

***Pamita hannahdaltonae* gen. nov., sp. nov.
from Baltic amber (Odonata: Amphipterygida)**

Michael L. May & Frank Louis Carle

Department of Entomology, Cook College, Rutgers University, 93 Lipman Drive,
New Brunswick, NJ 08901 USA. <may@aesop.rutgers.edu>

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ABSTRACT

The first known amphipterygid-like zygopteran from amber is described. Although its provenance is not known with certainty, we feel confident in attributing it to the Baltic amber deposits of northern Europe. It thus represents the first Old World Tertiary amphipterygidan and substantially extends the known geographic range of the taxon. Based on current knowledge its phylogenetic position cannot be ascertained reliably, but its possible relationships are discussed. It shares a mixture of characters with extant species including Amphipterygidae, Diphlebiidae, Thaumato-neurinae and Lestoideinae.

INTRODUCTION

The relationships of the Zygoptera placed by Bechly (1996) in the Amphipterygida have been a matter of uncertainty and controversy, both among themselves and with other Zygoptera, for many years (Selys 1853; Calvert 1913; Tillyard & Fraser 1938; Fraser 1957; Davies & Tobin 1984; Novelo-Gutierrez 1995; Bechly 1996). Members of the group exhibit a variety of unusual adult and larval traits, and in many cases these have been difficult to characterize as plesiomorphic or apomorphic. It is our hope that knowledge of the new taxon described here ultimately may contribute to a better understanding of this fascinating assemblage of zygopterans.

Relatively few fossil Odonata are known from amber, and nearly all of these are Zygoptera (Poinar 1996; Bechly 1998), undoubtedly because they are weaker fliers and thus more likely to become entangled in resin than are Anisoptera. Bechly (1998) listed 10 known Odonata specimens from Dominican (dated to 25-45 Mya) and 22 from Baltic (40-50 Mya) amber deposits. Of the zygopterans that can be identified with extant families, most are Coenagrionidae (or at least Coenagrionoidea), although at least two are probable lestids and one a euphaeid. Heretofore, none have been attributed unequivocally to Amphipterygida. In this paper we describe from Baltic amber a female amphipterygid, with a nearly complete head, thorax and legs, plus the bases of the abdomen and wings.

METHODS

The specimen was examined using a Wild M5 stereomicroscope and photographed with a Nikon CoolPix 4300 digital camera. All measurements were made using a ruler from photographs taken normal to the surface to be measured and appropriately calibrated by photographing the ruler, and drawings were also traced from photographs; measurements are in millimeters. Counts and qualitative characters were assessed by direct observation. Specimens of extant Amphipterygida and their possible relatives (Bechly 1996) were measured and observed directly and from figures of wings in Munz (1919) and Fraser (1957); relative measurements of fossil wings, except *Protamphipteryx basalis* Cockerell (see below), were made using drawings from the literature. Terminology for body morphology follows Westfall & May (1996), except abdominal segments are designated S1-S10, while that for venation follows Riek & Kukolova-Peck (1984), except that the compound vein forming the leading edge of the wing is simply designated as the costa, C.

Pamita hannahdaltonae gen. nov., sp. nov.
(Figs 1a-d, Plate IV)

Etymology

The genus name, a feminine noun, is the name of a figure from Buddhist mythology, the mother of Devadatta; the latter is also the name of an extant amphipterygid genus. The specific epithet, a Latinized genitive feminine noun, honors Hannah Dalton, the daughter of Richard Levey, the discoverer of the specimen.

Specimen examined

Holotype female: a Zygoptera specimen consisting of the thorax and legs, most of the head, and the basal portions of the abdomen and all four wings. Preserved in amber, believed to be Baltic in origin (see below), but locality and date of collection unknown. Deposited in the collection of the American Museum of Natural History, NY, USA; Specimen # AMNH Ba05-1.

Diagnosis

The new taxon is compared in Table 1 to all extant and fossil genera placed in Amphipterygida (sensu Bechly 1996). The Table also includes the extant *Lestoidea*, placed by Bechly (1996) in Coenagrionomorpha, Hypolestidae, but regarded by Fraser (1957) as a pseudolestid; *Protamphipteryx*, known only from a fragment of one wing from the Eocene-age Green River Formation of Wyoming (Cockerell 1920) and not treated by Bechly; and the newly described Palaeocene genus, *Latibasalia* (Petrulevicius & Nel 2004). We excluded the Mesozoic fossil genera *Triassolestes* and *Steleopteron*, included implicitly or explicitly in Amphipterygidae by Fraser (1957) but treated as well outside Amphipterygidae by Carle (1982) and as perhaps not belonging to Zygoptera by Bechly (1996). No single venation character is unique to *P. hannahdaltonae*, but the species shares the distal widening

of the RA-RP₁ space only with the very different *P. basalis* (see below) and differs markedly in many characters from any other taxon. Note that the Table is intended only as a diagnostic tool, not as an indicator of phylogeny or character polarity.

Description

The specimen is contained in a polished piece of amber 46.5 mm long and approximately 14 x 22 mm at the larger end, 11 x 14 mm at the smaller. In addition to the zygopteran, the amber piece contains a small midge (Diptera: Nematocera) and an ant (Hymenoptera: Formicidae), both apparently intact.

Entire thorax and all six legs preserved intact but surface details largely obscured by heavy investment of “Verlummung” – a milky coating apparently arising from chemical or physical reactions and characteristic almost exclusively of Baltic amber (D. Grimaldi pers. comm.). Head also intact except dorsal portion of left eye and small rim of epicranium bordering eye, evidently destroyed during polishing. Abdomen truncated at amber surface about midway along S3. Likewise each wing

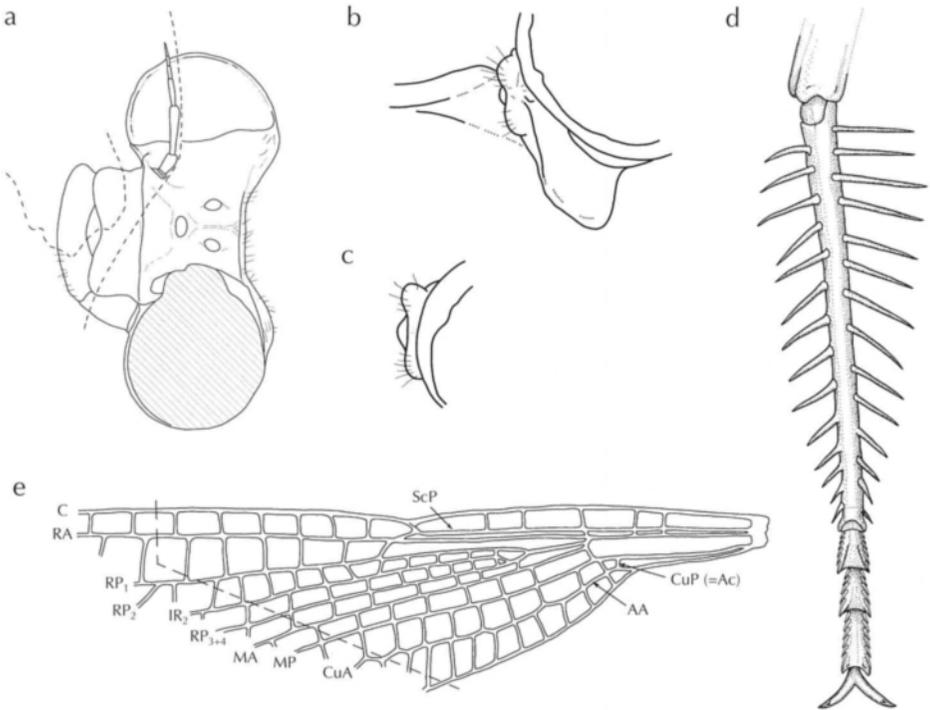


Figure 1: *Pamita hannahdaltoneae* gen. nov., sp. nov. from Baltic amber — (a) dorsal view of head. Dashed lines indicating position of cracks in matrix that partially obscure nearby structures; these areas had to be filled in freehand based in part on oblique views; (b) posterior lobe of prothorax in dorsal and (c) oblique dorsolateral views, partly obscured by left eye; (d) right mesotibia – showing tibial armature; (e) right forewing; view of area distal to dashed line distorted by curvature of matrix and filled in freehand based on non-orthogonal views.

truncated: right front $8\frac{1}{2}$ cells beyond nodus along the costa and obliquely to about even with the nodus along the posterior margin; left front at level of nodus on costa and curving slightly basad near posterior edge; and hindwings at about level of arculus (right wing) or distal end of discoidal cell (left wing).

Head: about twice as wide as long, dorsal surface with numerous scattered setae, especially on labrum, occipital ridge well developed, occipital lobes slightly protuberant, interocular distance 2.6 mm (Fig. 1a). Epicranium with lateral ocelli on distinct prominences, 0.95 mm apart and 0.73 mm from median ocellus, measured from centers; postfrontal suture well-developed, ecdysial line apparently present but partly obscured. Frons rounded; right antenna intact, with lengths of three basal segments in approximate ratios of 1:1.4:1, more distal flagellar segments indistinct but probably three present. Postclypeus with small, shelf-like projections on each side in lateral half, possibly exaggerated by slight dorsoventral compression, labrum narrowed basally, margin smoothly rounded. Right mandible not visible in dorsal view and probably missing. Labium with deep median groove to base but with distal cleft, if present, obscured. Color pattern obscured.

Thorax: prothorax partly obscured by head, apparently without unusual ornamentation, margin of hind lobe (Fig. 1b, 1c) with trapezoidal projection, slightly excavated medially. Pterothorax rather short but broad and deep, middorsal carina with anterior bifurcation at slightly more than $\frac{1}{4}$ distance from mesostigmal laminae to antealar crest. Mesostigmal laminae largely hidden beneath prothorax and head. Mesopleural sutures visible, more lateral thoracic sutures, if present, obscured, color pattern obscured. Legs relatively short, femora and tibiae with row of spurs on each side that are about three times as long as intervening spaces near tibial base but become markedly and progressively shorter toward apex (Fig. 1d), protibiae with well-developed "cleaning combs"; tarsal claws each with small but distinct inferior tooth. Color of legs largely obscured but uniformly dark brown where visible.

Wings: hyaline. Venation described from right forewing (Fig. 1e) unless otherwise noted. Five antenodal crossveins (Ax) between C and Sc at about 0.26, 0.34, 0.49, 0.67 and 0.78 distance from wing base (wb) to nodus (nd), basal 3 (2 in left wing) aligned with crossveins between Sc and R and forming costal braces. Nodal crossvein strongly oblique, well braced; first postnodal crossveins not strengthened, no distinct nodal cell (Petrulevicius & Nel 2004) present. Postnodal crossveins (Px) not aligned, RA and RP₁ diverging distal to nd. Arculus (arc) at 0.50 distance from wb to nd. Space between RA and RP distal to arc (antesubnodal space) without crossveins. Fork of RP₁₋₂ and RP₃₋₄ 0.34 distance from arc to nd, IR₂ apparently branching from RP₃₋₄ (not RP₁₋₂) just beyond first fork. Basal cell between RP and MA short, ending less than 1 cell beyond end of discoidal cell. Fork of RP₂ from RP₁ barely visible before cut edge of wing, between Px 6 and 7 (between C and RA) or 5 and 6 (between RA and RP₁) distal to nodus. Discoidal cell quadrate, uncrossed, 0.35 times as long as distance from arc to nd. Discal brace (connecting MA and CuA at end of discoidal cell) well-developed, transverse; discal nodus (Carle 1982) clearly present. Subquadrangle 3-celled. "Anal crossing" (base of CuP) distal to branch of AA from posterior wing margin by distance (0.8 mm) greater than its own length (0.25 mm); no crossveins in space basal to anal crossing. Basal cell between branch of AA and posterior wing margin short, not extending beyond arcu-

lus. CuA/CuP+AA gradually diverging forward from wing margin, with single row of 10 cells between it and posterior wing margin basal to nd.

Abdomen: abdominal base without unusual morphological features. Color pattern partly visible, consisting of broad pale lateral stripe on each side of S2, narrower pale stripes in corresponding position of S3 extending as far as segment is preserved.

Measurements: head 6.2 mm (max. across eyes) x 3.0 mm (occipital ridge to anterior margin of labrum); thorax, including prothorax 7.2 mm long x 3.5 mm high (values approximate since anterior and ventral margins were estimated); mesotibia 4.5 mm; wing petiole (base to origin of vein AA) 3.6 mm; distance from wing base to nodus 10.3 mm.

DISCUSSION

The amber piece containing this damselfly was purchased as jewelry from a commercial dealer, and its origins are not known. It is certainly not counterfeit, however, because the included damselfly is unlike any extant species, and the presence of abundant *Verlumung* on the surface of the specimen identifies it with near certainty as genuine Baltic amber (D. Grimaldi pers. comm.). Thus *Pamita hannahdaltonae* very probably inhabited northern Europe around 40-50 million years ago. Extant Amphipterygida, under the broadest possible definition of the taxon, are found in Central America (*Amphipteryx*, *Thaumatoneura*), northern South America (*Rimanella*), West Africa (*Pentaphlebia*), Southeast Asia to southern China (*Devadatta*, *Philoganga*, *Pseudolestes*), and Australia (*Diphlebia*, *Lestoidea*). Fossil species are from China (*Conqingia*), Brazil (*Euarthistigma*), Argentina (*Latibasalia*), and the western US (*Dysagrion*, *Petrolestes*, *Phenacolestes*, *Protamphipteryx*).

The species clearly belongs to the Amphipterygida, and could also be placed in the more restricted Amphipterygidae, sensu Fraser (1957), based on the number and arrangement of the Ax and the separation of RP₁₋₂ and RP₃₋₄ occurring nearer to the arc than to the nd. It is difficult or impossible at present to place *Pamita* within this assemblage, however, as Novelo-Gutierrez (1995) showed that larval characters are a much more reliable guide to affinities among many Amphipterygida than is venation. It should be noted that Bechly's (1996) classification relies mostly on adult characters (necessarily so for fossil species) and that, among the extant species listed in Table 1, the larva of *Pseudolestes* is unknown. It is thus uncertain that all the genera listed are closely related, and we have preliminary evidence suggesting that the Amphipterygida may be paraphyletic (K.M. Kjer, F.L. Carle and M. May unpubl.). Nevertheless, we made the Table as inclusive as possible to facilitate a broad comparison among taxa.

Several venational and other features separate *Pamita* from any extant species. Characters differ widely among genera and adult character polarities are poorly known, so phylogenetically meaningful resemblances are hard to detect. Some features of *Pamita* that stand out merely because the character states are uncommon among these taxa include: (1) intermediate length of discoidal cell – shared with *Pseudolestes* and *Thaumatoneura*; (2) multicelled subquadrangle – shared with *Devadatta* and some *Thaumatoneura*; (3) absence of doubled cells before nd and posterior to CuA – shared with *Devadatta*, *Pseudolestes*, and *Rimanella*; (4) very short basal cell in fork of AA – shared in less extreme degree with *Thaumatoneura*;

Table 1. Comparison of character states of *Pamita* with those of corresponding characters of other extant and fossil putative Amphipterygidae. Note that for purposes of comparison we accepted as part of this group genera (e.g., *Pseudolestes*, *Thaumtoneura*, *Latibasalia*) that are placed there with considerable doubt. — Character list: (1) number of antenodal crossveins in costal space; (2) number of antenodal crossveins in subcostal space; (3) position of arculus as fraction of distance from wing base to nodus; (4) position of RP₁₊₂-RP₃₊₄ fork as fraction of distance from arculus to nodus; (5) discoidal cell length as fraction of distance from arculus to nodus; (6) number of cells composing discoidal cell; (7) shape of discoidal cell: quadrate (qd); slightly trapezoidal (tr±); distinctly trapezoidal (tr++); (8) number of cells in subquadrangle; (9) number of crossveins in space basal to anal crossing (base of CuP); (10) distance of anal crossing beyond fork of AA from posterior wing margin: further than its own length (>), less than or equal to its own length (<), or at or before fork (-); (11) number of crossveins in RA-RP (antesubnodal) space; (12) basal-most space between RP₃₊₄ and MA with (+) or without (-) crossveins before end of discoidal cell; (13) length of basal-most space between RP₃₊₄ and MA relative to length of discoidal cell; (14) RA-RP₁ beyond nodus markedly divergent (+) or not markedly divergent (-); (15) number of cells before nodus between CuA and wing margin; (16) number of doubled cells before nodus between CuA and wing margin; (17) length of basal cell in fork of AA from posterior wing margin as fraction of distance from wing base-nodus; (18) number of cells between nodus and origin of RP2 (number in RA-RP₁ space | number in C-RA space); (19) vein from which IR₂ diverges: RP₃₋₄ (0), RP₁₋₂ (1); (20) relative length of three basal antennal segments (1st:2nd:3rd); (21) shape of margin of hind lobe of pronotum: with pronounced median lobe (0), smoothly rounded (1), with prominent lamellate lateral lobes (2), slightly undulate with very low rounded median lobe (3). (*only male examined); (22) tibial spurs, basally at least, twice as long as intervening spaces (+) or distinctly less than twice as long as intervening spaces (-); (23) frons rounded (ro), inclined (in), or angulate (an); ^A – abruptly rounded, approaching state “an”; ^B – postfrontal suture obsolete; ^C – postfrontal suture present.

	1	2	3	4	5	6	7	8
<i>Pamita</i>	5	2-3	0.50	0.34	0.35	1	qd	3
Extant genera								
<i>Amphipteryx</i>	7-9	3	0.46	0.16	0.22	1	tr++	1
<i>Devadatta</i>	6-8	4-7	0.55	0.18	0.50	4	tr±	3-4
<i>Diphlebia</i>	5-7	2	0.34	0.17	0.19	1	qd	1
<i>Lestoidea</i>	2	2	0.50	0.30-0.41	0.32-0.46	1	qd	1
<i>Pentaphebia</i>	5	2	0.55	0.20	0.18	1	tr±	1
<i>Philoganga</i>	11-16	14-20	0.39	0.33	0.13	1	qd	1
<i>Pseudolestes</i>	2	2	0.54	0.17	0.34	1	tr±	1
<i>Rimanella</i>	2-3	2	0.46	0.29	0.12	1	tr++	1
<i>Thaumtoneura</i>	3-4	2	0.36	0.85	0.28	1	qd	1-2
Other fossil genera								
<i>Congqingia</i>	2	2	~0.45	0.35	0.19	1	tr±	1
<i>Dysagrion</i>	4	2	0.36	0.61	0.10	1	tr±	1-2
<i>Euarchistigma</i>	2	2	0.64	0.81	0.77	1	qd	1
<i>Latibasalia</i>	2	2	?	?	?	?	tr++	?
<i>Petrolestes</i>	2	2	~0.35	0.40	0.17	1	tr±	1
<i>Phenacolestes</i>	5	2	0.45	0.63	0.24	1	tr±	2
<i>Protamphipteryx</i>	6	2	0.33	0.47	?	?	?	?

	9	10	11	12	13	14	15	16
<i>Pamita</i>	0	>	0	-	1.1	+	9	0
Extant genera								
<i>Amphipteryx</i>	0	>	1-3	+	0.88	-	10-11	2
<i>Devadatta</i>	3	<	2-3	+	0.48	-	7-8	0
<i>Diphlebia</i>	0	<	0	-	1.0	-	10	5
<i>Lestoidea</i>	0	n/a	0	-	2.3	-	1	n/a
<i>Pentaplebia</i>	0	-	0	-	1.5	-	11	2
<i>Philoganga</i>	0	>	10-12	-	2.4	-	15	6
<i>Pseudolestes</i>	0	<	0	-	0.91	-	7	0
<i>Rimanella</i>	0	>	0	-	4.4	-	11-12	0
<i>Thaumatoneura</i>	0	-	0-1	-	5.8	-	13	11

Other fossil genera

<i>Congqingia</i>	0-1	?	0	-	3.9	-	12	2
<i>Dysagrion</i>	0	>	0	-	5.0-6.9	-	14	12
<i>Euarchistigma</i>	0	<	0-1	-	1.1	-	3	0
<i>Latibasalia</i>	?	?	0	?	~2-3	-	?	?
<i>Petrolestes</i>	0	>	0	-	3.8	-	12	9
<i>Phenacolestes</i>	0	>	0	-	3.0	-	8	3
<i>Protamphipteryx</i>	0	?	0	?	?	+	?	?

	17	18	19	20	21	22	23
<i>Pamita</i>	0.036	5½ 6½	0	1.0:1.4:1.0	0	+	ro
Extant genera							
<i>Amphipteryx</i>	0.069	5 5	1	1.0:1.2:1.5	2	+	ro ^A
<i>Devadatta</i>	0.082	3½ 4½	1	1.0:0.67:0.72	1	-	in ^B
<i>Diphlebia</i>	0.075	½ 1½	1	1.0:3.6:0.66	1	+	ro
<i>Lestoidea</i>	n/a	1½-2½ 1½-2½	0,1	1.0:2.5:1.6	0	+	ro
<i>Pentaplebia</i>	0.18	1 2	1	1.0:2.2:--	1	+	an
<i>Philoganga</i>	0.074	1½-2½ 2½	1	1.0:3.0:0.91	1	-	ro
<i>Pseudolestes</i>	0.19	5 4	1	seg2>3>1	1	+	?
<i>Rimanella</i>	0.16	1-2 1-2	1	1.0:1.7:1.9	1*	-	ro
<i>Thaumatoneura</i>	0.054	>20	0,1	1.0:1.1:0.91	3	+	in ^C

Other fossil genera

<i>Congqingia</i>	~0.2	1-2½ 1-1½	?	?	?	?	?
<i>Dysagrion</i>	0.19	2½ 2	0	?	?	?	?
<i>Euarchistigma</i>	0.14	12-15 14-18	0	?	?	+	?
<i>Latibasalia</i>	?	6-13 7-16	1	?	?	?	?
<i>Petrolestes</i>	0.28	2 1½	0	?	?	?	?
<i>Phenacolestes</i>	0.21	5½ 5½	0	?	?	?	?
<i>Protamphipteryx</i>	0.13	6 5½	1	?	?	?	?

n/a – not applicable because of reduced venation of *Lestoidea*

(5) origin of IR_2 from RP_{3+4} rather than RP_{1+2} – shared with minority of *Lestoidea*, *Diphlebia* and *Thaumatoneura* individuals; and (6) intermediate relative length of antennal segment 1 – shared with *Amphipteryx*, *Rimanella*, and *Thaumatoneura*. On the other hand, it differs markedly from each of these genera in some other characters (Table 1). The quadrate discoidal cell suggests that *Pamita* may not be closely related to Amphipterigidae s.str. (Bechly, 1996), but in some genera (e.g., *Devadatta*) within the latter family the distal end of the quadrilateral is often only very slightly oblique. Obviously any placement is highly speculative until clear synapomorphies among adult characters are identified for the various amphipterygidan taxa.

From its description, the very incomplete *Protamphipteryx basalis*, which is also of approximately the same geologic age, appears similar to *P. hannahdaltonae* in sharing an apparently unique synapomorphy, the distal divergence of RA and RP_1 beyond the nodus. Examination of the type (and unique example) of *P. basalis*, however, reveals that the divergence is less marked than in the present species. More importantly, in *P. basalis* the arculus is positioned midway between the two costal braces, and RP_1 curves sharply forward near its base, so that it nearly touches RA just beyond the fork of IR_2 . Furthermore, although the posterior margin of the wing is poorly preserved, it appears that it was probably nearly unpetiolated. These characters distinguish *P. basalis* markedly from *P. hannahdaltonae* and from all other amphipterygidans. A note further describing this interesting fossil is in preparation.

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