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Morphology of female external genitalia in *Phenes raptor* (Odonata: Petaluridae)

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The exoskeleton of the female genitalic region in *Phenes raptor* is described based on light microscopy and scanning electron microscopy. It is shown that in this species the pattern of sclerites, articulations, processes, and apodemes is overall the same as in other ovipositor-bearing Odonata, i.e. Zygoptera, the anisozygopteran *Epiophlebia*, and the anisopteran Aeshnidae. However, many morphological details differ among all these taxa. Fifty-four characters were scored for *P. raptor* in order to be included in a previously compiled dataset for phylogenetic analysis of ovipositor-bearing Odonata. These characters include only few specific similarities between *P. raptor* and either Aeshnidae or *Epiophlebia*. Instead, *P. raptor* shows a number of features that are unique among ovipositor-bearing Odonata. Absence of serration on the ovipositor in *P. raptor* and reduction of the interlocking mechanism connecting the two first valves medially is probably correlated with the endosubstratic egg-laying of the female. The ovipositor bears numerous sensilla of different shape, which probably detect suitable places for oviposition.

Keywords: Odonata; dragonfly; morphology; ovipositor; *Phenes raptor*; Petaluridae; Anisoptera

Introduction

Extant Odonata are generally subdivided into three groups: the species-rich Zygoptera and Anisoptera, and the Anisozygoptera, with the sole extant genus *Epiophlebia*. Zygoptera are viewed either as paraphyletic with respect to Anisoptera and *Epiophlebia* (e.g. Pfau, 2002; Saux et al., 2003; Trueman, 1996), or as a monophyletic group (e.g. Bybee et al., 2008; Carle et al., 2008; Dumont et al., 2010; Fleck et al., 2008; Rehn, 2003). A sister-group relationship of *Epiophlebia* and Anisoptera (together called Epiprocta) is recently strongly favoured (e.g. Dumont et al., 2010; Fleck et al., 2008; Rehn, 2003) but not universally accepted (e.g. Carle et al., 2008). The monophyly of Anisoptera is beyond doubt, being supported both by morphological and molecular data (e.g. Dumont et al., 2010; Rehn, 2003). Phylogenetic relationships among families within Anisoptera remain disputed (e.g. Bechly, 1996; Bybee et al., 2008; Carle, 1982, 1995; Fleck & Nel, 2003; Lohmann, 1996; Misof et al., 2001; Pfau, 1991, 2005; Trueman, 1996).

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Odonata show a wide range in the morphology of their female genitalia. A highly complicated female genitalic region that includes a well-developed ovipositor is found in all Zygoptera, in *Epiophlebia*, and in the Aeshnidae, Petaluridae (see St. Quentin, 1962), and Austropetaliidae among the Anisoptera ("ovipositor-bearing Odonata"). While most species from these taxa lay their eggs into living plant tissue (endophytic oviposition), the Petaluridae and some Aeshnidae use another egg-laying strategy (see below). Information on the oviposition of the Austropetaliidae is unavailable. Anisopteran taxa apart from the aforementioned ones have the female genitalia strongly modified (such as Cordulegastridae) or greatly simplified (such as Libellulidae) (see e.g. Asahina, 1954).

Despite the potentially great phylogenetic information content of the female genitalic region, phylogenetic reconstructions of Odonata have not yet considered this character system in much detail. Therefore, Klass (2008) compiled a dataset where 79 characters of the female abdomen, mostly the genitalic region, are scored for a sample of ovipositor-bearing Odonata: 13 zygopterans, two aeshnids, and *Epiophlebia superstes*. The possible phylogenetic evidence from manual evaluation of these characters was discussed, but there was much incongruence. Matushkina (2008a) performed a very preliminary phylogenetic analysis of 70 oviposition-related characters in 33 species of Odonata, including 28 zygopterans, four aeshnids, and *Epiophlebia superstes*; the results suggest that oviposition-related characters support some of the traditional groupings of Odonata. During the last five years the authors of this work started to collaborate in the field of genital morphology of insects; one of their goals is to establish a comprehensive dataset on female genitalia in Odonata. The Petaluridae is one of the ovipositor-bearing odonatan families still missing in this attempt.

Petalurids are large anisopteran dragonflies, distributed in Japan, New Zealand, Australia, Chile, SW Argentina, and North America (Garrison et al., 2006; Steinmann, 1997). Adults inhabit bog and woodlands, where they perch on trees or fly over streams (Garrison et al., 2006). The females lay eggs into fairly loose substrate such as moss, among grass roots, into decaying vegetable matter, or into wet ground ("endosubstratic deposition"; Garrison et al., 2006; Winstanley, 1981). The larvae show an obligatory semi-terrestrial lifestyle, which is unique among extant dragonflies. They live in burrows in stream banks or in depressions under wet leaves and damp pieces of wood (Garrison et al., 2006; Winstanley, 1981; Winstanley & Rowe, 1980).

The family Petaluridae is composed of 11 extant species classified into five genera. The known fossil record starts *c*.160 million years ago in the Jurassic (Nel et al., 1998). Petaluridae is generally recognised as a monophyletic group, but its placement within the Anisoptera is quite controversial. Several authors considered Petaluridae as the sister group to the rest of Anisoptera (e.g. Bechly, 1996; Rehn, 2003; Trueman, 1996), while other authors placed petalurids within different anisopteran subgroups (e.g. Bybee et al., 2008; Carle et al., 2008; Lohmann, 1996; Pfau, 1991, 2005). Indeed, the petalurids are characterised by a complex mosaic of plesiomorphic and apomorphic features. St. Quentin (1962) regarded the ovipositor of Petaluridae as the most primitive in Odonata. However, Pfau (1991) emphasised that the ovipositor of *Petalura* sp. is only "relatively primitive", being intermediate between the endophytic zygopteroid-aeshnoid ovipositor and the moderately reduced and distinctly modified cordulegasteroid ovipositor.

This study aims to thoroughly describe the general construction and the microsculpture of the ovipositor in the petalurid *Phenes raptor* Rambur, 1842, and to compare this data with current information on other ovipositor-bearing Odonata (Klass, 2008; Matushkina, 2004, 2008b, c; Matushkina & Gorb, 1997, 2002). Characters related to the ovipositor and some other parts of the female postabdomen will be scored for *Phenes raptor* in order to be included into the dataset for phylogenetic analysis compiled recently by Klass (2008). The results of this study will fill the most striking gap in Klass's and Matushkina's datasets and represent an important step towards establishing a female genitalia character matrix for analysing odonatan relationships.

Material and methods

Terminal abdominal segments of two females of *Phenes raptor* were examined. Dried postabdomina were soaked with Bouin's fluid for a few months for softening and elastification of the cuticula. Then postabdomina were washed in distilled water and dissected in the median plane. The two halves were macerated in 10% KOH, and examined in glycerine under a stereo microscope. For the scanning electron microscope (SEM) study the cuticular parts of one female were washed in distilled water, dehydrated in a graded ethanol series, air-dried, sputtered with gold-palladium and examined with the scanning electron microscopes LEO 1530VP, Hitachi S-4800 and Zeiss EVO-50 SEM.

Morphological terms and abbreviations follow the insect-wide approach in Klass (2008) (see also e.g. Klass, 2003; Klass & Ulbricht, 2009), with few additions marked with an asterisk in Abbreviations. Terms by Klass (2008) are given in standard type; corresponding terms used by NM in previous publications are given in parentheses.

Abbreviations

ac9, ac10	antecosta of S9 (anterior carina of 9th tergite, partly), and antecosta of S10, respectively
ag	accessory gland
al	aulax (ventral part of tongue-and-groove interlocking mechanism on gonapophyses of S8 and S9 called the olistheter): groove on gonapophysis of S8
b	far posterior lateral expansion of tergite 8
ba8	posterior lateral apodeme of laterocoxosternum of S8
ca, CA	central apodeme between coxae of S9 and its sclerotised part, respectively (internal sclerite, or posterior intervalvula)
CX8	coxa of S8 (medial part of basal plate of ovipositor)
CX9	coxa of S9 (sclerotisation of paired third, or lateral valve of ovipositor)
da	anterodorsal apodeme of tergum of S9, on anterior segmental border
dl	dorsal lobe of gonoplac of S9
dt10	dorsal tendon of antecosta of S10
et10	ventrolateral tendon of antecosta of S10
fa	anterolateral apodeme of coxa of S9 (anterior apophysis of third valves of ovipositor)
fcs	(*) field, or cluster of campaniform sensilla on ventromesal surface of stylus of S9
fhs	(*) field of short hair sensilla on expanded base of gonapophysis of S9
ft	tendons flanking central apodeme ca, between coxae of S9
g	anteroventral extension of sclerite of gonapophysis of S9, bearing anterior end of rhachis
ga	anterior apodeme of coxa of S8
gl9	gonoplac of S9 (third valve of ovipositor)
gp8, gp9	gonapophyses of S8 and S9 (first and second valves of ovipositor)
GP8, GP9	sclerites of gonapophyses of S8 and S9
gt	anterior tendon of coxa of S8, mesal to apodeme ga
j	(*) ventral extension of antecosta of S9, connecting tergite TG9 with anterior part of laterocoxa of S9
la	posterolateral apodeme of coxa of S9 (posterior apophysis of third valves of ovipositor)

LCa9   anterior part of laterocoxa of S9 (anterior part of gonangulum, lateral part
                of basal plate of ovipositor)
LCp9   posterior part of laterocoxa of S9 (posterior part of gonangulum, elongated
                sclerite)
LS8   laterocoxosternum of S8 (sternite of S8)
pa8   anterior lateral apodeme of laterocoxosternum of S8 ('sternal' apophysis)
PS9   poststernum on ventral hind margin of S9
rh   rhachis (dorsal part of tongue-and-groove interlocking mechanism on
                gonapophyses of S8 and S9 called the olistheter): ridge on gonapophysis
                of S9
sl9, SL9   stylus of S9 and its sclerotisation, respectively (stylus)
ta   (*) tendon upon central apodeme ca
TG8, TG9   terga of S8 and S9, respectively
TG10+LP   tergum of S10 fused with surmised anterolateral sclerites of "paraproct"
                (S10)
ty7, ty8, ty9   transverse external ridge on posterior part of tergum of S7, S8 and S9,
                respectively

Results

Description of female genitalic region of Phenes

The anterior part of tergite 8 (TG8) is normally sclerotised. The short posterior part behind the transverse ridge with a row of denticles ty8, however, is much more weakly sclerotised – very weak in the median portion but moderately strong in the lateral portions. The heavier lateral parts are somewhat expanded posteroventrally (i.e. a weakly developed extension b is present) but they do not reach the articulations between the tergite of S9 (TG9) and sclerites LCa9 (Figures 1a, 2a, c).

On the ventral side the long anterior part of S8 bears a large uniform sclerite, the laterocox-osternite LS8; this is usually called the sternite of S8, but most of it consists of the laterocoxal sclerotisations of this segment, while a true sternal component may be included but cannot be demonstrated (Klass, 2008, section 6.4.1, figure 63). The anterior apodeme pa8 as well as the postspiracular apodeme ba8 are strongly developed (Figure 1b).

The ventral border area between S8 and S9 bears two paired sclerites which are separated by a narrow ribbon of membrane, without any articulation, and connect the bases of gonapophyses of S8 with laterocoxosternite LS8 and tergite TG9 (Figures 1, 2a). The plate-like anteromesal sclerites are the coxae CX8. Left and right CX8 are fully separated. Along its anterior margin each CX8 forms a shallow transverse apodeme ga. The mesal part of apodeme ga, which is demarcated by a small notch, bears a tendon gt; the tendon is sclerotised basally (part of CX8) and membraneous apically (Figure 2a, b). The posterior margin and especially the posteromesal corner of sclerite CX8 is in close contact with the sclerotisation GP8 of gonapophysis gp8. The posterolateral sclerites are the heavy antelaterocoxae LCa9, which belong to S9. Dorsolaterally each LCa9 splits into a level anterior extension and into a narrow, thickened posterior extension (j, the thickening likely represents a ventral part of antecosta ac9); the latter is somewhat movable relative to the remainder of LCa9 and eventually continues into the tergal part of the antecosta of S9 (Figure 2a). The mesoventral tip of LCa9 forms a slightly movable articulation with the sclerotisation of gonapophysis gp8 (at e in Figure 2a).

The gonapophyses of S8, the gp8 (first valves), are curved dorsad, with sub-acute tips and slightly expanded bases (Figures 1, 3a, c, d). Basally, the anterior end of the cleft between the gp8 of the two sides is roughly at the level of the articulation between sclerites GP8 and LCa9
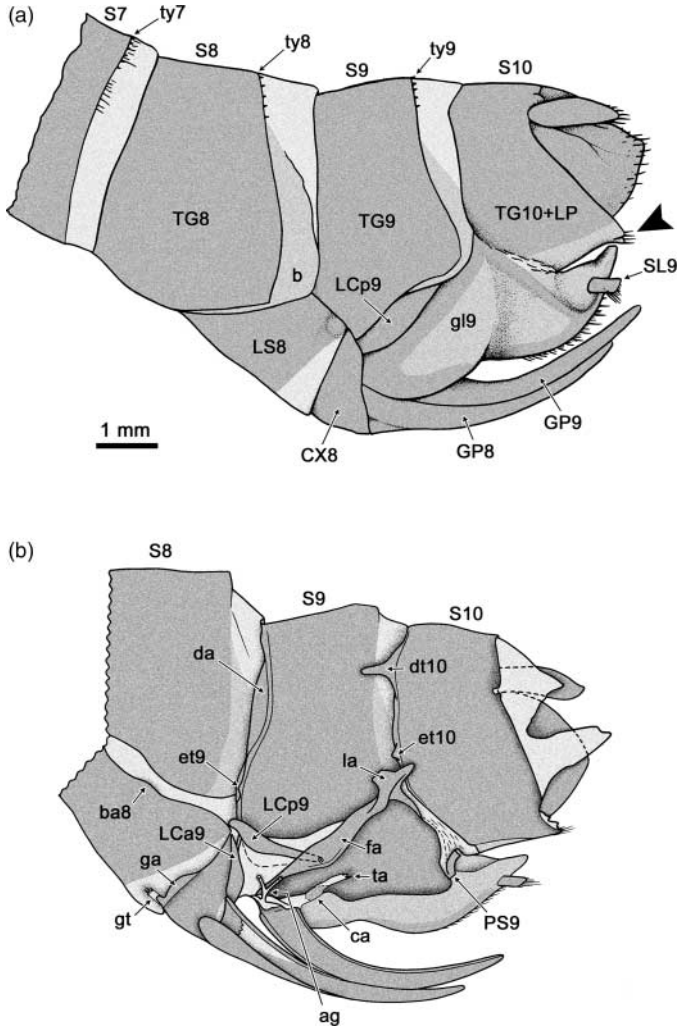
Figure 1.   Female postabdomen of *Phenes raptor*: (a) lateral view; (b) medial view. Grey scale corresponds to degree of sclerotisation. Arrowhead in (a) marks ventral bulge on posteroventral wall of S10.

(at e in Figure 2a). The sclerotisations GP8 of the left and right gonapophyses 8 are entirely separated from each other at their bases, both dorsally (Figure 2b) and ventrally (Figure 2a); there is also no median sclerite (cf. MS in Klass, 2008, e.g. figure 32) between them at the ventral base. At its sclerotised mesal base, each gonapophysis gp8 is folded dorsally and laterally (part x in Figures 1b, 2a, b, d). This part of the gonapophysis is sclerotised (part of GP8) and has a smooth mesal surface, i.e. interdigitating ribs for keeping the two gp8 together (cf. gy in Klass, 2008, e.g. figures 29, 36) are absent. The dorsal basal margin of sclerotisation GP8 is not straight, but there is a deep membraneous notch (in Figure 2b this membrane is retained on the right side but cut out on the left). The entire exposed (i.e. ventral and lateral) surface of gp8 is also smooth, i.e. any cuticular ridges or teeth (such as tm8 and gz8 in Klass, 2008) are absent; however, there are numerous coeloconic and campaniform sensilla scattered over the entire surface (more frequent apically; Figure 4). The ventromesal edge of the basal part of gonapophysis gp8 shows a sparse vestiture of long hairs. The dorsolateral edge of each gp8 forms a longitudinal groove (aulax al) that provides a sliding interlock with the rhachis of the gonapophysis of S9, the gp9 (Figure 2b).
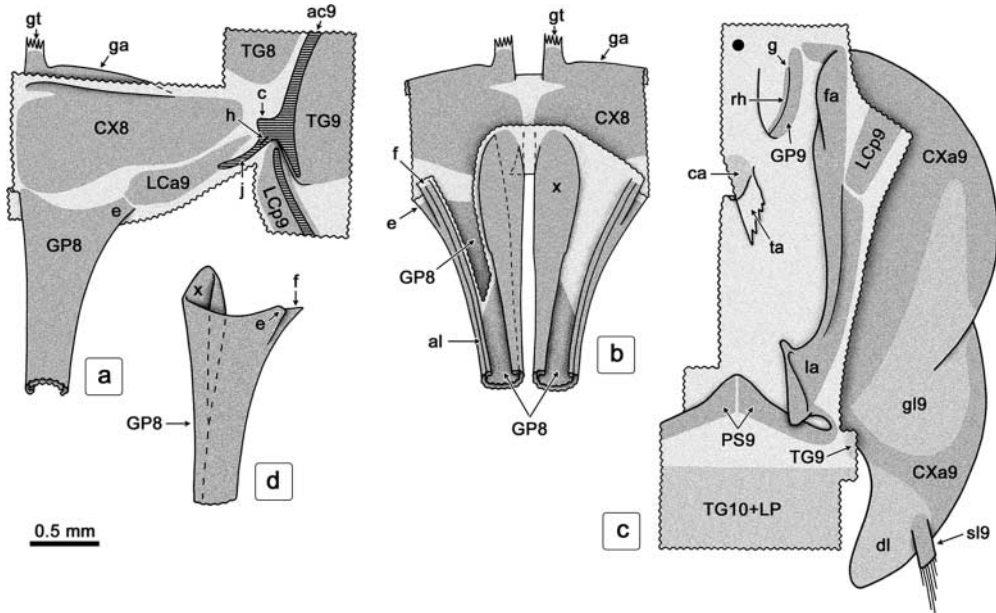
Figure 2. Details of female postabdomen of *Phenes raptor*, diagrammatically: (a) segmental border area S8–9 of left side, ventral view, ladder-like ribbons represent internal ridges based on thickening of cuticle; (b) coxae CX8 and bases of gonapophyses gp8, dorsal view; (c) right gonoplac gl9 and elements around its base, dorsal view with gonoplac forced dorsolaterad, black spot indicates orifice of common duct of accessory glands; (d) basal part of left gonapophyseal sclerite GP8, ventral view, surrounding membranes not shown. Grey scale in (c) corresponds to degree of sclerotisation.

The anterior end of the aulax is located on a short basal extension (f) of the GP8 sclerotisation, and immediately lateral to this point, sclerite GP8 forms a lateral basal extension (e) bearing the GP8-LCa9 articulation (Figure 2a, b, d).

Tergite 9 bears a heavy ridge near its anterior margin, the dorsal antecosta ac9; upon ac9 there is an anterodorsal apodeme da and a tendon et9 (both very weakly developed), and most ventrally ac9 forms an anteriorly directed extension c. When the transition area between antelaterocoxa LCa9 and TG9 is artificially broken, a thin but firm cuticular fibre is detached at the lateral end of extension j; this probably represents the strip called h in Klass (2008, e.g. figures 26, 27) (Figure 2a), which marks the border between LCa9 and TG9. The short part of TG9 behind the transverse row of denticles ty9 is altogether weakly sclerotised, but the sclerotisation is somewhat heavier in the lateral portions of this area (Figures 1, 2c). The posteroventral corners of these sclerotisations are somewhat expanded towards the posterior bases of the gonoplacs (sheathing valves; see the part of TG9 shown in Figure 2c).

The gonapophyses of S9 (gp9, second valves) are curved dorsad – in contact with gonapophyses gp8 – and have rather blunt tips (Figures 1, 3a, c, d); the two gp9 are separated from each other down to their very base, and there is also no connection between the sclerotisations (GP9) of the two gp9. The ventrolateral edges of the gp9 form a longitudinal rail, the rhachis rh, for the sliding interlock with the aulax al of gonapophyses gp8. The anterior end of the rhachis – placed on a small extension g of sclerite GP9 – is located distinctly posterior to the anterior end of the gonapophyseal sclerotisation GP9 (Figure 2c). The pair of accessory gland (ag) ducts is, near the opening, fused into a common duct which opens at midline at the level of the base of gp9 (Figures 1b, 2c) – a condition so far not reported for ovipositor-bearing Odonata. The exposed (i.e. dorsal and lateral) surfaces of gonapophyses gp9 are smooth, with numerous sensilla of different shapes, the density of which increases apically (Figure 4). The base of each gp9 is
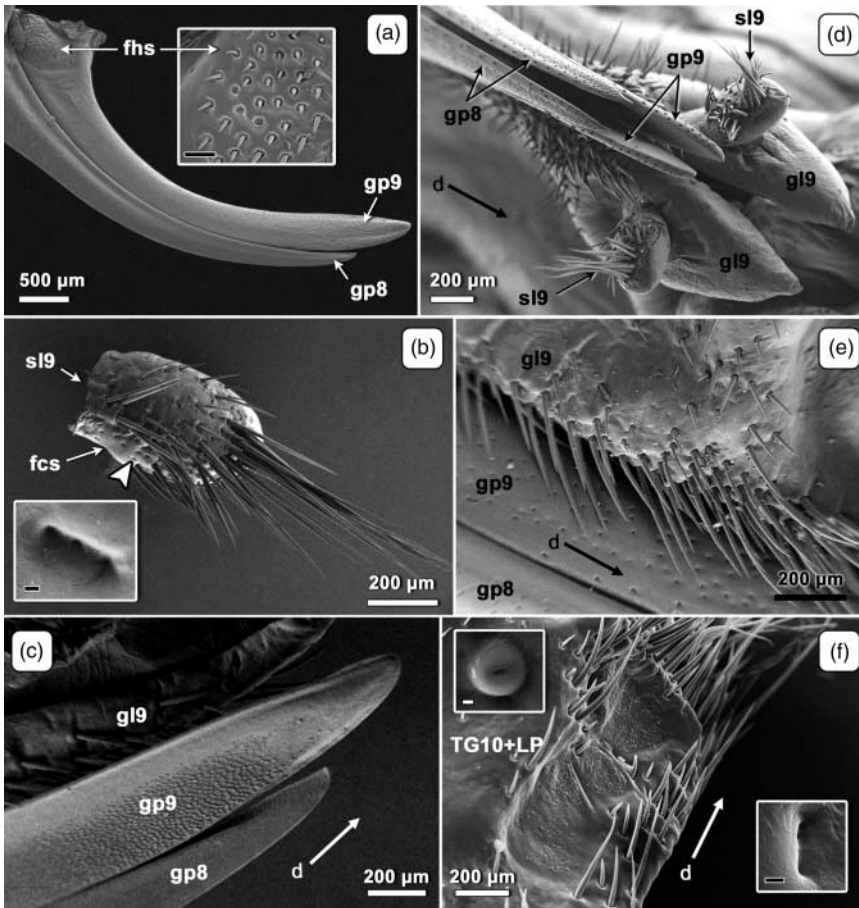
Figure 3. Scanning electron micrographs of the ovipositor of *Phenes raptor*: (a) lateral view of gonapophyses S8 and S9 – inset shows field of short hair sensilla; (b) stylus of S9 – inset shows single campaniform sensillum; (c) mesal view of gonapophyses in apical area; (d) ventral view of distal parts of gonapophyses and gonoplacs of S9; (e) lateral view of ventral edge of gonoplac of S9; (f) ventrolateral view of ventral bulge of S10 – insets show campaniform sensilla of different shape. d: distal direction. Arrowhead in (b) marks sensillum enlarged in inset. Scale bars of insets: (a) 8 μm, (b, f below) 2 μm, (f above) 3 μm.

slightly expanded, and on the proximal half of the expansion bears a field fhs of short setae upon its exposed surface (Figure 3a).

The gonoplacs gl9 (sheathing or third valves of S9) have a transverse depression demarcating the proximal from the distal parts, which are thus both a bit convex (Figures 1, 2c). The distal parts of the gonoplacs cover the tips of both pairs of gonapophyses laterally in the resting position. All the exposed externally visible parts of the gonoplacs gl9 are sclerotised by the large main sclerite of coxa 9, CXa9 (Figure 2c), but the central lateral and the distal portions are distinctly weakened (see lighter areas in Figure 2d). The tip of the gonoplac forms a slightly set-off lobe (dl in Figure 2c), which is weakly sclerotised dorsally; this sclerotisation is fully continuous with sclerite CXa9, while part of it likely corresponds to sclerite CXb9 of other Odonata (cf. Klass, 2008, figures 7, 39, 46–61). The mesal face of the gonoplac, which is in contact with the gonapophyses, is membraneous. From the sclerotised lateral base of each gonoplac arise two conspicuous apodemes, the weakly developed fa anteriorly and the triangular la, with a widened internal end, posteriorly (Figures 1b, 2c). The ventral edge of the gonoplac is densely covered with robust, sharp setae directed posteriorly; these are short on the proximal part of the edge but
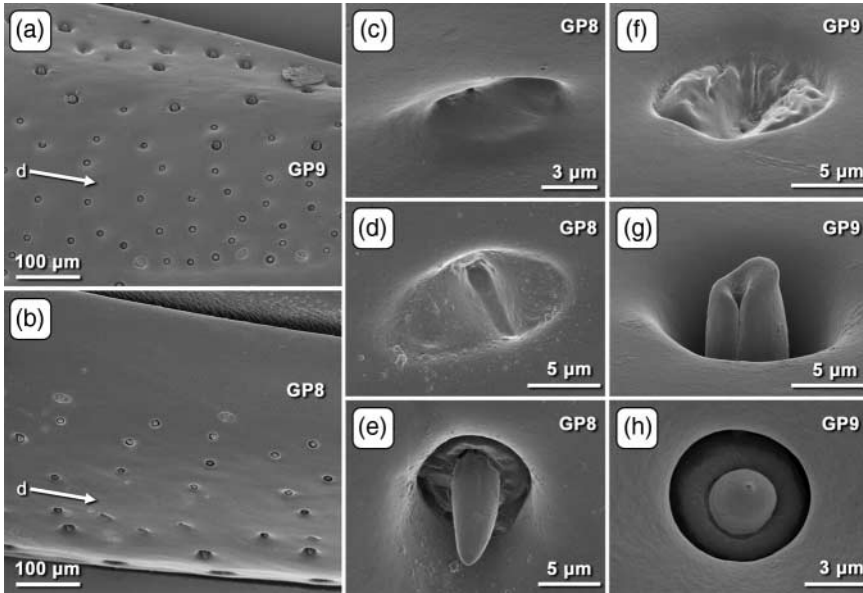
Figure 4.   Scanning electron micrographs of sensilla on gonapophyses of *Phenes raptor*: (a) lateral view of gonapophysis of S9; (b) lateral view of gonapophysis of S8; (c)–(e), sensilla of gonapophysis of S8; (f)–(h) sensilla of gonapophysis of S9. d: distal direction.

longer on its distal part (Figure 3d, e). Solitary campaniform sensilla are scattered over the lateral (external) gonoplac wall dorsal to the setae.

The membraneous mesal walls of the gonoplacs continue, towards the midline, into a wide membrane lying above the gonapophyses. Far anteriorly in this membrane lies a median infolding (apodeme ca) that is weakly sclerotised (sclerite CA) and bears a pair of lobe-like membraneous tendons (ta) (Figures 1b, 2c).

A firm transverse sclerite, the poststernum of S9, PS9, is located between the posterior gonoplac bases and is divided into two halves by a median strip of membrane (Figures 1b, 2c). The anteroventral margin of sclerite PS9 is bilobate, and its posterodorsal margin lacks a transverse fold, which in some other Odonata provides transverse stiffening between the posterior gonoplac bases of the two sides. The lateral ends of the two PS9 halves are quite narrowly but almost immovably fused with the main gonoplac sclerites CXa9.

The paired postlaterocoxa LCp9 is a ribbon-like sclerite extending lengthwise from the anteroventral corner of tergite TG9 to the margin of sclerite CXa9 at the lateral base of the gonoplac (Figure 1b); an internal ridge runs along it (anterior part seen in Figure 2a). Sclerite LCp9 reaches far anteriorly alongside TG9, to the area where TG9 is also in contact with extension j of sclerite LCa9 (Figure 2a). Where LCp9 and TG9 meet they are fused and almost immovable relative to each other. However, there is no direct contact between LCp9 and LCa9. The posterior end of sclerite LCp9 is movably articulated upon a small notch in the margin of CXa9 – quite far anterior to the base of apodeme la (Figure 2a, c).

The stylus sl9 is very short, essentially cylindrical, but with an obliquely truncated tip (Figure 3b, d). Its sclerotisation SL9 is hardly movable relative to the CX9 sclerotisations surrounding its base. The ventral surface of sl9 is covered with robust, apically directed setae of various lengths, and the apex of sl9 bears a tuft of very long setae. Campaniform sensilla are scattered over the ventral surface of the stylus (more densely near the base). The cluster fcs of campaniform sensilla is not clearly bordered (Figure 3b).

S10 is entirely sclerotised by a ring TG10+LP, but the sclerotisation of the ventral wall including the median projection is weaker (Figures 1, 2c, 3f). The ventromedian projection of S10 is poorly developed, represented only by a low bulge (Figure 3f). The antecosta of S10, ac10, is absent ventral to the short tendon et10 upon the tergal part of TG10+LP. The ventral membrane between sclerites PS9 and TG10+LP is rugose and bears neither sclerotisations nor melanisations (no sclerite IT9, cf. Klass, 2008, figures 46–61). The dorsal tendon dt10 on the anterior margin of sclerite TG10+LP is huge and entirely sclerotised, though corresponding tendons are lacking in S8 and S9. The ventrolateral region of TG10+LP bears robust sharp setae directed posteriorly and campaniform sensilla of two different shapes scattered among the setae.

Characters of Klass (2008) scored for **Phenes**

Characters are numbered and defined following Klass (2008). From the previously published dataset characters were selected that are related to the ovipositor (12–24 and 38–64), and most of those that refer to the structure of the segment wall of S8, S9 and S10 (9–11, 65–68). If necessary, supplementary explanations are provided for these characters – especially if a new state has to be defined for *Phenes*. In addition, some new characters are herein defined (80–86); for these all defined states are explained, and scoring for all taxa studied in Klass (2008) is given. As in Klass (2008), we are using instructive abbreviations for character states, which for analysis have to be replaced by 0, 1, 2 etc.

Char. 09. Presence of extension b on posteroventral corner of tergum of S8: [sho] short. Note: The posterolateral margin of TG8 has a very weak but broad sclerotisation, which is situated posterior to the row of denticles ty8; this is clearly expanded ventrally towards articulation TG9-LCa9, but it does not reach the articulation.

Char. 10. Presence of post-spiracular apodeme ba8 on lateral margin of laterocoxosternum LS8: [dst] distinct.

Char. 11. Presence of median process pp8 on posterior margin of laterocoxosternum LS8: [abs] absent.

Char. 12. Location of origin of tendon gt: [sct] arising from distinct sclerotisation on anterior margin or anteromesal corner of coxa CX8.

Char. 13. Extension of base of apodeme ga of CX8 towards midline: [lon] reaching and continuing through area of origin of tendon gt, which thus originates from mesal part of apodeme ga.

Char. 14. Interrelation between coxae CX8 of the two sides: [sep] entirely separated by membrane.

Char. 15. Interrelation between coxae CX8 and antelaterocoxae LCa9: [sep] separated by membrane, not articulated upon each other.

Char. 16. Extension to the anterior of cleft between gonapophyses gp8 of the two sides: [ime] anterior end of cleft roughly at the level of articulation GP8-LCa9.

Char. 17. Size of sclerite MS at ventral gp8 bases (i.e. at anterior end of cleft between gonapophyses of S8): [abs] absent.

Char. 18. Interrelation between sclerites MS and GP8 at ventral gp8 bases: inapplicable.

Char. 19. Interrelation between sclerites GP8 of the two sides at dorsal gp8 bases: [sep] separated by membrane.

Char. 20. Condition of GP8 sclerotisation at dorsal gp8 bases: [mes] with deep, broad membraneous notch.

Char. 21. Presence of oblique ridges gy on mesal face of gp8: [abs] absent.

Char. 22. Condition of ridges gy on basal mesal face of gp8: inapplicable.

Char. 23. Presence of saw-teeth tm8 distolaterally on gp8: [abs] absent.

Char. 24. Presence of ridges gz8 distolaterally on gp8: [abs] absent.

Char. 38. Presence of spine sa on antelaterocoxa LCa9 near its articulation with sclerite GP8: [abs] absent.

Char. 39. Anterior extension of postlaterocoxa LCp9: [lon] reaching articulation between tergum TG9 and antelaterocoxa LCa9 (Figure 2a). Note: LCa9 is in contact with TG9 only in the area of h (upon antecosta ac9, via extension j). LCp9 does not reach this point directly, but reaches the posterior flank of the bulge on ac9 from which extensions j and c diverge.

Char. 40. Interrelation between tergum TG9 and anterior part of postlaterocoxa LCp9: [cnt] connected by sclerotisation that is as heavy as that of the two sclerites in this area.

Char. 41. Interrelation between ante- and postlaterocoxa, LCa9 and LCp9: [sep] separated by membrane, two-piece "gonangulum". Note: The criteria for connection (= one-piece gonangulum) or separation of sclerites LCa9 and LCp9 are discussed in Klass (2008, pp. 118–120); only a connection of LCa9 and LCp9 mesal to strip h (Figure 2a) represents a true connection between these two sclerites that is not mediated by parts of tergite TG9.

Char. 42. Interrelation between gonapophyses gp9 of the two sides: [sep] free from each other down to the very base.

Char. 43. Extension of row of saw-teeth tm9 along dorsal edge of gonapophysis gp9: inapplicable (see below Char. 81).

Char. 44. Location on gonapophyseal sclerite GP9 of extension g bearing anterior end of rhachis rh: [pos] distinctly farther posteriorly than anterior tip of GP9.

Char. 45. Presence of tendon ft flanking apodeme ca: [abs] absent. The tendons ta that in *Phenes* are placed on apodeme ca (see Char. 82) are not homologous with the ca-flanking tendons ft of Zygoptera, since they probably provide attachment to different muscles.

Char. 46. Presence of posteriad-directed extension i at base of sclerite GP9: [abs] absent. Note: extension so far only found in *Epiophlebia* (Klass, 2008, i in figure 41).

Char. 47. Location of opening(s) of accessory glands ag of the two sides: New state [mid] right and left ducts of accessory glands unite into an unpaired common duct shortly internal to the orifice (Figure 1b), which is thus located at midline (at the same anteroposterior level as the paired openings in other ovipositor-bearing Odonata).

Char. 48. Location of articulation between sclerites CXa9 and LCp9: [ant] distinctly anterior to lateral base of apodemela.

Char. 49. Presence of dorsal gonoplac sclerite CXb9: New state [ews] embedded in weak sclerotisation. Note: in the entire distal part of the gonoplac – posterodorsal to the stylus base – the cuticle is uniformly weakly sclerotised (stronger than "typical" membrane but weaker than "normal" sclerites) (Figure 2c); this sclerotisation is confluent with sclerite CXa9, but part of it represents (by position) a weakly sclerotised CXb9.

Char. 50. Interrelation between distal parts of sclerites CXa9 and CXb9: inapplicable due to lacking differentiation of sclerite CXb9 (see Char. 49).

Char. 51. Presence of sclerite CXc9 beside base of stylus sl9: inapplicable. Note: sclerites CXc9 are, when present, tiny in other Odonata. Since in *Phenes* the sclerotisations of the gonoplac and of the stylus (CXa9 and SL9) are largely confluent, it is impossible to score the presence or absence of a CXc9.

Char. 52. Shape of stylus sl9: [cyl] straight, cylindrical, tip not widened.

Char. 53. Presence of tubercles/projections on distal ventral edge of gonoplac gl9: [abs] absent.

Char. 54. Condition of tubercles/projections on distal ventral edge of gonoplac gl9: inapplicable.

Char. 55. Presence of setal tuft on tip of stylus sl9: [dst] distinct.

Char. 56. Presence of sclerite PS9: [dst] distinct.

Char. 57. Condition of midline of sclerite PS9 in its posterodorsal part: [mes] membraneous, PS9 thus divided into two articulated halves.

Char. 58. Presence of posterodorsal, inward-directed transverse fold on sclerite PS9: [abs] absent.

Char. 59. Shape of anteroventral margin of PS9: [bil] with deep median incision.

Char. 60. Extension of connection between lateral part of PS9 and gonoplac sclerite CXa9: [ime] moderately broad.

Char. 61. Presence of sclerite IT9 between sclerite PS9 and sclerite ring TG10+LP of S10: [abs] absent. Note: there are several membranous folds in this region, but neither sclerotisations nor melanisations.

Char. 62. Interrelation between sclerite IT9 and posteroventral corners of tergum TG9: inapplicable due to the absence of IT9. Note: in context with this character it is of interest that the posterolateral corners of TG9 are expanded ventromesad in *Phenes*; the same expansion is, in *Lestes*, *Drepanosticta*, and *Epiophlebia*, the precondition for the fusion of TG9 with the median IT9 and thus the formation of a sclerite ring around the hind part of S9 (Klass, 2008, figures 48, 50, 51). For adequate consideration of the tergal expansions, the formulation of an additional character is recommended (see Char. 84).

Char. 63. Presence of circumferential internal ridge xr on posterior part of S9, on TG9 and IT9: [abs] absent (compare Klass, 2008, figures 50, 51).

Char. 64. Condition of ventral part of sclerite ring TG10+LP of S10: [wan] ring closed with very weak sclerotisation in anteromedian ventral part.

Char. 65. Presence of ventral antecostal ridge ac10 on sclerite ring TG10+LP: [abs] absent.

Char. 66. Presence of dorsal tendon dt10 on sclerite ring TG10+LP: [dst] distinct.

Char. 67. Presence of bulging outfolding and tubercles or of more massive/elaborate projections on posteroventral part of sclerite ring TG10+LP: New state [ime] intermediate. Note: median projection represented only by a weakly sclerotised low bulge.

Char. 68. Presence of posteromedian dorsal process dp on sclerite ring TG10+LP: [abs] absent.

Char. 80. Anterior extension of apodeme ga: [sho] short and transverse, only slightly surpassing the anterior margin of coxa CX8; [lon] longer, strongly surpassing the anterior margin of coxa CX8. State [sho] in *Phenes*; state [lon] in all Odonata studied by Klass (2008).

Char. 81. Presence of row of saw-teeth, tm9, along dorsal edge of gonapophysis gp9: [abs] absent; [dst] distinct. State [abs] in *Phenes*; state [dst] in all Odonata studied by Klass (2008; compare character 43 therein, which relates to the extension of the tm9 row).

Char. 82. Presence of tendon ta on apodeme ca: [abs] absent; [dst] distinct. State [dst] in *Phenes*; state [abs] in all Odonata studied by Klass (2008). Tendons ta differ from tendons ft (Klass, 2008, figure 39) by their position upon rather than beside apodeme ca.

Char. 83. Sclerotisation of tendon gt: [scl] at least basal part of gt sclerotised; [meb] gt entirely membraneous. State [scl] in *Phenes*; state [meb] in all Odonata studied by Klass (2008).

Char. 84. Presence of sclerite expansion on posteroventral corner of tergum of S9: [abs] absent, [dst] distinct. State [dst] in *Phenes* and most likely in *Lestes*, *Drepanosticta* and *Epiophlebia* (see Char. 64); state [abs] in all other Odonata studied by Klass (2008). The expansion may be serially homologous to sclerotisation b in S8 (see Char. 9), though the functional context is necessarily very different.

Char. 85. Dorsal upfolding of basal mesal wall of gonapophysis gp8 of S8: [dst] distinct; [abs] absent. State [dst] in *Phenes* (Figure 2b: fold bordering area x laterally); state [abs] in all Odonata studied by Klass (2008, figures 28, 29, 37).

Char. 86. Notch dividing lateral part of antelaterocoxal sclerite LCa9: [dst] distinct; [abs] absent. State [dst] in *Phenes* (Figure 2a: the notch separates an anterior tongue-like branch of LCa9 from a posterior branch = extension j that is limited to the course of the ventral antecosta ac9); state [abs] in all Odonata studied by Klass (2008, figures 26, 27, 32, 33, 36: the ventral antecosta is running along the undivided lateral part of LCa9).

Discussion

The female genitalic region of the petalurid *Phenes* shows the same overall structure as also found in other ovipositor-bearing Odonata, i.e. the Zygoptera, *Epiophlebia* and Aeshnidae (and perhaps Austropetaliidae, on which detailed data are lacking). This means that there are essentially the same sclerites present, and the same articulations between them; there is the same set of processes, and also tendons and apodemes are usually found in the same places. As it is true for the comparison among other ovipositor-bearing Odonata (see Klass, 2008), however, *Phenes* shows numerous peculiarities in the structural details of its female genitalia; some of these agree with conditions in certain other taxa, while others are unique to *Phenes*.

A summary comparison of the morphology of the female genitalia in *Phenes* and other ovipositor-bearing subgroups of Odonata is presented in Table 1 (for detailed data on the various Aeshnidae and Zygoptera studied see table 1 in Klass, 2008). A phylogenetic analysis of these data should await detailed studies on those Odonata that have an ovipositor that is strongly modified (Cordulegastridae) or strongly simplified (most of the remaining anisopteran families). However, in the following some characters of particular interest in the contexts of phylogenetic relationships or mode of oviposition will be highlighted. While there is no accurate study of the musculature in *Phenes* yet, some evidence on the arrangement of muscles of its ovipositor can be inferred from skeletal morphology.

Unique features of **Phenes** *female genitalia*

Our study of *Phenes* has revealed some features that are in contrast to all previously studied ovipositor-bearing Odonata. Most striking is the terminal fusion of the left and right outlet ducts of the accessory glands, ag, of S9 (character 47, Figure 2c). In the other taxa the ducts remain separated down to their orifices, and only the distance of the orifices from the midline of the body varies (closer to the midline in *Epiophlebia* and *Lestes* than in others; Klass, 2008). This character bears some relevance to the interordinal relationships in Insecta and on the structures associated with accessory glands in the insect ground plan, as explained in Klass (2008, pp. 106–107). Furthermore, the character is of functional significance: the outlet ducts in other ovipositor-bearing Odonata open close to the anterior end of the rhachis of gonapophysis 9 (see Klass, 2008, figures 39, 40), and in *Lestes* with its further mesally located gland apertures there are grooves linking the apertures to the rhachis base. While the function of the secretions has remained unknown, the link with the rhachis base suggests that the secretions enter the olistheter. In *Phenes*, however, there is no such link evident between gland aperture and rhachis base. It remains to be studied whether this implies a change in the function of the gland secretions.

Another unique feature of *Phenes* is the presence of tendons ta upon the central apodeme ca (character 82, Figure 2c). Tendons ta may evidence a particularly strong condition of the muscle attached to ca (muscle 32, cf. Klass, 2008, figure 19). This muscle was found in all ovipositor-bearing Odonata; it is particularly large in aeshnids (Matushkina, 2008b; Matushkina & Gorb, 1997), where, however, tendons ta are absent.

Phenes has a very short apodeme ga on coxa CX8 (character 80, Figure 2a); this may imply a reduction of the muscle known to be attached to ga in all other ovipositor-bearing Odonata studied so far (see muscle 17 in Klass, 2008, figure 19). It protracts the gonapophyses of S8 and S9 from the gonoplacs.

The posterolateral apodeme lt of the coxa of S9 shows a fairly complicated shape in *Phenes*; this might indicate an elaborate differentiation of the muscle running from the tergite TG9 to this apodeme (see muscle 29 in Klass, 2008, figure 19). The muscle is divided in two branches

Table 1.   States of studied characters in *Phenes* (bold type) compared with other ovipositor-bearing Odonata, following dataset of Klass (2008) and current study. Explanations of characters are given in the text. Abbreviations for character states after Klass (2008). Slash indicates a polymorphism (left one is the most frequent state), * – new state of character, # – new character, ? – state needs to be proofed by SEM. For the polarity of characters see Klass (2008).

Number of character	Character states			
	Phenes	*Aeshnidae*	*Epiophlebia*	*Zygoptera*
9	**sho**	abs	**sho**	lon/**sho**
10	**dst**	**dst**	**dst**	abs/ids/**dst**
11	**abs**	**abs**	dst	**abs**
12	**sct**	meb	ime	**sct**/meb/ime
13	**lon**	sho	sho	sho/ime/**lon**
14	**sep**	**sep**	**sep**	**sep**/cnt
15	**sep**	**sep**	cnt	art/**sep**
16	**ime**	vlo	lon	**ime**/sho
17	**abs**	sml/**abs**	sml	ime/lar/sml
19	**sep**	**sep**	cnt	cnt/ime
20	**mes**	div/**mes**	div	ent
21	**abs**	dst	dst	dst/**abs**(?)/ids
23	**abs**	**abs**	ids	dst/**abs**(?)
24	**abs**	**abs**	dst	dst/ids/**abs**(?)
38	**abs**	**abs**	dst	**abs**/ids
39	**lon**	**lon**	**lon**	sho/ime/**lon**
40	**cnt**	**cnt**	**cnt**	**cnt**/sep
41	**sep**	**sep**	cnt	**sep**
42	**sep**	**sep**	cnt	**sep**
44	**pos**	**pos**	ant	ant/**pos**
45	**abs**	**abs**	**abs**	dst
46	**abs**	**abs**	dst	**abs**
47	**mid** *	rem	adj	rem/adj
48	**ant**	**ant**	pos	pos
49	**ews** *	**abs**/dst	ids	dst/ids
51	**ids**	**ids**/dst	**ids**	dst/**ids**
52	**cyl**	**cyl**	con	clu/ime/**cyl**
53	**abs**	**abs**	dst	dst
55	**dst**	**dst**	abs	abs/**dst**
56	**dst**	**dst**/abs	**dst**	**dst**
57	**mes**	**mes**	**mes**	scl
58	**abs**	**abs**	**abs**	dst/ids/**abs**
59	**bil**	**bil**	**bil**	**bil**/stt/ime
60	**ime**	brd	brd	ntw/brd/**ime**
61	**abs**	dst/ids	dst	**abs**/dst
63	**abs**	**abs**	**abs**	**abs**/dst
64	**wan**	**wan**/opn	opn	cls/wpo
65	**abs**	**abs**	**abs**	dst/**abs**
66	**dst**	abs	**dst**	abs
67	**ime** *	dst/abs	dst	abs
68	**abs**	**abs**	**abs**	**abs**/ids/dst
80#	**sho**	lon	lon	lon
81#	**abs**	dst	dst	dst
82#	**dst**	abs	abs	abs
83#	**scl**	meb	meb	meb
84#	**dst**	abs	abs	abs/**dst**
85#	**dst**	abs	abs	abs
86#	**dst**	abs	abs	abs

in aeshnids and undivided in all zygopterans and *Epiophlebia* (Matushkina, 2004, 2008b, c; Matushkina & Gorb, 1997).

Further peculiarities of *Phenes* are the lack of saw-teeth tm9 on gonapophysis gp9 (character 81; see below), the sclerotisation of tendon gt located upon the anterior edge of coxa

CX8 (character 83), the extensive dorsal upfolding of the basal mesal wall of gonapophysis gp8 of S8 (character 85), and the laterally notched condition of the antelaterocoxal sclerite LCa9 (character 86).

All the unique features of the *Phenes* female genitalia presently appear as autapomorphies of this taxon. However, with the study of further Petaluridae genera and of Austropetaliidae the same characters may yield important evidence on the relationships among these taxa.

Female genitalia compared between Aeshnidae *and* Phenes

Among the ovipositor-bearing Odonata for which the female genitalia have been studied in detail, *Phenes* and the Aeshnidae are the only representatives of Anisoptera. One would thus expect that these two taxa share some apomorphic features, which would also provide further support to the taxon Anisoptera. However, there is hardly any such evidence from the characters we studied. *Phenes* and Aeshnidae show a complete separation between the gonapophyseal sclerites GP8 of the two sides (Figure 2b), while in *Epiophlebia* and Zygoptera at least some extent of connection is present at the dorsal gonapophyseal bases (Klass, 2008, figures 28, 37, character 19). While separation might appear as an anisopteran autapomorphy, outgroup comparison with other Insecta clearly suggests the separated, anisopteran condition to be plesiomorphic (see Klass, 2008, section 6.4). Similarly, the far anterior location of the articulation between sclerites LCp9 and CXa9 (Figure 2c) is shared between *Phenes* and Aeshnidae, while the articulation is further posterior in both *Epiophlebia* and Zygoptera (Klass, 2008, figures 39, 41, character 48), but outgroup comparison suggests the former, anisopteran condition to be plesiomorphic – although with some doubt (Klass, 2008, section 6.5). Only the absence of sawing devices on gonapophyses of S8 (tm8 and gz8) might tentatively be considered as an anisopteran autapomorphy (characters 23, 24).

Female genitalia compared between Epiophlebia *and* Phenes

Klass (2008) reported that *Epiophlebia* shows a number of features that are unique among ovipositor-bearing Odonata, being in contrast to both zygopterans and anisopterans, which conform with regard to these characters. However, since outgroup comparison does not allow for clear polarisation of most of the respective characters, phylogenetic evidence from them is presently unclear.

Most importantly, *Epiophlebia* is unique in showing a fusion between the sclerites LCa9 and LCp9, whereby it possesses a one-piece gonangulum. *Phenes* conforms with the remaining ovipositor-bearing Odonata, where either or both of these sclerites can be fused with the anterolateral part of tergite TG9 but a direct connection between LCa9 and LCp9 is absent. This character is of wider importance, because a one-piece gonangulum has been proposed as an autapomorphy of the dicondylic insects (see Hennig, 1969). However, the presence of a bipartite "gonangulum" in all ovipositor-bearing Odonata except for *Epiophlebia* puts this into question (see Klass, 2008, pp. 118–120).

Further features in which *Epiophlebia* is unique among ovipositor-bearing Odonata are an additional fusion of sclerite LCa9 (anterior part of gonangulum) with the coxa of S8, CX8 (Klass, 2008, figure 36, character 15); a basal fusion between the two gonapophyses of S9, gp9 (Klass, 2008, figure 41, character 42); a tongue-like posterodorsal extension i of the gonapophyseal sclerite of S9, GP9 (Klass, 2008, figure 41, character 46); a median process, pp8, on the hind margin of the laterocoxosternum of S8, LS8 (character 11); and a spine, called sa, on sclerite LCa9 (Klass, 2008, figure 36, character 38; a trace of spine sa, however, is also found in the zygopteran *Diphlebia*). Also in all these characters *Phenes* agrees with the conditions found in the remaining ovipositor-bearing Odonata.

On the other hand, a distinct Xth-segmental tendon dt10 has so far been known only from *Epiophlebia*, while in the present paper this element has also been found in *Phenes*. Furthermore, besides *Epiophlebia*, *Phenes* is the only ovipositor-bearing odonatan known to have adaptations for postabdominal abutment during oviposition both on the edges of the gonoplacs and on the ventral side of S10, as explained in the following section.

Oviposition behaviour and its morphological correlates in **Phenes** and other Odonata

There is a pattern of morphological and behavioural attributes related to oviposition that is common to Zygoptera, *Epiophlebia* and (most) Aeshnidae and thus likely represents a ground plan pattern of (crown group) Odonata (in agreement with Bechly et al., 2001). The core of this pattern is endophytic oviposition, where the female penetrates the plant tissues with the gonapophyses of genital segments S8 and S9 (first and second valves; cutting valves) of its well-developed ovipositor, and then inserts eggs into the slits prepared. Penetration into plant tissue is achieved by sawing movements of gonapophyses gp8 and gp9, which are pushed forward and drawn backward alongside each other. Coordination of these movements is enabled by the aulax al and rhachis rh, which provide a mutual sliding interlock between gp8 and gp9 on each side, by the ridges gy, which interlock the basal parts of the two gonapophyses gp8 (but are of varied distinctness throughout the groups here in question; see Klass, 2008) and by the ridges on the apical and ventral parts of gonapophyses gp8 ("apical lock" and "ventral lock" in Matushkina & Lambret, 2011). To ease penetration during these movements the gonapophyses gp9 and usually also the gp8 bear some saw-like sculpture upon their exposed surfaces (tm8, gz8, and tm9 in Klass, 2008). Generally, a well-organised positioning of eggs in endophytic clutches was reported for all three above-mentioned odonatan taxa (Matushkina, 2007). A particular clutch pattern can be specific to particular families (Hellmund & Hellmund, 1991) or genera (some Lestidae: Matushkina & Gorb, 2000) and can be used as a character in phylogeny reconstruction. The stereotyped sequence of oviposition movements defining a clutch pattern is controlled by campaniform sensilla on the ventrolateral surface of the stylus near its base upon the gonoplac; these sensilla have also been reported for members of all three above-mentioned odonatan subgroups (Matushkina, 2008c; Matushkina & Gorb, 2000, 2002; Matushkina & Lambret, 2011).

To prevent the sawing movements of the gonapophyses from causing the abdomen to slide along the plant substrate, the female abuts against the substrate with certain parts of the postabdomen, the bearing edge ("Stützkante" *sensu* St. Quentin, 1962). Throughout the ovipositor-bearing Odonata, the bearing edge can be in two very different positions: Zygopterans contact the substrate with the ventrally directed (morphologically mesal) surface of the gonoplacs (sheathing = third valves; Matushkina, 2004; Matushkina & Gorb, 2000), which bears many small denticles or few (or a single) larger processes. In the anisopteran Aeshnidae, in contrast, the contact is established with the ventral surface of S10 (St. Quentin, 1962), which bears teeth (often upon a large bulge) or larger processes, thus showing considerable variation (e.g. St. Quentin, 1962). While this seems to indicate a fundamental difference for endophytic oviposition in Zygoptera and the anisopterans concerned, *Epiophlebia* bridges the two conditions by showing differentiations in both areas: the gonoplacs bear a sclerotised protuberance with short setae, robust setae, and campaniform sensilla; and the ventral side of S10 bears many robust setae (Klass, 2008; Matushkina, 2008c). This seems to indicate that both areas contact the substrate during egg laying, while none of them is strongly challenged by this function.

Petalurid dragonflies, though they are equipped with a well-developed ovipositor, practise endosubstratic oviposition, i.e. females do not cut plant tissue but push their ovipositor into mud, moss, decaying vegetable matter or leaf litter to lay their eggs (the same is true for some aeshnids; Garrison et al., 2006; St. Quentin, 1962). With this derived mode of egg-laying, some

of the morphological attributes listed above have undergone reduction while others have been maintained. In *Phenes* the aulax-rhachis interlock between gonapophyses gp8 and gp9 is well developed, but the basal interlock between gonapophyses gp8 is absent (no ridges gy). Neither the gonapophyses of S8 nor those of S9 have any sculptural elements for sawing, and the gonapophyses are smooth. Campaniform sensilla at the stylus base have been retained. At the same time, the sensory equipment of the *Phenes* ovipositor is extremely rich and diverse. Taking into account the unique semi-terrestrial habitat of the larvae, probably sensilla of different shape are involved in the detection of the particular parameters demanded for suitable places for oviposition. With regard to the bearing edge, the situation in *Phenes* is similar to *Epiophlebia*: similarly shaped setae and campaniform sensilla occur both on the gonoplacs and ventrally on S10. In this way, both *Epiophlebia* and *Phenes* seem to constitute morphological and functional links between the zygopteran and the aeshnid types of bearing edges.

Acknowledgements

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