

## Morphological re-examination of *Epiophlebia laidlawi* (Insecta: Odonata) including remarks on taxonomy

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*Epiophlebia* is the only known taxon of Odonata that is neither part of the damselflies (Zygoptera) nor dragonflies (Anisoptera). Previously, two species of *Epiophlebia* were recognized, restricted to areas in Japan (*Epiophlebia superstes*) and the Himalayas (*Epiophlebia laidlawi*). Recently, the group gained attention with the description of new species from China – *Epiophlebia sinensis* and *Epiophlebia diana* – while a subsequent genetic study suggested only one species of *Epiophlebia*. To clarify these conflicting hypotheses this study focused on the under-recorded *Epiophlebia laidlawi*. This study elucidated the morphology of this species in comparison to *Epiophlebia superstes*, representing the first comparative study of *Epiophlebia* species. Furthermore, it presents notes on the taxonomic conditions of this group. With this study, a first step is made to resolve the confusion regarding the taxonomic status of the described *Epiophlebia* species. A number of anatomical characters – for example the different shape of the vertex of the head, the distinct colour patterns of the head, thorax and the abdomen or the differences in the shape of the hamulus anterior and posterior in the secondary male genitalia – confirmed the species status of *E. laidlawi* and underlined its distinctness from *E. superstes*. However, in the Chinese species *E. sinensis* and *E. diana* a re-examination is advised; especially in *E. diana* the species status is questionable.

**Keywords:** dragonfly; Epiophlebiidae; “Anisozygoptera”; taxonomic notes

### Introduction

Generally, Odonata can be divided into three subordinate taxa: dragonflies (Anisoptera), damselflies (Zygoptera) and the taxon of *Epiophlebia* (Asahina, 1954; Büsse et al., 2012; Hennig, 1959). Historically, the extant species of *Epiophlebia* were grouped together with fossil taxa, forming the “Anisozygoptera” (Nel, 1993). This name relates to the conspicuous mixture of anisopteran and zygopteran characters found in its extant species (Asahina, 1954; Büsse et al., 2012; Ruppell & Hilfert, 1993; Xylander & Günther, 2003). It has however been shown by Carle (1982) as well as Nel (1993), that the Anisozygoptera are a paraphyletic assemblage, and the taxon is thus invalid.

*Epiophlebia* is neither part of the damselflies nor the dragonflies (Bybee, Ogden, Branham & Whiting, 2008), but is the sister group of the Anisoptera, forming the monophylum Epiprocta (Bechly, 1996; Carle, 1982; Lohmann, 1996; Rehn, 2003). The group currently contains four species: *Epiophlebia superstes* Sélys, 1889 and *Epiophlebia laidlawi* Tillyard, 1921 as well as the recently described *Epiophlebia sinensis* Li & Nel, 2012 and *Epiophlebia diana* Carle, 2012.

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The ancestors of *Epiophlebia* were at their peak in the Mesozoic era (Carpenter, 1992; Nel, 1993) and the extant species of *Epiophlebia* are considered to be relict species (Asahina, 1954; Davies, 1992; Mahato, 1993). Their disjunct distribution (Büsse et al., 2012) is restricted to large areas of Japan in the case of *E. superstes* (Asahina, 1954; Tabaru, 1984), to the Himalayas for *E. laidlawi* (Asahina, 1961, 1963; Brockhaus, 2015; Brockhaus & Hartmann, 2009; Dorji, 2015; Nesemann, R.D.T. Shah, D.N. Shah & Sharma, 2011) and to China and North Korea for *E. sinensis* (Fleck et al., 2013; Li et al., 2012) and *E. diana* (Carle, 2012). While the Japanese *E. superstes* has been thoroughly studied by Asahina (1954) and more recently the head anatomy examined by Blanke, Beckmann and Misof (2012) as well as Blanke, Büsse and Machida (2015), little is known about *E. laidlawi*, which was described by Tillyard (1921) based on a single larva. The adult of *E. laidlawi* was studied by Asahina (1963) and the larvae by Asahina (1961) and more recently the thorax by Büsse, Helmker & Hörschemeyer (2015). Asahina (1963) suggested that the following characters could be used to distinguish adult *E. laidlawi* from *E. superstes*: “Colouration more brownish with fewer yellow markings; male genitalia differ especially in the shape of the hamulus posterioris; apical process of the eighth sternite less developed in the female; wings slightly longer” (p. 19). Asahina (1961) listed the following differences for *E. laidlawi* larvae: “Body size slightly larger; third antennal segment relatively longer and thicker than in *E. superstes*; antero-lateral angle of the pronotum rounded in an obtuse angle in *E. laidlawi*, angle in *E. superstes* sharply pointed anteriorly. The fore femur is longer and much wider in *E. laidlawi* and the lateral spines of abdominal segments seven through nine are well protruded into a round process in *E. superstes* and undeveloped in *E. laidlawi*” (p. 445). Four of these larval characters could not be confirmed by supplementary study of anatomy in Büsse et al. (2012) – the descriptions of Nesemann et al. (2011) refer to coloration only. Furthermore, the comparative studies on the musculature of the head (Blanke et al., 2015) and the thorax (Büsse et al., 2015) of *E. superstes* and *E. laidlawi* larvae reveal no significant differences between them.

The description of *E. diana* is only based on larvae and is therefore difficult to separate from *E. sinensis*, as the larva of the latter species is unknown, a possibility not considered by Carle (2012). A number of odonatologists have expressed doubt concerning the taxonomic status of these two *Epiophlebia* species (Dijkstra, 2013). The species status of *E. sinensis* however, seems more justified, even though a re-examination including proper figures of important distinguishing characters is certainly necessary (Li et al., 2012).

The recent description of *E. sinensis* and *E. diana* (Carle, 2012; Li et al., 2012) and the DNA analysis of three *Epiophlebia* species (Büsse et al., 2012) have provided new insights into this group. The results of Büsse et al. (2012) show an unexpected similarity of DNA sequences (18s, 28s, ITS1, ITS2, CO2) for separated species and therefore tentatively suggest that *E. laidlawi* and *E. sinensis* are allopatric populations of *E. superstes*. These results indicate the need for a morphological re-examination and reconsideration of the status of these species. The aim of this study is therefore to elucidate the morphology of *Epiophlebia laidlawi*, particularly among the adults (Asahina, 1963) and to compare anatomical characters with the other described species, especially *E. superstes*. Furthermore, taxonomic notes help to provide insights into these equivocal doubtful species status definitions.

## Materials and methods

The following adults and larvae of *Epiophlebia laidlawi* Tillyard, 1921 were studied:

- Eleven larvae, three adult females and three adult males from the Davies Collection of the University Museum of Zoology (UMZ-Cam), University of Cambridge, UK.

- One adult male from the Collection of the Dragonfly Kingdom Nature Park (DNP), Shimanto City, Japan.
- Ten larvae from the collection of the Hindu Kush Himalayan Benthological Society (HKHBS), Kathmandu, Nepal.

The following adults and larvae of *Epiophlebia superstes* Sélys, 1889 were studied for comparison:

- Nine larvae, two adult females and two adult males from the Collection of Systematic Entomology (CSE), Graduate School of Agriculture, Hokkaido University Sapporo, Japan.
- Four larvae, two adult females and two adult males from the Davies Collection of the University Museum of Zoology (UMZ-Cam), University of Cambridge, UK.

More information regarding the studied specimens is available in Supplemental Table S1. Furthermore, some general measurements are available in Supplemental Table S2 – these help to underscore some morphological statements. Due to the small sample size it is not possible to apply statistical analyses to these morphological data; therefore, they only show trends in the measured characters

Data for comparison of *Epiophlebia sinensis* Li & Nel, 2012 and *Epiophlebia diana* Carle, 2012 appear in the original descriptions (Carle, 2012; Li et al., 2012).

Photographs were taken with a Keyence Digital Microscope VHX600 (Keyence, Osaka, Japan) at the Department of Mineralogy, Georg-August University, Göttingen, Germany or at the respective museum using a Canon 550D (Canon, Tokio, Japan) with a Metz MB 15 MS-1 Makrolave digital ring flash (Metz, Zirndorf, Germany); entirely mounted on a Cullmann NANOMAX 200 T traveller tripod (Cullmann, Langenzenn, Germany) to perform stacking photography using an Apple Macintosh Airbook (Apple, California, USA) and Helicon Remote and Helicon Focus software (HeliconSoft Ltd, Kharkov, Ukraine). All images were subsequently processed in Photoshop CS3 (Adobe System Inc., San José, CA, USA).

The juvenile stage in Odonata, Ephemeroptera and Plecoptera is generally referred to as a naiad following the terminological suggestions in Bybee, Hansen, Büsse, Wightman and Branham (2015). However, since Asahina (1954, 1961, 1963) followed Tillyard's (1921) suggestion, discussed also in Sahlén et al. (2016) and Büsse & Bybee (2016), to call the juvenile stage of Odonata a larva, this terminology is used to guarantee ease of comparison. Nomenclature and terminology are from Snodgrass (1935), if necessary supplemented by Asahina (1954) or Matsuda (1970).

## Results

Dissections of the rare specimens were not authorized; consequently only partial analysis of body parts that are difficult to access was possible. In undissected condition, some characters therefore remain unavailable (especially mouthparts and male genitalia). This study focused on the differences between the species of *Epiophlebia* and provides figures (Figures 1–7) showing the major differences between *E. laidlawi* and *E. superstes* as well as overview photographs in the supporting information (Supplemental Figures S1–S16). Due to the comparative morphological focus, no descriptions are provided for a general/identical anatomical overview of *Epiophlebia*; the copious work of Asahina (1954) is recommended for this purpose. All characters are developed in both male and female specimens, unless otherwise indicated.

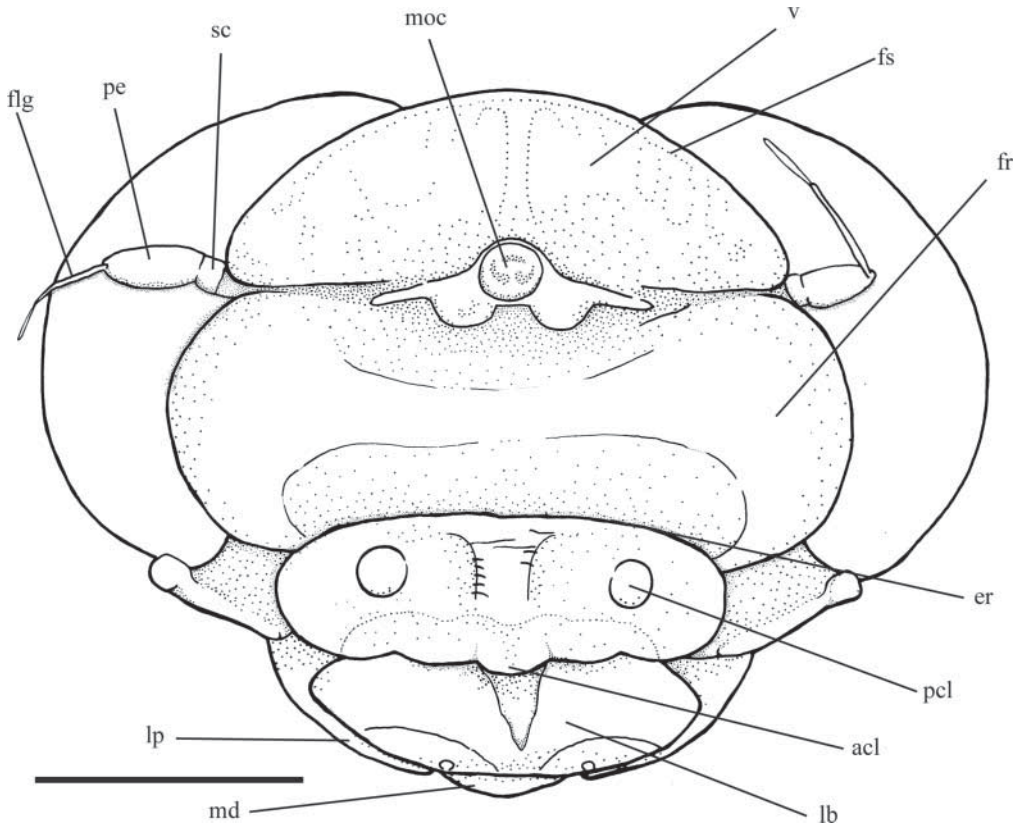


Figure 1. Drawing of the head of *Epiophlebia laidlawi*, frontal view. Hairs not drawn. Abbreviations: acl, anteclypeus; er, epistomal ridge; flg, flagellum; fr, frons; fs, frontal suture; lb, labium; lp, labial palp; md, mandible; moc, median ocellus; pcl, postclypeus; pe, pedicel; sc, scape; v, vertex. Scale = 0.5 cm.

### **Anatomical characters of adult *Epiophlebia laidlawi***

#### *Head*

The sclerotized orthognathous head is noticeably covered with a brownish coat of hair (Supplemental Figure S3). The head is spherical in shape and mainly composed of laterally located, convex compound eyes that are not medially contiguous. The three ommatidia display a general uniform size. The posterior part of the occiput between the compound eyes steeply declines to the foramen. The occipital tubercles are distinctly developed in the male, while being less developed in the female (Figures 2, 3(A, B) and Supplemental Figure S4). The postfrontal and premandibular ridges merge into each other; the junction is not distinctly separable. The premandibular ridge runs around the posterior part of the compound eyes and dorsoanteriorly to the mandibular articulation. The most prominent character of the head of *Epiophlebia* is the elevated transverse ridge (vertex) of the postfrons (Supplemental Figure S5), which is U-shaped and medially nearly pointed from dorsal view (Figures 2 and 3(A, B)). From frontal view, a small median convexity at the base of the vertex is visible. The antefrons is semicircular and medially vaulted, forming a medial tapered ridge (Figures 1 and 3(A, B)). The clypeus is divided into anteclypeus and postclypeus. The latter is strongly sclerotized, whereas the anteclypeus is weakly sclerotized. The sclerites of the anteclypeus are weakly developed. The clypeofrontal ridge is planar but distinctly visible. The shape of the labrum might be unique within the Odonata; it is short but

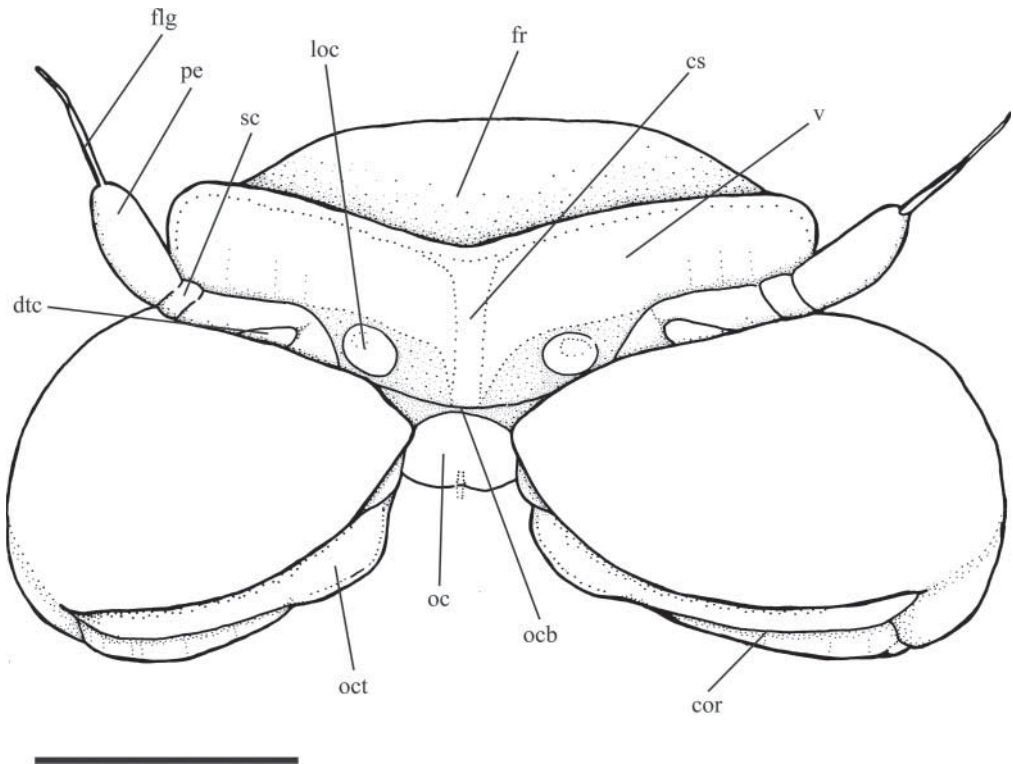


Figure 2. Drawing of the head of *Epiophlebia laidlawi*, dorsal view. Hairs not drawn. Abbreviations: cor, circumcircular ridge; cs, coronal sulcus; dtc, dorsal tentorial cavity; flg, flagellum; fr, frons; loc, lateral ocellus; oc, occiput (dorsal part); ocb, occipital bar; oct, occipital tubercle; pe, pedicel; sc, scape; v, vertex. Scale = 0.5 cm.

broad, with the lateral sides protruding transversally. Thin brownish hair covers the labrum completely. The vertex separates the normally triangular co-arranged ocelli. The median ocellus is located in front of this – atypical for Odonata – elevated vertex; lateral ocelli are hidden behind the vertex in frontal view. The antennae are composed of five antennomeres. The first antennomere (scape) is cylindrical and arises from the posterolateral part of the antefrons. The second antennomere (pedicel) is broad, distinctly flattened dorsoventrally and can be up to four times longer than the scape. Long hairs cover the flattened pedicel at the lateral edges. Antennomeres 3–5 (flagellum) are developed and extremely slender. The first flagellomere is approximately half as long as the pedicel, second flagellomere a third to half as long as the first flagellomere and the third flagellomere half as long as the second (Figure 2). Without dissection, mandibles are difficult to describe; they are triangular-shaped from dorsal view. The anterior mandibular articulation is located at the tri-border region of the postclypeus, the antefrons and the genae. The posterior mandibular articulation is located at the hindmost part of the mandible at the end of the premandibular ridge. The dorsal tentorial pits are located posterior, close to the antennae; the anterior tentorial pits are connected with the epistomal and pleurostomal ridges and the posterior tentorial pits are located directly beneath the occipital foramen. The basic parts of the maxillae are visible but hardly describable in detail. However, they display the same characteristics as in *E. superstes* (Asahina, 1954; Blanke et al., 2012). The labium covers the mouthparts ventrally and consists of the postmentum and prementum. The postmentum is enlarged. The small end hooks (Asahina, 1954; Blanke et al., 2012) are difficult to distinguish, but the movable hooks, which conclude the labial palps, are prominent. The glossa and paraglossa are merged and form

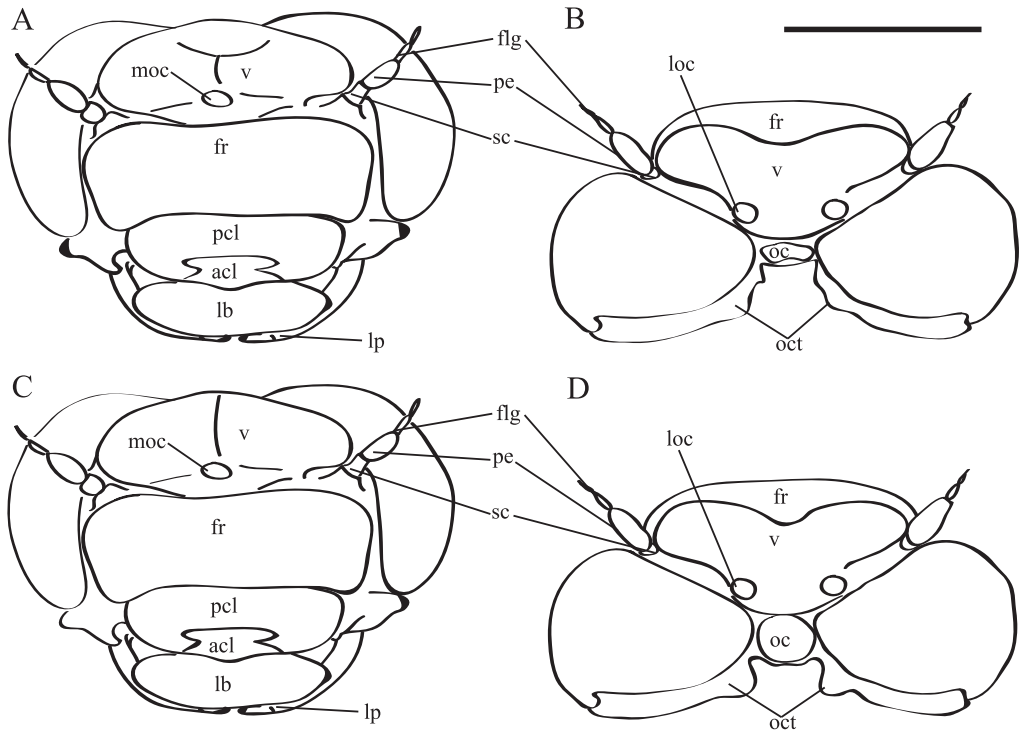


Figure 3. Schematic drawing showing the major differences of the head in: A, B, *Epio-phlebia laidlawi*; and C, D, *Epio-phlebia superstes*. A, C, frontal view; B, D, dorsal view. (On the basis of Figures E1 and E2 and Plate 1 in Asahina, 1954.) Abbreviations: acl, anteclypeus; flg, flagellum; fr, frons; lb, labium; lp, labial palp; loc, lateral ocellus; moc, median ocellus; oc, occiput (dorsal part); oct, occipital tubercle; pcl, postclypeus; pe, pedicel; sc, scape; v, vertex. Scale = 0.8 cm.

the median lobe (Blanke et al., 2012); the beginnings of both structures are recognizable between the movable hooks. No yellow markings, only different shades of brown and grey, characterize the otherwise black head of *E. laidlawi* (Supplemental Figures S3–S8).

### Thorax

The eyes cover the cervical sclerites and the prothoracic tergite is straight and sparsely developed (Supplemental Figure S4). The anterior lobe is small and ridge-like and the pronotum is slightly convex and extends laterally. The prothoracic pleurites coalesce with the tergum. The separation of the epimeron and episternum is indistinctly developed and the epimeron runs anteroventrally and forms the praecoxale. The sternite of the prothorax is broadly developed and the sternal pit is recessed. The majority of the prothoracic sternite is formed by the basisternum 1, the cranial part of the base of the coxae. The small furcasternum 1, located posterior to the latter, separates the left and right coxa. It is followed by the intersternite, which forms the transition to the mesosternite. The cranialmost part of the pterothoracic tergite is the acrotergite 2, followed posteriorly by the dorsal carina and is enclosed laterally by the mesostigmata. The acrotergite 2 is medially punctuated with the pit of the tergal apophysis 2. The small prescutum 2 is located cranial to the pit of the tergal apophysis 3 and connected to the humeral plate 2. The humeral plates are axillary sclerites at the wing base. The centre of the mesothorax forms the rhomboidal scutum 2, which is connected to the radius and axillary plate 2 by their lateral branches. The scutellum 2 is located posterior to the scutum 2. The scutellum is the origin of the axillary cords, which

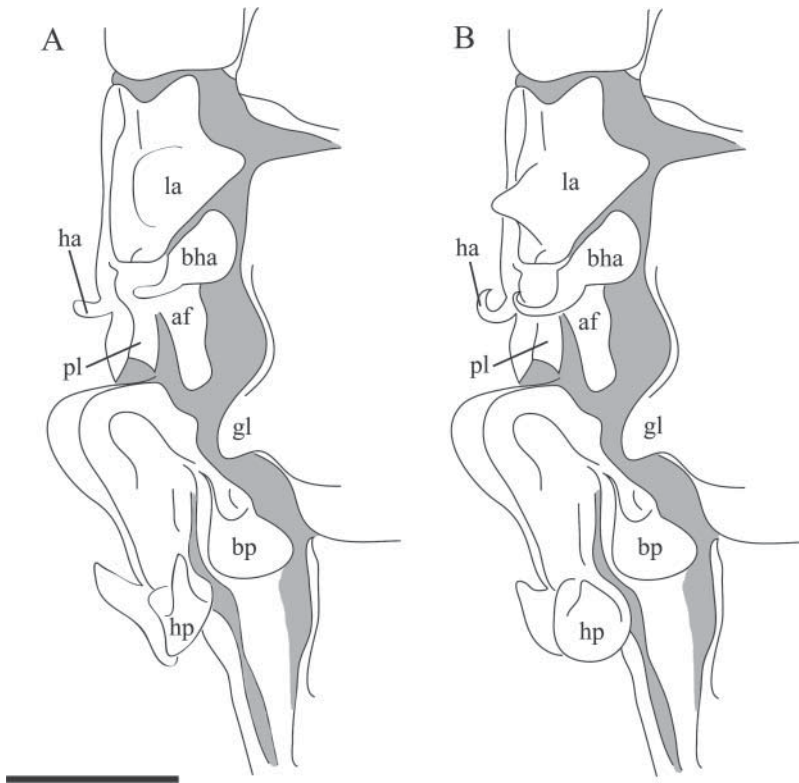


Figure 4. Schematic drawing showing the major differences of the secondary male genitalia in: A, *E. laidlawi*; B, *E. superstes*. (On the basis of Figure E54 and Plate 36 in Asahina, 1954.) Abbreviations: af, anterior frame; bha, base of hamulus anterior; bp, base of 'penis'; gl, genital lobe; ha, hamulus anterior; hp, hamulus posterior; la, lamina anterior; pl, processus ligoideus. Scale = 0.5 cm.

run laterocaudally and connect the scutellum to the anal veins. The scutellum 2 is followed by the large and trapezoidal postnotum 2. The structures of the metathoracic part of the pterothorax are in general identical to those of the described mesothoracic part. The prescutum 3 is overlaid by the posterior edge of the postnotum 2. Compared to the postnotum 2, the postnotum 3 is only weakly developed.

The pleurites of the pterothorax are tilted posterior and are characteristic for adult Odonata (Büsse, Genet & Hörschemeyer, 2013; Matsuda, 1970; Pfau, 1986). The collar carina, antelar carina and sinus as well as the apical carina are only slightly developed and located on the broad episternum 2. The two-branched wing process 2 is located dorsally to the distinct mesopleural ridge and articulates with the wing base. The metathoracic spiracle is located posterior to the end of the interpleural ridge. The latter also demarcates the epimeron 2 from the episternum 3. This ridge ends more or less at one third of the dorsoventral expansion of the pterothorax. The wing process 3 is similar in shape but distinctly smaller than wing process 2. The pterothoracic sternites of *E. laidlawi* display the same characteristics as in *E. superstes* (Asahina, 1954).

Thorax coloration is characterized by two yellow stripes: the mesepisternal and the metaepisternal one. The rest of the thorax is dark brown with a ventral gradient to lighter brown. The posterior part of the epimeron 3 is a lighter shade of brown as well (Supplemental Figures S4–S6).

The legs display a colour gradient. The coxa, trochanter and two-thirds of the femur are lighter brown than the rest of the femur. The tibia and tarsi are nearly black. The base of the coxa is

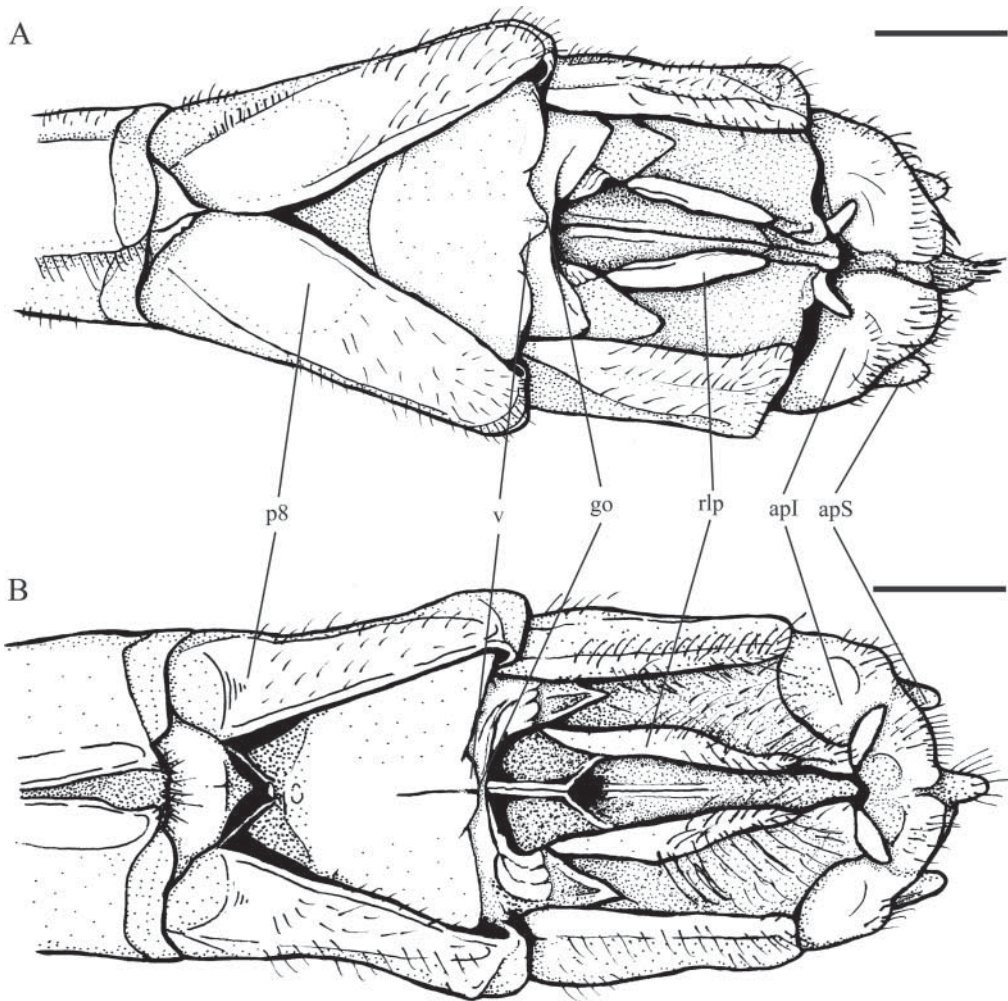


Figure 5. Drawing of the apical male abdomen, ventral view. A, *Epiophlebia laidlawi*; B, *Epiophlebia superstes*. Abbreviations: apl, appendages inferior (epiprocts); apS, appendages superior (cerci); go, gonad opening; p8, pleurite segment 8; rlp, rudiment of larval paraprocts; v, valvule. Scale = 0.3 cm.

dark brown as well. The femora are cylindrical, ventrally with two rows of small spines. The assemblage of semicircular tubercles on the dorsal side of the femur is unique in *Epiophlebia* species (Asahina, 1954, 1961). The nearly rectangular tibia provides two rows of strong and long spines running laterally on the flat dorsal side (Supplemental Figure S5).

The wing venation is a highly variable character system, even within one individual. Single specimens of *Epiophlebia* display distinct differences in their wing venation between the left and right wing. I therefore question the taxonomic usefulness of this character system at least in *Epiophlebia*; also because it has shown a high amount of convergence in Odonata (Ballare & Ware, 2011; Blanke, Greve, Mokso, Beckmann & Misof, 2013; Fleck, Brenk & Misof, 2008).

### Abdomen

The abdomen of *E. laidlawi* is cylindrical and composed of 10 segments. Segments 3 to 6 have almost the same length and shape and are laterally compressed, whereas segment 8



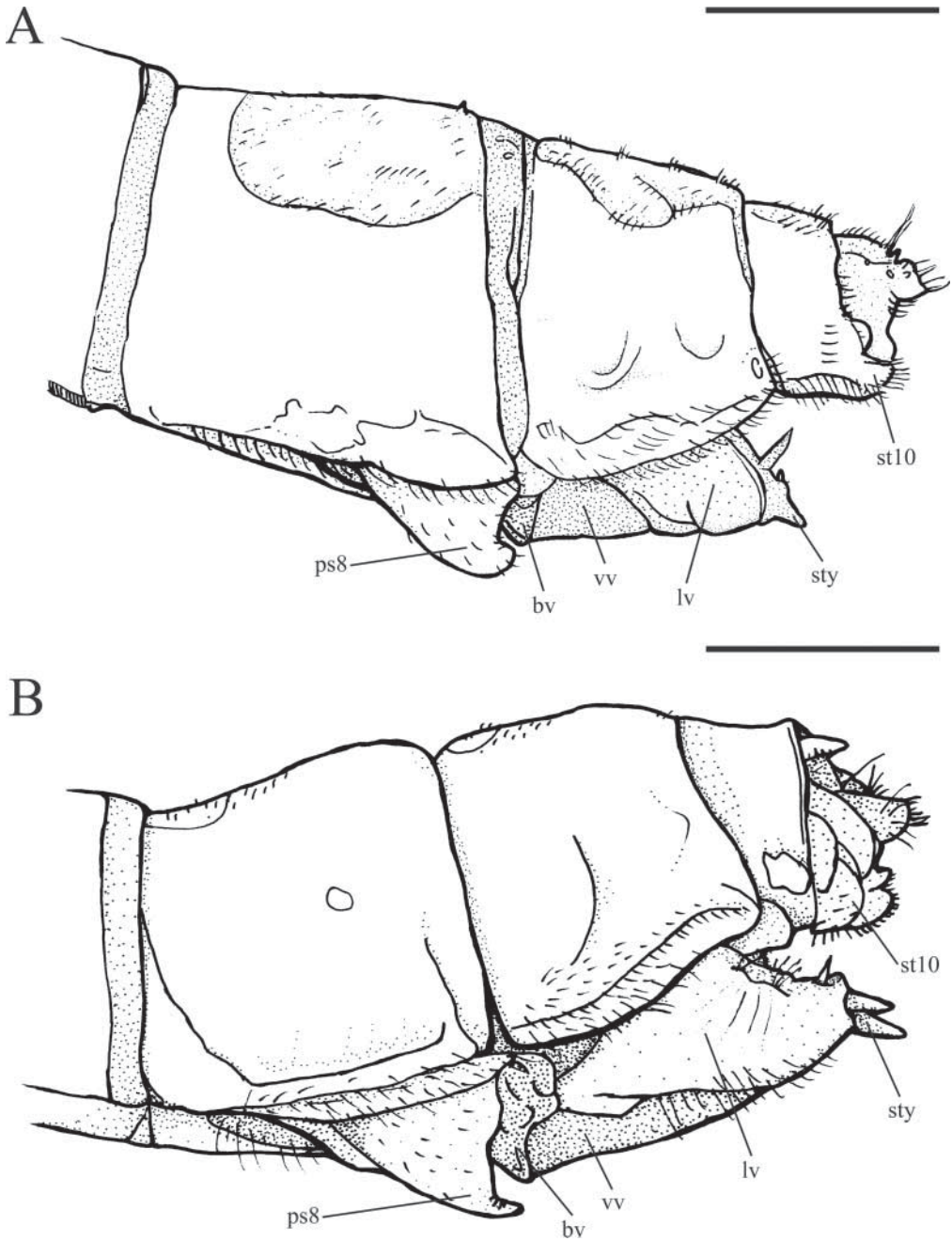


Figure 6. Drawing of the apical female abdomen, lateral view. A, *Epiophlebia laidlawi*; B, *Epiophlebia superstes*. Abbreviations: bv, basivalvula; lv, lateral valvula; ps8, process of sternite 8; st10, sternum 10; sty, stylus; vv, ventral valvula. Scale = 0.3 cm.

broadens towards segment 9. Segments 8 and 9 are therefore funnel-shaped. The coloration of the abdomen is brownish with a dorsoventral colour gradient to nearly black towards the tip of the tergite. Segments 2–8 each show a more or less yellow triangular distal dorsal spot. Segment 9 shows an indistinct, often very dark, yellow spot at the same location. Laterally

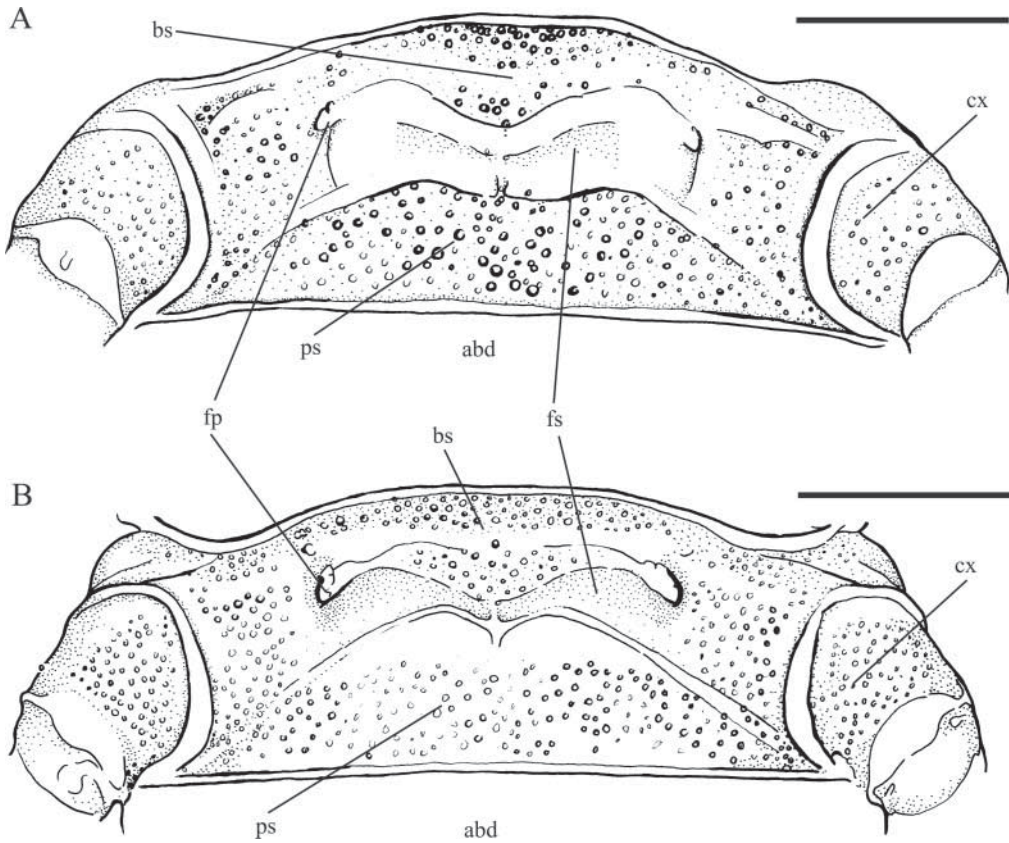


Figure 7. Drawing of the prothoracic sternite of larvae, ventral view. A, *Epiophlebia laidlawi*; B, *Epiophlebia superstes*. Abbreviations: abd, abdomen; bs, basisternum; cx, coxa; fp, furcal pits; fs, furcisternum; ps, poststernum. Scale = 1 cm.

segments 2–8 show lighter brownish spots that appear almost transparent (Supplemental Figures S1, S2 and S7).

Generally, the secondary male genitalia are situated on abdominal segments 2 and 3 (Supplemental Figure S6), starting at the anteriormost part with a shield-shaped plate, the lamina anterior. This lamina anterior has a convex elevation in the centre. The hamuli anterior are bump-like and short (Figure 4(A)). Some of the internal structures are difficult to distinguish, but, as far as noticeable in the undissected condition (Supplemental Figure S6), display the same characteristics as *E. superstes* (Asahina, 1954). The most characteristic part of the secondary male genitalia is the hamulus posterior, which is anchor-like (Figure 4(A)). The primary male genitalia are located at sternite 9 and are partly covered by the surrounding valves. The rudiment of larval paraprocts (Asahina, 1954) display only a few hairs and form two equal sides of a triangle-like structure (Figure 5 and Supplemental Figure S9). The caudal appendages of abdominal segment 10 display the same characteristics as *E. superstes* (Asahina, 1954). The superior appendages (cerci) are short and rudimentary with notched apical parts. The inferior appendage (epiproct), however, is strongly developed. The other structures of the male abdomen of *E. laidlawi* are similar to *E. superstes* (Asahina, 1954).

The female genitalia are located at abdominal segments 8 and 9. The ovipositor resembles that of *E. superstes* (Asahina, 1954), except that the process of sternite 8 of *E. laidlawi* resembles a blunt hook (Figure 6 and Supplemental Figure S8).

### ***Anatomical characters of Epiophlebia laidlawi* larvae**

The general appearance of the larvae of *Epiophlebia* resembles that of Anisoptera. The early instars are more rounded and the body, especially the abdomen, becomes more and more slender during ontogenesis. During ontogenesis, the wing buds, legs and the abdomen elongate and the late instars look cigar-shaped (Supplemental Figures S11–S16). This kind of development is commonly known for a number of different Anisoptera (e.g. Aeshnidae). The cuticle is thick and covered with small wart-like protruding structures (Figure 5 and Supplemental Figure S11). The coloration of *Epiophlebia* larvae is variable in comparable instars; generally they are light brown in the early instars and darken during development (Nesemann et al., 2011). The dorsal part of the body is slightly rounded, whereas the ventral part is flattened to cling to stone surfaces.

#### *Head*

The head is obconical from lateral view, with the most anterolateral part covered by compound eyes. The clypeofrontal ridge runs posterior slightly descending and the postfrontal ridge and the coronal ridge are well developed. Due to the strongly developed compound eyes, the postoccipt is a small semicircular sclerite and the encircling premandibular ridge obscure dorsally at the lateral sides of the head. The prominent fan-shaped labrum (seen from above) is anteroventrally flattened with pointed tips and from a lateral view is visor-like. The antenna is five segmented; the scape is broad and short, whereas the pedicel is approximately as broad as the scape, but at least twice as long. The flagellum is at least as long as the scape and the pedicel; the first segment of the flagellum (third antennomere) is longer than the second and third flagellomere together and distinctly thicker. The mandible of *E. laidlawi* is divided into incisor and molar lobe and displays the same characteristics as in *E. superstes* (Asahina, 1961; Blanke et al., 2015); the counting of teeth is impossible in the undissected condition. The maxillary palpus is depressed. The labium of *E. laidlawi* displays the same characteristics as *E. superstes* larvae, it has a nearly rectangular shape and narrows towards the end (Asahina, 1961; Blanke et al., 2015). The lateral margin of the prementum is sinuous and the premental cleft is distinctly developed and varies in length. The movable hooks are well developed and the labium, known as the prehensile mask, fits perfectly into the ventral body.

#### *Thorax*

The prothorax and the merged meso- and metathorax – known as the syn- or pterothorax (Matsuda, 1970) – are distinct. The tergum is divided into notum (anterior part) and postnotum (posterior part), these parts display an irregular pattern on their surface – resembling engraved graphical characters (Supplemental Figures S11 and S14). At the anterolateral edge of the notum, strong spearhead-like processes are directed cranially. The acrotergites of the pterothorax are less developed and the gap between the left and right side of the thorax is small. The rectangular mesotergite is developed to a rather compressed and cone-shaped sclerite (Asahina, 1954). From a lateral view, the tergal convexities of the prothorax, which serve as muscle attachment points (Büsse & Hörnschemeyer, 2013), are distinctly visible. The prothorax increases in a blunt angle from caput to pterothorax. The thoracic ridge resembles the description of *E. superstes* (Asahina, 1954); however, they seem to be more distinct in *E. laidlawi*. The sternites are well developed and the furcal pits are conspicuous. The anterior part of the basisternum is slightly depressed to accommodate the closed prehensile mask. The anterior ridge of the metathoracic poststernum declines steeply from the lateral sides of the segment border, resembling an incised volcano cone anterior of the median line. The proximal one-third of the poststernum is free from

the wart-like protrusions that normally cover the whole body; nevertheless, the distal two-thirds of the poststernum are covered with those (Figure 7, Supplemental Figures S13 and S16). The internal cuticular structures as well as the thorax musculature of *E. laidlawi* and *E. superstes* larvae are studied in Büsse et al. (2015). The femora are dorsoventrally flattened with a distinct median ridge; the femora in the early instars are 2–2.5 times longer than they are broad and approximately three times as long as broad in the late instars. The surface of the femora is rather smooth.

### Abdomen

The abdomen is more rounded in the early instars and becomes elongated during development, though the abdomen of late instars is somewhat cigar-shaped. The shape is cylindrical but ventrally flattened. Each tergite is arched whereas the sternite is flat. The stridulatory organ is as Asahina (1954) describes it for *E. superstes* and displays no differences between *E. laidlawi* and *E. superstes*. However, the shape and extent of development of this organ in the different segments (3–7) varies significantly between the instars and also between individuals of the same size; due to a different development or deterioration. The most prominent character is the rounded process on the dorsolateral side of segments 7 to 9 (Asahina, 1961) (Supplemental Figure S11). The anal appendages resemble the state found in *E. superstes* (Asahina, 1954). The apices of the epiproct are slightly divided and the paraprocts do not touch each other apically; a small cleft always remains.

## Discussion

### Morphology of adults

The anatomical investigation of *E. laidlawi* larvae (Asahina, 1961) and adults (Asahina, 1963) confirm the sister-group relationship between *E. laidlawi* and *E. superstes*. These studies show a few distinctive discriminating characters (Asahina, 1961, 1963). I can confirm most of the adult characters and differences between *E. superstes* and *E. laidlawi* found by Asahina (1963). Furthermore, I add some important additional characters for discrimination of the two species (see also Table 1).

Generally, the coloration is black with more yellow stripes in *E. superstes* and more brownish with fewer yellow stripes in *E. laidlawi* (Supplemental Figures S1 and S2). It is obvious that the yellow markings in *E. superstes* correspond to the lightest brownish parts of *E. laidlawi*. This fact suggests an ancestral colour ground pattern in *Epiophlebia* resembling the condition in *E. superstes* (e.g. Supplemental Figure S5 or S8). *E. superstes* is covered with black and yellow hairs, whereas *E. laidlawi* displays less hair, which is brown.

Furthermore, the differences in body size found by Asahina (1961, 1963) can be supported – *E. superstes* seems to be slightly smaller compared to *E. laidlawi*. In numbers, the body size of *E. laidlawi* compared to *E. superstes* is 17.53% longer (small sample size, see Materials and methods). The head width and the wingspan however are comparable (cf. Supplemental Table S2).

The head of adult *E. laidlawi* is coloured in different shades of brown up to black without any yellow markings, opposed to the black coloured head with yellow mouthparts, antefrons and vertex of *E. superstes*. As mentioned above, the mouthparts, antefrons and vertex of *E. laidlawi* are lighter brown (Supplemental Figure S3–S6). The vertex is V-shaped in *E. superstes* and U-shaped in *E. laidlawi*. In detail, the vertex of *E. laidlawi* is slightly vaulted from a frontal view, whereas a distinct cutting line is visible in *E. superstes* (Figures 1, 3 and Supplemental Figure S3).

Table 1. Major morphological differences of *Epiophlebia* species.

Character	<i>E. superstes</i>	<i>E. laidlawi</i>	<i>E. sinensis</i>
<i>Adult</i>			
Size	Smaller	Larger	Smaller
General coloration	Blackish with more yellow markings	Brownish with less yellow markings	Blackish with more yellow markings
Vertex	U-shaped	V-shaped	U-shaped
Antefrons	Padded	Keeled	Padded
Hamulus posterior	Scorpion's stinger	Anchor-like	Scorpion's stinger?
Hamuli anterior	Long and hook-like	Short and blunt	?
Abdominal process (sternite 8)	Sting-like	Hook-like	?
Paraproct	Few rows of hair	Hairy	?
Epiproct	Hairy	Hairy	Hairless
Abdominal coloration	Blackish	Brownish	Reddish
<i>Larva</i>			
Size	Larger?	Smaller?	?
General coloration	Darker	Lighter	?
Flagellomere	Maximally as long as the second and third together or shorter	First longer than the second and third together	?
Spearhead-like processes on notum	Not so	Depressed posterolaterally	?
Anterior ridge of the metathoracic poststernum	Like a light hollow	Incised volcano cone like	?
Dorsolateral edges segments 7–9	Protruding and pointed	Rounded	?
Apices of the epiproct	Divided distinctively	Divided slightly	?

The antefrons is proximally keeled in *E. laidlawi* and padded in *E. superstes*. It is medially vaulted in *E. laidlawi*; it increases from all sides to medial, whereas in *E. superstes* it is more or less a consistent convexity (Figures 2, 3 and Supplemental Figure S4). The apical occipital region is convex in *E. superstes* and steeply declining to the foramen in *E. laidlawi* (Figures 2, 3 and Supplemental Figure S4). The occipital tubercles are distinctly developed in *E. laidlawi*, though they seem to be less developed in the female. By contrast, Asahina (1963) describes this characteristic conversely – the occipital tubercle seems to be less developed in the male. This character might therefore represent intraspecific variation and not sexual dimorphism, due to the contradicting descriptions. However, this weak hypothesis needs further testing with a larger sample size.

The coloration and yellow markings on the thorax differ significantly between *E. superstes* and *E. laidlawi*. The specimens of *E. superstes* show more and distinct yellow markings, especially visible from a lateral view (Supplemental Figure S5). In *E. laidlawi* there is only one lateral and one dorsal yellow marking and generally more brownish than black. In contrast the thorax of *E. superstes* shows additional ventrolateral markings and yellow spots on the coxae and the prothorax.

The coloration of the abdomen of *E. laidlawi* is different compared to *E. superstes*. The coloration of the abdomen is brownish with a dorsoventral colour gradient to nearly black towards the tip of the tergites, whereas the colour of *E. superstes* is black all over (Supplemental Figure S7). Segments 2–8 display a more or less yellow triangular distal spot dorsally. Segment 9 displays an indistinct, often faded yellow spot at the same location. In *E. superstes* segment 2 displays a bottom up yellow T, segments 3–6 display broad yellow distal spots, which stretch laterally. Segments 7–9 display two yellow spots each, which are almost connected medially (Supplemental Figures S1 and S2). Laterally, segments 2–8 display lighter brownish spots in *E. laidlawi* that appear almost transparent (Supplemental Figures S7 and S8). In *E. superstes*,

there are proximolateral yellow triangle-like spots. From a ventral point of view, a yellow line on the entire abdomen from proximal to distal is visible in *E. superstes*; in *E. laidlawi* this body part is dark brown. The reddish coloration of *E. sinensis* at the ventral abdominal side (segments 6–10) is the most prominent difference from *E. superstes* and *E. laidlawi* (Li et al., 2012). However, the coloration might be influenced by different storage situations within the museum collections; the impact of UV light especially can cause artefacts like bleaching.

The abdominal segments 3–6 are laterally compressed and the 7th is funnel-shaped in both *E. superstes* and *E. laidlawi*. Asahina (1954), however, describes the laterally compressed development for segments 3–5 in *E. superstes* only. The compression of abdominal segments might be an artefact of specimen drying, storing and handling within the museums collections.

In the male, the hamulus posterior is anchor-like in *E. laidlawi* and looks like a scorpion's stinger in *E. superstes* (Figure 4). The hamuli anterior are long and hook-like in *E. superstes* in contrast to the shorter and blunt development in *E. laidlawi* (Figure 4). The elevation in the centre of the lamina anterior is more protruding and like a pointed ridge in *E. superstes*. By contrast, in *E. laidlawi*, it is a flattened convexity (Figure 4). The caudal appendages of *E. laidlawi* are rounded and have a more uniform shape. In *E. superstes*, additional ventral lobes are developed (Figure 5 and Supplemental Figure S9). The rudiment of larval paraprocts (Asahina, 1954) of *E. laidlawi* display some rows of hairs at the base only. They form the two equal sides of an isosceles triangle (ventral view) and are slightly hooked (lateral view) (Figure 5 and Supplemental Figure S9). In *E. superstes* they run parallel (ventral view), are straight-lined (lateral view) and coated with hair. The pleurites start covering the sternites at sternite 8 in *E. laidlawi* and in *E. superstes* at sternite 7. As a consequence thereof, the angle of the closing pleurite (segment 8) is steeper in *E. laidlawi* and flatter in *E. superstes* (Figure 5 and Supplemental Figure S9). *E. sinensis* epiproct shows only few hairs, whereas the epiprocts of *E. superstes* as well as *E. laidlawi* show a distinct hairiness.

The abdominal process on sternite 8 in the female *E. superstes* is distinctly sharper and sting-like, whereas it is rounded, blunt and hook-like in *E. laidlawi* (Figure 6 and Supplemental Figure S8). However, it is significantly developed; Asahina (1963) describes it as a small bulge only.

*Epiophlebia* species display a conspicuous mixture of zygopteran and anisopteran characters as mentioned in the literature (Asahina, 1954; Bechly, 1996; Lohmann, 1996; Ninomiya & Yoshizawa, 2009) and shown herein. The compound eyes, which are situated close to each other, but not connected medially, and the general robust construction is distinctively anisopteran-like, whereas the uniform size of the ommatidia and the weakly developed sclerites of the anteclypeus are zygopteran-like. The strongly developed movable hooks are unique for recent *Epiophlebia* and might represent an ancestral character. The thorax, however, is two-parted; the general anatomy, like the wing base sclerites, displays anisopteran characteristics (Ninomiya & Yoshizawa, 2009), whereas the pterothoracic structures of the tergum as well as the wing shape and its venation are typically zygopteran-like (Asahina, 1954). The female genitalia resemble the ovipositor-system in Aeshnidae (van der Weele, 1906).

### **Morphology of larvae**

The proposed sister-group relationship between *E. laidlawi* and *E. superstes* is also supported by distinct larval characters (Asahina, 1961). I can corroborate most of the differences found in the larvae of *E. laidlawi* and *E. superstes* by Asahina (1961). Furthermore, I add some additional characters for discrimination (see also Table 1).

Generally, *E. superstes* larvae appear distinctly darker at least in the ultimate and penultimate instars; they are nearly black in *E. superstes* and brown in *E. laidlawi* (Nesemann et al., 2011).

The size differences mentioned by Asahina (1961), that *E. laidlawi* is bigger than *E. superstes*, are difficult to corroborate. The indeterminate larval stages make it nearly impossible to directly compare the instars. However, in the data presented here (cf. Supplemental Figure S2) the ultimate (penultimate) stage of the larvae of *E. superstes* is 4.3% bigger (small sample size, see Materials and methods).

The first flagellomere (third antennal segment) is longer than those of the second and third combined and is distinctly thicker in *E. laidlawi*. This first flagellomere in *E. superstes* is either equal in length or shorter than the second and third together combined; it is also thinner than in *E. laidlawi*. The first flagellomere is extended and broader in *E. laidlawi* compared to *E. superstes*. The scape and pedicle have the same length or are longer than the first flagellomere in *E. laidlawi*, not always longer as Carle (2012) proposes. The labium displays no significant differences.

The acrotergites of *E. laidlawi* are less developed and the gap between the left and the right side of the thorax is small. The acrotergite of *E. superstes* by contrast is more prominent and robustly developed; therefore, the gap between the two sides of the thorax seems to be broader. However, this character changes during ontogenesis and is therefore difficult to evaluate.

The prothorax widens in a blunt angle from caput to pterothorax in *E. laidlawi* and is distinctly steeper in *E. superstes* (Asahina, 1961) (cf. Supplemental Figure S12). The spearhead-like processes on the anterolateral edge of the notum are slightly depressed posterolaterally in *E. laidlawi* and not so in *E. superstes* (cf. Supplemental Figures S11 and S14). The anterior ridge of the metathoracic poststernum of *E. laidlawi* steeply declines from the lateral sides of the segment border and resembles an incised volcano cone anterior at the median line. In *E. superstes*, the ridge declines less steeply and resembles a shallow hollow anterior at the median line (Figure 7). In *E. superstes*, the whole poststernum is covered with wart-like protrudings, whereas the proximal one-third of the poststernum in *E. laidlawi* is free of them (Figure 7 and Supplemental Figures S13–S16).

The median ridge of the femora seems to be less distinct in *E. superstes*, furthermore, the dorsolateral edge of the femora displays small convexities over the entire length.

The length of the femora in *E. superstes* is 2–2.5 times longer than it is broad in the early instars and up to four times longer in the ultimate instars. The femora of *E. laidlawi* is broader than that of *E. superstes*; it is 2–2.5 times longer than it is broad in the early instars and up to three times longer in the ultimate instars. The differentiation of *E. diana* (2.5 times longer than broad) and *E. laidlawi* (always three times longer than broad) from Carle (2012) is therefore inexplicable. It is important to notice here that the holotype of *E. diana* used for these measurements is an ultimate instar.

The processes of the dorsolateral edges of segments 7–9 are rounded in *E. laidlawi* and more protruding and pointed in *E. superstes* (Asahina, 1961). The shape and extent of development of the stridulatory organ in the different segments (3–7) varies significantly between the instars and also between individuals of the same size, possibly due to differences in development and/or mechanical wear and deterioration.

The apices of the epiproct are divided, only slightly in *E. laidlawi* and distinctively in *E. superstes* as already mentioned by Asahina (1961). The paraprocts of *E. superstes* are connected with each other apically, whereas the paraprocts of *E. laidlawi* are not contacting each other; a small cleft always remains.

### **Taxonomic conclusions**

The mentioned differences in the anatomy of *E. superstes* and *E. laidlawi* are significant – some of them represent strong isolating mechanisms, like the shape of the male genitalia.

The main differences between *E. sinensis* and *E. superstes* (relative to *E. laidlawi*) are the rufism – reddish brown coloration – on the last segments of the abdomen and the missing hairiness of the epiproct of *E. sinensis* (Li et al., 2012). The coloration of the abdomen – especially yellow and red – often represents a warning coloration rather than intraspecific recognition (Ishizawa, 2005, 2007, 2008); therefore coloration often is no isolating mechanism. Furthermore, there are countless examples of colour variation in the same species, for example in Japanese damselflies (Ishizawa, 2000; Watanabe, 1991; Watanabe & Taguchi, 1990). However, there are certain examples in Odonata where abdominal coloration may play roles in establishing and maintaining intraspecific recognition (cf. Corbet, 1999). Unfortunately, the material of *Epiophlebia sinensis* is extremely scarce – I recommend a re-examination to establish more anatomical characteristics to substantiate the species status.

The description of *Epiophlebia diana* is problematic because some of the characters that supposedly distinguish *E. diana* from *E. laidlawi* (Carle, 2012) are questionable. The length of the scape and pedicle, the sinuous margins of the prementum and the abdominal lobes – which protrude on segment nine – are supposed to separate *E. diana* from *E. laidlawi* (Carle, 2012) but are found to be identical between the species herein. Furthermore, the significance of numerical characters like: “epiproct ca.  $0.6 \times$  length of paraprocts, male epiproctal processes slightly divergent, cerci ca.  $0.5 \times$  length of epiproct” (Carle, 2012, p. 77) at a sample size of two larvae of *E. diana* and two for comparison of *E. laidlawi* is questionable – because variations between larvae of the same species are common (Corbet, 1999). At the current state *E. diana* is from a morphological point of view a junior synonym of *E. laidlawi* – a substantial re-examination is inevitable. Unfortunately, a reinvestigation is impossible because the two larvae of *E. diana* are missing (F.L. Carle, describer of *E. diana* as well as J.J. Dombroskie of the Cornell University Insect Collection, New York, USA – personal communication, July, 2016).

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## Supplemental data

Supplemental data for this article can be accessed at <http://dx.doi.org/10.1080/13887890.2016.1257442>

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