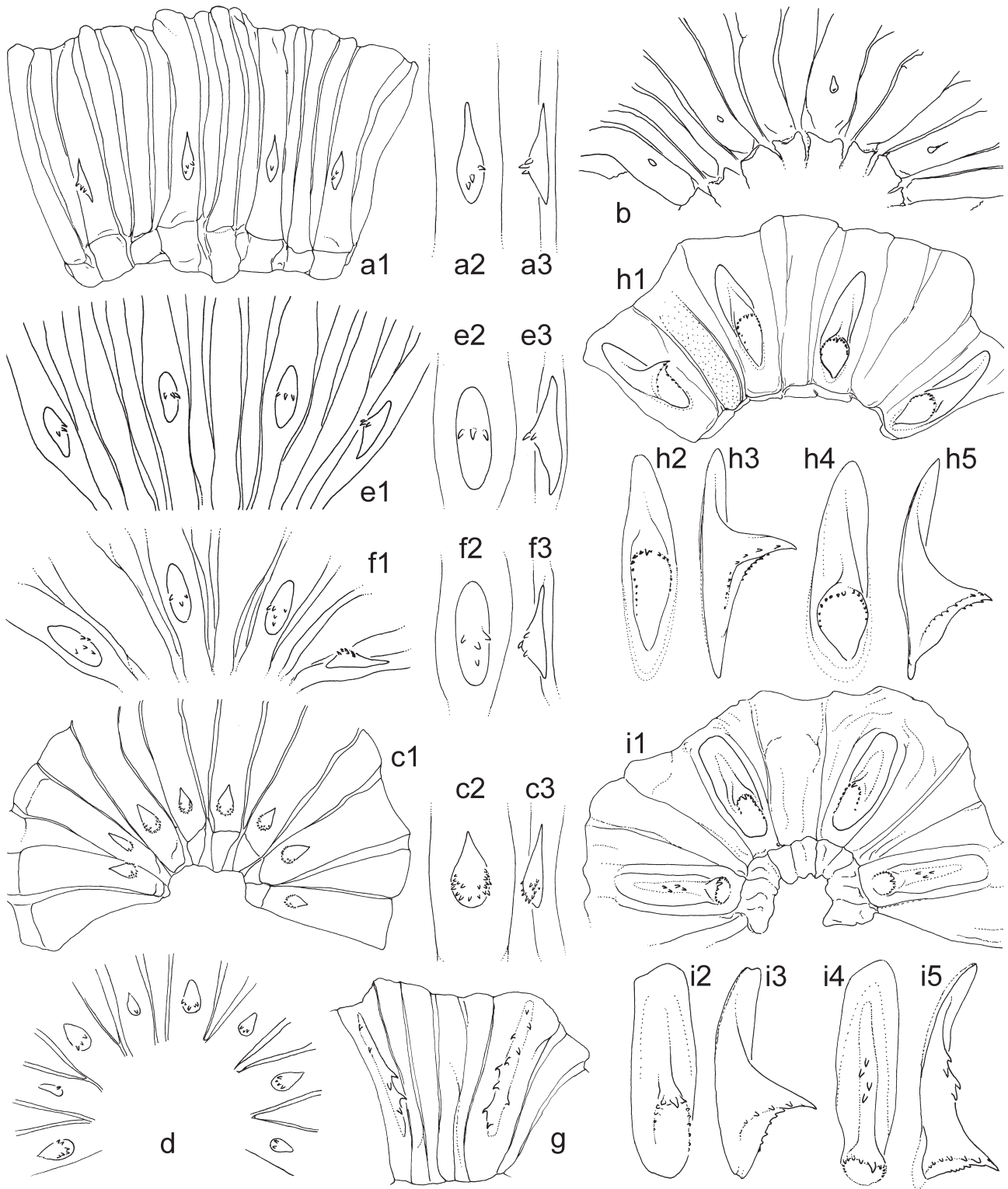


Fig. 13. Larval proventriculi, anterior side directed to the top (all proventriculi complete except g with two from four dental folds), detail of sclerotizations, view perpendicular to fold (a2, c2, e2, f2, h2, h4, i2, i4), same in lateral view (a3, c3, e3, f3, h3, h5, i3, i5), sclerotization of dorsal dental folds (h2, h3, i2, i3), sclerotization of ventral dental folds (h4, h5, i4, i5), lateral opening (h1), ventral opening (i1). – **a.** *Phenes* (coll. FLECK). **b.** *Phenes* (SMNS). **c.** *Tachopteryx* (F-1). **d.** *Tachopteryx* (F-3). **e.** *Archipetalia*. **f.** *Boyeria irene*. **g.** *Gomphus vulgatissimus*. **h.** *Neopetalia*. **i.** *Chlorogomphus risi*.

Character (4) is not applicable for the Carinitibiata since the nodus of *Neopetalia* and that of most Cordulegastridae is placed at the middle of the wing length or is slightly distally shifted. For the Cordulegastridae the character is apparently rather variable among individuals of a given species, and the nodus can appear sometimes well distally shifted.

Character (5) is useless to define the Carinitibiata and even the Brachystigmata since the approximation of the eyes is similar in *Neopetalia* and most of the Cordulegastridae, and since Chlorogomphidae have rather well separated eyes.

Character (6) is strongly subject to homoplasy. It is present in Cordulegastridae, even if less marked than that of Chlorogomphidae. In numerous Cavilabiata: Euryalpida it reaches the same development as that found in Cordulegastridae, and it is distinctly weaker developed in numerous other ones, including most of the Libellulidae, some 'Corduliidae' like *Rialla*, *Idionyx*, *Austrocordulia*, etc., and at least the Gomphomacromiidae: *Archaeophya* and the Synthemiistidae: *Synthemiopsis* and *Eusynthemis*. The character is also variable within Gomphidae (for example the inflation is rather well developed in *Onychogomphus forcipatus* and totally absent in *Davidius nanus*) and within Aeshnidae (well developed in *Oligoaeschna pryleri*, rather weakly developed in *Planaeschna milnei*).

Character (7): The Chlorogomphidae apparently do not have an intraocellar lobe, and only a rather well developed posterior inflation is visible which resembles that of some Gomphidae; in this case the vocabulary used by CARLE (1995), "posterior inflation of the intraocellar lobe" versus "gomphid postocellar ridge", is maybe only a semantic artefact since the non-homology of these characters is not demonstrated. The intraocellar lobe of *Neopetalia* is distinctly less developed than that found in Cordulegastridae and could be considered as 'more primitive', representing a kind of intermediate stage between Chlorogomphidae and Cordulegastridae (thus an intraocellar lobe could have evolved three times independently).

Character (8): As already mentioned, this character is secondarily lost in Cordulegastridae. It is also secondarily lost in Libellulidae for which no atrophied keel is even recognizable (possible convergence with Petaluridae, Austropetaliidae and Aeshnidae), and lost or atrophied in one pair of legs of several other Euryalpida like *Williamsonia*, some *Somatochlora*, *Hemicordulia*, *Idionyx*, *Cordulephya*, *Austrophya*, *Archaeophya*, etc. This proves that the character is also somewhat subject to homoplasy.

Character (9): Glossal processes are clearly present in *Chlorogomphus suzukii*, and more Chlorogomphidae must be checked to evaluate their importance within the family. The character is also homoplastic since it is present in Gomphidae, and variously expressed in Aeshnidae (for example, very distinct glossal processes are present in *Gynacantha japonica*, whereas they are absent in *Anax imperator*).

Character (10) is not receivable because erroneously stated and only applicable for the ground plan of Trichodopalpida Bechly, 1996. The great reduction of the Chlorogomphidae ovipositor is an independent event convergent to Gomphidae and the most derived Euryalpida. The ovipositor of *Neopetalia*, even if somewhat modified, is strongly similar and homologous to that of Cordulegastridae, basal Gomphomacromiidae and Synthemiistidae. The presence of a well visible apical remnant of V3 (sensu PFAU 1991) (and strongly developed V1 and V2) in *Synthemiopsis* (an Euryalpida) tends to prove independent simplifications within Cavilabiata.

Chlorogomphidae

This family has the following plesiomorphies:

(1) Functional articulation of molar lobe of the left larval mandible (Fig. 17d–f) (unique plesiomorphy within Cavilabiata). – The molar lobe of the left mandible even if somewhat specialized, is rather similar to that of *Epiophlebia* with a strong tooth 'a', a well individualized tooth 'b' and five teeth 'm' (plesiotypic arrangement). This lobe is clearly moveable in all checked Chlorogomphidae. Moveable larval molar lobes are also plesiomorphically present in Epiophlebiidae (Fig. 17a, b), Gomphidae and most Zygoptera. The molar lobe of the right mandible of all Chlorogomphidae is unique and strongly transformed, with complete reduction of the 'm' teeth, the strong reduction of the 'b' tooth and with the tooth 'a' enormously developed and strongly bent toward exterior (Fig. 17c). This huge tooth with strong eccentricity is probably greatly submitted to tearing constraints during mastication; therefore, non-mobility and reinforcement of the tooth is a necessity to prevent distortions and possible damages, the molar lobe is consequently secondarily not articulated. The process of sclerification and loss of mobility of the right mandible is not homologous to that of higher Cavilabiata. Contrary to non-gomphid Anisoptera, the strongly modified chlorogomphid molar lobe of the right mandible is well individualized, and even if not moveable, the fusion with the rest of the mandible is not totally achieved since the limit of the lobe is very distinct with a very thin paler area still visible and the presence of a non-obiterated suture. This strongly suggests a recent event non-homologous to that of non-gomphid Anisoptera.

(2) Mandibles only moderately narrowed distally, similar to Epiophlebiidae and Gomphidae (Fig. 17a–d).

(3) Ventral dental folds of proventriculus with median elongated rasp-like dentition (Fig. 13i1, i4, i5) (unique plesiomorphy within Cavilabiata). – Homologous elongated rasp-like dentition is present in Epiophlebiidae, Gomphidae and in the ground plan of Zygoptera (see Fig. 13g).

(4) Sclerotized plate of the dental folds, especially the ventral ones, at least slightly more elongated than in other Cavilabiata (Fig. 13i). – Elongated sclerotized plates

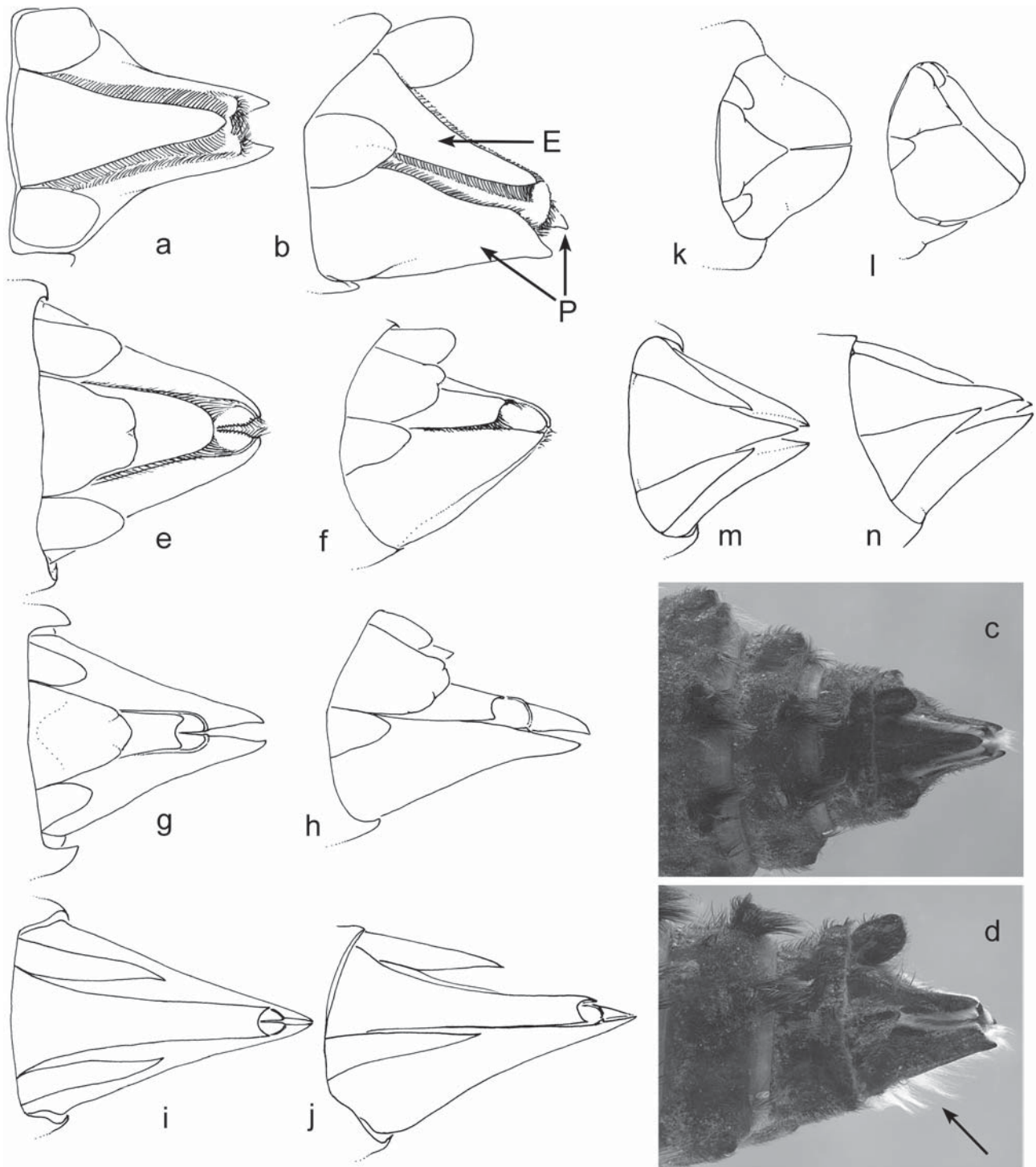


Fig. 14. Larval anal pyramids, dorsal (a, c, e, g, i, k, m) and dorso-lateral (b, d, f, h, j, l, n) views. – **a–d.** *Phenes*. **e, f.** *Tachopteryx*. **g, h.** *Phyllopetalia apicalis*. **i, j.** *Aeshna mixta*. **k, l.** *Epiophlebia superstes*. **m, n.** *Onychogomphus forcipatus*. – The arrow (d) indicates the ventral brush of hair-like setae. E = epiproct, P = paraprocts.

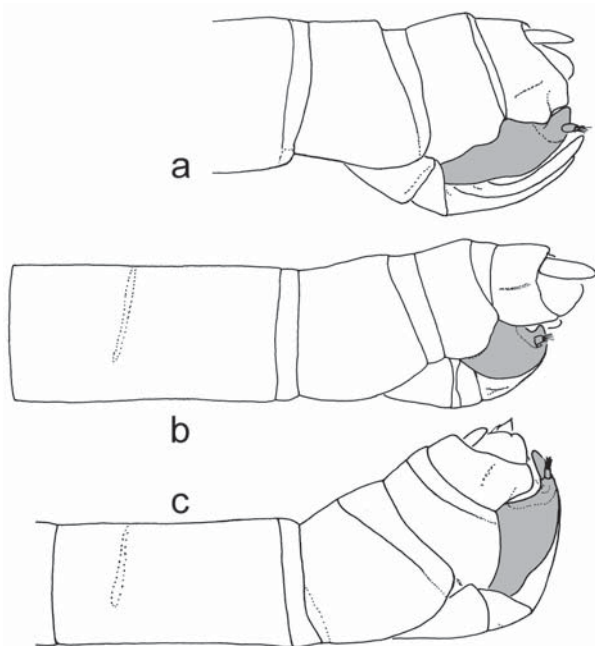


Fig. 15. Ovipositors (V3 grey coloured). – **a.** *Phenes* (modified from GARRISON et al. 2006). **b.** *Tachopteryx*. **c.** *Uropetala chiltoni*.

wearing denticles are present in Epiophlebiidae, Gomphidae and in the ground plan of Zygoptera; they are independently shortened in Siphonoprocta taxon nov. (see below) and higher Libelluloidea.

(5) Gills of the plesiomorphic simplex type (contra BECHLY 1996). – Organization very close to that found in *Neopetalia* and Cordulegastridae.

(6) Frons of adults in frontal view very transverse, rather low and only moderately bilobed, similar to that of Gomphidae, Petaluridae and Epiophlebiidae (unique within Cavilabiata).

(7) Adult with eyes distinctly more separated than other Cavilabiata (except the Libellulidae: *Diastatops* which clearly presents a reversion).

(8) No true intraocular lobe (contra CARLE 1995). – Like Gomphidae, the Chlorogomphidae possess a postocellar inflation close to lateral ocelli, but it cannot be considered as intraocular lobe. The median ocellus is distinctly detached from the inflation and the inflation is not directly in contact with the lateral ocelli because they are separated by a furrow, furthermore the inflation takes place distinctly behind the lateral ocelli and not between them.

In the light of these plesiomorphies, any of them being unique within the Cavilabiata, the Chlorogomphidae must be considered occupying a very basal position. They should be considered as the sister group of all remaining Cavilabiata. Nevertheless, it cannot be ruled out that they possibly represent also the sister group of the Cordulegas-

troidea stat. nov., on the base of possible synapomorphies like (1) the presence of two strong divergent teeth on the distal margin of the prementum, (2) the strongly irregular dentition of the labial palps (unique within Epiproctophora), (3) similarities in the structures of the male vesica spermalis, etc. (FLECK in prep.).

CARLE (1995) and BECHLY (1996) place the Chlorogomphidae as sister group of the Eurypalpida Bechly, 1996, on the basis of following characters:

- (1) Sectors of arculus approximate.
- (2) Arculus rather straight and posterior part (cross-vein) distinctly shorter than anterior part.
- (3) Oblique pterostigmal brace indistinct or obsolete, if present shifted distally beneath the pterostigma.
- (4) Wings with relatively short pterostigmata that cover only 1–3 complete cells.
- (5) In the hindwing the so-called “gaff” (= basal CuA before its branching) strongly prolonged.
- (6) In the hindwing CuAa further shortened with less than four posterior branches.
- (7) Anal loop widened.
- (8) Nodus shifted at least somewhat distally in forewing.
- (9) Presence of several accessory cubito-anal crossveins.
- (10) RP3/4 and MA parallel with only one row of cells even between the most distal parts of these veins.
- (11) Males with characteristic derived type of peg-like setae (tumidotrichae) on meso- and metatibiae.
- (12) Male tibial keels more than $\frac{1}{3}$ length of protibiae and more than $\frac{1}{5}$ length of meso- and metatibiae.
- (13) Larval proventriculus with inner denticles of dorsal lobes directed medially.
- (14) Larval rectal gills of the lamellate duplex type.
- (15) Ligula of the male secondary genitalia without longitudinal keel.

These characters are considered unconvincing because of the reasons given below. Some works (among others: FLECK 2004, FLECK et al. 2008) have demonstrated that wing characters are much more subject to homoplasy than previously assumed. Furthermore I agree with BECHLY (1996) himself indicating that “certain basal stem group representatives of Eurypalpida strongly suggest that the derived states of the anal loop, pterostigma and the arculus are convergences between Chlorogomphoidea and Eurypalpida”.

Character (1) is a convergence, since the basal fossil Chlorogomphida-Mesochlorogomphidae (*Hispanochlorogomphus*, *Mesochlorogomphus*) and some basal Eurypalpida (*Araripebellula*, *Rencordulia*, etc.) do not have more approximate sectors of the arculus than those of Cordulegastroidea stat. nov.

Character (2) is found in many Aeshnidae, numerous Gomphidae and some Stenophlebiptera, thus its phylogenetic importance is questionable. Its absence in the

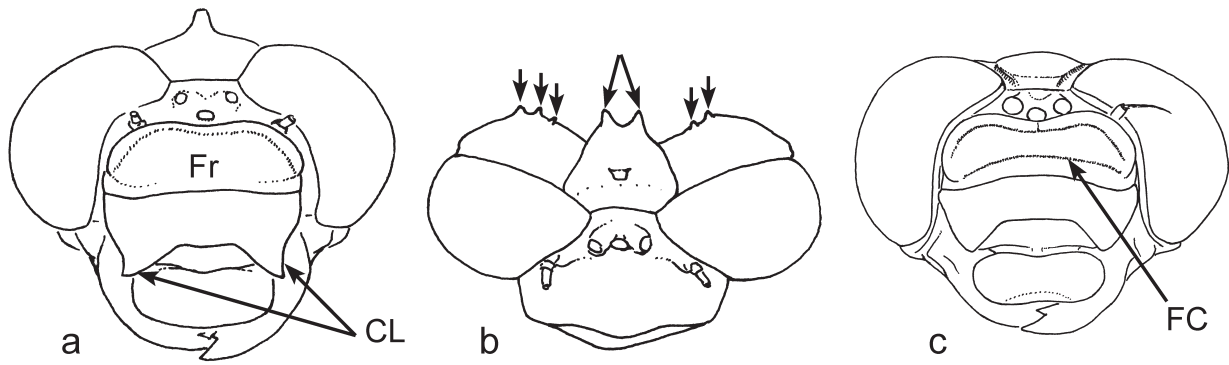


Fig. 16. Adult heads. – **a, b.** *Phenes* (modified from GARRISON et al. 2006), frontal (a) and dorsal (b) views. **c.** *Tanypteryx pryeri*, frontal view. – Arrows indicating the pair of occipital horns and the postocular spines. CL = clypeal lobes, FC = lower frontal carina, Fr = frons.

Hemeroscopidae and the Juralibellulidae Huang & Nel, 2007 and in some basal Eurypalpida like the fossil genus *Rencordulia* would moreover suggest a convergence between the Chlorogomphidae and other Brachystigmata.

Character (3) is highly homoplastic and useless since the brace vein is absent in Cordulegastridae, in some Isophlebiopoda, in some Heterophlebiopoda and in a few Aeschniidae, and present in some recent basal

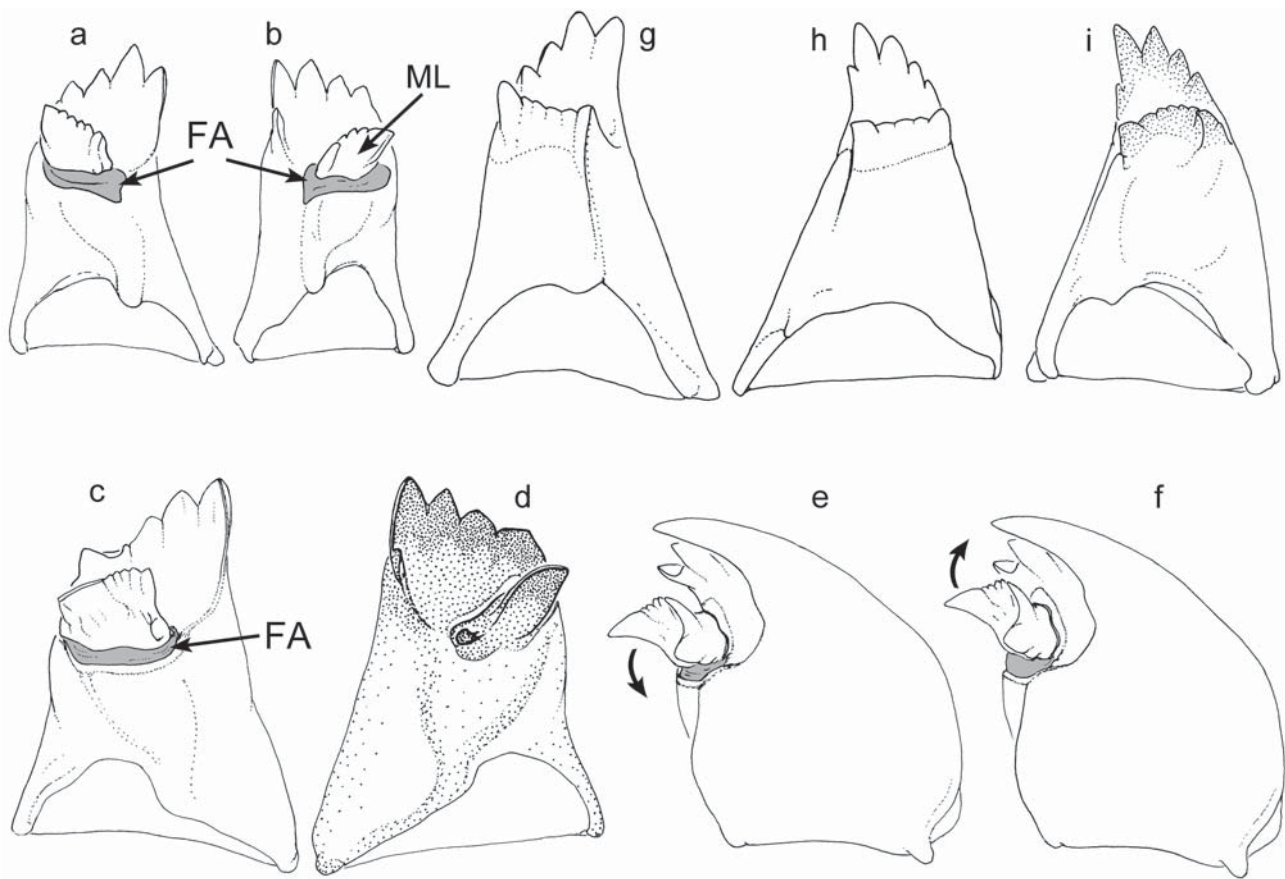


Fig. 17. Larval left (a, c, g) and right (b, d, e, f, h, i) mandibles, internal (a–d, g–i) and ventral (e, f) views. – **a, b.** *Epiophlebia superstes*. **c–f.** *Chlorogomphus risi*. **g, h.** *Phenes*. **i.** *Phyllopetalia* sp. – Flexible area coloured in grey. Arrows indicating the movements of the molar lobe. FA = flexible area, ML = molar lobe.

Chlorogomphidae, and in several more advanced Cavilabiata like the fossil family Araripelibellulidae, and the recent families Synthemistidae and Gomphomacromiidae s. str.

Character (4) is greatly homoplastic in the whole order. Short pterostigmata are found for example in most of the Zygoptera, Epiophlebiidae, numerous Aeshnidae and several Gomphidae. The length of the pterostigma is particularly variable within Cordulegastridae: short and covering about 2 or 3 cells in *C. brevistigma* and most of *C. erronea*, and covering 2½ to 4½ cells depending on the individual in most of the species (*C. bidentata*, *C. insignis*, *C. maculata*, *C. godmani*, *C. diadema*, *C. obliqua*, *C. dorsalis*, etc.). The pterostigmata of *Neopetalia* are not longer than those of several Chlorogomphidae, and are covering about 3 cells (between 2½ and 4 cells). Several large Chlorogomphidae have a rather long pterostigma covering more than 3 cells.

Character (5), visible in Chlorogomphida, is considered to be correlated with the independently evolved great enlargement of the anal loop and cubito-anal field of this group, which are variable within the clade Cavilabiata. The “gaff” of the most basal living Chlorogomphidae (having a rather small anal loop and not enlarged cubito-anal field) is not longer than the one of Neopetaliidae and Cordulegastridae. Some basal Brachystigmata, belonging to the fossil families Hemeroscopidae and Juralibellulidae, have also a rather short “gaff”. The recent basal families Synthemistidae and Gomphomacromiidae have in their groundplan a shorter “gaff” than that of most Chlorogomphida, also strongly suggesting convergences of Chlorogomphida with Trichodopalpida Bechly, 1996, but also with Aeshnidae and fossil Aeschniidae.

Character (6) is not applicable since it is present also in Neopetaliidae and several Cordulegastridae. It is furthermore strongly subject to homoplasy within the Anisoptera since it is present in some modern Petaluridae, apparently most of the Austropetaliidae, several Aeshnidae and numerous Gomphidae, and reversed in a few females of large species of Chlorogomphidae.

Character (8), rather homoplastic and present in Chlorogomphidae, is probably a convergence with higher Cavilabiata, Aeshnidae: Gomphaeschninae and several Gomphidae. Its absence in several groups of Eurypalpida and Brachystigmata (like the fossil families Araripelibellulidae and Juralibellulidae) also strongly suggests convergences between Chlorogomphidae with higher Cavilabiata.

Character (9) is useless since it is absent in most of Cavilabiata and could be considered as a convergence between a few taxa within this clade.

Character (10) is clearly highly homoplastic and of little value. It is present in several Gomphidae and Aeshnidae, and reversed or primitively absent in some basal Eurypalpida like the fossil *Rencordulia*, most of the Synthemistidae, some Gomphomacromiidae, and some basal ‘Corduliidae’ like *Apocordulia*, *Austrocordulia*,

Lathrocordulia, *Micromidia*, etc. Lastly, RP3/4 and MA are still slightly divergent in the basal Chlorogomphida: Mesochlorogomphidae, also strongly suggesting convergence between Chlorogomphidae and higher Cavilabiata.

Character (11) is not applicable since tumidotrichae are also present in Cordulegastridae. Since they are present in some Gomphidae, it is not impossible that tumidotrichae belong to the groundplan of Anisoptera, and are independently lost in several groups.

Character (12) is invalid since tibial keels are considered belonging to the groundplan of Cavilabiata, or even to the ground plan of Anisoptera.

Character (13) is considered by me as not founded because the inner denticles of the dorsal lobes of the proventriculus are apparently strictly similar in the studied specimens of Cordulegastridae, Neopetaliidae and Chlorogomphidae (see Fig. 13h, i).

Character (14) is, as already mentioned above, erroneous since Chlorogomphidae have simplex type of gills.

Character (15) is also present in Gomphidae and Neopetaliidae and strongly suggests correlation with atrophied ovipositors. This character is not really applicable to Eurypalpida since the ligula is strongly reduced in this group and with possibly different function.

Siphonoprocta **taxon nov.** (= Aeshnata + Petalurida, all sensu BECHLY 1996)

Etymology: In reference to the larval anal pyramid transformed into a respiratory siphon.

The recent Petaluridae, and the recent sister groups Aeshnidae and Austropetaliidae (for synapomorphies of Aeshnidae and Austropetaliidae see CARLE 1995 and BECHLY 1996) are gathered in the clade Siphonoprocta on the basis of the following potential synapomorphies:

(1) Loss of the molar articulation of the larval mandible, convergent to Cavilabiata non-Chlorogomphidae. – A molar articulation is present in Epiophlebiidae, Gomphidae and Chlorogomphidae, and belongs to the ground plan of Anisoptera and Cavilabiata.

(2) Larval mandibles strongly narrowed distally and rather well curved with its ventral side, in internal view, distinctly concave (Fig. 17g, h, i). – The right mandible of Cordulegastridae and Neopetaliidae is also rather well narrowed distally and somewhat slightly curved, however not as strong as in Siphonoprocta, and represents a convergence.

(3) Dental folds of proventriculus with mound-like sclerotized lobe carrying in the ground plan a few denticles in the median part (Fig. 13a, d, e, f) (unique within Epiproctophora). – The dental folds of the Siphonoprocta are not homologous to those of Cavilabiata (contra CARLE 1995). The mound-like sclerotization of Siphonoprocta is small and rounded, the entire sclerotized plate is bulged and has in its median part and slightly distally a few denticles (groundplan). This structure can be considered as

a strong contraction of the plesiomorphic elongated rasp-like sclerotized plate of the dental fold (Fig. 13g). The dental folds of Cavilabiata are strongly different, the sclerotized plate of a dental fold is very large and the huge tooth-like structure is placed on a large and relative plane plate (Fig. 13h, i). This plate presents only in its median part a longitudinal protuberance, low and only faintly marked anteriorly, it is growing posteriorly to give the well developed tooth-like structure. The strongly armed plates of the Cavilabiata can be considered as a lateral enlargement of the primitive thinner rasp-like sclerotization with a strong posterior specialization, this posterior part giving the tooth-like structure carrying aligned denticles along the posterior edges. The most primitive state of this structure is still encountered in the ventral dental folds of Chlorogomphidae (Fig. 13i1, i4, i5). – **Remarks:** (a) The proventriculus of one larva of *Phenes* presents small lobes (Fig. 13b). As I already observed this phenomenon in one larva of *Archipetalia*, even if less atrophied, and as in the other larva the lobes are nearly identical to those found in most other Petaluridae, Austropetaliidae, and most Aeshnidae (Fig. 13a, d, e, f), it is probable that the small observed lobes are atypical. – (b) The autapomorphic dentition of the proventricular lobes of *Tachopteryx* is without doubt due to a secondary hyper-development since the antepenultimate instar larva presents lobes similar to other Petaluridae (Fig. 13d).

(4) Anal pyramid modified as a siphon (Fig. 14a–j) (unique within Epiproctophora, secondarily reversed in some lotic Aeshnidae; primitively the anal pyramid is not siphon-like, see Fig. 14k–n). The siphon is formed by the gutter-shaped epiproct and elongate paraprocts with an inner siphon carina that anteriorly exactly corresponds to the lateral margin of the epiproct (contra CARLE 1995, considering the terminalia forming a dorsally directed vent as an autapomorphy of the Petaluridae). These lateral margins of the epiproct are furnished with a dense row of setae in Petaluridae, possibly a primitive condition, since distinct rows of setae are still visible in Austropetaliidae. This structure is functional for the direct air capture at the water surface or for an amphibian life.

(5) Terminalia with ventro-medial hair brush (Fig. 14d) (contra CARLE 1995). I consider this structure as a possible synapomorphy of the Siphonoprocta, since it is not only present in Petaluridae, but also present in *Archipetalia*, *Austropetalia*, and as a less developed structure in all other Austropetaliidae.

(6) Styli of ovipositor brush-like, carrying a terminal dense tuft of long and sub-parallel setae (apparently unique within Odonata). The Zygoptera and the Epiophlebiptera have styli not brush-like.

Additional putative synapomorphies:

(7) Tibiae of adult male with complete loss of tibial keel (convergent to Libellulidae). – This character is until now

not polarisable because of its absence in the recent outgroups and the unsolved position of the Gomphidae. Tibial keels are possibly in the ground plan of the Anisoptera, but the validity of this character depends on its knowledge in outgroup fossil taxa like Stenophlebiptera and basal fossil Anisoptera like Juragomphidae or Liassogomphidae, and also of the definitive position of the Gomphidae.

(8) Frons of adults with a large transverse carina between dorsal margin of the frons and clypeus, delimiting a kind of depression between it and the dorsal edge of the frons. – If this character is a reversion in *Phenes*, it could be a synapomorphy of the Siphonoprocta because it is present in non-Pheninae Petaluridae, Austropetaliidae – even if less marked – and several Aeshnidae – also less marked.

(9) Larval abdomen with hairy dorso-lateral tubercles ('Zottenhöcker') in the ground plan. – This character is present and well expressed in *Phenes*. It probably also belongs to the ground plan of Austropetaliidae (distinct 'Zottenhöcker' are present in *Archipetalia*, and smaller ones in *Austropetalia* and most *Phyllopetalia*). Lastly, small 'Zottenhöcker' are also visible in a few Aeshnidae like *Telephlebia* (atavism?).

4.2.4 Conclusion

The position of the Gomphidae is not resolved in the present study because of many conflicting characters. The presence of the unique rasp-like larval proventricular dentition and other putative plesiomorphies suggest that the Gomphidae could be the sister group of all remaining Anisoptera. Alternatively, the presence of tibial keels of the male and a part of characters presented by BECHLY (1996) suggest that the Gomphidae could be the sister group of Cavilabiata. Lastly, it is not impossible that the Gomphidae represent the sister group of the Siphonoprocta if on the one hand the presence in the ground plan of lateral abdominal protuberances anterior to the segment 7 and on the other hand complete fusion of the larval abdominal sternite 9 with the post-pleurite correlated to a perseverance of the pre-pleurite are accepted as possible synapomorphies. The work of FLECK et al. (2008) supports this last hypothesis and the monophyly of the Siphonoprocta. Their results and those of CARLE et al. (2008) and BYBEE et al. (2008) support also the Chlorogomphidae as not belonging to the Brachystigmata.

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