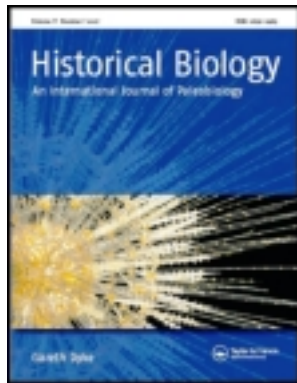


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***Vetuformosa buckleyi* n. gen., n. sp. (Ephemeroptera: Baetidae; Vetuformosinae n. subfam.), a new subfamily of mayflies in Early Cretaceous Burmese amber**

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A new subfamily, genus and species of mayflies, *Vetuformosa buckleyi* n. gen., n. sp. (Ephemeroptera: Baetidae; Vetuformosinae n. subfam.), are described as the first representative of the family Baetidae from Early Cretaceous Burmese amber. The female fossil is characterised by unusually long antennae, two pairs of gonostyli representing a primitive appendiculate ovipositor, sensory patches on sternites 8, 9 and 10, protuberances on the egg chorion and the absence of a costal projection on the hind wing. This is the first documentation of such long antennae and a primary ovipositor in the Ephemeroptera.

Keywords: mayfly appendiculate ovipositor; sensory patches; Burmese amber; Early Cretaceous baetid

Introduction

Mayflies are one of the most commonly encountered insect groups in moving and still water. The aquatic young (larvae, naiads or nymphs) ingest diatoms and desmids, whereas the winged adults have vestigial mouthparts and do not feed. The adults live only a few days at most and spend their time mating and egg laying. Mayflies are unique among insects in undergoing a moult in the adult stage. The larva moults into a winged preimago, which moults again to reach the sexually mature adult (imago) (Morgan 1930; Needham et al. 1935).

A small female baetid mayfly imago in Early Cretaceous Burmese amber is described in the present study. The fossil taxon contains several noteworthy features not known to occur on extant mayflies, namely the especially long antennae, sensory patches on sternites 8, 9 and 10 and two pairs of gonostyli forming a primitive appendiculate ovipositor.

Materials and methods

The amber piece weighs 1.5 g and is roughly rectangular in shape with the greatest length of 19 mm, greatest width of 15 mm and greatest depth of 5 mm.

The amber was obtained from a mine first excavated in 2001, in the Hukawng Valley, southwest of Maingkhwan in Kachin State (26°20' N, 96°36' E) in Burma (Myanmar). This new amber site, known as the Noiye Bum 2001 Summit Site, was assigned to the Early Cretaceous, Upper Albian, on the basis of paleontological evidence (Cruikshank and Ko 2003), placing the age at 97–110 mya. Nuclear magnetic resonance spectra and the presence of araucaroid

wood fibres in amber samples from the Noiye Bum 2001 Summit site indicate an araucarian (possibly *Agathis*) tree source for the amber (Poinar et al. 2007). Observations, drawings and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 600 ×. Higher rank group names use the McCafferty classification (Sun et al. 2006). Names for sections of the thorax follow Kluge (2004).

Description

The specimen is complete, well preserved and perfectly positioned in the amber. One of the two caudal filaments is disconnected but adjacent to the fossil. Although the specimen is an imago with fully developed eggs, remnants of the subimago cuticle with some microtrichia are retained on portions of the left forewing.

The main apomorphies of the Baetidae present on the fossil are the transformation of the forewing vein MA2 into an intercalary vein and the hind tarsi with only three movable joints (Kluge 2004).

Order: Ephemeroptera
Suborder: Pisciforma McCafferty
Superfamily: Baetoidea Leach, 1815
Family: Baetidae Leach, 1815
Subfamily: Vetuformosinae Poinar new subfamily
Type genus: *Vetuformosa*, new genus
Diagnosis: Same as type genus since monotypic.
Vetuformosa: Poinar new genus
Type species: *Vetuformosa buckleyi* n. sp.

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Diagnosis

Body minute; antennae elongate, 3.8 times head length, with multisegmented flagellum; legs well developed; tibio-patellar suture fused on forelegs but distinct on middle and hind legs; fore tarsus four-jointed; mid and hind tarsi three-jointed; claws on all legs dissimilar; forewings hyaline, without colour pattern, with few cross veins and single intercalary marginals; R2 forked twice; hind wing small, with three longitudinal veins, lacking costal process and cross veins; hind margin of both wings fringed with short hairs, two pairs of gonostyli surround vulva on sternite VIII; sensory patches on tip of sternite VIII, posterior margin of sternite IX and base of sternite X; caudal filaments long, over five times body length; paracercus rudimentary, single segmented.

Etymology

Vetu is from the Latin ‘vetus’ for old and formosa is from the Latin ‘formosus’ for beautifully formed.

Comments

The fossil taxon shows some similarities, such as small size, presence of single marginal intercalaries and distinct patella-tibial sutures only on the middle and hind legs, with the Late Cretaceous Taimyr amber baetid, *Palaeocloeon taimyricum* (Kluge 1997) that was placed in the fossil subfamily Palaeocloeoninae (Kluge 1997, 2004). However, *Vetuformosa* differs from *Palaeocloeon* with its longer antennal flagella (over three times head length; whereas in *Palaeocloeon*, it is only 1.5 times head length), the presence of gonostyli on abdominal sternite VIII and sensory patches on the tip of sternite VIII, the posterior margin of sternite IX and at the base of sternite X. Also, there is no costal spur on the hind wing of *Vetuformosa* as on *Palaeocloeon* and R3 in the forewing forks twice in *Vetuformosa*, but is a simple intercalary vein in *Palaeocloeon*.

***Vetuformosa buckleyi* Poinar n. sp. (Figures 1–8)**

With characters listed in the generic diagnosis: all measurements are in microns unless otherwise noted.

Material examined

Holotype female; body brown, legs yellow; total body length, 1.8 mm; forewing length, 2.5 mm. Male and larva unknown.

Head

Small, length, 155; compound eyes rounded, protruding; antenna relatively long in relation to head; scape broad, glabrous, length 40; pedicel narrowed slightly at tip, glabrous, 74 long; flagellum multisegmented, 458 long,

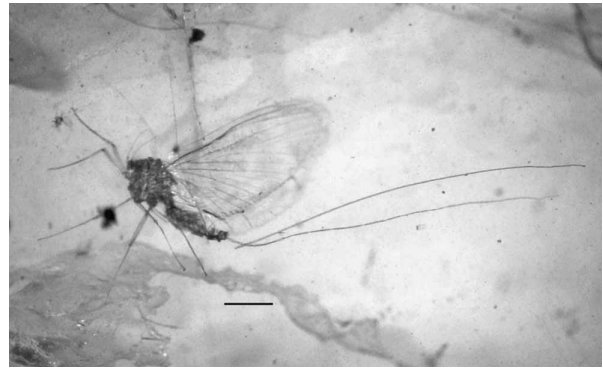


Figure 1. *Vetuformosa buckleyi* in Early Cretaceous Burmese amber; bar = 707 μ m.

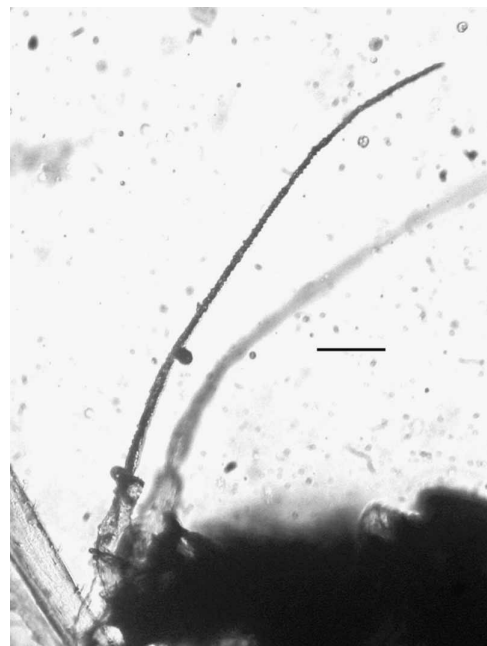


Figure 2. Left antenna of *V. buckleyi* in Early Cretaceous Burmese amber. Note the elongate flagellum; bar = 54 μ m.

segments beaded (as if formed by string of minute beads), glabrous.

Thorax

Compact, length, 130, greatest width, 90; anternotal protuberance reduced; mesonotal suture distinct; anterior and posterior medioscutal nodes and posterior sutural protuberance distinct; metanotum with scutellum and phragma; other mesonotal sutures not decipherable (see Figure 4); foreleg with coxa and trochanter distinct, less so in middle and hind legs; femora flattened; profemur (406 long) shorter than mesofemur (490 long) and metafemur (539 long); propatella (length, 140) fused with protibia; protibia (490 long) shorter than mesotibia (630 long) and metatibia (630 long); mesopatella (140 long) and metapatella (140 long) with distinct suture; tarsal formula

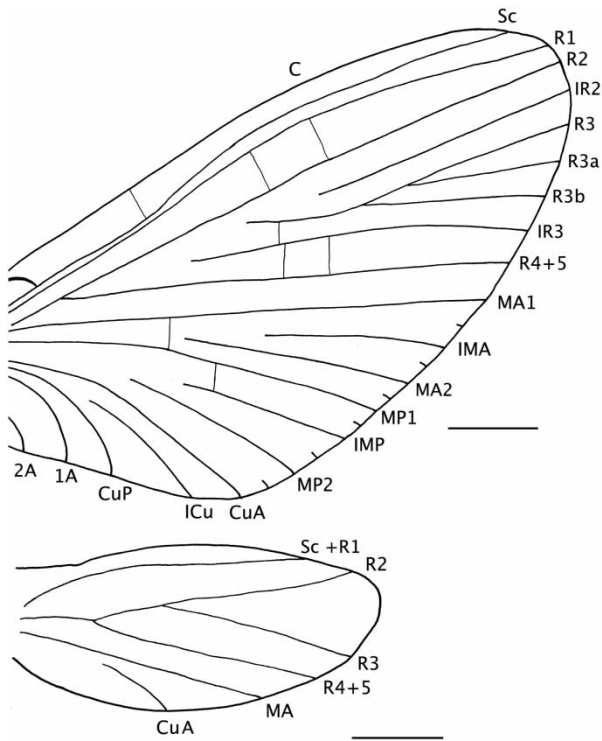


Figure 3. Forewing and hind wing of *V. buckleyi* in Early Cretaceous Burmese amber. Forewing bar = 333 μm ; hind wing bar = 160 μm .

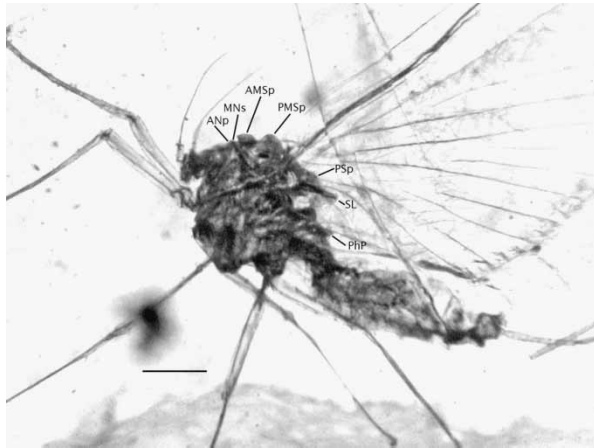


Figure 4. Thoracic structures of *V. buckleyi* in Early Cretaceous Burmese amber. ANp, antennotal protuberance; AMSp, anterior medioscutal protuberance; MNs, mesonotal suture; PhP, posterior phragma; PMSp, posterior medioscutal protuberance; PSp, posterior scutal protuberance; SL, scutellum; bar = 329 μm .

4-3-3; tarsal lengths: foreleg: basitarsus, 154, second tarsomere, 67, third tarsomere, 76, fourth tarsomere, 91; middle leg: basitarsus, 57; second tarsomere, 69; third tarsomere, 92; hind leg: basitarsus, 53; second tarsomere, 47; third tarsomere, 79; claws on all legs dissimilar; foreleg with one short pointed claw and one larger blunt-tipped swollen claw; middle leg with one swollen claw and

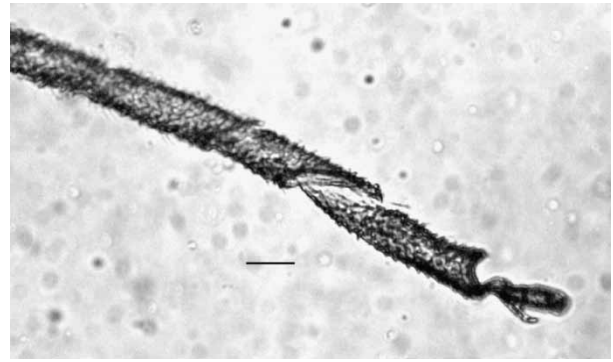


Figure 5. Foretarsus of *V. buckleyi* in Early Cretaceous Burmese amber. Note dissimilar claws; bar = 20 μm .

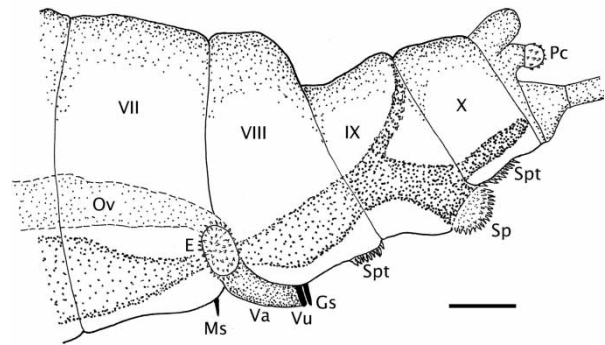


Figure 6. Abdominal segments VII–X of *V. buckleyi* in Early Cretaceous Burmese amber: E, egg (only outer egg shown); Gs, gonostyli (only outer pair shown); Ov, oviduct; Ms, mating spine; Pc, paracercus; Sp, sensory pad; Spt, sensory patch; Va, vagina; Vu, vulva; bar = 55 μm .

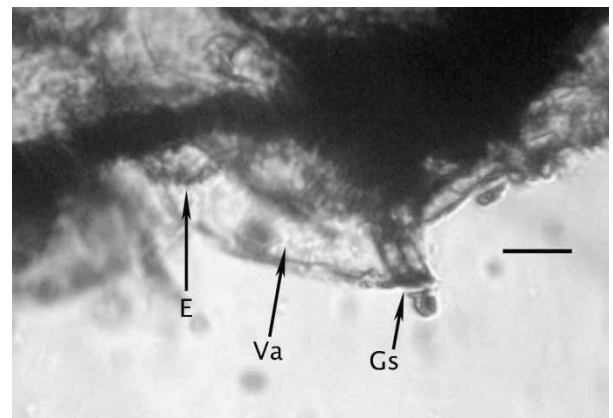


Figure 7. Egg (E), vagina (Va) and outer pair of gonostyli (Gs) of *V. buckleyi* in Early Cretaceous Burmese amber; bar = 26 μm .

one thickened pointed claw, both subequal in length; hind leg with one swollen claw and one stout pointed claw.

Wings (Figure 3)

Sc free, visible for entire length; vein MA2 transformed to intercalary vein, MA1 unforked, with two basally unattached free veins behind it; some short basally

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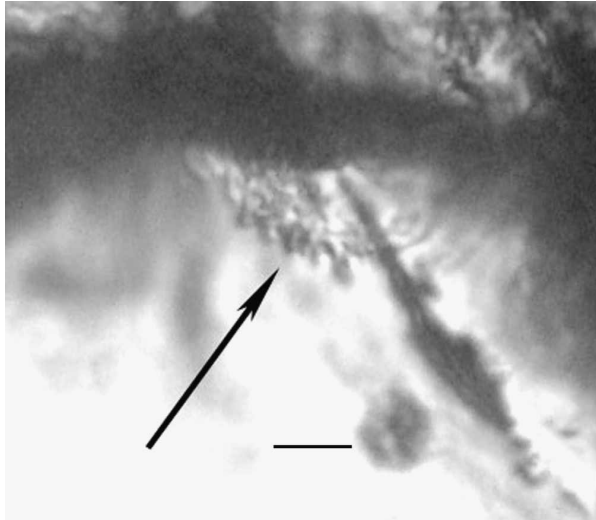


Figure 8. Protuberances (arrow) on egg chorion of *V. buckleyi* in Early Cretaceous Burmese amber; bar = 14 μm .

detached single marginal intercalaries in the centre of six interspaces; R2 with a series of intercalary veins, two of which branch off from a third; 1A extending to the hind margin of wing; bases of MA2 and MP2 atrophied.

All wings are present but only one hind wing is decipherable; venation of forewings identical; forewing length, 2.5 mm; costa with strong brace vein; Sc, R1 and R2 simple to wing margin; R2 followed by intercalary vein IR2; R3 free at base, with two forks (R3a and R3b); R4 + 5 and MA1 simple to wing margin; MA1 followed by intercalary vein IMA; MA2 free, extending only half distance to base; MP1 simple to base, followed by intercalary vein IMP; MP2 free at base; CuA extends to base, followed by intercalary vein ICu; CuP, 1A and 2A all simple to base, all ending at hind wing margin; cross vein connecting lower third of C with Sc, two cross veins connecting R1 with R2; one cross vein connecting R3b with IR3, two cross veins connecting IR3 with R4 + 5; one cross vein connecting MA1 with MA2; one cross vein connecting MP1 with IMP; 6 (possibly more) single marginal intercalaries positioned between veins CuA and MA1; hind margin fringed with short hairs.

Hind wing length, 683; greatest width, 315; with three longitudinal veins; Sc + R1 simple to margin; Rs with two forks, resulting in R2, R3 and R4 + 5; MA simple to base; CuA free at base; hind margin fringed with short hairs; costal projection not observed.

Abdomen (Figures 6 and 7)

Brown, partially cleared, but with little distortion; 11 segmented; paired oviducts enter vagina (common gonadal chamber, oviductus communis and vestibulum) at apex of sternite VII; two pair of non-articulated gonostyli flank the vulva (gonopore, exit aperture and

gonadal opening) on middle of sternite VIII; single egg in terminus of both oviducts; single mating spine at distal edge of sternite VII; tip of sternite VIII bearing short sensory patch; posterior margin of sternite IX (anal plate) with large sensory pad; base of sternite X with sensory patch; eggs elliptical, lengths, 45 and 50, widths, 28 and 32; chorion covered with protuberances; terminus with paired caudal filaments (cerci) extending 5.2 mm in length; caudal filaments covered with short spines orientated posteriorly; paracercus rudimentary, represented by round-tipped stub covered with minute projections.

Diagnosis: same as for genus

Type: Holotype deposited in the Buckley amber collection (accession number E-6).

Type locality: Amber mine at the Noiye Bum 2001 Summit Site in the Hukawng Valley, southwest of Maingkhwan in Kachin State (26°20' N, 96°36' E) in Burma (Myanmar).

Etymology: The specific name 'buckleyi' honours Ron Buckley, who allowed the author to study this valuable fossil and has made additional Burmese amber specimens available for scientific study in the past.

Discussion

This fossil was placed in a separate subfamily, because of its unique features, which include the extremely long antennae in relation to its head (Figure 2), the presence of an appendiculate ovipositor accompanied by sensory patches (Figures 6 and 7) and the protuberances on the egg chorion (Figure 8). The long antennae may be a carry over from the immature stages, because elongated larval antennae are considered an apomorphy in the Baetoidea (Ogden et al. 2009).

The specimen is considered an adult female and not a subimago, even though the hind margins of both wings are fringed with short hairs. Subimagos usually have the outer and hind edges of their wings fringed with a row of fine cilia and the wing surface is covered with falciform microtrichia (Edmunds and McCafferty 1988). Some adult extant mayflies retain cilia on the wing margins (Edmunds and McCafferty 1988) and the short hairs on *Vetuformosa* only occur on the hind margin of the wings. There are remnants of the subimago cuticle retained on portions of the left forewing and these remnants possess microtrichia. Falciform microtrichia is of normal occurrence on the wing surface of subimagos (Edmunds and McCafferty 1988). There are no microtrichia on any other portion of the wings of *Vetuformosa*.

The chorion of mayfly eggs can be smooth or has various types of ornamentation (Needham et al. 1935). The surface may be reticulate, punctate, maculate, tuberculate or with overlapping plates (Koss 1968). Many mayflies, including species of *Heptagenia* Hatch and *Cloeon* Leach,

have nodes (tubercles) on their eggs. In extant forms, these nodes contain coiled strings with terminal knobs that adhere to various substrates when the egg is placed in water. The chorion of the two eggs of *Vetuformosa* is covered with short, uneven protuberances. No extant mayflies were reported to have such a chorion surface. It is unknown what function these may have served during oviposition.

The short, tubular vagina formed by the fusion of the paired oviducts at the distal portion of sternite VII terminates at the vulva in the middle of sternite VIII. Two pairs of sturdy, non-articulated gonostyli flank the vulva. The tips of the first pair are rounded, but those of the second pair are pointed. These gonostyli are considered to represent a primitive appendicular ovipositor (ovipositor formed from appendicular parts of abdominal segments 8 and/or 9; Torre-Bueno 1989).

The egg valves on some mayflies are prolonged and grooved, and together with a depression in sternum 8, they form a common passageway for the eggs, but these modifications are not considered ovipositors and differ from the condition in *Vetuformosa* (Needham et al. 1935). In his discussion on the genital system of mayflies, Kluge (2004) considered that a tubular unpaired vagina by itself could represent a secondary ovipositor.

However, the combination of a vulva with gonostyli in *Vetuformosa* represents a primary, appendicular ovipositor, which was never reported in mayflies (Brinck 1956; Kluge 2004). Such an appendicular ovipositor represents a highly unique character for the fossil taxon and a new character state for Ephemeroptera. The gonostyli, along with the elongate antennae and sensory patches, make *Vetuformosa* unique among mayflies. Some of the larger Paleozoic mayflies, such as the Upper Carboniferous *Triplosoba pulchella* (Brongniart) and the Lower Permian *Protereisma permiana* Sellards, had relatively long antennae, but relative to the head or body length, not as long as that of *Vetuformosa*. There is no mention of gonostyli or sensory patches on Paleozoic mayflies (Tshernova 1991; Carpenter 1992).

Most adult female mayflies lay their eggs on the water surface rather than attaching them to any fixed objects (Koss 1973). However, there are five basic types of ovipositional behaviour in extant mayflies (Sivaramakrishnan and Venkataraman 1985; Encalada and Peckarsky 2007). These ovipositional behavioural types were called splashers, bombers, dippers, floaters and landers (Encalada and Peckarsky 2007). The fossil probably belongs to the 'lander' category. Extant 'landers' go underwater and lay eggs on a submerged substrate or rest on an object at the waterline and deposit her eggs on a substrate just beneath the water line. Morgan (1930) noted that a female *Baetis* sp. that entered the water to deposit her eggs was quite selective regarding the proper ovipositional site and underwent a 'tour of inspection' by touching various substrates with the tip of her abdomen. It is possible that

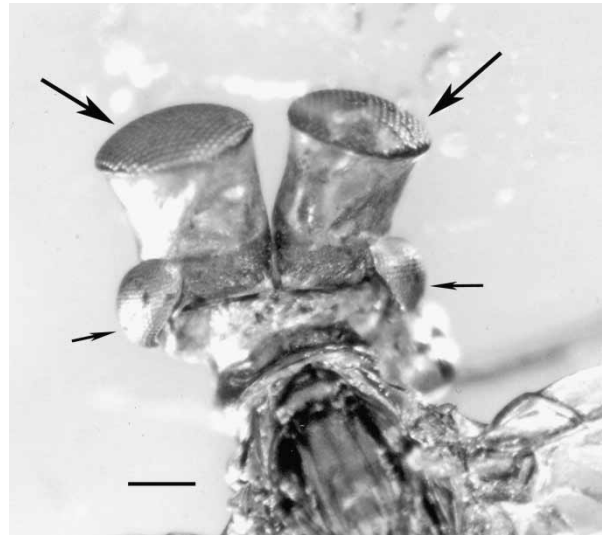


Figure 9. Eyes on a male baetid in Tertiary Dominican amber. Upper large arrows show upward-directed turbinated eyes. Lower, small arrows show lateral eyes. Poinar amber collection accession number Ep-3-13; bar = 184 μ m.

Vetuformosa was also selective in choosing a special site for her eggs that facilitated the use of the gonostyli as well as the sensory patches on sternites 8, 9 and 10 (Figure 6). Such sensory areas have not been observed on extant mayflies to the best of my knowledge. These features, together with the projections on the egg chorion, suggest that *Vetuformosa* had a rather specialised ovipositional site.

The fossil record of the Baetidae is rather sparse and was reviewed by McCafferty (1997), who characterised the oldest fossil of the family in Lebanese amber dated at 135 million years. The Taimyr amber subfamily Palaeocloeoninae is the only baetid known from the Late Cretaceous (Kluge 1997, 2004). Aside from these specimens, some Tertiary baetids occur in Baltic and Dominican (Figure 9) amber and a Pliocene species was reported from Australia (McCafferty 1997).

The present report is the only record of the family Baetidae from Early Cretaceous Burmese amber. Other mayflies in Burmese amber were described in the families Prosopistomatidae (Sinitschenkova 2000) and Australiphemeridae (McCafferty and Santiago-Blay 2008).

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