

A new *Epiophlebia* (Odonata: Epiophlebioidea) from China with a review of epiophlebian taxonomy, life history, and biogeography

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> Abstract

Epiophlebia diana **sp.n.** is described from larval specimens collected in the mountains of western Sichuan Province, China. Epiophlebian taxonomy, life history, and biogeography are reviewed, and keys provided for determination of the known adults and larvae of *Epiophlebia* Calvert, 1903. Classification of *Epiophlebia* is revised as follows: *Epiophlebia* s.str. with *E. superstes* (Selys, 1889) [type species] and *E. sinensis* Li & Nel, 2012; and *Rheoepiophlebia* **subgen.n.** with *E. laidlawi* Tillyard, 1921 [type species] and *E. diana* **sp.n.** Behavioral, ecological and paleontological information is also evaluated and members of *Epiophlebia* acknowledged to have inhabited small high elevation streams of the east Palaearctic for possibly 180 million years. Likely reasons are proposed for the enduring survival of *Epiophlebia*, its lack of a fossil record and the extinction of related groups.

> Key words

Epiophlebia, *Rheoepiophlebia*, extinction, biogeography, living fossil.

1. Introduction

Traditionally Odonata include Anisoptera (dragonflies), Zygoptera (damselflies), *Epiophlebia* Calvert, 1903, and a diverse array of fossil forms, among which are both the largest known insects and the oldest known creatures to fly (BRAUCKMANN & ZESSIN 1989; CARPENTER 1992). Fossil dragonflies not only allow the intricate wing venation of Odonata to be correctly homologized with that of other Pterygota (CARLE 1982a; RIEK & KUKALOVÁ-PECK 1984), but offer excellent out-group taxa for character state polarization in Odonata s.str. (REHN 2003). However, even with an extensive fossil record, the systematic position of the enigmatic *Epiophlebia* has changed dramatically over the last century. *Epiophlebia* was considered a zygopteran (SELYS 1889; NEEDHAM 1903; TILLYARD 1914, 1917), an anisopteran (NEEDHAM 1930; LEW 1933), or placed within the artificial group “Anisozygoptera Handlirsch” (HANDLIRSCH 1906–08, 1939; TILLYARD 1925, 1929; TILLYARD & FRASER 1940) along with several Jurassic fossil taxa.

In his monograph on the morphology of *Epiophlebia* ASAHINA (1954) established a separate superfamily for Epiophlebiidae based on its phylogenetic isolation and morphological uniqueness. From related fossil evidence it is apparent that *Epiophlebia* has been genetically isolated since the Lower Jurassic, and this has resulted in a curious combination of plesiomorphy and autapomorphy. This is illustrated by a few wing features of *Epiophlebia*: petiole of hind wing well developed, costa widened at nodus, pterostigmata strongly convex posteriorly, and hind wing with one or two cell rows between CuA and wing margin. *Epiophlebia* also lacks a discal nodus, an often overlooked ventral membranous area along the discal brace, yet some wing flexibility is achieved by a slight flattening of the pleat at the discal brace, and although the costal nodus is hinge-like its flexibility is limited particularly in the forewings by a minimal nodal fissure (CARLE 1982a). Additional autapomorphies include: labrum widened distally, genae with lateral tubercles, antennae five seg-

mented with pedicel elongate and flattened, postfrons with transverse shield-like intraocellar ridge, male occipital region with antitandem lobes, male epiproct with ventral and dorsal rami, male gonocoxae elongate, female abdominal segment 8 with midventral apical spur, and several autapomorphies of the female genitalia listed by KLASS (2008: p. 133). The copulatory apparatus of *Epiophlebia* is bizarre. It includes paired elongate posteriorly directed hamuli with swollen studded hooked apices (penis) and a median process (the homologue of the anisopteran ligula and the zygopteran penis) of abdominal sternum two, and a somewhat bottle shaped sperm vesicle (anisopteran penis) at the anterior end of abdominal sternum three (SCHMIDT 1915; PFAU 1971; CARLE 1982b). Remarkable plesiomorphic character states include: labial end hook occasionally two segmented (though more usually one segmented), well developed glossae and paraglossae, and a trilobate hypopharynx (ASAHINA 1949). *Epiophlebia* larvae are unique in that the antennae are five segmented, the head has well developed paralabial ridges, and they can produce sound by rubbing the inner apex of the femora against lateral abdominal files (Figs. 1E, 2E, 3E). Plesiomorphic character states of *Epiophlebia* larvae include wing pads without a branch of the RA tracheae crossing over the RP trachea, abdomen without transverse muscles (ASAHINA 1954), simple rectal gills, and proventriculus with 16 to 18 well developed denticulate lobes.

Several apomorphies found in extant Odonata support a sister group relationship between Anisoptera and *Epiophlebia* (CARLE 1982a, 1995; CARLE & KJER 2002; REHN 2003; KLASS 2008), as do diverse molecular markers (CARLE et al. 2008). "Anisozygoptera" was considered polyphyletic by CARLE (1982a), who rearranged the three suborders of Odonata into Zygopteroids and Anisopteroids, the latter of which includes *Epiophlebia*, based on several characters including tandem hold and associated modifications of the male terminalia. BECHLY (1996) also considered "Anisozygoptera" polyphyletic, but with Tarsophlebioidea Handlirsch, 1908 sister to a group including Zygoptera, Anisoptera and *Epiophlebia*. In contrast, NEL et al. (1993), BECHLY (1995) and (FLECK et al. 2004) represented "Anisozygoptera" as merely paraphyletic, with Tarsophlebioidea sister to Anisopteroids.

The genus *Epiophlebia* currently includes three described species: *Epiophlebia laidlawi* Tillyard, 1921 from India, Nepal and Bhutan; *Epiophlebia superstes* (Selys, 1889) from Japan; and *Epiophlebia sinensis* Li & Nel, 2012 recently described from northeastern China (LI et al. 2012). Adult *Epiophlebia* are rather rare in collections perhaps due to short flight seasons, isolated habitats, and atypical lifestyles. However, the first larval specimens of *Epiophlebia* from India, China and Japan were already collected before 1930

(TILLYARD 1921; NEEDHAM 1930; CARLE 1983a), and the second known *Epiophlebia* species, *E. laidlawi*, was described based on the original larval specimen collected in India. Here, a new species of *Epiophlebia* is described from larval specimens collected by "Dr. David C. Graham in the mountainous regions of western Szechuan" (NEEDHAM 1930). Unfortunately, Needham misidentified larvae of *Epiophlebia* as Gomphidae (CARLE 1983a), and the significance of these larvae from south-central China was not realized. The new species is compared to larval specimens of both *E. superstes* from Japan and of *E. laidlawi* from the type locality near Sonada in India, and determined to be more similar to the Himalayan species. Selected diagnostic features are illustrated for all known *Epiophlebia* larvae in Figs. 1–3.

2. *Epiophlebia diana* sp.n.

Fig. 3A–E

Material. Holotype: ultimate female larva in ethanol, China, mountains of western Sichuan, Dr. "D. C. Graham" collector; deposited in Cornell University Insect Collection. Additional material: one penultimate male larva (collected with holotype). Adult unknown.

Etymology. Diana – an allusion to the highland huntress and protectress of humankind, who if despoiled, will presage the destruction of mankind by their own handiwork, just as Actaeon was devoured by his own hunting dogs.

Description (ultimate female larva, holotype). Compactly built, somewhat limpet-shaped with granulate cuticle and head and thorax rather austropetalidlike. Total length 26.5 mm, abdomen including terminalia 15.5 mm, hind femur 6.2 mm, prementum 5.7 mm.

Ground color light brown with abdominal pattern in darker brown. Head wider than prothorax and slightly narrower than synthorax, labrum wider than frons, slightly scooplike with shallow median indentation; genae produced forward well beyond anterior margin of compound eyes and ventrally formed into a granule lined ridge along prementum; frontoclypeal region with low transverse ridge; antennae short, ca. 1.8 mm long, and tightly appressed to face, scape and pedicel together as long as first flagellar segment (Fig. 3A); prementum ca. $2 \times$ as long as wide at base (Fig. 3C), distally triangularly produced to hair fringed edge with deep median tightly appressed cleft, lateral margins strongly sinuate with dorsally directed flange in basal half; labial palps with movable hook slightly shorter than distance from base of movable hook to

base of palp, palps rounded-truncate apically with ca. 15 triangular teeth along inner margin; labium in resting position extended into a pocket along anterior edge of mesosternum; occipital lobes well-developed, produced into anterolateral recesses of pronotum.

Anterolateral angle of prothoracic tergum blunt, ventral paracoxal lobes of mesothorax blunt; femora strongly flattened, forefemur ca. $2.5 \times$ as long as wide (Fig. 3B), foretibia with inner apical brush of hairlike setae; wing-cases parallel, extended posteriorly as far as hind margin of abdominal segment 4; tarsi three jointed.

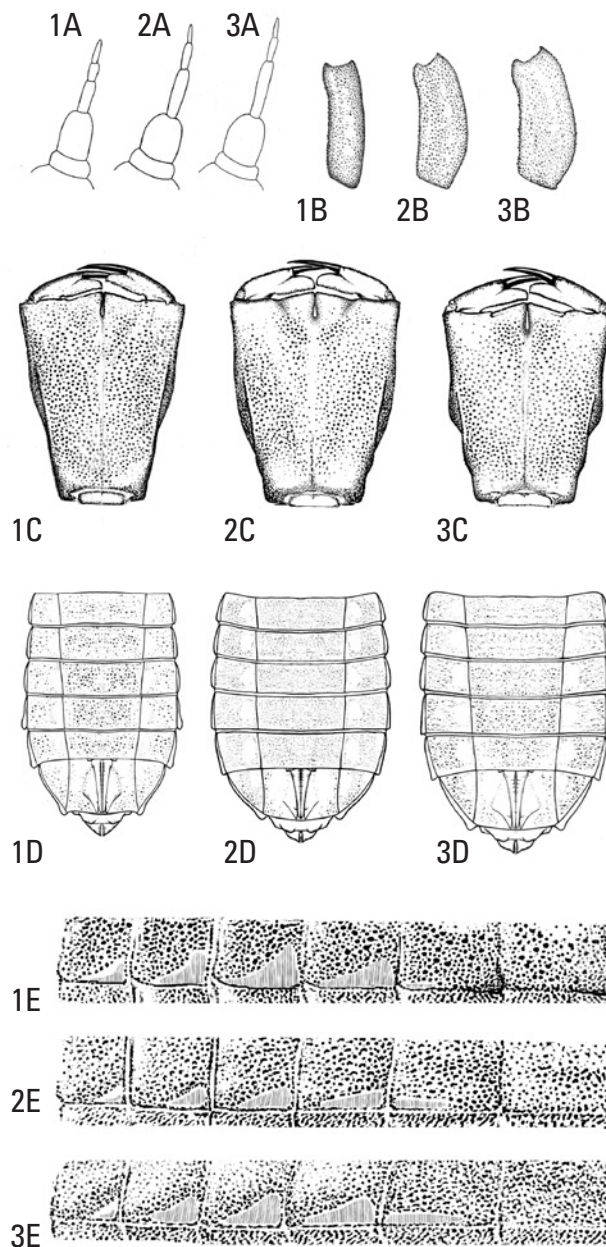
Abdomen similar to that of *Lanthus* in outline (Fig. 3D), widest on segment 7, abdominal terga 3 to 10 with low medial ridge; proventriculus 16-lobed: 8 minor folds with 2–3 teeth alternating with 8 major folds with clusters of 4–8 teeth, minor lobes typically alternating with teeth separated and together, major ventral lobes with 5–8 teeth and major dorsal lobes with 4–5 teeth; abdominal stridulatory file of segment 3 vestigial and surrounded by smooth area ca. $1/3$ length of segment, that of segment 4 ca. $1/2$ as high as long, and that of segment 7 ca. $3/4$ length of segment (Fig. 3E); lateral abdominal lobes on segment 7 vestigial, moderately developed on 8, and well developed on 9 (Fig. 3D), lateral ridges of segments 7–9 with small irregular spines; paraprocts 1 mm long with hair lined inner surface, epiproct ca. $0.6 \times$ length of paraprocts, male epiproctal processes slightly divergent, cerci ca. $1/2 \times$ length of epiproct.

Description (penultimate male larva). Same as holotype, with the following exceptions: Total length 21.1 mm, abdomen including terminalia 11.9 mm, hind femur 5.4 mm, prementum 4.5 mm including palps. Femora relatively wider than in ultimate instar, wing pads extended to near middle of abdominal segment 2.

Material used for comparison. *Epiophlebia superstes*: male and female ultimate and penultimate larvae, Shimizu Japan, 21-XII-1993, H. Karube collector; *Epiophlebia laidlawi*: male and female ultimate and penultimate larvae, Sonada India, 14-IV-1988, G. Patel collector.

3. Key to known larvae and adults of Epiophlebiidae

1 Adult: body black with labrum, postclypeus, antefrons, and interocellar ridge largely yellow, with long curved dorsal mesanepisternal stripes, with metepisternal yellow stripes extended below spiracles, with well developed ventral metepimeral stripes, and with well developed ventral, lateral, and middorsal abdomi-



Figs. 1–3. Larvae of *Epiophlebia* species. 1: *Epiophlebia (Epiophlebia) superstes*. 2: *Epiophlebia (Rheoepiophlebia) laidlawi*. 3: *Epiophlebia (Rheoepiophlebia) diana* sp.n. In each figure (A) dorsal view of right antenna, (B) dorsal view of right prothoracic femur, (C) ventral view of prementum, (D) ventral view of abdominal segments 4–10, and (E) lateral view of abdominal segments 3–8 showing stridulatory surface.

nal yellow markings; forewing postnodals typically 12–15, costal side of quadrilateral subequal in length to arcular brace, abdomen 37–42 mm, posterior hamuli with apical lobe shorter than wide, male tergum 10 without middorsal longitudinal carina, male epiproct extended beyond apex of cerci and with ventral rami subacute.

– Larva: cuticle with larger granulations dark brown; antennal pedicel ca. $2.0 \times$ as long as wide, longer than first flagellar segment (Fig. 1A); prementum ca. $2.4 \times$ as long as basal width (Fig. 1C); anterolateral angle of prothoracic tergum and ventral paracoxal lobes of mesothorax acute; femora not strongly flattened, forefemur ca. $3.4 \times$ as long as wide (Fig. 1B), foretibial brush with palpiform setae; abdominal stridulatory file of segment 3 well developed, that of segment 4 ca. as high as long, and that of segment 7 vestigial (Fig. 1E); abdomen with lateral abdominal lobes 7 and 8 well developed (Fig. 1D), male epiproctal processes strongly divergent

..... *Epiophlebia (Epiophlebia)* – 2

Type-species: *Epiophlebia superstes* (Selys), originally named as *Palaeophlebia superstes* Selys (CALVERT 1903).

Larva of *E. sinensis* Li & Nel not yet known.

1' Adult: body brown with straight dorsal mesanepisternal and short metepisternal yellow stripes, and with vestigial ventral metepimeral stripes and vestigial mid-dorsal abdominal spots, forewing postnodals typically 8–11, costal side of quadrilateral longer than arcular brace, abdomen 45–47 mm, posterior hamuli with apical lobe longer than wide, male tergum 10 with mid-dorsal longitudinal carina, male epiproct not extended beyond apex of cerci and with ventral rami blunt.

– Larva: cuticle with granulations light brown; antennal pedicel ca. $1.5 \times$ as long as wide, shorter than first flagellar segment (Figs. 2A, 3A); prementum ca. $2.0 \times$ as long as basal width (Figs. 2C, 3C); anterolateral angle of prothoracic tergum and ventral paracoxal lobes of mesothorax blunt; femora strongly flattened, forefemur 2.5 – $3.0 \times$ as long as wide (Figs. 2B, 3B), foretibial brush with hairlike setae; abdominal stridulatory file of segment 3 vestigial and surrounded by triangular smooth area, that of segment 4 ca. $1/2$ as high as long, and that of segment 7 well developed (Figs. 2E, 3E); abdomen with lateral abdominal lobes 7 and 8 vestigial (Fig. 2D, 3D), male epiproctal processes slightly divergent

..... *Rheoepiophlebia* subgen. nov. – 3

Type-species: *Epiophlebia laidlawi* Tillyard.

Adult of *Epiophlebia diana* sp.n. not yet known.

2 Adult: abdominal segment 6 laterally beyond antecostal suture and segments 7–10 and terminalia dark brown to black with dorsal yellow spots of segments 8–10 distinct

..... *Epiophlebia (Epiophlebia) superstes* (Selys)

Distribution: Japan: Honshu, Hokkaido, Kyushu, Shikoku.

Flight season: 3-IV-1990, Shikoku (H. Karube collector) to July, Hokkaido (ASAHINA 1950).

2' Adult: abdominal segment 6 laterally beyond antecostal suture and segments 7–10 and terminalia ferruginous, with dorsal pale spots of segments 8–10 obscure

..... *Epiophlebia (Epiophlebia) sinensis* Li & Nel

Distribution: China: Zheng-nan-gou stream, Heilongjiang province.

Flight season: 20–21-VI-2010, Shahezi Zhen (Qiming Li collector).

3 Larva: labrum with anterior margin entire, scape and pedicel together longer than first flagellar segment (Fig. 2A), prementum with lateral margins slightly sinuous, premental cleft as long as ventral width of palp at midlength (Fig. 2C), forefemur ca. $3.0 \times$ as long as wide (Fig. 2B), abdominal stridulatory file of segment 7 ca. $1/2$ length of segment (Fig. 2E), lateral abdominal lobes slightly protrudent on segment 9 (Fig. 2D)

.... *Epiophlebia (Rheoepiophlebia) laidlawi* Tillyard

Distribution: India: Darjeeling; Nepal: Chitre, Shivapuri Hills, Daman, Helambu, Phulping; Bhutan: Thimphu, Taba, Haa, Trongsa (TILLYARD 1921; ASAHINA 1963; TANI & MIYATAKE 1979; SAVILLE 1990; SHARMA & OFENBÖCK 1996; NESEMANN et al. 2008; BROCKHAUS & HARTMANN 2009).

Flight season: 2-V-1979, Shivapuri Hills (O. Tominaga & N. Doi collectors) to 1-VII-1963, Chitre (T. Haruta & A. Hara collectors).

3' Larva: labrum with anterior margin widely indented, scape and pedicel together as long as first flagellar segment (Fig. 3A), prementum with lateral margins strongly sinuous, premental cleft longer than ventral width of palp at midlength (Fig. 3C), forefemur ca. $2.5 \times$ as long as wide (Fig. 3B), abdominal stridulatory file of segment 7 ca. $3/4$ length of segment (Fig. 3E), lateral abdominal lobes protrudent on segment 9 (Fig. 3D)

..... *Epiophlebia (Rheoepiophlebia) diana* sp.n.

Distribution: China: mountains of western Sichuan province.

Flight season: unknown.

4. Epiophlebian life history

According to ASAHINA (1950), upon hatching the shrimp-like prolarva of *Epiophlebia superstes* is active and able to flip itself a distance of 10 cm. After having reached the water surface the prolarval exuvia is cast and the first instar larva sinks to the stream bed. A total of 14 larval instars were estimated by TOKUNAGA & ODAGAKI (1939), and it was determined that five to eight years are required for larval development depending on conditions in the larval habitat. During early larval development *E. superstes* larvae cling to the stones of rushing torrents, with larger instars favoring larger stones in faster current (ASAHINA 1950). In contrast the larvae of *E. laidlawi* occur in smaller streams with slower current (TANI & MIYATAKE 1979). However, current velocity for all *E. laidlawi* sites was rather high according to BROCKHAUS & HARTMANN (2009), and ranged from 15 cm/sec in pools to 200 cm/sec in riffles. The distinct aquatic habitat requirements of these species from the two subgenera apparently mirror differences in larval morphology. The greater development of the ventral occipital ridges and antero-ventral mesothoracic lobes in *E. superstes* apparently is required to more firmly support the labium in faster currents, where the labium is necessarily extended and retracted during feeding. However, the femora of both *Rheoepiophlebia* species are more strongly flattened than in *E. superstes*, and in the recessed position overlap the trochanter of the following leg to form a sort of suction disk. This morphology may function to prevent these larvae from being washed from their small upstream habitats during periods of high flow. In contrast, the legs of *E. superstes* are narrower and in the recessed position form a small streamlined disk apparently adapted for moving in faster currents. In addition, FURUKAWA (1934) supposed that the ventral setae of the paraprocts function as adhesive organs, but these setae (found in all known *Epiophlebia* larvae) point outward about the respiratory opening, and may instead act as a filtering device for water entering the rectal gill chamber.

Epiophlebian larval behavior during the ultimate instar is unique when compared to other Odonata. For *E. superstes* it is known that emergence is preceded by a period of up to five months during which the larvae leave the water and crawl about in the terrestrial environment near the parent stream (TOKUNAGA & ODAGAKI 1939). This unusual shift in larval habitat is also suspected in *E. laidlawi* because TANI & MIYATAKE (1979) were not able to find last instar larvae in the Shivapuri stream. In my experience larval stridulation is yet another unique feature of Epiophlebiidae among Odonata. It is not known whether larvae utilize stridulation to synchronize emergence, optimize habitat occu-

pancy, deter predation, or some other function such as flushing aquatic prey. In any case larvae do stridulate when disturbed, which suggests a protective or warning function. The stridulation sound can be artificially produced by holding the apices of the femora against the lateral abdominal files while bending the abdomen from side to side. The abdominal scraper is apparently formed from cuticle granulations that have been modified into transverse vertical ridges (Figs. 1E, 2E, 3E). The smooth areas about the anterior files apparently serve to enable a stress-free start to the stridulatory movement.

Transformation into the adult generally occurs in the morning on a streamside rock or stem with the larval body in a vertical position, but ASAHINA (1950) found exuvia on the bark of *Cryptomeria japonica* as far as ten meters from the larval habitat. As is usual for stream inhabiting Odonata, teneral show the greatest dispersal, with mature individuals eventually aggregating back toward the parent stream or to nearby streams. For example, a teneral female *E. laidlawi* has been collected at the top of the Shivapuri Hills about one km from the parent stream (TANI & MIYATAKE 1979), although mature adults are rarely collected far from suitable larval habitat.

Flight of *Epiophlebia* is swift and relatively efficient, but maneuverability and acceleration are far less than in Zygoptera or Anisoptera; and after a fifteen minute warm up period, flight can occur at 16°C, or even in the rain at lower temperatures than typical for extant Odonata (RÜPPELL & HILFERT 1993). Feeding flight occurs in the valley of the parent stream near treetop level, where early in the season small insects are fed on throughout the day. As the season progresses, feeding is limited to before 10:00 and to after 15:00 (ASAHINA 1950). The male search flight for females occurs during mid-day and is typified by a slow upstream flight close to the water surface, with the males weaving forward and back while inspecting suitable oviposition sites for mature females. Males pursue females as they fly between oviposition sites and grasp females with the typical anisopteran tandem hold. Mating is at rest and the huge hooked and studded apex of the posterior hamuli (penis) may not only function in sperm displacement, removal, and transfer, but could also damage the female reproductive tract and thus reduce the efficiency of future mating. Unlike other Odonata the male head of *Epiophlebia* has posterior anti-tandem lobes (CARLE 1996), which presumably prevent multi-tandem entanglements as sometimes observed in Lestidae.

Flight season is about a month in length (ASAHINA 1950), and varies significantly with latitude and elevation: for *E. superstes* it extends from late March in Kyusyu to July in Hokkaido, and for *E. laidlawi* it extends from early May until early July. *Epiophlebia superstes* and *E. laidlawi* (and thus perhaps the sub-

genera of *Epiophlebia*) apparently also differ in the substrate utilized for oviposition. *E. superstes* has been reported to oviposit in a wide variety of soft tissue plants, although oviposition is sometimes attempted in hard tissue. Chosen plants typically grow in wet and mostly shaded areas, less than one meter from the stream, and include several genera of spermatophytes: *Houttuynia* (Saururaceae), *Angelica* (Apiaceae), *Elatostema* (Urticaceae), *Trautvetteria* (Ranunculaceae), *Saxifraga* (Saxifragaceae), *Parasenecio*, *Petasites*, *Ligularia* (Asteraceae), *Lilium*, *Cardiocrinum* (Liliaceae), *Arisaema* (Araceae), and *Wasabia*, *Cardamine* (Brassicaceae); and a few bryophytes: *Dumortiera* (Dumortieraceae), *Conocephalum* (Conocephalaceae), and *Pellia* (Pelliaceae) (ASAHINA 1934, 1950; ASAHINA & EDA 1958, 1982; ASAHINA & SUGIMURA 1981; TAMAYA & MIYAKAWA 1984; TOKUNAGA & ODAGAKI 1939). However, suitable plants for oviposition are not known at the small streams in the Shivapuri Hills, one of the few localities where both adults and larvae of *E. laidlawi* have been found (TANI & MIYATAKE 1979). It is possible that suitable oviposition substrates may also include decaying logs, but ASAHINA (1982) has identified *Elatostema hookerianum* (Urticaceae) as the plant most likely utilized for oviposition in this region. Female *Epiophlebia* oviposit unaccompanied, and require a small opening of about one cubic meter above the oviposition site for access, possibly because of crude flight capabilities reported by RÜPPELL & HILFERT (1993). Oviposition in plant stems is preceded by trial thrusts, which, if successful, lead to a descent along the stem, after which eggs are laid from the bottom of the stem upward. ASAHINA (1934) reported that females would fly away without ovipositing when plants were found to be too solid. Similar plants are utilized by austropetaliids for oviposition (CARLE 1996), but the more weakly sclerotized epiophlebian abdomen apparently makes the process more time consuming and seemingly laborious. The eggs of each female are arranged in a sinuous row of up to about 1000 eggs maximum, with an egg deposited about every four seconds (ASAHINA 1950). The eggs are inserted with the anterior coarse end upward, are about 1/4 as wide as long, and average about 1.1 mm in length. Micropyles number 10–14 (reported as 12–14 by ANDO 1962) and are arranged about the anterior end in a subapical ring. Embryonic development is ca. 30 days at 20°C and 20 days at 25.5°C (ASAHINA 1950).

5. Epiophlebian biogeography

Lower Jurassic fossils of the epiophlebian sister group indicate that *Epiophlebia* are the survivors of an evo-

lutionary line that has been genetically isolated for at least 180 million years. Unfortunately, conclusive fossils are not known of *Epiophlebia* or of its Jurassic stem group. Several synapomorphies, including the widening of the MA-MP interspace, separate both *Epiophlebia* and its sister Anisopteroids from their Jurassic stem group (CARLE 1982a), which is currently known only from the Palaearctic (HAGEN 1862, 1866; BODE 1905; MARTYNOV 1925; PRITYKINA 1968, 1970, 1977, 1985; WHALLEY 1985; FLECK & NEL 2002; NEL et al. 2009). In turn, *Epiophlebia* is distinguished from its sister group Anisopteroids by the lack of several wing features related to increased vagility (CARLE 1982a). It is telling that even the most plesiomorphic of these more vagile Anisopteroids had already spread across Pangaea during the Jurassic, as evidenced by fossils from Antarctica to China (CARPENTER 1969; HANDLIRSCH 1920; PRITYKINA 1980; HONG 1983). *Epiophlebia*'s apparent failure to disperse more widely indicates that *Epiophlebia* had already specialized to inhabit isolated east Palaearctic highland streams during the early Jurassic. Lack of wing features including a discal nodus, a well developed nodal hinge, or an expanded hind wing anal field (CARLE 1982a) indicate a lower vagility of *Epiophlebia* when compared to its anisopteran contemporaries. The most plesiotypic extant anisopterans are the Austropetaliidae, which inhabit the mountain streams and spring seeps of the Southern Hemisphere (CARLE & LOUTON 1994; CARLE 1996; CARLE et al. 2008), suggesting that these southern habitats remained unoccupied until the basal radiation and dispersal of Anisoptera. Speciation for highland streams and associated low vagility has also likely prevented dispersal of *Epiophlebia* into the mountains of Europe or its dispersal across the North American/Okhotsk plate (SENO et al. 1996) from Japan to America. In contrast, nearby ecological associates of *Epiophlebia*, the anisopteran genera *Lanthus* Needham, 1897 (Gomphidae) and *Tanypteryx* Kennedy, 1917 (Petaluridae), occur exclusively in Japan and North America (CARLE 1980, 1986).

The known distribution of the subgenus *Epiophlebia* s.str. includes Japan and northeastern China, and the known distribution of *Rheoepiophlebia* subgen.n. includes the Himalayas and mountains of south-central China. Similar adult morphology of the northern species pair (*E. superstes* and *E. sinensis*) suggests that a vicariance event isolating them on either side of the Sea of Japan may be related to Pleistocene glaciation. In contrast, larvae of the southern species pair are easily distinguished compared to the difficulty often encountered when identifying dragonfly larvae to species. This indicates a much more ancient vicariance event, perhaps the formation of deep river valleys between the Himalayas and the mountains of south-central China.

Although the utility of epiophlebian autapomorphic features remains largely unknown, it is apparent that the unusual wings of epiophlebian are adapted for flight about cool high elevation habitats (RÜPPELL & HILFERT 1993). In addition, a streamlined larval body and a rheophilic lifestyle also enable *Epiophlebia* to exploit the stable environment and detritus based ecosystems of high elevation spring-fed seeps and streams. Unfortunately, this high energy environment is not conducive to fossil formation, thus explaining the current lack of *Epiophlebia* from the fossil record. As streams descend mountain valleys ambient temperature rises, gradient decreases and sediment accumulates in pool areas (VANNOTE et al. 1980), thus forming the habitat utilized by the borrowing larvae of gomphid, cordulegastrid and chlorogomphid populations (CARLE 1983b). These sentinels patrol along the upper limit of lowland aquatic ecosystems dominated by advanced anisopteran competitors which together help restrict *Epiophlebia* to its mountain retreats.

Fortunately for *Epiophlebia* its habitat is an ideal shelter from the perturbations of global extinction events such as meteor impacts and extreme volcanism, which result in extended periods of reduced sunlight (ALVAREZ et al. 1980; KNOLL et al. 2007). The environmental stability afforded small stream communities from emerging ground water and a persistent flow of energy and nutrients from detritus based ecosystems (CARLE 1982c) is strongly contrasted by temporary lentic ecosystems, which although often highly productive are dependent on reliable sunlight and rainfall. For example, extinction of all Stenophlebioidea Pritykina, 1980 and Aeschnidioidea Carle & Wighton, 1990 is associated with large size, a stalking larval feeding mode, and an apparent lentic habitat preference (CARLE & WIGHTON 1990; ZHANG 1999). A synergism favoring an exposed feeding mode and the utilization of relatively predator free temporary aquatic habitats would explain the lack of concealed larvae among fossil Stenophlebioidea and Aeschnidioidea, but would eventually also expose these giant dragonflies to the environmental perturbations associated with major extinction events. In contrast, the diversification of Anisoptera and the prolonged survival of Epiophlebiidae are associated with small size, secretive larval feeding modes, the environmental stability of emerging ground water, and the persistent flow of energy and nutrients through detritus based ecosystems.

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