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THE LARVA OF *AMPHIPTERYX* AND A RECLASSIFICATION OF AMPHIPTERYGIDAE *SENSU LATO* BASED UPON THE LARVAE (ZYGOPTERA)

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Larvae of *Amphipteryx longicaudata* González-Soriano and *Amphipteryx* sp. from Mexico, are described and compared to the genera *Devadatta, Pentaphlebia, Rimanella, Philoganga* and *Diphlebia*. Ecological and biogeographical comments are provided. A new reclassification of Amphipterygidae and Diphlebiidae based upon larval characters is proposed. The Amphipterygidae is redefined and is divided into 2 subfamilies: Amphipteryginae (*Amphipteryx* and *Devadatta*) and Pentaphlebiinae sfam.n. (*Pentaphlebia* and *Rimanella*); these 4 genera share a notable apomorphic character unique among all odonates: the gill tufts of the larvae. On the other hand, *Diphlebia, Philoganga* and *Lestoidea* are put together in the Diphlebiidae; they lack the gill tufts and exhibit many other features in common which are not shared with the Amphipterygidae (s. str.). The taxon Rimanellidae is suppressed. Brief diagnoses for the new groupings and detailed illustrations of the larvae and of adult wings are also given.

INTRODUCTION

As FRASER (1955) pointed out, "the family Amphipterygidae has been regarded as an archaic remnant of a once world-wide circumtropical fauna". According to DAVIES & TOBIN (1984), it consists of four genera: *Amphipteryx* (Central America), *Devadatta* (Orient), *Pentaphlebia* (Ethiopia), and *Philoganga* (SE Asia). This clearly shows a relict distribution.

After SELYS' orginal description of *Amphipteryx agrioides* in 1853, this genus remained monotypic until the recent discovery of *A. longicaudata* by GONZALEZ-SORIANO (1991) from the mountains of Oaxaca, Mexico and a probably new species from Hidalgo, Mexico (Dr E. González, pers. comm.). GONZALEZ-SORIANO (1991) assigned erroneously the suffix -us to the new species he described as *A. longicaudatus*. The generic name is feminine (J. De Marmels, pers.

comm.), therefore, on the basis of the articles 32d and 34b of the 3rd ed. of the International Code of Zoological Nomenclature, the spelling must be changed to *A. longicaudata*. According to Dr T.W. Donnelly (pers. comm.) *A. agrioides* occurs in Guatemala and there are two more undescribed species, one from Chiapas, Mexico and the other from Honduras in Central America. Thus, there is a total of five species.

In 1985 I received two final instar larvae preserved in 80% ethanol, one from the state of Chiapas, the other from the state of Jalisco. At first glance, when I saw these larvae I thought that they were extremely rare because of the shape of the epi- and paraprocts and the presence of tufts of filamentous gills. By a process of elimination and according to the literature (e.g.: FRASER, 1955; GEIJSKES, 1940), I concluded that they belonged to *Amphipteryx*. Later on, I collected larvae of *A. longicaudata* at the type locality, although I was not successful in rearing them; also I collected medium-aged larvae of the new species from Hidalgo.

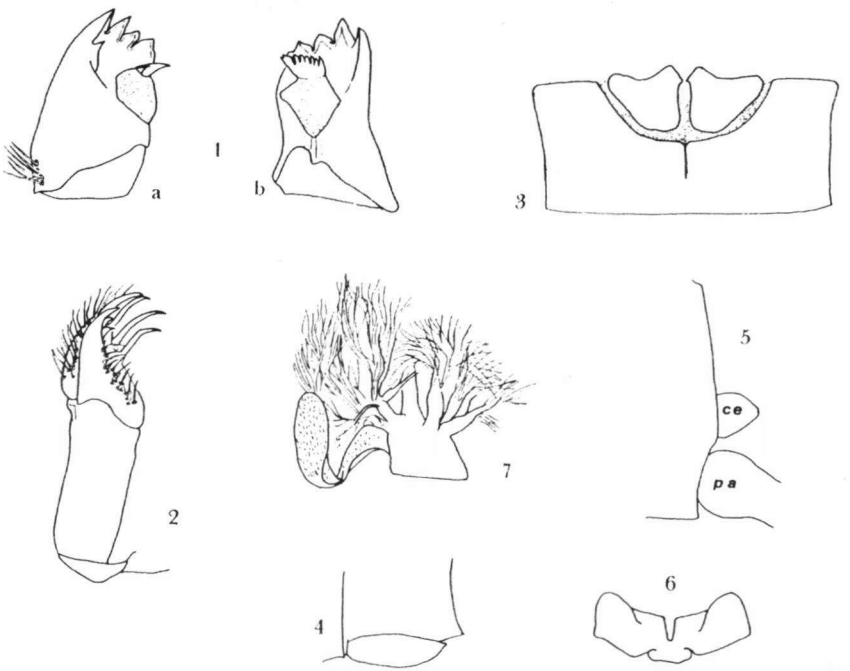
AMPHIPTERYX LONGICAUDATA GONZALEZ-SORIANO

Figures 1-8, 10-12, 17a, 18A, 19A, 20A, 25a, 26a, 27a, 28A, 29A, 30A, 31a,b

M a t e r i a l. – 9 larvae (4 ♂, 5 ♀). MEXICO: Jalisco, Río Cuitzmala, 23-III-1985 (1 ♀ ultimate instar), A. Cantú leg.; Oaxaca, 84 km on route 175 Tuxtepec-Oaxaca, 1735 m, 13-VI-1992 (8 young instars), R. Novelo leg. Deposited in author's collection.

DESCRIPTION. – Larva yellow-brown to brown, body stout and short, densely covered with very minute scale-like setae; abdomen cylindric, tapering gradually caudad.

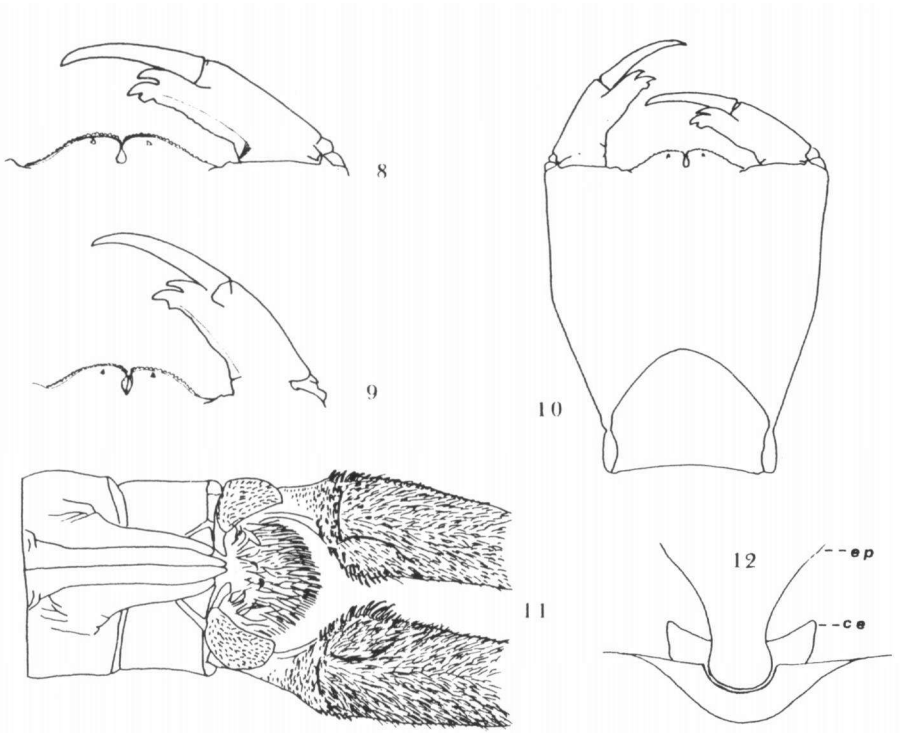
H e a d. – 1.5 times wider than long (Fig. 17a), posterior border widely concave, cephalic lobes set with small scale-like setae except in small glabrous areas; eyes prominent, quite rounded; labrum reddish-brown, trapezoid, its anterior border convex with a brush of robust hair-like setae; in ventral view the epipharynx appears slightly concave (Fig. 27a). Antennae 6-jointed (Fig. 30A; also cf. Fig. 14) (although the sixth apparently but not really subdivided), shorter than head, scape and pedicel short and stout, densely covered with small scale-like setae, slightly more obscure than other segments, flagella segments slender, covered with hair-like setae, first flagella segment the longest of all antennal segments, ratio of length of antennal segments: 0.95, 0.75, 1.0, 0.60, 0.50, 0.50. Mandibles biramous (Figs 1, 18A), external branch of the right mandible with 5 cuspids, internal branch with one large, acutely-pointed, upwardly-directed tooth and a very small one at its base (Fig. 1a); external branch of the left mandible with 4 cuspids, internal one with 7 (Fig. 1b). Maxillary palp hairy and one spine at distal end; galeolacinia with four long, robust, incurved dorsal hooks and three small but robust incurved ventral hooks, both rows of hooks preceded basally by long, stout setae (Fig. 2). Labium yellow-brown with hinge extending to posterior margin of prosternum; prementum longer than wide (Figs. 10, 25a), narrowed basally, thence gradually widening until 0.50 the length, then slightly concave and



Figs 1-7. Details of the morphology of *Amphipteryx longicaudata* larva: (1) mandibles, ventral view; a=right, b=left; – (2) right maxilla, ventral view; – (3) sternite 10, male; – (4) left lateral view of abdominal segment 9 of male, showing the knob of vestigial gonapophyse; – (5) apical margin of segment 10 of the male, left lateral view; c=cercus, pa=base of paraproct; – (6) male cerci, dorsal view (caudal appendages removed); – (7) gill tuft, ventral view. – [The dotted areas in Figs 1 and 3 are membranous]

again widening to reach its maximum width at apical end; sides covered with very minute spiniform setae their entire length; ligula moderately prominent (Figs 8, 10, 19A, 25a), its anterior border serrated, median cleft small, V-shaped, a small spine on each side of the median cleft; no premental setae; palp without setae (Figs 8, 10, 20A, 25a), its external border almost smooth, only a few minute scale-like setae at base, internal border very slightly serrated (almost imperceptible), sharp as a cutting-edge (Fig. 8), distally ending in three hooks, the median the largest and the internal one the smallest, the movable hook long and sharply pointed (Fig. 20A).

T h o r a x. – Covered densely with minute scale-like setae giving it a very fine granular aspect. Anterior margin of pronotum more or less straight, anterior corners forming a 90° angle with the anterior margin (Fig. 26a); sides straight and



Figs 8-12. Details of the morphology of *Amphipteryx* larvae: (8) dorsal aspect of the ligula and right palp of *A. longicaudata*; – (9) the same, *Amphipteryx* sp. (Chiapas); – (10-12) *A. longicaudata*: (10) prementum, dorsal view; – (11) sternites 9-10 of the female showing the gonapophyses, gill tufts, and basal halves of paraprocts; – (12) dorsal view of female cerci; ce=cercus, ep=base of epiproct.

convergent posteriorly; posterior margin widely rounded. Synthorax robust, quadrate, more or less obscure without any definite color pattern. Anterior and posterior wing sheaths extending over the basal 0.30 and 0.70 respectively of abdominal segment 6. Legs short and slender, densely covered with scale-like setae, uniformly coloured; apical borders of procoxae and protibiae with a brush of robust setae, mainly on internal sides in the latter; posterior margin of apical border of protibiae with two robust spines, 8 and 12 in meso- and metatibiae respectively; tarsi 3-jointed, claws simple with pulvilliform empodium.

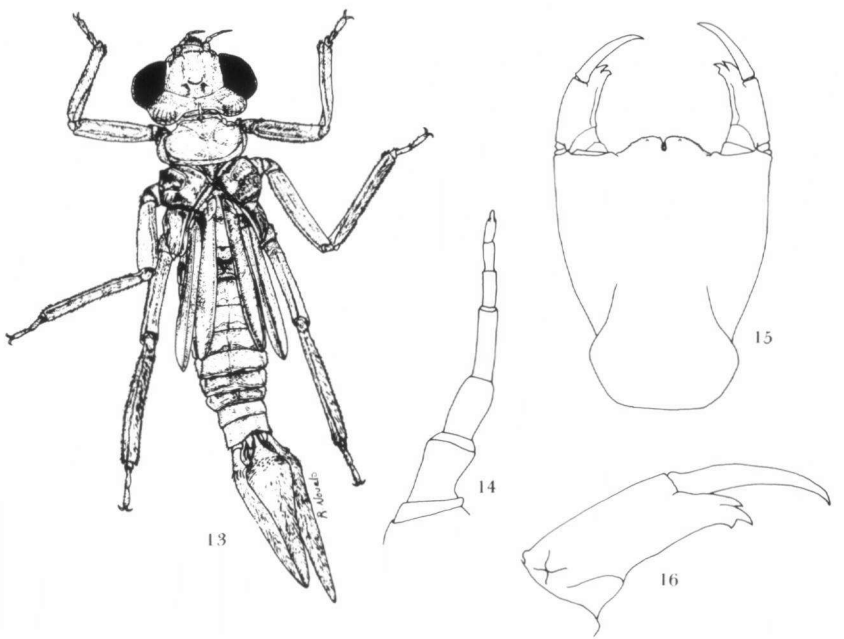
A b d o m e n. – Tergites brown, a narrow, white, longitudinal middorsal line throughout; sternites yellow. Basal segments wider, gradually narrowing caudad; 3-9 with a lateral carina covered with scale-like setae; this carina more or less straight except on 8 where it is notably convex (cf. Fig. 13). No lateral spines or dorsal hooks. Male gonapophyses rudimentary (Fig. 4), only represented by one small knob on each side of genital pore. Female gonapophyses well developed,

slightly exceeding posterior margin of sternite 10; lateral valvae the shortest, their apices, in ventral view, convergent (Fig. 11). Sternite 10 formed by an apical semicircular membranous area and 4 sclerotized plates as follows: 2 large lateral plates fused at basal midline and 2 small, subtriangular plates occupying the apical 0.70; the membranous area separating the large plates from the smaller plates as well as each small plate (Figs 3, 31b).

Caudal appendages. – Male cerci short, in lateral view conical, bluntly tipped (Fig. 5); in dorsal view wider than long, other features as in Figure 6. Female cerci short, in dorsal view subrectangular, transversally enlarged, with an external conical projection (Fig. 12). Epiproct and paraprocts yellowish-brown, their tips light yellow, inflated, long, tapering caudad (Figs 28A, 29A), densely covered with scale-like setae (Fig. 11). Basal 0.14 of paraprocts narrowed, resembling a pedicel, then abruptly swollen and thence gradually tapering, ending in a long, blunt tip (Fig. 29A); the swollen part covered with long, flat scale-like setae, its internal side excavated (Fig. 11). Epiproct similar to paraprocts but inflated portion 0.75 wider than in paraprocts (Fig. 28A); ventral side of the swollen part bulging, with one short, longitudinal furrow on each side of midline; the crest of this bulging with a tuft of long, scale-like setae. Paraprocts 15 per cent longer than epiproct. The accessory gills comprise a pair of tufts lying between the bases of the epi- and paraprocts (Fig. 11); the tufts are yellowish to lilac in color and 1.0 to 1.15 mm long when extended (Fig. 7). The base of each tuft is cylindrical with three sets of stems; a dorsal one with three stout stems in a circular manner; a latero-external one with one stem only and a posterior one with six stems arranged in a single row arising from a strap-like process which terminates in a sclerotized, upturned plate. Forking of stems to the tip is dichotomous except the first of the dorsal stems which is trichotomous. Lamina supra-analis absent. The gizzard in *A. longicaudata* has 32 folds (16 major and 16 minor), the same number that LIEFTINCK (1971) mentioned as common for recent amphipterygids; the major folds in *A. longicaudata* bear rows of 8-9 minute denticles, while some folds minor exhibit 2 and others 5 denticles.

Measurements (in mm) (mature larva). – Total length (including paraprocts) 27; abdomen (without app.) 11; maximum width of head 5.3; hind femur 5.1; paraprocts 6.75-7.0; epiproct 6.0.

ECOLOGY. – Larvae of *A. longicaudata* were found among rough gravel in sites where the water flow was rapid. At least in Oaxaca, they inhabit small, shallow creeks running throughout the montane cloud forest. Dr. T.W. Donnelly (pers. comm.) collected juvenile stages of *Amphipteryx* in tangles of leaf trash found at the lip of small waterfalls in Guatemala. In a medium-aged larva of *A. longicaudata* three small trichopteran larvae (apparently Rhyacophilidae) were found in the gizzard.



Figs 13-16. *Amphipteryx* sp. (Chiapas): (13) last instar larva (♂); – (14) left antenna; – (15) prementum, dorsal view; – (16) left palp, ventral view.

AMPHIPTERYX SP.

Figures 9, 13-16

Material. – 1 larva (♂) ultimate instar. MEXICO: Chiapas, Río Mixcum, 23-III-1985 (♂), H. Velasco leg. Deposited in author's collection.

DESCRIPTION. – Larvae reddish-brown (Fig. 13). In other features strikingly similar to *A. longicaudata*. Epiproct and paraprocts reddish-brown.

Measurements (in mm). – Total length (including epi- and paraprocts): 23; abdomen (without app.): 8; maximum width of head: 5.0; hind femur 4.5; right paraproct 7.1 (the left one apparently abnormally developed cf. Fig. 13); epiproct 6.1.

DISCUSSION

Larvae of *Amphipteryx longicaudata* and *Amphipteryx* sp. (from Chiapas) are extremely alike and only slight differences separate them. *A. longicaudata* has the internal end hook of the labial palp larger, the serrations of the internal border of the labial palp and ligula are more conspicuous (cf. Figs 8-9), and the body is larger in length. Also the larva of *Amphipteryx* sp. is reddish-brown whereas that of *A. longicaudata* is yellow-brown. The larvae of *Amphipteryx* (sp.n.?) from

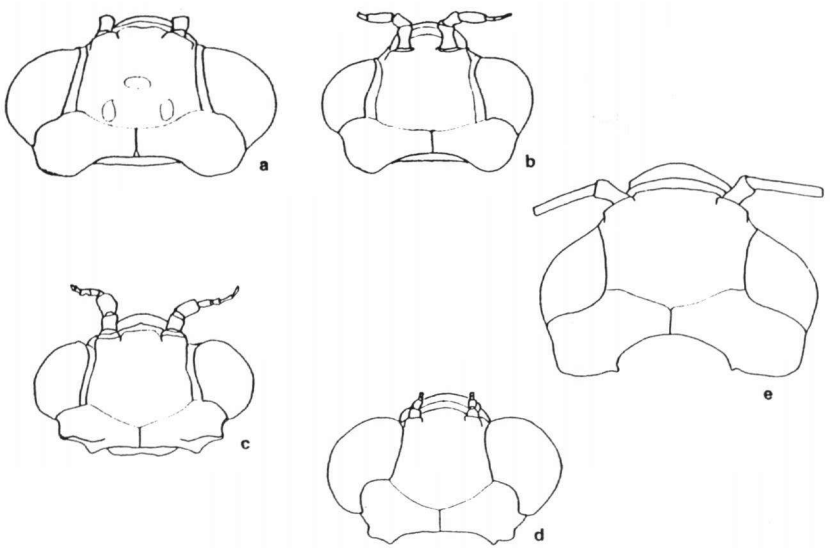


Fig. 17. Heads of Amphipterygidae (a-d) and Diphlebiidae (e): (a) *Amphipteryx longicaudata*; – (b) *Devadatta argyoides*; – (c) *Pentaphlebia stahli*; – (d) *Rimanella arcana*; – (e) *Diphlebia euphaeoides*.

Hidalgo differ from *A. longicaudata* only in the more angular cephalic lobes of the former.

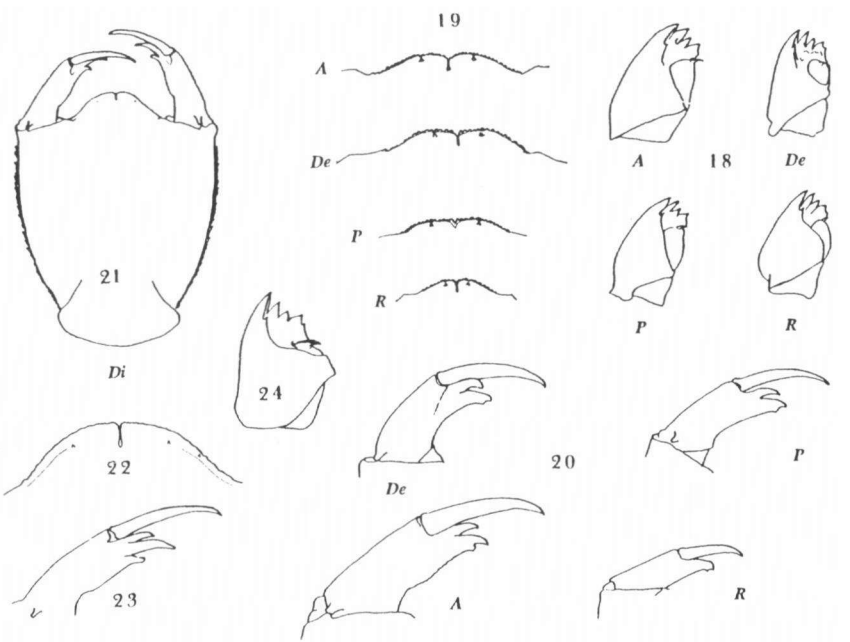
BIOGEOGRAPHY

I have larvae of *Amphipteryx* from the states of Chiapas, Oaxaca, Jalisco and Hidalgo. The distribution of this genus is fragmentary like that of the montane cloud forest. Adults and larvae of *A. longicaudata* have been collected at the Sierra de Juárez in Oaxaca, Mexico but it seems that the distribution of this species extends to northwest Mexico at least as far as the state of Jalisco (the mature larva I received in 1985 agree well in features with those collected by myself at the type locality). Larvae of the supposed new species from the state of Hidalgo (situated on northeast Mexico) are more alike to specimens from Oaxaca and Jalisco than that from Chiapas. A preliminary analysis shows vicariance in their distribution. Perhaps the sharp barrier which separates *A. longicaudata* and *Amphipteryx* sp.n.? (from Hidalgo) from the *Amphipteryx* sp. from Chiapas is the zone of warm lowlands of the Istmo de Tehuantepec in Oaxaca; in this area the conditions of humidity and temperature are unfavorable for the establishement of the cloud forest with which *Amphipteryx* is usually closely associated.

SYSTEMATICS

Since SELYS (1853) founded the present family Amphipterygidae (originally

named as Légion *Amphipteryx*) to include the unique genus *Amphipteryx*, several genera have been added to this family from time to time: *Devadatta* and *Diphlebia* (SELYS, 1859); *Pentaphlebia* (FÖRSTER, 1909) and *Philoganga* (FRASER, 1938). NEEDHAM (1933) described the genus *Rimanella* (Needham) and considered it as allied to *Hypolestes*. GEIJSKES (1940) described the larva of *Rimanella arcana* and this indicated a close relationship not to the Lestidae but to the Megapodagrionidae and Amphipterygidae. WATSON (1966) considers *Rimanella* referable to Amphipterygidae on the basis of the gill tufts of the larva and LIEFTINCK (1971) came to the same conclusion in his study on the phylogeny of the family. DAVIES & TOBIN (1984) established the family Rimanellidae (to include the unique genus *Rimanella*), basing their decision only upon adult characteristics (Dr. J.A.L. Watson, pers. comm.). They distinguished the Philoganginae from the Amphipteryginae on, among other features, the lack of gill tufts in *Philoganga*. *Diphlebia* (Diphlebiidae) also lacks gill tufts but *Rimanella* has them. Dr J.A.L. Watson (pers. comm.) states "the gill tufts, developed from the laminae sub-anales, are an apomorphic feature, yet the classification of DAVIES & TOBIN (1984) implies that they are not". I agree with this comment and, in the following section I will try to resolve the problem.



Figs 18-24. Details of the morphology of Amphipterygidae (18-20) and Diphlebiidae (*Diphlebia euphaeoides*) (21-24): (18) right mandibles, ventral view; – (19) ligulae, dorsal view; – (20) left palpi, dorsal view; A=*Amphipteryx*, De=*Devadatta*, P=*Pentaphlebia*, R=*Rimanella*; – (21) Prementum, dorsal view; – (22) ligula, dorsal; – (23) left palp, dorsal; – (24) right mandible, ventral.

RELATIONSHIPS

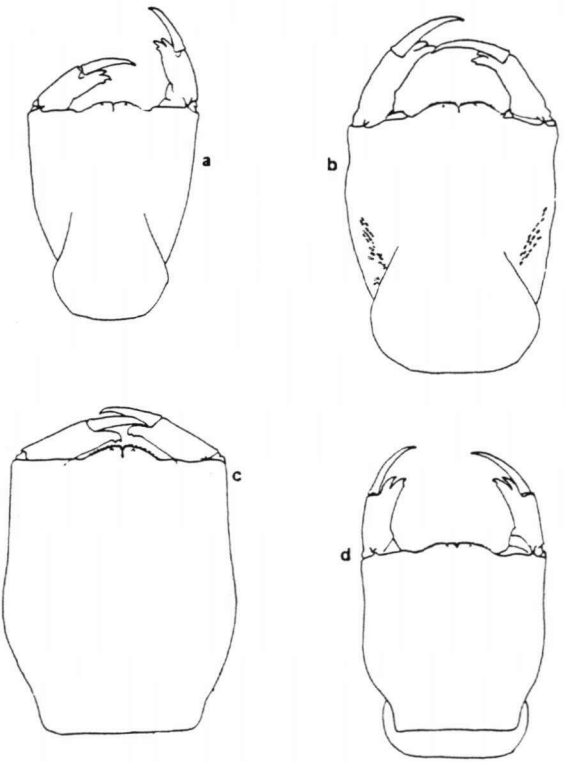


Fig. 25. Prementa of Amphipterygidae, dorsal view: (a) *Amphipteryx*; – (b) *Devadatta*; – (c) *Rimanella*; – (d) *Pentaphlebia*.

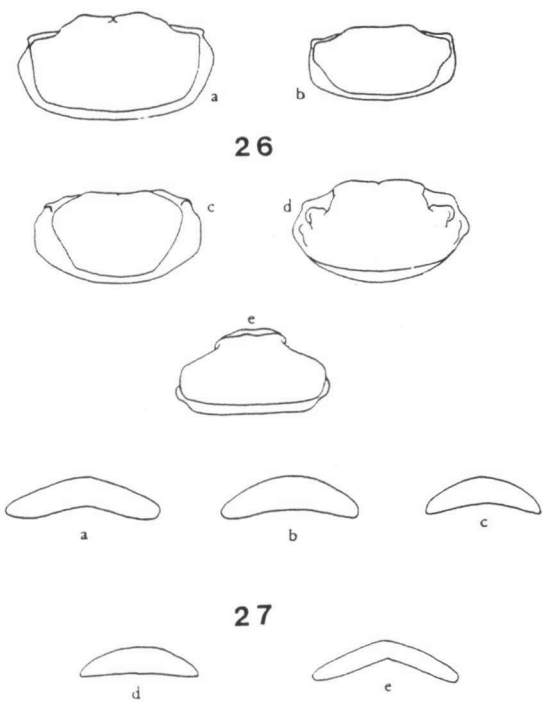
The larva of *Amphipteryx* shows a close resemblance to that of the Oriental genus *Devadatta*, as was suggested by LIEFTINCK (1971). They agree in many aspects but mainly in the structure of the gill tufts and in the shape of epi- and paraprocts (cf. Figs 28A, De; 29A, De). In both genera the bases of the gill tufts are cylindrical and there is a strap-like process ending in a sclerotized plate; the lamina supra-analis is absent; the epi- and paraprocts are saccoid in form bearing a cover of scale-like setae, which in *Devadatta* appear to be mechanoreceptors (WATSON, 1966). Details of morphology are provided for comparison in Figures 17a,b; 18A,De; 19A,De; 20A,De; 25a,b; 26a,b; 27a,b; 28A,De; 29A,De; 30A,De; 31-32. It is interesting to note that adults of both genera show pterostigmata with the basal side strongly slanting.

On the other hand, DAVIES & TOBIN (1984) put the genus *Pentaphlebia* into the subfamily Amphipteryginae together with *Amphipteryx* and *Devadatta*, using adult characteristics. However, there are many differences between larvae of *Pentaphlebia* and those of the other two genera (Tab. I) (see Figs 17-20, 25-34 for comparison).

After a detailed analysis of the larvae, I suggest that *Pentaphlebia* is the closest relative of *Rimanella* taking into account the following features: (1) cephalic lobes sharp (Figs 17c,d); – (2) prementum subrectangular (R) or subquadrate (P) (Figs 25c,d); – (3) pronotum elliptical (Figs 26c,d); – (4) sternite 10 entire (Figs 33-34); – (5) enlarged paraprocts (Figs 29P,R); – (6) general structure and details of the gill tufts; – (7) lamina supra-analis present (reduced in *Rimanella*,

Table I
Main larval differences in Amphipteryginae

Structure	*Amphipteryx-Devadatta*	*Pentaphlebia*
Pedicel	Not hyptertrophied	Hyptertrophied
Femora	Rather cylindrical	Strongly flattened
Dorsal protuberances on abdomen	Absent	Present
Sternite 10	Subdivided	Entire
Epiproct	Almost as long as paraprocts	Very short with respect to paraprocts
Paraprocts	Saccoid	Triquetral
Stem of gill tufts	Issuing from a strap-like process and ending in a sclerotized plate	Issuing from a papilla and not ending in a sclerotized plate
Cerci	Plate-like, closely apposed in the midline	Not plate-like nor closely apposed in the midline
Lamina supra-analis	Absent	Hypertrophied



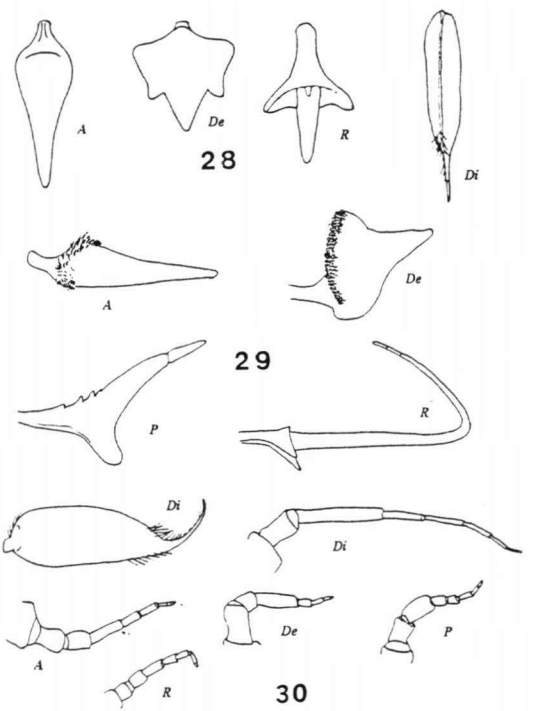
Figs 26-27. Details of the morphology of Amphipterygidae (a--d) and Diphlebiidae (e): (26) pronota; – (27) labra-epipharynx, ventral view: (a) *Amphipteryx*; – (b) *Devadatta*; – (c) *Pentaphlebia*; – (d) *Rimanella*; – (e) *Diphlebia*.

hypertrofied in *Pentaphlebia*) (cf. WATSON, 1966, p. 14, figs 6-7).

As WATSON (1966) pointed out in his excellent paper, "the gill tufts appear to be homologous structures, all being derived from the lamina sub-analis, and not found in any other Odonata". They are present in *Amphipteryx, Devadatta, Pentaphlebia* and *Rimanella*. This apomorphic character plus other important details of the morphology, such as type of setae, size of antenna, shape of prementum and ligula, length of sternite 10 and others, are strong evidence of a common ancestry. Thus, for all these reasons, I suggest that the family Rimanellidae proposed by DAVIES & TOBIN (1984) should disappear, and that a new sub-

family, Pentaphlebiinae, of the Amphipterygidae should be erected, containing the genera *Pentaphlebia* and *Rimanella*. The former is the type genus by priority.

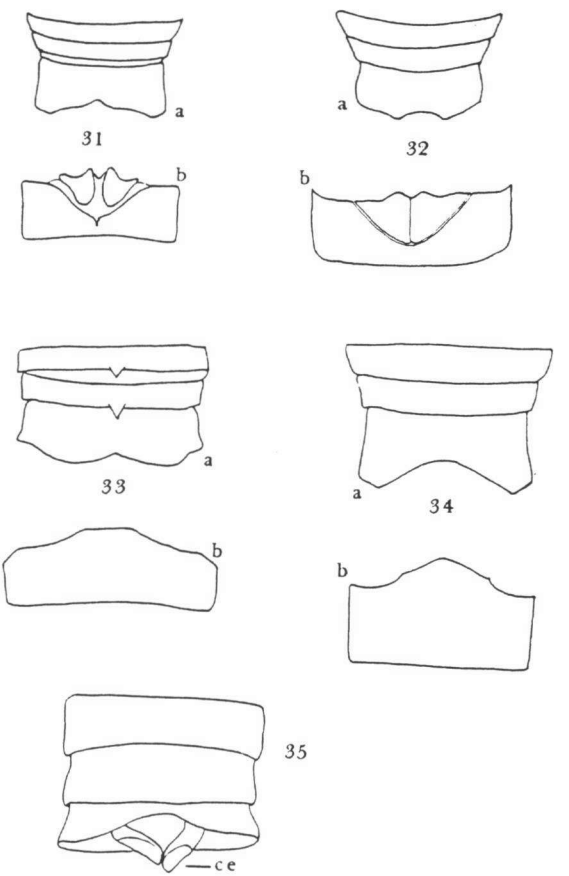
PENTAPHLEBIINAE (new subfamily) – Larvae perlid-like. – H e a d with cephalic lobes sharp (Figs 17c,d); prementum subquadrate or subrectangular (Figs 25c,d), sides with the apical half straight, widening to the base. – T h o r a x: Pronotal disk elliptical (Figs 26c,d). – A b d o m e n with or without dorsal protuberances (Figs 33a, 34a); sternite 10 entire (Figs 33b, 34b). Epiproct short as compared to paraprocts (cf. Figs 28R, 29R), both triquetral; paraprocts tapering caudad, with a subbasal internal (Fig. 29R) or external process (Fig. 29P), tips long (Fig. 29P) or extremely long (Fig. 29R). The bases of the gill tufts are elliptical in section, with or without tubercles, stems of tufts issuing from a papilla. Lamina supra-analis present, hypertrophied or reduced (cf. WATSON, 1966, p. 11, fig. 4; p. 14, figs 6--7).



Figs 28-30. Details of the morphology of Amphipterygidae (A, DE, R, P) and Diphlebiidae (Di): (28) epiprocts, dorsal view; – (29) left paraprocts, dorsal view (A, De, P, Di), ventral view (R); – (30) right antenna. – [A=*Amphipteryx*; De=*Devadatta*; P=*Pentaphlebia*; R=*Rimanella*; Di=*Diphlebia*].

On the other hand, larvae of *Philoganga* show a remarkable resemblance to those of *Diphlebia*, but not to the other genera mentioned above. Larvae of both of these genera share many features in common, according to the descriptions and illustrations provided by FRASER (1938) and ASAHINA (1967) of *P. montana* and *P. vetusta* respectively, when compared to specimens of *D. euphaeoides* that I could analyze directly. It is interesting to note the difficulty of finding resemblances in detail between larvae of *Philoganga-Diphlebia* and the other four genera studied here. The apparently unique characteristic is purely ecological, since all of the genera inhabit torrential mountain streams, usually clinging under the rocks and gravel.

Likewise, Dr. T.W. Donnelly called my attention to the fact that the genus *Lestoidea* belongs with the other Amphipterygids. FRASER (1956) considered the larva of *L. conjuncta* as amphipterygoid, and provided a partial figure of the prementum of *Diphlebia lestoides* for comparison. According to his brief and general description and to his illustration of the larva of *L. conjuncta*, I consider it to be more closely related to the Diphlebiidae than to the Amphipterygidae. With respect to the adults, *L. conjuncta* shows a strongly reduced wing venation compared to that in the Diphlebiidae and Amphipterygidae (cf. Figs 36-42 and Tab. II). However, it is interesting to note the similarity of the three intercalary radial veins between RP1 and RP2 which are proportionally spaced in *L. conjuncta* and *Diphlebia* (see Figs 41 and 42).



Figs 31-35. Details of the morphology of Amphipterygidae and Diphlebiidae: (31) a=tergites 8-10; – b=sternite 10 of *Amphipteryx*; – (32) idem, *Devadatta*; – (33) idem, *Pentaphlebia*; – (34) idem, *Rimanella*; – (35) tergites 8-10 of *Diphlebia*; ce=cerci.

On the light of the larval evidence, I propose that *Philoganga* should be removed from the Amphipterygidae and included in the Diphlebiidae together with *Lestoidea.*

DIPHLEBIIDAE. – Larvae perlid-like; body and legs strongly flattened. – Head: ventral margin of eyes with (Diphlebiinae) or without (Lestoideinae) rows of strong spines; mandibles flattened ventrally with (Diphlebiinae) or without (Lestoideinae) strong, sharp spines; occiput strongly concave (Fig. 17e); cephalic lobes large (Fig. 17e); antennae 7-jointed, longer than head, the pedicel being notably longer than other antennal segments (Fig. 30Di); prementum broad and ovate, with strong marginal spines (Diphlebiinae) (Fig. 21) or square and without

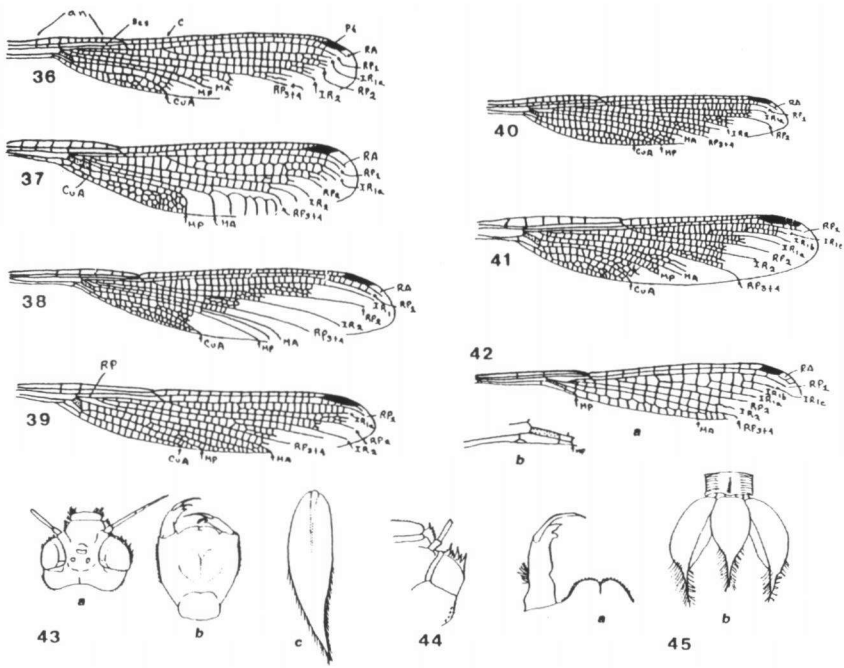
Table II
Some features of the wing venation of Amphipterygidae and Diphlebiidae

Genera	No. of cross veins in scs*	quadrangle	Length of RP until the origin of RP3+4	Origin of RP2 (at or distad of nodus)	Shape of pterostigma	Position of nodus	No. of costal antenodals	No. of subcostal antenodals
Amphipteryx	none	not crossed	short**	3-4 cells	anterior side strongly slanting; 3-4 cross-veins surmounting it	at basal 0.34	7-9	3
Devadatta	none	crossed	short	3-4 cells	as above; 3 cross-veins	at basal 0.34	6-7	4-7
Pentaphlebia	none	not crossed	short	from slightly beyond to one cell	parallel--sided; no cross-veins	at basal 0.33	5	2
Rimanella	none	not crossed	long*** (1-1.5 cells)	slightly beyond	slightly slanting anteriorly; 1-2 cross-veins surmounting it	at basal 0.38	2-3	2
Diphlebia	none	not crossed	short	at nodus	parallel-sided; no crossveins	at basal 0.42	6	2
Philoganga	11	not crossed	long (3 cells)	2-3 cells	as above	at basal 0.42	11-12	14-17
Lestoidea	none	not crossed	short	1.5 cells	slightly slanting anteriorly; no cross-veins	at basal 0.35	2	2

scs*: subcostal space (see Fig. 36); – short**: less than 1 cell long; – long***: more than 1 cell long.

such spines (Lestoideinae); labial palp with three (Diphlebiinae) (Fig. 23) or two (Lestoideinae) well developed end hooks; ligula prominent (Figs 21-22). – T h o r a x robust, broad and flattened (Diphlebiinae) or bulky (Lestoideinae). – A b d o m e n: Segment 10 as long as 9 (Fig. 35); epi- and paraprocts saccoid, soft, without scale-like setae (Figs 28Di, 29Di); gill tufts lacking; cerci slender, digitiform (Dephlebiinae) (Fig. 35) (uncertain for Lestoideinae).

The relative closeness of the two genera of Diphlebiinae is enhanced by the fact that the resting habits of adults, with widespread wings, is common to *Diphlebia* and *Philoganga* (FRASER, 1938; ASAHINA, 1967), and is rather unusual in the Zygoptera. Moreover, the nodus in both genera is placed at 0.42 from



Figs 36-45. Details of the morphology of Amphipterygidae and Diphlebiidae: (36-42) wing venation of: (36) *Amphipteryx agrioides*, FW; – (37) *Devadatta argyoides*, FW; – (38) *Pentaphlebia stahli*, FW; – (39) *Rimanella arcana*, FW; – (40) *Philoganga montana*, HW; – (41) *Diphlebia lestoides*, FW; – (42) *Lestoidea conjuncta*: a=hind wing; – b=posterior border of base of wing; – (43) *Philoganga vetusta*: a=head; – b=prementum; – c=paraproct; – (44) detail of head of *Philoganga montana*; – (45) details of *Lestoidea conjuncta* larva: a=palp and ligula; – b=tergite 10, epi- and paraprocts. – [Figs 36, 40-42 redrawn from MUNZ (1919); 37 and 44 and 38 and 45 after FRASER (1938; 1955, respectively); 39 after NEEDHAM (1933); 43 after ASAHINA (1967). The terminology of wing venation is following the interpretation of RIEK & KUKALOVA-PECK (1984) but adapted by the author (cf. NOVELO-GUTIERREZ et al., 1988)].

the wing's base, while in the other genera it is more basal (cf. Tab. II). Traditionally, several classificatory schemes have been proposed, based mainly on adult wing venation (TILLYARD & FRASER, 1939; DAVIES & TOBIN, 1984). In Table II and Figures 36-42 I summarize and illustrate the wing venation in order to demonstrate that it is not useful in grouping genera.

Summary of the proposed new scheme:

DIPHLEBIIDAE	AMPHIPTERYGIDAE
Diphlebiinae	Amphipteryginae
Diphlebia	*Amphipteryx*
Philoganga	*Devadatta*
Lestoideinae	Pentaphlebiinae
Lestoidea	*Pentaphlebia*
	Rimanella

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REFERENCES

ASAHINA, S., 1967. Notes on two amphipterygid dragonflies from Southeast Asia. *Dt. ent. Z.* (N.F.) 14(3/4): 323-326.

DAVIES, D.A.L. & P. TOBIN, 1984. *The dragonflies of the world.* Vol. 1. *Zygoptera, Anisozygoptera.* Soc. Int. Odonatol., Utrecht.

FÖRSTER, F., 1909. Beiträge zu den Gattungen und Arten der Libellen. *Jb. nassau. Ver. Naturk.* 62: 211-235.

FRASER, F.C., 1938. Additions to the family Amphipterygidae (Order Odonata). *Proc. R. ent. Soc. Lond.* (B)7: 137-143..

FRASER, F.C., 1955. The Megapodagriidae and Amphipterygidae (Odonata) of the African continent. *Proc. R. ent. Soc. Lond.* (B)24: 139-146.

FRASER, F.C., 1956. The nymphs of Synlestes tropicus Tillyard, Chorismagrion risi Morton, Oristicta filicicola Tillyard and Lestoidea conjuncta Tillyard: with description of the female of the latter and further notes on the male. *Austr. Zool.* 12(3): 284-292.

GEIJSKES, D.C., 1940. Notes on Odonata of Surinam. 1. Rimanella arcana Needham and its nymph (Odon. Zyg.). *Revta Ent., Rio de J.* 11(1/2): 173-179.

GONZALEZ-SORIANO, E., 1991. A new species of Amphipteryx Selys, 1853 from Oaxaca, Mexico (Zygoptera: Amphipterygidae). *Odonatologica* 20(4): 465-470.

LIEFTINCK, M.A., 1971. Some unusual features of amphipterygid larvae and their possible phylogenetic significance. *Abstr. Pap. 1st Europ. Symp. Odonatol., Gent.* pp. 31-32.

MUNZ, P.A., 1919. A venational study of the suborder Zygoptera (Odonata) with keys for the identification of genera. *Mem. Am. ent. Soc.* 3: 1-78+20 pl.

NEEDHAM, J.G., 1933. Dragonflies from Mt. Duida and the Venezuelan border. *Am. Mus. Nov.* 664: 1-6.

NOVELO-GUTIERREZ, R., O. CANUL-GONZALEZ & J. CAMAL-MEX, 1988. Los odonatos del estado de Quintana Roo, México (Insecta: Odonata). *Fol. ent. mex.* 74: 13-68.

RIEK, E.F. & J. KUKALOVA-PECK, 1984. A new interpretation of dragonfly wing venation based upon Early Upper Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wing. *Can. J. Zool.* 62: 1150-1166.

SELYS LONGCHAMPS, E. de, 1853. Synopsis des caloptérygines. *Bull. Acad. r. Belg.* 20 (Annexe): 1-73.

SELYS LONGCHAMPS, E. de, 1859. Additions au Synopsis des Caloptérygines. *Bull. Acad. r. Belg.* (2)7: 437-451.

TILLYARD, R.J. & F.C. FRASER, 1939. A reclassification of the order Odonata. Based on some new interpretations of the venation of the dragonfly wing. Part II. *Aust. Zool.* 9(3): 195-221.

WATSON, J.A.L., 1966. The structure and function of the gill tufts in larval Amphipterygidae (Odonata: Zygoptera). *J. Morphol.* 120(1): 9-21.