



# Revised systematics, phylogeny, and paleontology of the mayfly family Baetiscidae (Insecta: Ephemeroptera)

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## Abstract

The systematics of all known extant and fossil taxa of the mayfly family Baetiscidae is reviewed. Previously described fossil Baetiscidae are critically reviewed and their systematic position is re-evaluated. Added herein is the description of *Balticobaetisca bispinata* sp. nov., a new fossil mayfly from Eocene Baltic Amber. Also described for the first time is the putative adult of *Protobaetisca bechlyi* Staniczek, 2007 from the Cretaceous Crato Formation of Brazil. Based on external morphological characters of nymphs and adults, we present the first integrated cladistic analysis of both fossil and extant Baetiscidae, which revealed the monophyly of the respective fossil and extant genera and their phylogenetic splitting sequence as *Cretomitarcys* + (*Protobaetisca* + (*Balticobaetisca* + *Baetisca*)).

## Keywords

Baltic amber, Crato Formation, cladistics, imago, mayflies, new species, nymph, taxonomy

## 1. Introduction

The Baetiscidae, or “armored mayflies” (Insecta: Ephemeroptera) currently comprise ten valid extant species (Pescador and Berner 1981). They are a well-defined monophyletic group (Pescador et al. 2009): their hind wings are of almost circular shape, and adult stages have a bispinate prosternal projection; both characters are generally regarded as autapomorphies of the group (Pescador et al. 2009). Their nymphs have developed a

characteristically shaped, massive notal shield, which dorsally covers most abdominal segments to form a breathing chamber (Notestine 1993). Its sister group, Prosopistomatidae, has a similar mesonotal “carapax” (Barber-James 2009), but unlike in Baetiscidae, it is smooth and without lateral spines and projections. These pronounced spines in Baetiscidae are most probably an apomorphic adaptation to prevent or obstruct devouring

by fish and other predators. Apart from the notal shield as such, potential synapomorphic characters of the two groups are the significant enlargement of the labial postmentum in the nymphs (own observation, but see also Pescador and Berner 1981 and Barber-James 2010), and the characteristic apomorphic forewing venation in which CuP is shifted distally of the wing tornus (Kluge et al. 1995). A close relationship between Baetiscidae and Prosopistomatidae had already been proposed by Lameere (1917). Later, Edmunds and Traver (1954) also supported this classification under the new rank Prosopistomatoidea. While some authors had proposed different phylogenies for the two families (Landa and Soldán 1985, McCafferty 1991), a sistergroup relationship of Baetiscidae and Prosopistomatidae has by now been accepted by most other authors (Kluge 1995, McCafferty 1997, 2001, Kluge 2004, Staniczek 2007, Pescador et al. 2009) and was finally also corroborated by genomic data (Ogden et al. 2009). Other names coined for this monophyletic group were Baetiscoidea (Peters and Hubbard 1989), Posteritorna (Kluge 1995), and Carapacea (McCafferty 2004).

The distribution of extant Baetiscidae is limited to the Nearctic realm (Berner and Pescador 1980). However, recent discoveries of fossil Baetiscidae and Prosopistomatidae greatly improved the knowledge of these mayflies (see also Table 1): *Balticobaetisca velteni* Staniczek and Bechly, 2002 and *Balticobaetisca stuttgartia* Godunko and Krzemiński, 2009 were described from Eocene Baltic Amber (see Staniczek and Bechly 2002; Godunko and Krzemiński 2009). *Protobaetisca bechlyi* Staniczek, 2007 was described in the nymphal stage from a single compression of the Crato Formation in Brazil (Staniczek 2007). Formally undescribed fossil nymphs from the Cretaceous of Australia had been placed within Siphonuridae (Jell and Duncan 1986). *Cretomitarcyis luzzi* Sinitshenkova, 2000 had been described as polymitarcyid mayfly from Cretaceous amber of New Jersey and was later placed in a newly established family Cretomitarcyidae within Prosopistomatoidea by McCafferty (2004). Staniczek (2007) discussed a placement of both of these Australian and North American fossils within Baetiscoidea. Finally, a monotypic genus and species *Myanmarella rossi* Sinitshenkova, 2000 from Cretaceous amber of Myanmar was attributed to Prosopistomatidae, followed by *Proximicorneus rectivenius* Lin et al., 2018.

In this contribution, we describe *Balticobaetisca bispinata* **sp. nov.**, another new fossil species of Baetiscidae from Eocene Baltic Amber. We also describe the putative adult of *Protobaetisca* Staniczek, 2007 from the Cretaceous limestones of Crato, Brazil, which had been only known in the nymphal stage, and comment on its taphonomy. Secondly, we also re-analyse the characters of previously described fossil Baetiscidae and incorporate the confirmed fossil Baetiscidae into an integrated cladistics analysis. This first phylogenetic analysis of Recent and extinct Baetiscidae is aimed to improve our understanding of the early evolution of these enigmatic mayflies and their past and present distribution.

## 2. Material and methods

### 2.1. Materials

**Table 1** lists the extant and fossil taxa of Baetiscidae (and some Prosopistomatidae for outgroup comparison) that were analysed either from literature or (whenever possible) from the actual investigation of loaned (type) specimens.

#### The material is housed in following institutions

- AMNH** – Invertebrate Zoology Collection of the American Museum of Natural History, New York, USA
- CCHH** – private collection of Christel and Hans Werner Hoffeins, Hamburg, Germany
- CNUB** – Key Lab of Insect Evolution & Environmental Changes, Capital Normal University, Beijing, China
- NHM** – The Natural History Museum, London, UK
- NMVP** – Palaeontological Collection, Museum of Victoria, Melbourne, Australia
- PIN** – Paleontological Institute of the Russian Academy of Sciences, Moscow, Russian Federation
- SMF** – Senckenberg Naturmuseum, Frankfurt, Germany
- SMNS** – Staatliches Museum für Naturkunde, Stuttgart, Germany

The holotype of *Balticobaetisca bispinata* **sp. nov.** described in this study is a male subimago embedded in Eocene Baltic amber. It is part of the private collection Christel and Hans Werner Hoffeins (CCHH), Hamburg, Germany, which is accessible for scientific research and which will be eventually transferred to a public museum in due course. The fossil has the present inventory number BaB 1373/1. Due to its fragility, the piece of amber was additionally embedded in epoxy resin to seal the specimen from oxygen and prevent mechanical damage. It originates from an unknown Eocene deposit of Baltic amber (Figs 1–3; Table 1; Table S1).

The paratype of *B. bispinata* **sp. nov.** is a male subimago, which is housed in the collection of Senckenberg Naturmuseum Frankfurt (SMF), Frankfurt, Germany, under inventory number SMF Be 411. Struve (1960) presented a first general view of this specimen under its former inventory number SMF VI 90 (for more details on labeling see Supplementary Material 1, Fig. S1). This specimen embedded in Eocene Baltic amber originates from the Samland [Sambia] Peninsula at the south-eastern shore of the Baltic Sea, Kaliningrad Region, Russian Federation. It was part of a small Baltic amber collection donated to the Senckenberg Museum in 1908 by Arthur von Gwinner, a prominent sponsor of SMF at the turn of the 19<sup>th</sup> to 20<sup>th</sup> century.

The respective single nymphal and adult specimen of the Cretaceous species *Protobaetisca bechlyi* Staniczek, 2007 both originate from unknown outcrops in the vicinity of Nova Olinda municipality, Ceará State,

**Table 1.** Fossil taxa described in Prosopistomatoidea (for details see also Discussion).

Type Material	Taxon and reference	Inventory number	Ontogenetic Stage	Provenance	Age
<b>Baetiscidae Edmunds and Traver, 1954</b>					
Holotype	<i>Protobaetisca bechlyi</i> Staniczek, 2007	SMNS 66620	Nymph	Crato Formation Brazil	Cretaceous Aptian approx. 113 Ma
	[The Crato Fossil Beds of Brazil: 182, fig. 11.6g; Fig. 7 and 8]				
Holotype	<i>Protobaetisca bechlyi</i> Staniczek, 2007	SMF VI 993	[putative] Adult, sex unknown	Crato Formation Brazil	Cretaceous Aptian approx. 113 Ma
	[adult described in here; Fig. 7]				
Holotype	<i>Balticobaetisca velteni</i> Staniczek and Bechly, 2002	SMNS BB-2376	Female imago	Baltic amber Europe	Eocene Lutetian 34–48 Ma
	[Stuttgarter Beitr. Naturk., Ser. B, 322: 7, figs 1–10]				
Holotype	<i>Balticobaetisca stuttgartia</i> Godunko and Krzemiński, 2009	SMNS BB-2394	Male imago	Baltic amber Europe	Eocene Lutetian 34–48 Ma
	[Aquatic Insects, 31, Suppl. 1: 126, figs 1–5, Table 1]				
Holotype	<i>Balticobaetisca bispinata</i> <b>sp. nov.</b>	CCHH BaB 1373/1	Male subimago	Baltic amber Russian Federation	Eocene Lutetian 34–48 Ma
	[described here; Figs 1–3, Table S1]				
Paratype	<i>Balticobaetisca bispinata</i> <b>sp. nov.</b>	SMF Be 411	Male subimago	Baltic amber Russian Federation	Eocene Lutetian 34–48 Ma
	[described here; Fig. 4, Table S1]				
Formally undescribed	Siphonuridae? gen. nov.	NMVP103210	Nymph	Koonwarra Fossil Bed Australia	Cretaceous Aptian 116±5Ma
	[Jell and Duncan 1986; Mem. Ass. Australas. Palaeontol. 3: 126, figs 2A, 3E]				
Formally undescribed	Siphonuridae? gen. nov.	NMVP103209	Nymph	Koonwarra Fossil Bed Australia	Cretaceous Aptian 116±5Ma
	[Jell and Duncan 1986; Mem. Ass. Australas. Palaeontol. 3: 126, figs 2B, 3F]				
<b>Cretomitarcyidae McCafferty, 2004</b>					
Holotype	<i>Cretomitarcys luzzi</i> Sinitshenkova, 2000.	AMNH NJ-257	Adult male	New Jersey amber USA	Cretaceous Turonian 90 Ma
	[Studies on fossils in am- ber: 113, figs 1–5]				
<b>Prosopistomatidae Lameere, 1917</b>					
Holotype	<i>Proximicorneus rectivenius</i> Lin et al., 2018	CNU-EPHMA2017001	Female subimago	Burmese amber Myanmar	Cretaceous Albian 98.79±0.62 M
	[Cretaceous Research, 84: 402, figs 1–3]				
<b>Transferred taxa</b>					
Holotype	<i>Myanmarella rossi</i> Sinitshenkova, 2000	NHM In.20173	Adult female	Burmese amber Myanmar	Cretaceous Albian 98.79±0.62 Ma
	[Bull. Nat. Hist. Mus. London, Geol. 56(1): 25, figs 1, 2]				

Brazil. However, both specimens undoubtedly belong to the Nova Olinda Member of the Crato Formation (upper Aptian, Lower Cretaceous). The nymphal specimen (Fig. 6A, C, E) is the holotype of *Protobaetisca bechlyi*, housed at the State Museum of Natural History Stuttgart

(SMNS) under inventory number SMNS 66620 (see also Staniczek 2007: 182). The putative adult specimen is housed in the collection of Senckenberg Naturmuseum Frankfurt (SMF), Frankfurt, Germany, under inventory number SMF VI 993 (Fig. 7; Table 1).

## 2.2. Optical equipment, measurements, terminology

Material preserved in Cretaceous limestones was examined in dry condition and under a film of ethyl alcohol using stereomicroscopes Olympus SZX7 and Leica M205 C. Drawings of amber specimens were made with a camera lucida on a Leica M205 C stereomicroscope. Serial photographs with different focal planes were taken through a Leica Z16 APO Macroscope equipped with a Leica DFC450 Digital Camera using Leica Application Suite v. 3.1.8. Resulting photo stacks were processed with Helicon Focus Pro 6.4.1 to obtain combined photographs with extended depth of field. Photographs were sharpened, and contrast and tonality were adjusted using Adobe Photoshop™ version 23.1.1 (Adobe Systems Incorporated, San Jose, USA). Measurements of individual body parts were taken either by using an ocular grid or inferred from the photographs taken with a calibration scale (see Table S1). Anatomical terminology is mainly based on Kluge (2004) and Bauernfeind and Soldán (2012). Wing vein abbreviations: **C** – costa; **Sc** – subcosta; **RA** – radius anterior; **RP** – radius posterior; **MA** – media anterior; **MP** – media posterior; **CuA** – cubitus anterior; **CuP** – cubitus posterior; **A** – anal vein.

## 2.3. Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved, and the associated information viewed through any standard web browser by appending the LSID to the prefix ‘http://zoobank.org’. The LSID for this publication is LSID urn:lsid:zoobank.org:pub:2046ADA5-5456-45D8-AA27-4328496DAD5B.

## 2.4. Phylogenetic analysis

In order to perform an integrated phylogenetic analysis of fossil and extant Baetiscidae, the character matrix using morphological data of extant Baetiscidae used by Pescador et al. (2009) was modified and 14 additional characters were introduced (see Table S2 and Table S3). The combined data analysis included both nymphal and adult characters, with 36 characters in total. We analysed 14 ingroup taxa. Outgroup taxon was *Prosoptoma variegatum* as already used by Pescador et al. (2009). Parsimony methods were conducted using TNT 1.5 (Goloboff and Catalano 2016) (data matrix in Table S3). All characters were treated as non-additive and unordered. An exhaustive search was run under the implicit

enumeration command (collapsing rule applied), and implied weights, testing several concavity constant values ( $k=1-20$ ). The implied weights were used because they normally increase the stability and support compared to the equal weights scheme (Goloboff et al. 2008). Exhaustive and traditional searches without implied weighting were also applied for comparison. To estimate support of nodes, the Relative Bremer Support (RB) was calculated. All branches were collapsed with 15 additional steps than the shortest tree, generating 1168 trees. The nodes in which the RB value was higher than 60 were considered strongly supported; between 30 and 60 were considered moderately supported; and those less than 30, poorly supported (Hillis and Bull 1993). Also, 1,000 bootstrap (BT) pseudoreplicates were run, using the implicit enumeration search.

## 3. Results

### 3.1. Systematic Paleontology

**Class Insecta Linnaeus, 1758**

**Order Ephemeroptera Hyatt and Arms, 1891**

**Family Baetiscidae Edmunds and Traver, 1954**

**Genus *Balticobaetisca* Staniczek and Bechly, 2002**

**Type species.** *Balticobaetisca velteni* Staniczek and Bechly, 2002 [by monotypy] in Staniczek and Bechly 2002: p.7, figs 1–10.

**Species composition.** *Balticobaetisca velteni* Staniczek and Bechly, 2002 [type species; female imago, holotype BB-2376]; *B. stuttgartia* Godunko and Krzemiński, 2009 [male imago, holotype BB-2394]; *B. bispinata* **sp. nov.** [male subimago, holotype BaB 1373/1, male subimago paratype SMF Be 411]. Nymphs unknown.

**Type locality and horizon.** The pieces of amber with embedded holotypes of *B. velteni* and *B. stuttgartia* and *B. bispinata* **sp. nov.** originate from unknown Eocene deposits of Baltic amber; for information on the piece with the embedded paratype of *B. bispinata* **sp. nov.**, see below.

**Revised diagnosis.** Modified after Staniczek and Bechly 2002, Godunko and Krzemiński 2009, and characters of *B. bispinata* **sp. nov.** **ADULTS:** (1) abdominal tergum VI without mid-dorsal transverse elevation; (2) eyes without vertical bands; (3) wings without maculation; **in male** (4) two blunt claws of different size on each foreleg; (5) first segment of forceps with distinct projection of variable shape on inner margin; (6) penis lobes clearly separated

and apically tapered, blunt at the tip; **in female** (7) dissimilar claws (one hooked, one blunt) on each foreleg (8) sternum IX without apical cleft.

### *Balticobaetisca bispinata* sp. nov.

<http://zoobank.org/DDFF50E6-178E-43E7-B451-0BA19EF9DF89>

Figures 1–4; Table S1

“Eintagsfliege”, p 15, fig. 5, W. Struve (1960): Die Eroberung der Luft, in: Schmidt H. (ed.): Der Flug der Tiere. Verlag Waldemar Kramer, Frankfurt am Main: 9–40 [figured specimen herein designated as paratype of the new species].

**Material.** Holotype: BaB 1373/1 in coll. CCHH. Paratype: SMF Be 411 in coll. SMF (see also Supplementary Material 1, Fig. S1).

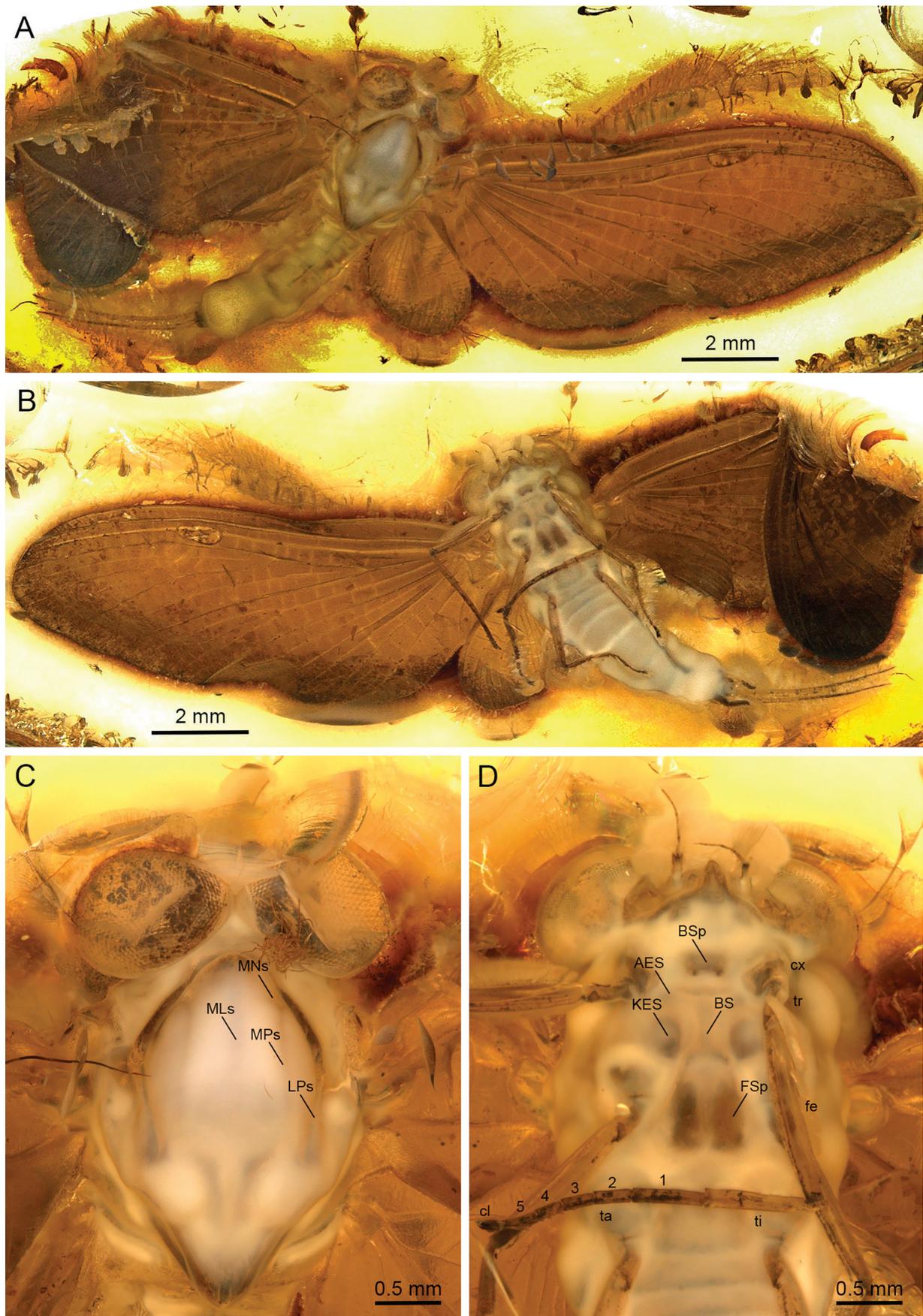
**Etymology.** The species epithet refers to the shape of the paired subapical process of the penis, which is sharply pointed at the tip.

**Diagnosis.** Male subimago (Figs 1A–D, 2A–D): (1) body length 6.80–7.50 mm; (2) from vein A1, 8–9 veins going to basitornal margin of forewing; (3) costal projection of hind wings distinctly prominent, widely rounded apically; (4) numerous simple and forked cross veins between C and Sc of hind wings; (5) forceps segment I with widely rounded hump on inner margin.

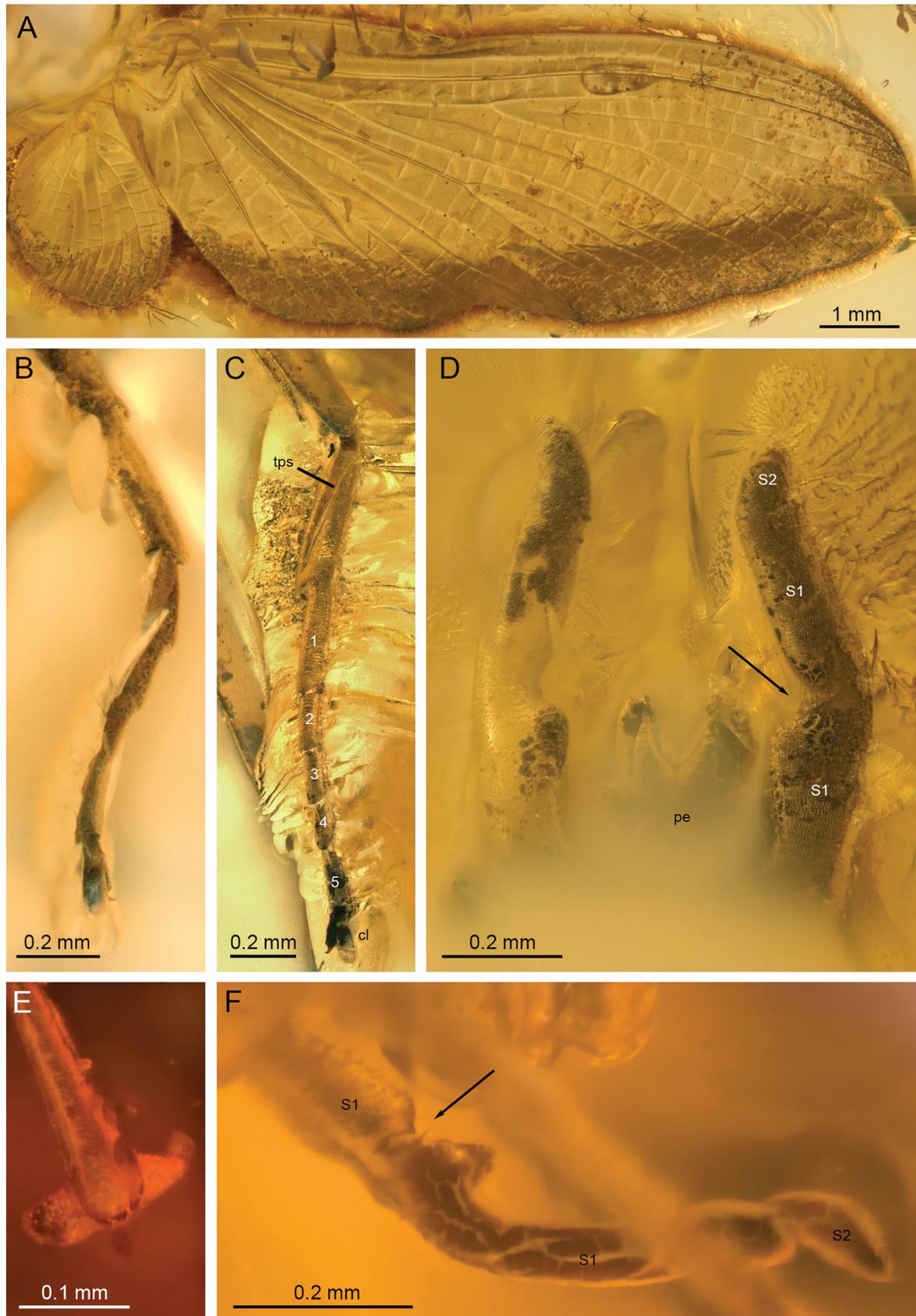
**Description of holotype.** Male subimago (Figs 1–3). Well preserved specimen visible in dorsoventral aspect. Head, thorax and abdomen covered by a whitish cloud of turbidity or so-called “Verlumung”, a milky emulsion surrounding the embedded carcass due to leaking gases and fluids during decomposition (Schlüter and Kühne 1975). Body completely preserved. Left forewing partly damaged, twisted centrally, covered by streaks and overlaying cracks of amber. Rest of body also surrounded by darkened bands and cracks. The subimaginal stage is indicated by the presence of microtrichia covering the wings and by a fringe of microtrichia along posterior wing margin. Additionally, the wings are not translucent, but markedly frosted (Fig 2). For complete measurements see Table S1.

Colouration relatively pale, dirty yellow to light brown, except of fore- and hind wings distinctly darker, coloured brown to dark brown; distal half of left forewing intensively dark brown to blackish. Due to “Verlumung”, body colouration slightly frosted. Femora relatively pale, yellow to yellowish-brown; tibiae and tarsi darker than femora, up to brown, with blackish maculation irregularly scattered. Abdominal segments unicoloured, dirty brown to greyish brown, segments VII–X fully covered by “Verlumung”. Genitalia only visible ventrally, due to streaks and cracks of amber mainly from dorsal side; natural colouration of genitalia most probably not preserved.

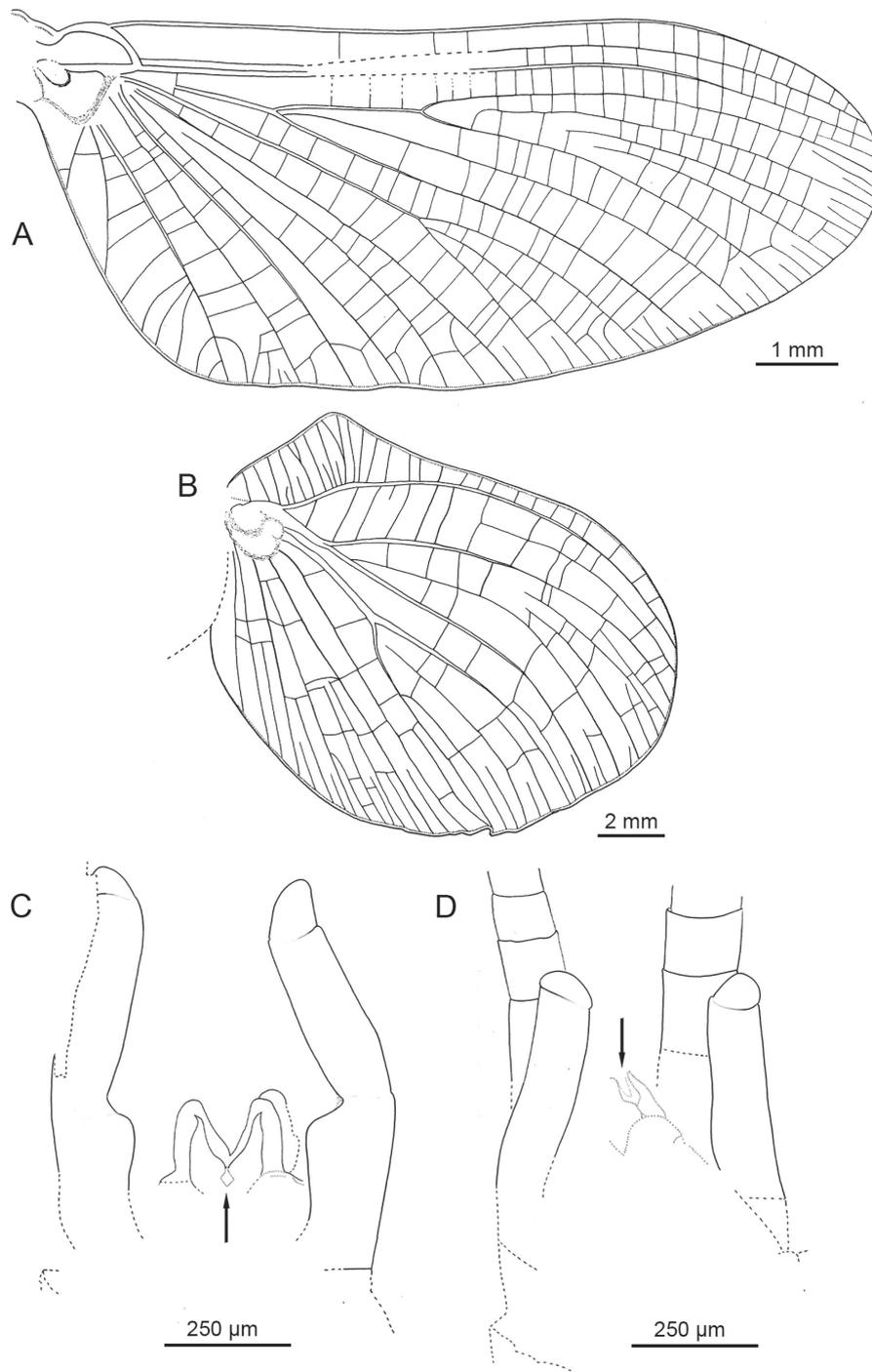
Head. Eyes large, well developed, indistinctly separated into two portions; medially contiguous at short distance, flattened laterally; hexagonal ommatidia of upper portion of eyes well distinguishable; no preserved bands or strips on eyes laterally; ocelli poorly visible due to streaks and cracks, relatively small; antennae short, not longer than length of head; facial keel relatively large (Fig. 1C and D). — **Thorax:** Prothorax mostly covered by “Verlumung”, relatively short; prosternum medially with strong bispinate projection between bases of forelegs (Fig. 1B and D). Mesothorax covered by “Verlumung”; details of lateral mesothorax not visible; mesonotum massive, with elongate medioscutum; sutures of mesonotum poorly recognizable; mesonotal suture [MNs] nearly transverse, laterally stretched backwards; medioparapsidal suture [MPs] slightly curved medially; lateroparapsidal suture [LPs] not elongate, curved outward distally, not reaching posterior scutal protuberance; mesobasis-ternum [BS] elongate; furcasternal protuberances [FSp] contiguous, without median impression. Metathorax short; metanotum reduced (Fig. 1C and D). — **Wings:** Forewing. Opaque, not translucent (Figs 1A, 1B; 2A; 3A, 3B), relatively narrow, with posterior margin slightly scalloped. Pterostigma with 11–13 simple veins only. Longitudinal veins well recognizable, including short marginal intercalaries; cross venation well developed. Venation of “posteritornous” condition, i.e. CuP and A1 end distally of wing tornus; RS, MA and MP triads well developed; RS field complete, with RSa2 diverting from RSa; RS and MA without common stem, basally approached; MA furcation nearly symmetrical, forked after 0.56–0.58 of its length; MP1 and MP2 without common stem; MA–CuA arise from the same point; base of CuP distant from CuA base; CuA and CuP nearly parallel centrally, slightly divergent distally, no cubital intercalaries; 6–7 simple veins going from A1 to basitornal margin; four cross veins between A1 and A2; anal veins except of A1 short, ending distally near wing base. Numerous free short intercalaries along of tornopical margin of forewing, and a smaller number of short marginal intercalary veins connected to longitudinal veins (Fig. 3). — **Hind wings:** Opaque, not translucent, nearly round, as long as 0.26× forewing length (Fig. 1A and B). Costal projection well developed, situated strongly proximally; widely rounded apically; numerous simple and forked cross veins between C and Sc, densely grouped in costal area; MA not forked, thus lacking MA triad; MP triad complete, MP fork situated nearly middle of vein length; CuA and CuP nearly parallel; at least three longitudinal veins and a few intercalaries in anal field. Cross venation well developed; numerous short and elongatemarginal intercalaries between RA and A1 (Fig. 3). — **Legs.** Subimaginal forelegs shorter than body. Patellotibial suture vestigial, present on middle and hind legs, absent on forelegs. Tarsi five-segmented; first tarsomere longest, well separated from foretibia, but fused with tibia in middle and hind legs. Tarsi of forelegs with paired blunt pretarsal claws, in each pair one foreclaw smaller than the other; middle and hind legs with one hooked and one blunt claw (Figs 1D, 2B, 2C). — **Abdomen:** Abdomen relatively short and



**Figure 1.** *Balticobaetisca bispinata* sp. nov., holotype, male subimago. Baltic amber (Eocene), coll. CCHH, BaB 1373/1. **A** Total dorsal view; **B** total ventral view; **C** head and thorax in dorsal view: MPs – medioparapsidal suture; MLs – median longitudinal suture; MNs – mesonotal suture; LPs – lateroparapsidal suture. **D** head and thorax in ventral view: BSp – probasisternal bispinate projection, AES – anepisternum; KES – katepisternum; BS – mesobasisternum; FSp – mesofurcasternal protuberance; left foreleg: cx – coxa, tr – trochanter, fe – femur, ti – tibia, ta – tarsus; 1–5 – tarsal segments, cl – pretarsal claw.



**Figure 2.** A–D: *Balticoabaetisca bispinata* sp. nov., holotype, male subimago. Baltic amber (Eocene), coll. CCHH, BaB 1373/1. **A** Right forewing in dorsal view, **B** right and **C** left hind leg: tps – tibiopatellar suture, 1–5 – tarsal segments; cl – pretarsal claw. **D** genitalia in ventral view: S1–S2: forceps segments; pe – penis lobes; arrow points to medial indentation at halflength of S1. **E** *Balticoabaetisca velteni* Staniczek and Bechly, 2002, holotype, female imago. Baltic amber (Eocene), coll. SMNS BB–2376. **(E)** Right foreclaw in dorsal view. **F** *Balticoabaetisca stuttgartia* Godunko and Krzeminski 2009, holotype, male imago. Baltic Amber (Eocene), coll. SMNS BB–2394. **(E)** Left forceps in dorsal view: S1–S2: forceps segments, arrow points to medial indentation at halflength of S1.



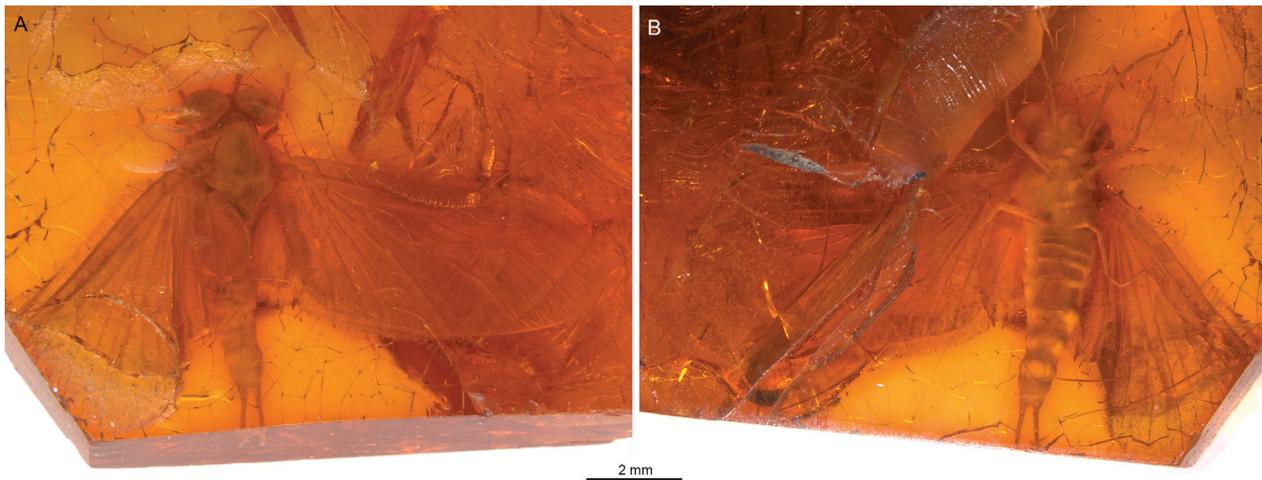
**Figure 3.** *Balticobaetisca bispinata* sp. nov., Baltic amber (Eocene). A–C Holotype, male subimago, coll. CCHH, BaB 1373/1. D Paratype, male subimago, SMF Be 411. A Right forewing in dorsal view; B right hind wing in dorsal view; C genitalia in ventral view. Arrow points to V-shaped cleft separating penis lobes; D genitalia in ventrolateral view. Arrow marks V-shaped cleft separating penis lobes. For further details of wing venation of Baetiscidae see also Staniczek and Bechly (2002) and Kluge (2004).

massive, moderately tapered distally. Segment I shortest, fused with metathorax; segments II–V relatively short, segments VI–VII enlarged and robust; segment VI largest; tergum VI without middorsal transverse evaluation; segment IX markedly enlarged, wider than adjacent segments. Cerci completely preserved, approximately two times shorter than body; paracercus very short, segmentation not recognizable (Fig. 1A and B).

**Genitalia.** Penis lobes partly covered by “Verlumung”. Two-segmented forceps well preserved. Segment I long, moderately expanding distally, with widely rounded hump on inner margin; apically of hump indented, superficially giving the appearance of segmentation; after this indenta-

tion, segment I distinctly bent inwards at half-length, so forcipes tilted towards each other. Distal segment short, as long as 0.22–0.24 of segment I length, only laterobasally with clear segment border towards segment 1, tapering apically, with widely rounded tip. Penis lobes well separated by wide, V-shaped cleft; each lobe moderately tapered apically, rounded at tip; both lobes with prominent subapical process, sharply pointed at the tip (Figs 2D, 3C).

**Description of paratype.** Male subimago (Figs 3D, 4). Well preserved and almost complete specimen visible in dorsoventral aspect. Piece of amber with numerous cracks and streaks. Head, thorax and abdomen covered with thin layer of “Verlumung”. Dense layer of “Verlumung” on



**Figure 4.** *Balticobaetisca bispinata* sp. nov., paratype, male subimago. Baltic amber (Eocene); SMF Be 411. **A** Total dorsal view; **B** total ventral view.

posterior half of abdomen, so details of genitalia poorly visible; shape of styliger basally not recognizable. Right forewing and both hind wings well preserved, complete; distal half of left forewing missing. A dense row of microtrichia along of posterior margin of wings. Wings not translucent, frosted. Legs well preserved, complete. Most part of cerci missing. For complete measurements see Table S1.

**Remarks.** Despite some differences in body size of the specimens (see Table S1), we attribute both male subimagines described here to the single species *B. bispinata* sp. nov., based on similarities in wings venation and shape of genitalia. It should however be noted that, unlike in the holotype, the upper portion of compound eyes in the paratype specimen is not contiguous dorsally, but separated by a narrow gap. Although genitalia are mostly covered by “Verlumung” in the paratype, the shape of the apical portion of the penis lobes and forceps resemble those of the holotype.

The new species described herein can be undoubtedly assigned to the genus *Balticobaetisca* Staniczek and Bechly, 2002 within Baetiscidae. In contrast to extant representatives of the subgenus *Fascioculus* Pescador and Berner, 1981 (genus *Baetisca*) (Pescador and Berner 1981), the upper portion of compound eyes is unicolorous and without stripes. The same character state is observed in the two other known species of *Balticobaetisca*, as well as in representatives of *Baetisca* s. str.

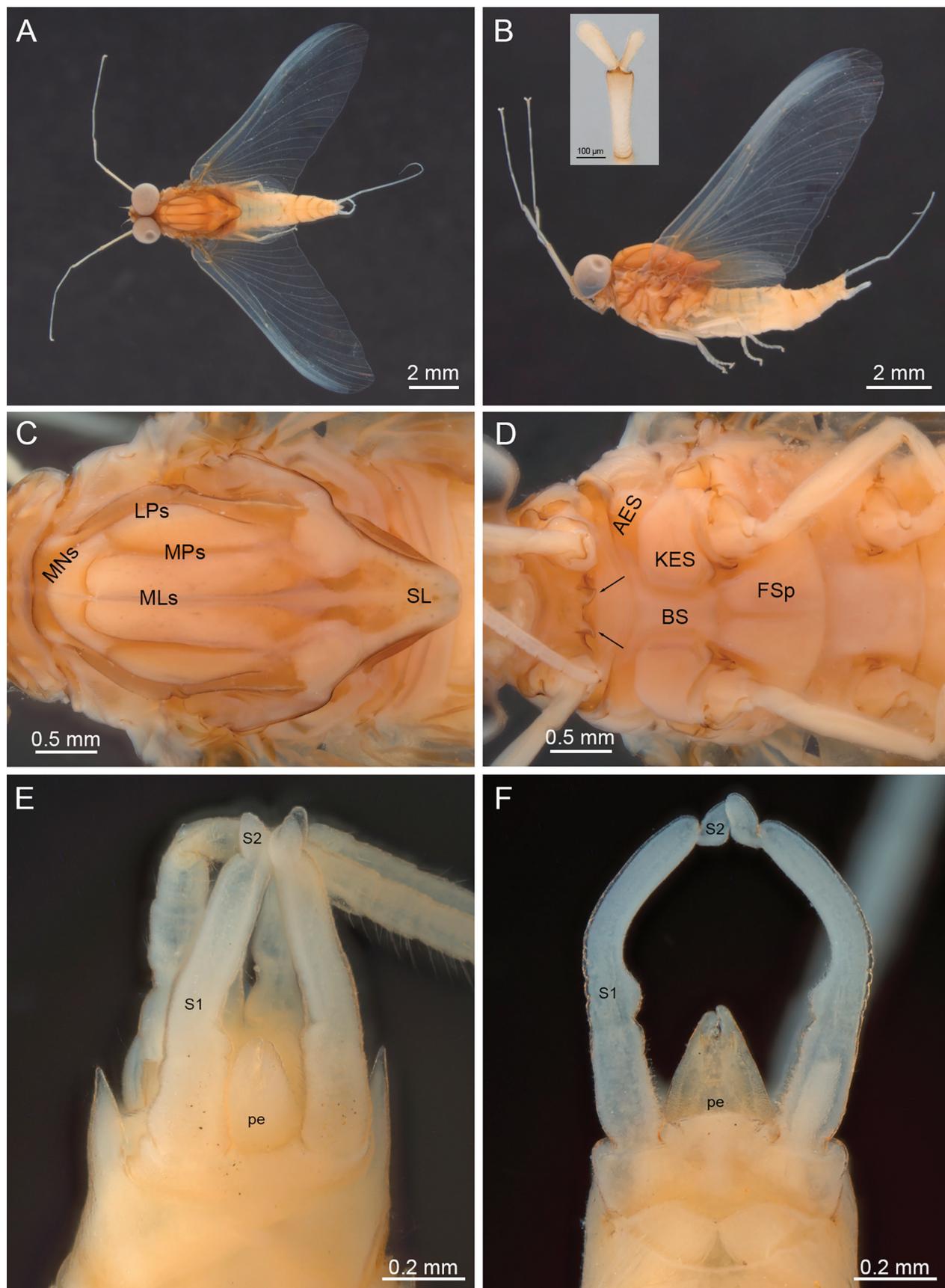
Like other taxa of Baetiscidae, *B. bispinata* sp. nov. has a prominent bispinate prosternal projection located between the bases of forelegs (Fig. 1D) and characteristically rounded hind wings (see also Kluge 2004, Staniczek and Bechly 2002). It is further characterized by the presence of (1) forewings with fully developed RS, MA and MP triads, and numerous intercalaries between RS and CuP (see Kluge 2004: 68, fig. 17B); (2) foretarsus with each of both paired claws blunt apically, similar to males of *Balticobaetisca stuttgartia* and extant species of *Baetisca*, both claws of one pair with different length to each other (see also Fig. 5B, inlay); (3) tergum VI of

abdomen without mid-dorsal transverse evaluation (see also Staniczek and Bechly 2002: 127, fig. 2) and (4) vestigial, not segmented paracercus (see Staniczek and Bechly 2002; Kluge 2004: 68–69, fig. 17).

*Balticobaetisca bispinata* sp. nov. can be distinguished from other representatives of the genus by (1) its smaller general size; (2) by having tarsomere I as the longest (tarsomere V is the longest in *Balticobaetisca velteni* and *Balticobaetisca stuttgartia*); (3) having shorter caudal filaments (half the length of *B. velteni* and *B. stuttgartia*); (4) shorter intercalaries between longitudinal veins (at least 3) compared to other *Balticobaetisca* representatives, and (5) lacking forked veins in the anal field unlike the other two species.

Up to now there was only a single male specimen of *Balticobaetisca* known: *B. stuttgartia* was established based on a specimen with complete genitalia that have well separated penis lobes, which are blunt at the tip (Godunko and Krzemiński 2009: 130). A similar shape of penis is described for *B. bispinata* sp. nov. (Fig. 2D), but the new species can be clearly separated from *B. stuttgartia* (Fig. 2F) by the first segment of forceps, which lacks the distinct triangular inner projection of segment I, as well as the general shape of both forceps segments (Fig. 2F, Godunko and Krzemiński 2009: 130).

A comparison of *B. bispinata* sp. nov. with *B. velteni* is limited, as only the opposite sex is described in both species (Staniczek and Bechly 2002). The female holotype of *B. velteni* however differs by the pattern of venation, especially of forewings, with a rich cross venation and numerous veins, mostly forked, going from A1 to the basitornal margin. The hind wings of *B. velteni* also have a less prominent costal projection and fewer cross veins in the costal field [in contrast to the costal projection of *B. bispinata* sp. nov., which is markedly protruding and proximally in the costal field with rich cross venation] (Staniczek and Bechly 2009: 7–8, figs 3–7). It also differs in the foreclaws, which are dissimilar (one hooked, one blunt) in *B. velteni* (Fig. 2E), but this may be a generic character, which is only present in the female sex (as also in females of extant *Baetisca*).



**Figure 5.** *Baetisca rogersi* Berner, 1940. USA, coll. SMNS EPH 009249A. A–B, F: male imago; C–E: male subimago. **A** general dorsal view; **B** general lateral view, inlay: paired right foreclaws enlarged in dorsal view; **C** mesothorax in dorsal view: MNs – mesonotal suture; LPs – lateroparapsidal suture; MPs – medioparapsidal suture; MLs – medioscutum; SL – scutellum. **D** thorax in ventral view: AES – anepisternum; KES – katepisternum; BS – basisternum; FSp – fucasternal protuberance, arrows mark bispinate projection of prosternum. **E–F** genitalia in ventral view: pe – penis; S1 – segment 1 of forceps; S2 – segment 2 of forceps.

**Table 2.** Adult characters of *Balticobaetisca* Staniczek and Bechly, 2002 (Ephemeroptera: Baetiscidae).

Characters	<i>Balticobaetisca velteni</i> Staniczek and Bechly, 2002 [female imago]	<i>Balticobaetisca stuttgartia</i> Godunko and Krzemiński, 2009 [male imago]	<i>Balticobaetisca bispinata</i> <b>sp. nov.</b> [male subimago]
<b>Measurements</b>			
Body length [mm]	8.50	9.75	6.80–7.50
Forewings length [mm]	9.80–10.10	11.60–11.75	8.30–10.5
Hind wings length [mm]	3.50–3.55	3.55–3.60	2.30–2.75
Hind/Fore wings length ratio	0.35	0.31	0.26–0.28
Forewings width/length ratio	0.42	0.44	0.42–0.44
Hind wings width/length ratio	0.23	0.26	0.26–0.28
<b>Head</b>			
Eyes	small, well separated	large, contiguous medially	large, contiguous medially or separated by narrow gap
Eyes [vertical bands]	absent	absent	absent
<b>Thorax</b>			
Prosternum [prominent bispinate projection]	present	present	present
Mesonotal suture [scutellum]	elongate	elongate	elongate
Mesothorax [anepisternum]	distinctly smaller than katapisternum	distinctly smaller than katapisternum	distinctly smaller than katapisternum
Mesothorax [furcasternal protuberances]	contiguous	contiguous	contiguous
<b>Forewing</b>			
Wings [colouration]	unicolorous, no maculation	unicolorous, no maculation	unicolorous, no maculation
Pterostigma [number of cross veins]	at least 15, dense row	8	11–13
Pterostigma [shape of veins]	mainly branched	1–2 forked, other unbranched	simple, unbranched
RS furcation [respectively to vein length]	0.18	0.13	0.13
MA furcation [respectively to vein length]	0.54	0.56	0.56–0.58
CuP and A1 [centrally]	divergent	nearly parallel	nearly parallel
A1 [number of veins arising to basitornal margin]	8–11	5–6	6–7
A1 [shape of veins arising to basitornal margin]	simple and forked veins	simple and forked veins	simple veins
A1–A2 [number of cross veins]	0	3–5	4–5
Intercalary veins between A1 and A2	6–10	1–2	absent
Intercalary veins between A2 and A3	absent	1–2	1
<b>Hind wing</b>			
Wing [shape]	nearly round	nearly round	nearly round
Costal projection [shape]	moderately prominent; rounded	prominent; widely rounded apically	prominent; widely rounded apically
C–Sc field [number of cross veins in costal area]	5–8	4–5	up to 12
C–Sc field [shape of cross veins in costal area]	simple	simple	simple and forked
C–Sc field [intercalary veins]	absent	absent	present
Free short marginal intercalaries	present	present	present
<b>Legs</b>			
Foretarsi [shape of claws]	dissimilar; one blunt, one pointed	both blunt	both blunt
<b>Abdomen</b>			
Mid-dorsal transverse evaluation of tergum VI	present	present	present
Sternum IX [in female]	without apical cleft	—	—
Paracercus	vestigial	vestigial	vestigial
<b>Genitalia (male)</b>			
Forceps segment I [inner projection]	—	triangular	widely rounded
Forceps segment II [shape]	—	nearly triangular	nearly conical
Penis lobes [shape]	—	blunt apically	blunt apically

Regarding body size, there remains the possibility that the described female of *B. velteni* and male of *B. bispinata* **sp. nov.** belong to the same species (Staniczek and Bechly 2002: 7–8). On the other hand, a clear difference in the venation of fore- and hind wings between *B. velteni*

and *B. bispinata* **sp. nov.** rather points to the presence of two different fossil species. Table 2 lists a detailed comparison of characters between *Balticobaetisca* representatives.

## Genus *Protobaetisca* Staniczek, 2007

**Type species.** *Protobaetisca bechlyi* Staniczek, 2007 [by monotypy] in Staniczek 2007: 182, fig. 11.6g.

**Specimens.** *Protobaetisca bechlyi* Staniczek, 2007 [type species; nymph, holotype SMNS 66620]; *P. bechlyi* Staniczek, 2007 [putative adult of unknown sex; SMF VI 993].

**Type locality and horizon.** Vicinity of Nova Olinda, southern Ceará state, northeast Brazil; upper Aptian, Lower Cretaceous, Nova Olinda Member, Crato Formation, Santana Group, Araripe Basin.

**Revised diagnosis.** As for type species, since monotypic (see below); modified based on Staniczek (2007) and characters redescribed in nymph and described in putative adult.

### *Protobaetisca bechlyi* Staniczek, 2007

= *Protobaetisca bechlyi* Staniczek, 2007: The Crato Fossil Beds of Brazil: window into an ancient world, p. 182, fig. 11.6g

**Revised diagnosis (Figs 6–7).** Modified based on Staniczek (2007) and on newly described characters of male nymph [holotype] and putative adult of *P. bechlyi*. **ADULT:** (1) body length 7 mm [as preserved]; (2) forewing length of approximately 6 mm, maximum width 3.5 mm [as preserved]; (3) forewing triangular-shaped, width/length ratio approximately 0.58 [as preserved]; (4) longitudinal venation of “posteritornous” condition; (5) MA slightly asymmetrical, fork located at 0.65 of wing length; (6) at least 15 simple and forked cross veins in pterostigma; (7) distinct short intercalary vein between MP2 and CuA; (8) CuP nearly parallel to A1, approaching close to each other; (9) at least five veins going from A1 to basitornal margin; (10) small (ratio of forewing/hind wing length of 1/5) rounded hind wings with prominent costal projection at base; (11) abdominal segment VI enlarged. **NYMPH:** (12) body length 8 mm [without caudal filaments], caudal filaments length 3 mm; (13) genal shelf of head not distinctly projected; (14) femur short, as long as 0.32 of tibia length; tarsus at least 0.50 of tibia length; preserved part of pretarsal claw at least 0.34 of tibia length; (15) notal shield without traces of dorsal or lateral spines; (16) abdominal segment X ventrally covered by well-preserved paired sclerites of triangular shape, rounded apically, markedly separated by narrow V-shaped incision, which may be interpreted either as genital buds (outgrowths of IX) or paraprocts.

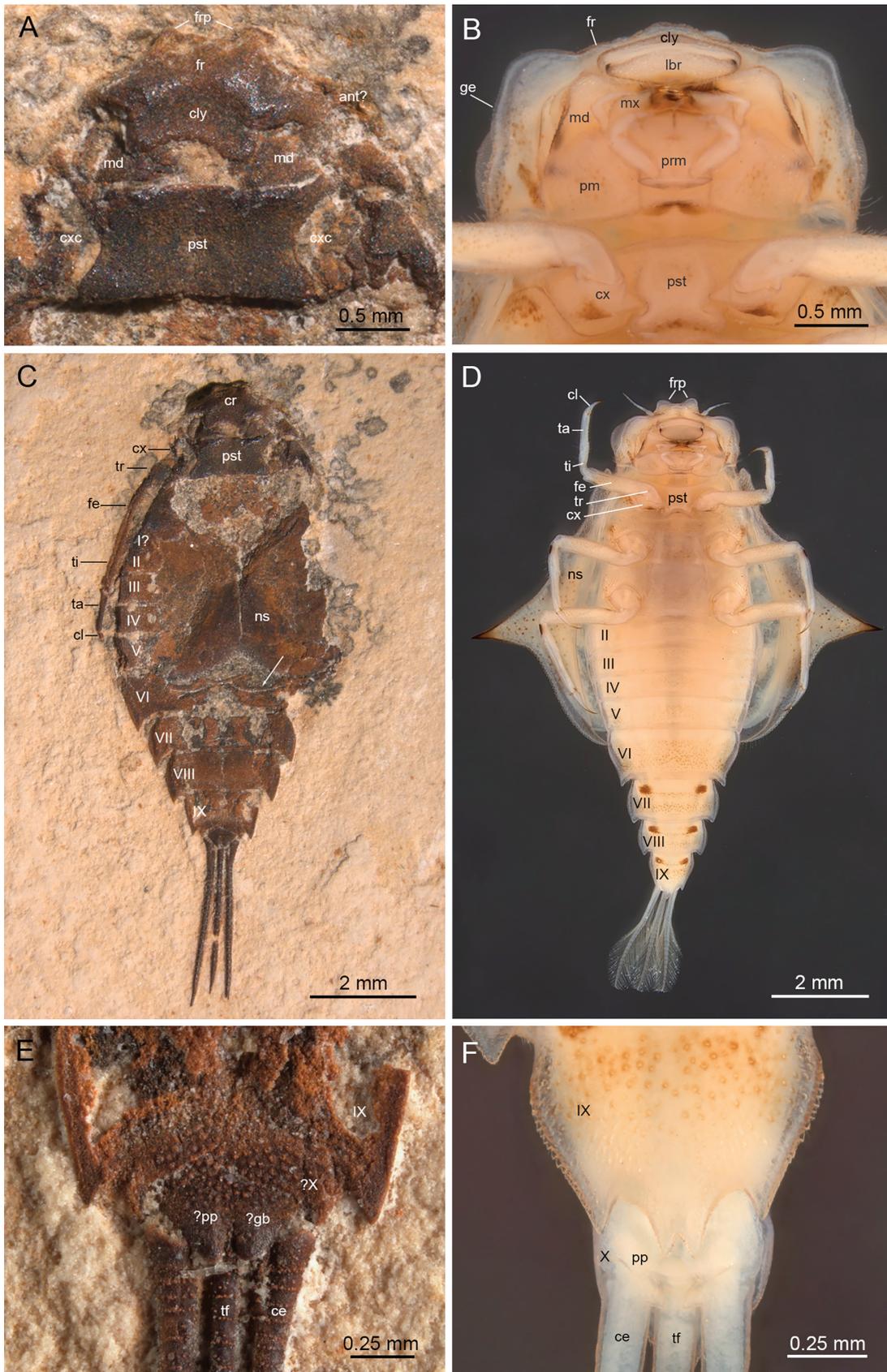
**Material.** Male nymph, holotype, SMNS 66620 adult, SMF VI 993.

**Redescription of holotype (male nymph; Fig. 6A, C, E).** Length of body 8 mm [without terminal filaments]. Length of cerci 3 mm. The nymph was initially described by Staniczek (2007) as a new species and attributed to

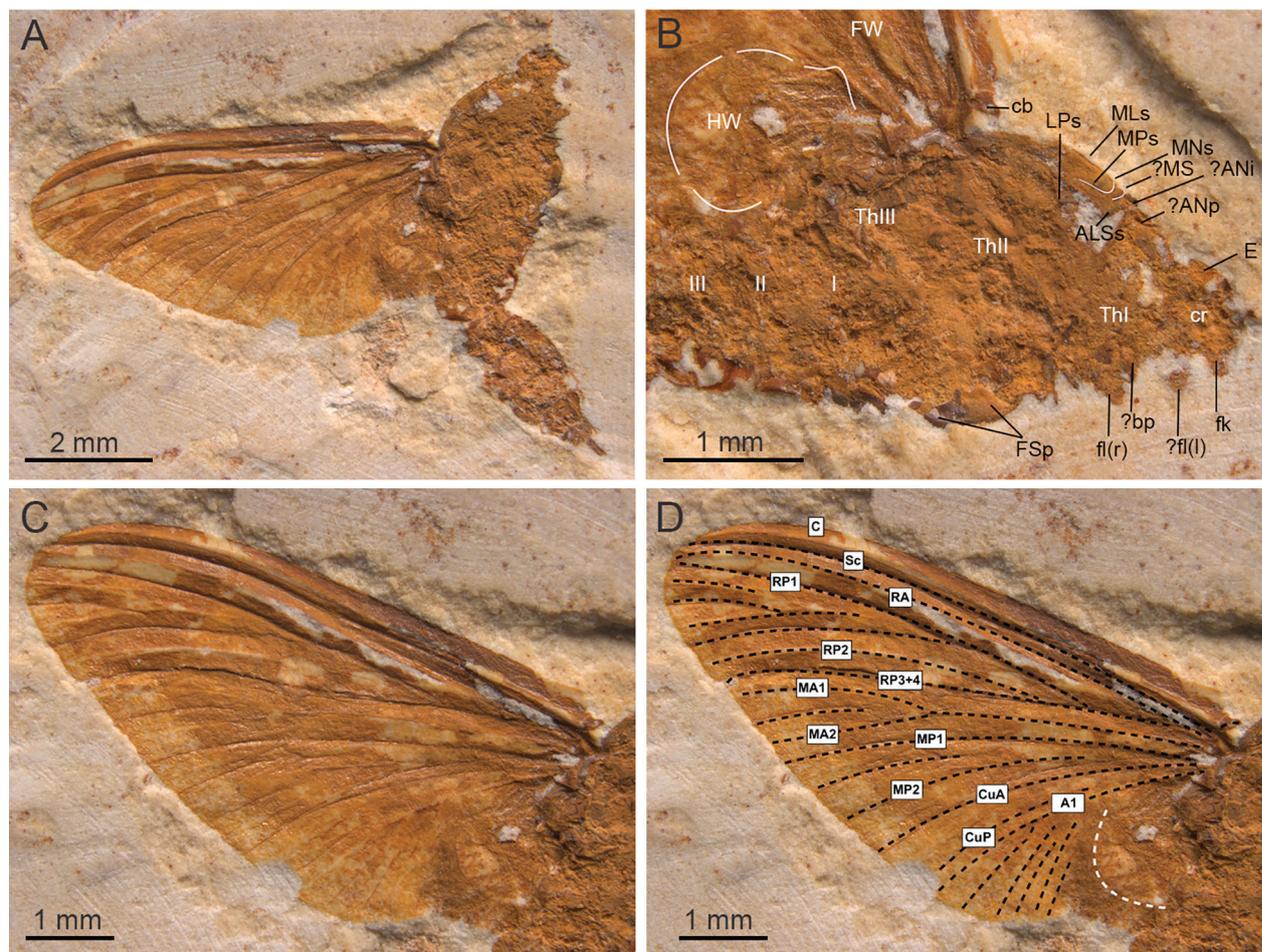
a new fossil genus within Baetiscidae. A thorough reinvestigation confirmed that the compressed specimen is visible from its ventral side, which implies an amended description and interpretation as follows: Relatively well-preserved nymph, visible from ventral side (see also Fig. 6 for interpretation). Body stout, nearly ovoid shaped (Fig. 6C). — **Head:** Poorly preserved, relatively large, head width at least 0.53× of head length; lateral portions of head moderately damaged; distinct remnants of frontal and genal projections; frontal projections relatively large, rounded apically, located close to each other; putative remnants of left antenna along left lateral side of head; basal antennal segments better visible; length of antenna at least 2/3× of head length; genal shelf not distinctly projected, not protruding above anterolateral margin of head. Head in ventrocaudal posture, ventral outer edge of cranium well visible, but labrum and other mouthparts mostly not preserved except of mandibles, maxilla not visible, labium probably lost (Fig. 6A). — **Thorax:** Prothorax well separated from head and anterior part of mesothorax, without traces of bispinate projection; prothorax relatively wide, at least 0.30× its length (Fig. 6A, C). Base of foreleg large; coxa and trochanter apparently robust; remnants of foreleg located along right side of nymphal body; femur short, about 0.32× of tibia length; tarsus shorter than tibia, at least 0.50× of tibia length; pretarsal claw stout and long, with preserved part as long as at least 0.34× of tibia length (Fig. 6C). Mesosternum and metasternum mainly lost, distinctly short. Mesonotum posteriorly extended to abdominal segment VI, forming a notal shield (or “carapace”); notal shield well recognizable from ventrally (as anterior abdominal sterna not preserved), with distinct outer margin on right side; notal shield robust, with widest part at half length; near posterior margin slightly narrower than at half length, without traces of dorsal or lateral spines (Fig. 6C). — **Abdomen:** Abdominal segments VI–IX with prominent posterolateral projections; no preserved traces of median spines; lateral margins of abdominal segments I–V slightly bent up; abdominal segment VI slightly enlarged, longest, with traces of transversal crest indicating the caudal closure of notal shield; segment VI covered approximately at 1/2 of its length by notal shield (Fig. 6C). Abdominal segment X ventrally covered by well-preserved paired sclerites of triangular shape (Fig. 6E), rounded apically, markedly separated by narrow V-shaped incision, which may be interpreted either as genital buds (outgrowths of IX) or paraprocts. Cerci and paracercus stout; swimming setae on both inner sides of cerci and paracercus, denser at half length.

### **Description of new putative adult (SMF VI993; Fig. 7).**

Length of body 7 mm; length of forewing approximately 6 mm, maximum width 3.5 mm. Imago of unknown sex. Specimen preserved in right lateral view with both forewings overlapping. Except of forewings, entire body of specimen poorly preserved, first abdominal segments not discernible, only base of cerci preserved. Right forewing is almost complete except of cubital and anal fields with venation poorly distinguishable. Traces of left forewing



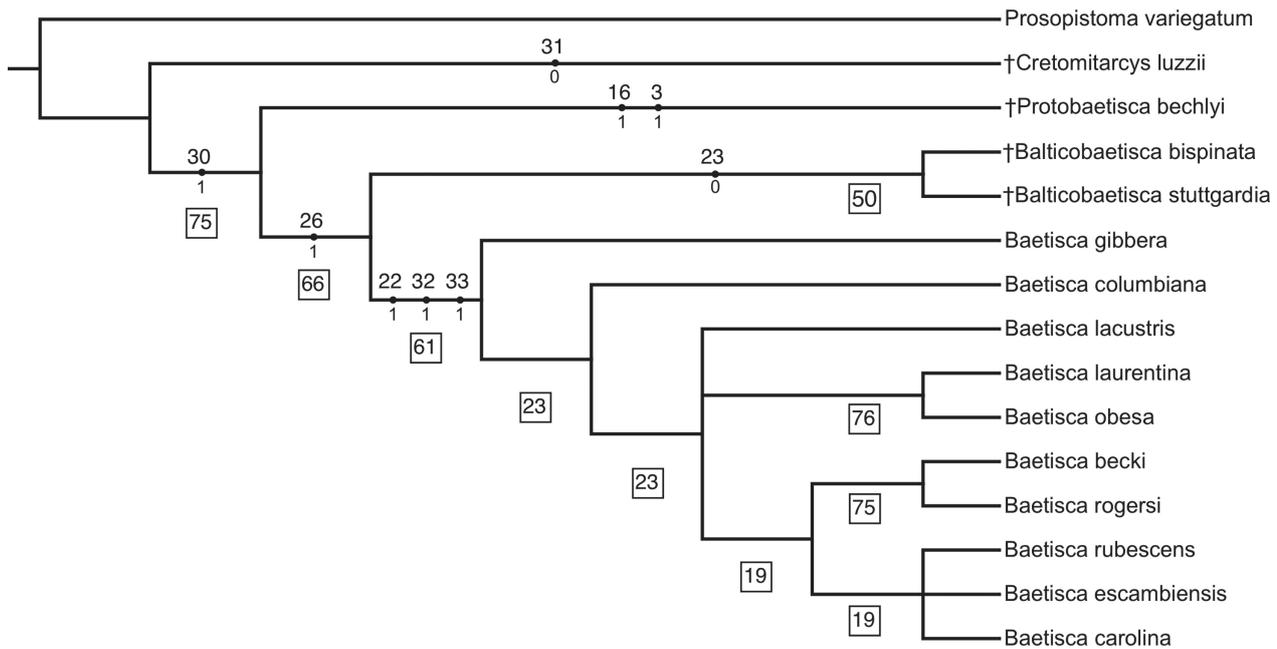
**Figure 6.** Nymphs of (A, C, E) *Protobaetisca bechlyi* Staniczek, 2007 (holotype, Lower Cretaceous, Upper Aptian, Crato Formation, holotype, SMNS 66620) and (B, D, F) *Baetisca rogersi* Berner, 1940, (USA, coll. SMNS). **A–B** head and prothorax, ventral view: ant – antenna; cly – clypeus; cx – coxa; exc – coxal cavity; fr – frons; frp – frontal projections; ge – gena; lbr – labrum; md – mandible; mx – maxilla; prm – prementum; pm – postmentum; pst – prosternum. **C–D** general ventral view: I–IX – abdominal segments I–IX; cr – head; cl – pretarsal claw; cx – coxa; fe – femur; frp – frontal projections; ns – notal shield; pst – prosternum; ta – tarsus; ti – tibia; tr – trochanter, arrow marks traces of transversal crest. **E–F** caudal end of abdomen, ventral view: IX–X – abdominal segments IX–X; ce – cerci; gb – genital bud; pp – paraproct; tf – paracercus.



**Figure 7.** *Protobaetisca bechlyi* Staniczek, 2007, putative adult specimen, sex unknown, SMF coll., SMF VI 993. **A** general lateral view; **B** head, thorax, wing bases and abdominal segments I–III, lateral view. Abbreviations in white colour: cr – head; ThI – prothorax; ThII – mesothorax; ThIII – metathorax; I–III – abdominal segments I–III; FW – forewing; HW – hind wing [wing shape marked by white lines on left half of photo]. Abbreviations in black colour: ALSs – anterolateral scutal suture; ANp – anteronotal protuberance; ANi – anteronotal transverse impression; bp – bispinate projection of prosternum; cb – costal brace; E – eye; fk – frontal keel; fl – foreleg [r – right; l – left]; FSp – furcasternal protuberance; LPs – lateroparapsidal suture; MLs – median longitudinal suture; MNs – mesonotal suture [white line indicates the placement and orientation of MNs/MPs]; MPs – medioparapsidal suture; MS – medioscutum [white lines on right half of photo indicate position of MS]. **C** right forewing, ventral side; **D** same with interpretation of venation (for vein abbreviations see Material and Methods).

venation partly overlapping with right forewing venation. Costal brace and basal part of costal field almost destroyed; longitudinal venation mostly preserved and distinguishable; cross veins poorly visible, especially in anal field. Hind wings partially superimposing forewings. Hind wing mostly damaged, with poorly preserved outline and trace of costal projection; venation almost lost. Legs completely missing, except of traces of putative trochanter of right and left foreleg. Because of poor preservation of eyes and lacking gonopods, the sex of this specimen is not determinable (Fig 7A). — **Head:** Relatively small; shape of eyes not distinguishable; preserved part of facial keel relatively short. — **Thorax:** Prothorax not widened, relatively narrow; mesonotum with trace of elongate medioscutum; putative sharply pointed [? bispinate] projection on ventral side of prothorax, close to pointed projection trace of putative trochanter. Border between pro- and mesothorax poorly recognizable; mesothorax distinctly large; mesonotal sutures poorly

preserved; shape of preserved part of MPs and putative MS similar to those in *Baetisca* (Fig 5A); lateral sclerites completely damaged; ventrally with traces of relatively elongate furcasternal projection. Metathorax short (Fig 7B). — **Wings:** Preserved forewing of triangular shape, relatively wide, with width/length ratio approximately 0.58 [as preserved]. Longitudinal venation well recognizable; cross venation well developed, occasionally poorly visible, present in all the fields of forewing. Pterostigma with at least 15 simple and forked cross veins; only simple veins between C and Sc proximally. RP basally forked at 0.30× of its length; RP2 basally forked at 0.29× of its length. Longitudinal venation with complete RP, MA and MP triads; RP and MA without common stem, basally approached; posteritornous wing condition: wing tornus situated basally of CuP and A1, A1 nearly parallel and close to CuP throughout remaining length. Furcation of MA slightly asymmetrical, fork located at 0.65 of wing length; iMP slightly closer to MP2 proximally; MP and



**Figure 8.** Strict consensus tree. Strict consensus of the one most parsimonious trees, from the analysis of 36 morphological characters from nymphs and adults of Baetiscidae. Numbers above and below circles (characters and their states, respectively) correspond to synapomorphies supporting branches (species of *Baetisca* with same resulting synapomorphies as those recovered by Pescador et al., 2009). Relative Bremer (RB) support values are located below branches, in black squares.

CuA without common stem; distinct short intercalary vein between MP2 and CuA; traces of short intercalaries in MA and MP fields poorly preserved; MP1 and MP2 without common stem; base of CuP markedly distant from CuA base; at least five veins branching from A1 to basitornal margin; A2, if preserved, most probably visible in basal part of wing (Fig. 7C, D). Ratio of hind wing / forewing length 1/5. Hind wing length 1 mm; rounded, almost circular appearance, with prominent costal projection near its base, rounded at tip (Fig 7B). — **Abdomen:** All abdominal terga and sterna poorly preserved; borders between segments I–IV poorly preserved, other segments with more or less preserved borders; segments IV–VI partly damaged; distal segments relatively large; segment VI the longest. Gonopods not preserved.

### 3.2. Phylogenetic analysis

We opted not to include the two nymphs from the Lower Cretaceous of the Koonwarra Fossil Bed because there were only three character states to score, collapsing all branches into polytomies. We have also excluded from the analysis the female holotype of *Balticobaetisca velteni* since the synapomorphy of *Balticobaetisca* is male related, and the input of *B. velteni* was generating a polytomy for this clade. Parsimony analysis under implied weights ( $k=3$ ) for the combined data matrix of nymphal and adult characters resulted in one most parsimonious tree, shown in Fig. 8. The same topology was also found under traditional and exhaustive search without implied weights.

**Remarks.** We have no hard evidence that the single nymph and single adult specimen of *Protobaetisca* re-

semble different life stages of the same species. However, the length of the adult body matches the length of the nymph, and the given rarity of these Baetiscidae in the Crato deposit prompted us to associate the stages and assign both life stages to the same species, also according to the low species richness of the deposit (Storari et al. 2021).

*Protobaetisca* shows several apomorphic characters of Prosopistomatoidea in both nymph and adult: the forewing is characterized by a typical posteritornous condition, with the wing tornus situated basally of CuP. The nymph features the apomorphic notal shield or carapace, which is characteristic of Prosopistomatoidea. In extant species, pronotum, mesonotum and wing buds are fused and extend across thorax and abdominal terga I–VI. Since the fossil nymph of *Protobaetisca* is fossilised in ventral aspect, the preserved prosternum prevents a direct view onto the anterior part of the notal shield, so we have no information on a possible fusion of pro- and mesonotum. However, the ventral margins between prosternum and adjacent head and mesosternum are distinct. As in other nymphs of Prosopistomatoidea, the abdominal segment VI is enlarged and has a transverse crest, which marks the posterior interlocking of the notal shield.

Further characters prove the systematic position of *Protobaetisca* within Baetiscidae: in the adult, it is the presence of the spine-like sternal projection between the bases of forelegs and the rounded shape of hind wings with prominent costal projection near its base, and the presence of a distinct trace of an elongate furcasternal protuberance. Similarly to other Baetiscidae, it shares the plesiomorphic complete forewing venation, including all branches and intercalaries of RP, as well as symmetrical furcation of MA close to the middle of the wing.

The adult of *Protobaetisca bechlyi* differs from extant *Baetisca* (including the subgenus *Fascioculus*) and extinct *Balticobaetisca* by (1) the shape and width/length proportion of forewing (for more details see Supplementary materials and taxonomy of *Balticobaetisca*); (2) the placement of MA fork, slightly asymmetrical, located at 0.65 of wing length; (3) the shape of CuP and A1, nearly parallel along their length, closely approaching to each other. The male nymph of *P. bechlyi* resembles extant species of *Baetisca* in the presence of frontal projections of head, and especially in the shape and extension of notal shield and proportions and shape of abdominal segments. However, unlike in extant nymphs of *Baetisca*, in *P. bechlyi* (1) the genal shelf is less protruding above anterolateral margin of head; (2) antennae are distinctly elongate; (3) lateral protuberances of notal shield are lacking; (4) notal shield is widest at half length and slightly narrowed towards posterior margin, and (5) there is a different ratio of foreleg segments, with longer tibia and shorter femur and tarsus.

### 3.3. Taphonomy

Given its rarity within a site otherwise rich in fossil mayfly specimens, *P. bechlyi* was probably allochthonous to the depositional paleolake of the Crato Formation. Moreover, Crato Lagerstätte is currently considered by most authors as a stratified lake with variable salinity and anoxic bottom waters, subject to occasional freshwater input at surface waters (Martill and Wilby 1993; Neumann et al. 2003; Varejão et al. 2019; Ribeiro et al. 2021). Extant *Baetisca* are sprawlers and clingers in running water pools and on margins of lotic-depositional streams, partially submerging themselves in the thin layer of silt and detritus that accumulates in calm shallows. They are fine-particle detritivores, feeding by collecting or scraping organic matter (Pescador and Peters 1974). Assuming similar ecomorphological preferences for *P. bechlyi* like extant nymphs of *Baetisca*, which favor more cold, acid watersheds, we do not consider an autochthonous presence of *Protobaetisca* directly in the paleolake to be likely. The habitat of *Protobaetisca* though may have been nearby and may have been connected to the depositional site of Crato (at least seasonally), in flooded lotic areas around.

Due to the presence of the massive notal shield and strong sclerotisation, nymphal Baetiscidae have a rather robust morphology, so they would probably be able to withstand mechanical disturbances and only disarticulating the most obviously delicate body parts (legs; antennae; caudal filaments) post mortem. The nymphal holotype of *P. bechlyi* in fact lacks most of its legs. Also lacking are most parts of meso- and metathorax and anterior abdominal segments. This central and lateral damage clearly points to necrolysis before its complete burial. The denaturation and consequent necrolysis of cuticle occurs faster in warmer waters (e.g. those of the depositional site of Crato) or while still in exposition between water-air during transport. Much longer flotation times along the water-air interface increase the likeliness to decompose under aerobic conditions (Wang et al. 2013). Consequent-

ly, we assume that the nymph underwent some transport and decay before it came to rest at the bottom of Crato paleolake.

The putative adult specimen of *Protobaetisca* is preserved with the wings upheld and is missing legs and caudal filaments. This is a typical position of specimens that died before reaching the water and not drowned by asphyxia (in the latter case showing both wings open and spread out) (unpublished data of APS). Previous experiments have shown that insects, which are transported onto the water surface in dead condition, are not likely to overcome the surface tension and sink, unless some physical agent causes that (e.g. transport currents; rain; wind) (Martínez-Delclòs and Martinell 1993). Most probably this was also the case in the adult *Protobaetisca* specimen. During transport on the water surface, it lost its delicate body parts and underwent decomposition. The abdomen shows signs of partial disarticulation and also the rest of body clearly went through some decay before final burial, and therefore lost its delicate body parts during transport and sinking.

## 4. Discussion

### 4.1. Phylogeny of Baetiscidae

As expected, *Cretomitarcys* is recovered as sister group to the remaining Baetiscidae included in the analysis, the latter synapomorphically featuring oval hind wings (30:0). *Cretomitarcys* also presented one autapomorphy, which is the absence of a costal projection on hind wing (31:0); followed by *Protobaetisca* that was recovered as sistergroup to the genera *Balticobaetisca* + *Baetisca*, supported by one synapomorphy, namely the rounded hind wing (30:1). *Protobaetisca* also presented two autapomorphies, which are the long antennae (3:1) and well-developed posterolateral projections of abdominal segments VI–VIII (16:1). *Balticobaetisca* was recovered as monophyletic sistergroup to *Baetisca*. Monophyly of *Balticobaetisca* was supported by a single synapomorphy, the presence of a triangular projection on the inner margin of forceps (23:0); *Balticobaetisca* + *Baetisca* shared elongate, narrower forewings as synapomorphies (26:1). Synapomorphies of *Baetisca* species are the approximated penis lobes (22:1), the presence of a middorsal transverse elevation on tergum VI (32:1), and in the female the presence of an apical cleft on sternum IX (33:1). The positions of the different *Baetisca* species were recovered unchanged as in Pescador et al. (2009).

### 4.2. Extinct taxa assigned to Prosopistomatoidea in literature and their systematic positions

The genus *Cretomitarcys* Sinitshenkova, 2000 was established for an alate male specimen found in Upper Cretaceous amber of New Jersey (Sinitshenkova 2000).

It was initially placed in a newly established subfamily Cretomitarcyinae within Polymitarcyidae. McCafferty (2004) realized the lack of the apomorphic basal curvature of MP2 and CuA in the forewings of *Cretomitarcys*, which is characteristic for all Ephemeroidea. On the other hand, based on the well-developed longitudinal venation of the hind wing he assumed closer relationships with Baetiscidae, and transferred *Cretomitarcys* to a new family Cretomitarcyidae McCafferty, 2004, within Prosopistomatoidea [= Carapacea *sensu* McCafferty (2004); = Posteritorna *sensu* Kluge (2004)].

Staniczek (2007) corroborated McCafferty's attribution of *Cretomitarcys* to Prosopistomatoidea based on the posterotornous wings and analysed a set of characters, which specified its phylogenetic position in the stemline of Baetiscidae. Some apomorphies of Baetiscidae are already present in this taxon, like the almost rounded hind wing with multiple intercalaries in all fields. Other characters remained plesiomorphic compared to other Baetiscidae, such as the gonopods made up of several segments and a basitarsus of the foreleg, which is still well-separated from the tibia (see also Sinitshenkova 2000, fig. 2). Consequently, Staniczek (2007) placed *Cretomitarcys* in the stemline of Baetiscidae (Staniczek 2007).

Examination of the specimen by ourselves has not been possible despite our efforts. As a result, we could not investigate and code further characters like the presence or absence of the bispinate projection of the prosternum in *Cretomitarcys*. Given the phenetic gap towards the remaining Baetiscidae and awaiting a thorough re-examination, we refrain to formally include this fossil in Baetiscidae for now. In any case, the preliminary phylogenetic analysis, though weakly, confirmed the position of *Cretomitarcys* as basal stemline fossil of Baetiscidae.

Two nymphs from the Lower Cretaceous of the Koonwarra Fossil Bed in Australia were reported by Jell and Duncan (1986: 118, 119, 126, figs 2A, 2B, 3E, 3F) as Siphonuridae? gen. nov., without formal establishment of new generic and species names. Later, Jell (2004) confirmed the attribution of these nymphs as undescribed new Siphonuridae. Kluge (2004) noted their similarities with Baetiscidae and suggested placement of these fossils within Prosopistomatoidea. Both nymphs are preserved in lateral aspect, and resemble in their outline extant nymphs of Baetiscidae, especially in the shape of the enlarged mesothorax that expands posteriorly to abdominal segment III in one of the specimens, and to segment VII in the second one. However, opposite to extant baetiscid nymphs, the pronotum appears to be well-separated from the mesonotum. Consequently, Staniczek (2007) based on the available published data concurred that the fossils belong to Prosopistomatoidea, possibly Baetiscidae. Pescador et al. (2009) reported the presence of a prominent transverse subapical ridge on the carapace based on analysis of figures 2 and 3 of original description published by Jell and Duncan (1986), suggesting a placement in the stemline of Baetiscidae.

The former placement can be additionally supported by the shape of their preserved forewing pads, which ac-

tually show remnants of venation. These show remarkable similarities to wings of Baetiscidae: a relatively narrow MA and MP field with MA almost symmetrically forked at almost half length and situated approximately middle to wing length; and a presumably posteritornous condition with first anal vein ending before tornus at toroapical margin of wing, with indistinct traces of veins going from AA to tornus and basitornal margin. Moreover, the hypognathous head features projections on gena and frons, and on abdominal segments VI–VIII there are strong, relatively large posterolateral spines well visible. However, in contrast to nymphs of extant species of *Baetisca* s.l., the fossil representatives most probably possessed legs with longest femora and tibia (Jell and Duncan 1986, figs 2A, 2B, 3E, 3F; Jell 2004: 12).

Sinitshenkova (2000) described the monotypic genus and species *Myanmarella rossi* Sinitshenkova, 2000 based on a poorly preserved adult female from Cretaceous Burmese amber and attributed it to Prosopistomatoidea due to forewings with multiple additional longitudinal veins and poorly developed cross venation. In fact, the doubled longitudinal veins pattern seems rather like an artifact as a result of fossilization in resin (N.J. Kluge, pers. comm.). Unfortunately, the specimen has been severely damaged during preparation and its posterior half of body and hind wings have been destroyed (for more information see Szadziewski 2004). Later, the specimen took further, when the piece of amber broke into several parts in 2016 (Dr. Claire Mellish, Curator of Fossil Arthropods at NHM, pers. comm.).

The systematic position of this taxon was unclear and only briefly commented on by Kluge (2004). Following Kluge (2004), we here attribute *M. rossi* to the subfamily Paleocloeoninae Kluge, 1997 (Baetidae), based on following characters: the strongly elongate antennal flagellum, at least 3 times longer than length of head, and 1.5 times longer than head width (fig. 1a in Sinitshenkova 2000); relatively wide forewings, widely rounded distally (see Supplementary Material 2, Fig. S2, and also Kluge 1997: 529, figs 16, 19; Sinitshenkova 2000: 26, figs 1d, e); forewing venation with solitary free intercalaries, depicted by Sinitshenkova (2000: 26, figs 1d, e) at least for RP sector; RP basally forked (at least at 0.25 of its length) and weakly developed, RP2 fork situated more proximally; unforked MA with free MA2; shortened MP2 beginning at marked distance from wing base, not connected with MP1; cubital venation with CuA clearly diverging from CuP basally, and presence of a single cubital intercalary vein (for more details of wing venation see Supplementary Material 2, Fig. S2, and also, e.g. Kluge 1997: 529, figs 16, 19; Kluge 2004: 97, fig. 27A; Sinitshenkova 2000: 26, figs 1d, e). However, unlike in *Palaeocloeon* from Upper Cretaceous Taymyr amber (type species *P. taimyricum* Kluge, 1997), the hind wings of *M. rossi* are narrower and elongate, lack a marked costal process (Sinitshenkova 2000: 27, figs 1f, g), and show only a widely rounded costal angulation (compare with Kluge 1997: 524, 532, fig. 17; Kluge 2004: 97, fig. 27B). On the other hand, the hind wing venation is reduced in *Myanmarella*, as it is typical for many baetoid taxa (also

Palaeocloeoninae), including RA fork, secondary furcation of RP, and absence of other triads and veins posterior to MP1 (Sinitshenkova 2000: 26, figs 1d, e).

At the same time, *M. rossi* is similar to *Vetuformosa buckleyi* Poinar, 2011 which is the second species of Baetidae described from Upper Cretaceous Burmese amber based on a single female subimago (Poinar 2011). Both specimens are similar in wing venation with a double-forked RA in the elongate and narrow hind wing that also lacks a costal process. Additionally, the antennal flagellum of both fossil taxa is distinctly long. Poinar (2011: 370, figs 2, 3) referred to the presence of these characters in *V. buckleyi* in contrast to *Palaeocloeon* with short flagellum and absence of the second RA fork as basis to place *V. buckleyi* in a newly erected subfamily Vetuformosinae (Poinar 2011).

Nevertheless, a shortened antennal flagellum is only present in males of *Palaeocloeon* (e.g. holotype specimen, see Supplementary material 2, Fig. S2), whereas females possess a relatively long antennal flagellum, which is at least 2.5 times longer than head length (e.g. paratype nr. 3 described by Kluge 1997: 529, fig. 9; Kluge 2004: 97, fig. 27C). Contrary to Poinar's assumption, the hind wings of *Palaeocloeon* have a double-forked RA, which is even better visible in the subimago. On the other hand, presumed features of *V. buckleyi* in female genitalia could indicate a separate systematic position within other Palaeocloeoninae described from Burmese amber.

In summary, none of the diagnostic criteria of *V. buckleyi* justify its placement in a separate subfamily. Therefore, we transfer this species to Palaeocloeoninae (= Vetuformosinae Poinar, 2011 **syn. nov.**). Thus, *M. rossi* can be considered the first reliable record of Baetidae from the Upper Cretaceous Burmese amber, and the second Mesozoic evidence of this subfamily after Kluge's (1997) discovery of *Palaeocloeon* in Taymyr amber. The adult characters discussed above indicate a possible synonymy of *Myanmarella* and *Vetuformosa*, and the available records suggest the widespread presence of Palaeocloeoninae in the Late Mesozoic.

### 4.3. Biogeographic considerations

As Recent Baetiscidae are confined to North America, these findings raised more complex interpretations on their biogeographical history. Initially of Pangean origin, the group radiated worldwide by dispersion and vicariance events. Its present restriction to North America may be explained as the result of continental extinctions, possibly even in fairly geologically recent times, i.e. by glaciation events during the ice ages. The extinction of *Protobaetisca* from the Lower Cretaceous of Gondwana probably took place during the K/Pg event by the end of Cretaceous; followed by the extinction of *Cretomitarcys* from the Upper Cretaceous of Laurasia due to local glaciations in North America. Finally, the extinction of *Balticobaetisca* in the Palearctic most probably took place during Pleistocene glaciations (Pescador et al. 2009).

## 5. Conclusions

*Balticobaetisca bispinata* **sp. nov.** constitutes the third known fossil species of *Balticobaetisca*, adding to current knowledge of the mayfly diversity during the Eocene. The first winged specimen putatively assigned to the Cretaceous genus *Protobaetisca* provides new information on character evolution of Baetiscidae. The cladistic analysis of Baetiscidae including its extinct representatives revealed that the most basal group of this clade is *Cretomitarcys* from the Upper Cretaceous of Laurasia, separated by the remaining Baetiscidae by only moderately rounded hind wings [apomorphic character for *Protobaetisca* + (*Balticobaetisca* + *Baetisca*)]. The monophyletic *Balticobaetisca* shares a triangular projection on the inner margin of forceps. As expected, considering its Eocene age (in contrast to the Mesozoic *Protobaetisca* and *Cretomitarcys*), *Balticobaetisca* is most closely related to its sistergroup *Baetisca*, sharing an elongated/narrower forewing in contrast to the basal groups and outgroup, which possess a more triangular forewing. Also shared are the presence of two differently sized blunt claws on the foreleg of males. Based on the fossil evidence, we concur with the biogeographical considerations presented by Pescador et al. (2009), in which the authors hypothesize a Pangean origin for Baetiscidae.

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## Supplementary material 1

### Figure S1

**Authors:** Staniczek AH, Storari AP, Godunko RJ (2022)

**Data type:** .tif

**Explanation note:** *Balticobaetisca bispinata* sp. nov., SMF coll., SMF Be 411, labels of paratype.

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**Link:** <https://doi.org/10.3897/asp.80.e82845.suppl1>

## Supplementary material 2

### Figure S2

**Authors:** Staniczek AH, Storari AP, Godunko RJ (2022)

**Data type:** .png

**Explanation note:** Species of Palaeocloeoninae Kluge, 1997 from Upper Cretaceous amber: (A, C, E) *Palaeocloeon taimyricum* Kluge, 1997, Taymyr amber, male imago, holotype [A, B], PIN coll.; *P. taimyricum*, female subimago, paratype nr. 3 [C], PIN coll.; (B, D, F) Palaeocloeoninae spp., Burmese amber, female imago [B, D], SMNS coll., BU–12 (specimen 4); female imago [F], SMNS coll., BU–12 (specimen 1). (A) head, thorax, wings and abdominal segments I–III in ventral view; (B) – general dorsal view; (C–D) – right forewing in dorsal view; (E) right hind wing in ventral view; (F) right hind wing in dorsal view. Abbreviations: (A–B) I–III – abdominal segments I–III; ant – antenna with long flagellum; BS – basisternum; E – male eyes [not divided into two portions, in contrast to other Baetoidea, except of Siphlaenigmatidae; for more details see Kluge 1997: 531, fig. 11; Kluge 2004: 101, fig. 27F]; fe1–fe3 – pro-, meso-, metafemur; FSp – furcasternal protuberances [contiguous, same character state in Siphlaenigmatidae, in contrast to other Baetoidea; for more details see Kluge 1997: 531, figs 11, 14; Kluge 2004: 101, fig. 27F]; FW – forewing; HW – hind wing; ti1–ti3 – pro-, meso-, metatibia; TPs – tibio-patellar suture. (C–E) cp – costal process; C – Costa; Sc – Subcosta; RA – Radius anterior; RP – Radius posterior; iRP – intercalary vein RP; MA – Media anterior; iMA – intercalary MA; MP – Media posterior; CuA – Cubitus anterior; CuP – Cubitus posterior; A1 – anal vein.

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**Link:** <https://doi.org/10.3897/asp.80.e82845.suppl2>

## Supplementary material 3

### Table S1

**Authors:** Staniczek AH, Storari AP, Godunko RJ (2022)

**Data type:** .pdf

**Explanation note:** Measurements of holotype and paratype of *Balticobaetisca bispinata* **sp. nov.** (Eocene Baltic amber).

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**Link:** <https://doi.org/10.3897/asp.80.e82845.suppl3>

## Supplementary material 4

### Table S2

**Authors:** Staniczek AH, Storari AP, Godunko RJ (2022)

**Data type:** .pdf

**Explanation note:** Measurements of holotype and paratype of *Balticobaetisca bispinata* **sp. nov.** (Eocene Baltic amber).

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## Supplementary material 5

### Table S3

**Authors:** Staniczek AH, Storari AP, Godunko RJ (2022)

**Data type:** .pdf

**Explanation note:** Matrix of morphological characters and states used for the phylogenetic analyses of Baetiscidae.

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