1 Evolution of sexual conflict in scorpionflies

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17 Abstract

18 Sexual conflict – opposite reproductive/genetic interests between sexes – can be a
19 significant driver of insect evolution. Scorpionflies (Insecta: Mecoptera) are models in sexual
20 conflict research due to their large variety of mating practices, including coercive behaviour
21 and nuptial gift provisioning. However, the role of palaeontology in sexual conflict studies
22 remains negligible, namely due to the paucity of well-preserved fossils. Here we describe
23 three male scorpionflies from Cretaceous and Eocene ambers. The structure of notal and
24 postnotal organs is analysed in extant and extinct forms; a depression below the base of the
25 notal organ in different panorpid species spatially matches the anterior fold of the female's
26 wing. Based on disparate abdominal configurations and correlations in extant relatives, we
27 posit that each new fossil taxon had a different mating approach along a nuptial gifting-
28 coercive spectrum. The Eocene specimen possesses extreme female clamping abdominal
29 armature, suggesting a degree of sexual coercion greater than in any other known scorpionfly,
30 extinct or extant. The fossil record of abdominal modifications in male scorpionflies
31 documents a relatively late evolution (Eocene) of long notal organs indicating oppressive
32 behaviour toward a female during mating. Our findings reveal a wider array of mating-related
33 morphological specialisations among extinct Panorpoidea, likely reflecting more diversified

past mating strategies and behaviours in this group, and represent first steps towards gaining a deep-time perspective on the evolution of sexual conflict over mating among insects.

Key words: mating strategies, Mecoptera, amber, Cretaceous, Eocene, new species, new genus, new family

INTRODUCTION

Sexual conflict between two conspecific sexes arises when divergent interests about the timing and duration of copulation, number of mating partners, or parental investment occur, provided that a trait enhancing the reproductive success (~fitness) of one sex may reduce that of the other (Arnqvist and Rowe, 2005). Currently more broadly defined as the sexually antagonistic selection of shared traits, the sexual conflict is now recognised as a “pervasive evolutionary selective force”, leading in many known instances to a male-female coevolution (Parker, 1979; Rostant et al., 2020). At the very core of this conflict lies the struggle for dominance over genetic control in offspring by each sex (Thornhill, 1976, 1979). The study of mating practices offer one of the most direct ways to address sexual conflict in nature. Two seemingly opposite (yet not necessarily mutually exclusive) mating-related strategies are observed in males: aggressive behaviour toward a female, which allows exerting domination while mating, and the nuptial gifting of food to allure and/or pacify a female during the time of copulation and sperm transfer (Lehmann, 2012; McCartney et al., 2013). Both coercive and nuptial gifting strategies appear costly to males because they are based on the differential allocation of limited sources (Liu et al., 2015); therefore, an exaggerated armature may hinder the overall fitness in a male (e.g., in rhinoceros and flour beetles a larger ‘weapon’ is negatively correlated with wing size; Yamane et al., 2011). In order to incline the female to mate, males show aggression (e.g. calopterygid damselfly; Cordero and Andrés 2002), intimidating behaviour (e.g. water strider; Han and Jabłoński, 2010), and may use special structures, as modified front legs to clasp the female wings (e.g. sepsid flies; Eberhard, 2002) or adhesive discs to secure grip on the female (e.g. diving beetles; Bergsten et al., 2001). Within coercive mating, extreme cases of aggressive behavior by males, which may cause damage or even death to the female, are known among insects and other invertebrate groups, such as true bugs (Siva-Jothy, 2006), water bugs, and camel-spiders (Arnqvist and Rowe, 2002; Hrušková-Martišová et al., 2010) or snails (Kimura and Chiba, 2015), but also among vertebrates (e.g., ducks: Brennan and Prum, 2012). Nuptial gifting is also widespread. Crickets and bush crickets (Orthoptera: Tettigonidea, Grylloidea) provide an edible gift

attached to a structure containing the sperms. Female consumes the nutritious part during fertilisation by the spermatozoans, the time for consumption correlating with that of fertilisation (Lehmann, 2012; McCartney et al., 2013). Males of other orthopterans offer thoracic secretions (Gryllidae; Bussire et al., 2005) or even their own hind wings as nuptial gifts (Haglidae; Eggert and Sakaluk, 1994; Sakaluk et al., 2004). Silk-wrapped nuptial gifts of prey are offered by spiders (Stlhandske, 2001) and dance flies (Diptera: Empididae; Preston-Mafham, 1999; Sadowski et al., 1999; LeBas and Hockham, 2005); the shining silk cover makes a gift more enticing and may deceive the female if it only contains a scarce – or even fully absent – edible portion (Ghislandi et al., 2017). In dobson flies (Megaloptera: Corydalidae), the species offering nuptial gifts have a ‘weapon’ armature used for fighting off the rivals smaller than in species whose males rely only (or mostly) on such armature (Liu et al., 2015). Among mecopterans, a gift of prey is offered by hangingflies (Bittacidae; Thornhill, 1976) and scorpionflies (*Panorpa* spp.; Gwynne, 1984); the latter may offer hardened salivary masses to the female instead (Thornhill, 1979; Bockwinkel and Sauer, 1994). Coercive and nuptial-gifting mating approaches can co-occur in same species, which then exhibits a mixed strategy that can serve as a model to study the trade-off between these two tactics (e.g., Tong and Hua, 2019).

Scorpionflies (Mecoptera: Panorpidae) are models in sexual conflict research. Their mating practices range from coercive to provisioning nuptial gifts, in extreme cases including mouth-to-mouth salivary transfer until the end of copulation (Zhong et al., 2015). Mecoptera are among the oldest holometabolous insects. They are known since the Permian, when they were a significant component of the flying insect fauna. Whereas scorpionflies flourished in the Mesozoic, most of their lineages rapidly declined during the Cenozoic. In fact, mecopterans are considered to have gone through a degree of extinction unparalleled among holometabolans (Grimaldi and Engel, 2005). Extant Mecoptera are classified in nine families, most of which are relict; only two lineages, Panorpidae and Bittacidae, are relatively species-rich. The Panorpidae appeared in the Late Jurassic (Ding et al., 2014) and currently represent the most diverse mecopteran lineage, with about 480 described species classified in seven genera (Bicha, 2018; Miao et al., 2018), i.e., c. 67% of extant mecopteran species.

In scorpionflies, the male behaviour towards the female may be coercive in such a degree that the expression ‘rape’ has been used in the past for describing their mating rituals (Thornhill, 1980). In any case, the role of a female in controlling mating and the eventual reproductive outcome appears more active and decisive than initially thought in the group, namely through precopulatory male choice, struggling behaviour to interrupt genital

connection, and the selective reception of sperm from gift-providing males (likely through spermathecal muscular action; Kock et al., 2009). The modifications of panorpid males enabling coercive mating behaviour include a diverse array of structures on different abdominal segments as well as thinned and elongate last segments of the abdomen. Some of these structures, the so-called notal and postnotal organs, effectively act as a ‘clamp’, grasping the female’s wing prior to and during the course of copulation (Figure 1A and B, Figure 1F). Depending on the size and shape of these organs in a species, the grasp is more or less coercive. Elongate abdominal segments enable the males to bend the abdomen over that of the female, while additional, usually paired abdominal structures referred to as anal horns are used to achieve and maintain the strained, twisted copulatory position of both abdomens for the long time required for sperm transmission, which could be more than three hours (Tong et al. 2018; Tong and Hua, 2019). Panorpid species with very long notal organs, capable of clamping the entire width of the female wing, only use coercion, so no food gifts are offered (Tong and Hua, 2019). In species with mixed strategies, it is the physical condition of the male which determines the followed strategy (Enquist and Sauer, 2001): older and weaker males, as well as smaller ones, primarily adopt an aggressive strategy toward a female, as they are either not able to obtain a prey as a gift or to fabricate it through salivary production, or their gift is often been stolen by a stronger male. Larger males also have an advantage over smaller ones when competing for dead arthropods that can be offered to a female or, if eaten by the male, allow to produce salivary masses. On the other hand, conspecific smaller males bear proportionally larger notal organs (Thornhill, 1990), which shows the genetic background of this negative allometry.

Here we describe three exceptional scorpionflies from three different Cretaceous and Eocene ambers deposits and each belonging to a distinct panorpoid lineage. The disparate abdominal configurations and specialisations in the new taxa allow us to extrapolate trends observed among extant relatives, discussing possible mating habits for the new fossils and previously described ones with preserved non-genitalic abdominal modifications (Willmann and Novokschonov, 1998; Archibald, 2010; Krzemiński and Soszyńska-Maj, 2012; Zhang et al., 2021). Additionally, the new taxa is of general evolutionary significance, including the description of a new extinct panorpoid family and the first orthophlebiid species described in amber.

RESULTS

Systematic Palaeontology

Mecoptera Packard, 1886

Panorpoidea Latreille, 1805

Panorpidae Latreille, 1805

Baltipanorpa Krzemiński and Soszyńska-Maj, 2012

Type species. *Baltipanorpa damzeni* Krzemiński and Soszyńska-Maj, 2012; Baltic amber.

Other species included. *Baltipanorpa oppressiva* sp. nov.; Baltic amber.

Baltipanorpa oppressiva Soszyńska-Maj and Krzemiński sp. nov. (Figures 1A–H)

Etymology. After “*oppressio*”, meaning “coercive” in Latin, referring to the most restraining notal organ ever found within Panorpidae. Gender is feminine.

Material. Holotype MP/2711, most part of the abdomen and wings preserved,

Locality and age. Baltic amber, middle Eocene (ca. 45 Ma).

Diagnosis. Wing membrane with dark maculations (vs. transparent in *B. damzeni*); notal and postnotal processes very long, reaching end of VII segment, notal process distally forked (vs. notal process shorter than postnotal, and not forked in *B. damzeni*); abdominal segment V slightly wider than long; tergite V medially bearing large, strongly recurved process (vs. tergite V without process in *B. damzeni*); segments VII and VIII thinned at base, not particularly elongate, about 3–4× as long as maximal width (vs. segments VII and VIII strongly elongate in *B. damzeni*).

Description. Body length 2.2 mm as preserved (only abdomen). *Head.* Antennae partly preserved with 14 cylindrical flagellomeres twice longer than wide. *Wings* (Figure 1A). Elongate and narrow, almost 3.5× longer than wide, at least 10 mm long, ~3 mm wide. *Forewing* (Figure 1G). Membrane bearing seven maculated areas, largest occupying the wing tip; Sc short and single reaching wing margin in midwing, opposite crossvein m-cu; costal area narrow; R_{1a} and R_{1b} surrounding pterostigmal area; Rs with five branches reaching wing margin, Rs₁₊₂ longer than R₃₊₄; fork of Mb more distal than fork of Rs, crossvein r₃₊₄–m₁₊₂ sinuous; M with four branches reaching wing margin, M₁₊₂ 13× longer than M₃₊₄, M₄ sharply curved at m-cu; Cu₁ and Cu₂ fused at base, with two crossveins between them; three anal veins, A₁ reaching wing margin proximal to origin of Rs. *Hind wing* (Figure 1H). Venation very similar to forewing, except for: Mb fused with Cu₁, A₁ proximally fused with Cu₂, only one cu2-a2. *Abdomen* (Figure 1A and B). Incomplete, longer than wings; first two segments are missing; notal and postnotal processes on tergites III and IV, respectively (Figure 1B), both processes very long (1.2 mm), about equal in length, reaching segment VII; notal process

with spine-like setae on inner surface's distal half (Figure 1B and C), bearing terminal fork curved posteriorly (Figure 1E); postnotal process terminally curved anteriorly, lodged between prongs of notal process (Figure 1B and C), bearing one very long seta at midlength of organ, and few shorter setae in basal part (Figure 1C and D); postnotal organ covered with short and blunt teeth, irregularly distributed on inner surface; tergite V medially bearing a large, strongly recurved process (horn, 300 μ m); abdominal segments VI–VIII moderately elongate, with fused tergites and sternites; segments VII–VIII narrower basally. *Genitalia* (Figure 1B). Genital bulb round; hypovalves narrow, not extending to apex of gonocoxite; gonostylus shorter than gonocoxite.

Remarks.

Orthophlebiidae Handlirsch, 1906

Burmorthophlebia Soszyńska-Maj, Krzemiński and Wang gen. nov.

Etymology. Combination of *Burmo*-, after Burmese amber, and *-orthophlebia*, after the genus *Orthophlebia* (from the Greek “phlebas”, φλέβας, meaning “veins”) to emphasize an alleged close relationship to this genus. Gender is feminine.

Type species. *Burmorthophlebia multiprocessa* sp. nov., by monotypy and present designation.

Diagnosis. Rostrum long and narrow; antenna with at least 30 flagellomeres. Fore- and hind wings with R_1 slightly curved in pterostigmal area towards anterior wing margin; R_s with five branches (vs. six and more in other genera of Orthophlebiidae), R_{s1+2} and R_{s3+4} very long (vs. much shorter in other genera of Orthophlebiidae) R_{s1} ascending, R_{s1+2} and R_{s2} almost at the same level. Forewing with Sc long and simple, reaching pterostigmal area; M with five branches; two crossveins present between M_4 and Cu_1 ; two anal veins. Hind wing with Sc single and simple, only reaching M_{3+4} forking; M with four branches; one anal vein. Abdominal segments VI–VIII moderately elongate; very short notal process on tergite III, not extending beyond end of this tergite; postnotal process absent; two hirsute postnotal areas on tergite IV; tergites VI and VII with a pair of distal appendages each. Genital bulb without stem part, gonostyli long and thin.

Burmorthophlebia multiprocessa Soszyńska-Maj, Krzemiński and Wang sp. nov. (Figures 2A–H)

Etymology. Species name highlights the unusual morphology of the holotype, possessing multiple processes on abdominal segments.

Material. Holotype MP/3721, male.

Locality and age. Kachin amber, Myanmar; earliest Cenomanian (98.8 ± 0.62 Ma), Late Cretaceous.

Diagnosis. As for the genus (*vide supra*).

Description. Body length 9.5 mm from frons to the end of gonostyli (Figure 2A). *Head* (Figure 2G). Three occipital bristles; rostrum 2 mm long, first five flagellomeres only slightly longer than wide, gradually becoming more elongate, distal visible flagellomeres 3× longer than wide; maxillary palp five segmented, palpomeres slim, ca. 4× longer than wide. *Thorax.* Legs with setae arranged in whorls, each bearing a pair of long tibial spurs; fifth tarsomere ca. 4× longer than fourth one, two pretarsal claws; first tarsomeres bear, no swellings on any leg. *Wings.* Proximally narrow and significantly broadening distally, 9.5 mm long and ca. 3.5 mm wide; wing membrane bearing a round, dark pigmented spot in medial sector. *Forewing* (Figure 2C). Sc and R₁ reaching pterostigmal area, two crossveins between C and Sc; Rs₁₊₂ almost 3× longer than Rs₁, Rs₃₊₄ longer than Rs₃ and Rs₄; M with five branches reaching wing margin, Mb forking beyond the Rs fork, M₁₊₂ 9× longer than M₃₊₄, M_{4a+b} 3.5× longer than M₃₊₄; two m₄-cu₁ crossveins, the most proximal slightly bending M₄; two crossveins between A₁ and A₂, A₃ not visible. *Hind wing* (Figure 2D) same as in forewing; Mb fused with Cu₁; second anal vein reduced or invisible. *Abdomen* (Figure 2E and F). Elongate, notal organ on abdominal tergite III wide at base and curved toward distal part; postnotal organ on tergite IV acutely elevated, composed of two areas of dense brush of short setae, distal part of tergite IV curved upward and covered with dense setation (Figure 2H); abdominal segment V ca. 1/3 longer than wide; segment VI ca. ½ longer (800 µm) than wide, bearing a pair of relatively large anal horns on posterior margin of tergum; distinct sinuous seam between tergites and sternites (Figure 2E and F); tergites and sternites VII–VIII fused; segment VII (1.3 mm) distinctly thinned at base and gradually broadening distally, horns on posterior tergum margin, opposite to them the sternite bears a process with dense setae; segment VIII ca. 2× longer than wide, sternite covered with setae. *Genitalia.* Genital bulb narrow (Figure 2E); gonostyli longer than gonocoxites, very thin at apex, covered with numerous setae; hypovalve broad; epandrium most likely with two processes.

Remarks. *Burmorthophlebia* gen. nov. differs from all other genera of the family Orthophlebiidae in number of veins in radial sector, and in unusually long veins Rs₁₊₂ and Rs₃₊₄ which are only terminally forked, at level of end of Sc. Wings of *Burmorthophlebia* are more narrow than in other orthophlebiids. Five veins in radial sector are present also in a recently established family Protorthophlebiidae (Soszyńska-Maj et al., 2020), but the rostrum

in this family is short (only c. twice as long as its maximum width), and VI-VIII abdominal segments in male are shorter than wide, while *Burmorthophlebia* has a long rostrum and elongate abdominal segments, both characters typical to orthoplebids.

Cantabridae Soszyńska-Maj, Pérez-de la Fuente, Krzemiński and Wang fam. nov.

Type genus. *Cantabra* gen. nov., by monotypy and present designation.

Diagnosis. Head with three pairs of long ocellar bristles, rostrum elongate; pronotum elongate, longer than head, bearing long bristles; Sc single, costal area narrow, R and M sectors with four branches in both wings, crossvein cu2-a2 present in hind wings; male abdomen much longer than wings, with elongate and narrow segments VI–VIII, tergites and sternites VII and VIII fused; male gonostylus without median tooth, with several minute denticles.

Remarks. The wing venation and general habitus of *Cantabra* gen. et. sp. nov. resemble those of the Panorpidae and Panorpididae. The new fossil species differs from panorpidids in the distinct body bristles, particularly those on head and thorax, an unusually elongate pronotum, clearly longer than the head (shorter in panorpidids), and the lack of median tooth on the inner surface of male gonostyli, instead bearing several minute denticles in a row. From panorpidids, *Cantabra* gen. et. sp. nov. differs in greatly elongate rostrum, elongate abdomen and fused VII and VIII abdominal segments. The remarkably elongate and narrow male abdomen of the new taxon resembles extinct family Holcorpidae, but differs from the latter in five veins in medial sector in both wings and less elongate abdominal segments VI-VIII (Archibald, 2010).

Cantabra Soszyńska-Maj, Pérez-de la Fuente, Krzemiński and Wang gen. nov.

Type species. *Cantabra soplao* sp. nov., by monotypy and present designation.

Etymology. After the Latin “cantabra” (“cantabrum” in masculine) meaning “from, or pertaining to, Cantabria” – i.e., the Autonomous Community of Spain where the El Soplao outcrop is located. Gender is feminine.

Diagnosis. As for the family (*vide supra*).

Cantabra soplao Soszyńska-Maj, Pérez-de la Fuente, Krzemiński and Wang sp. nov. (Figures 3A–G and Figures 4A–E)

Etymology. After the El Soplao amber outcrop, where the amber inclusion was found. The specific epithet is treated as a noun in apposition.

271 **Material.** Holotype CES-437, male.

272 **Locality and age.** El Soplao amber outcrop; middle Albian, Early Cretaceous (ca. 105 Ma).

273 **Diagnosis.** As for the genus (*vide supra*).

274 **Description.** Body length ~9.25 mm without antennae (Figure 3A). *Head* (Figures 3B and C).
275 Rostrum with preserved proximal part about 1.5× as long as that of head; 20 flagellomeres
276 preserved, all elongate, 2–3× as long as wide, covered with microsetae; three pairs ocellar
277 bristles on vertex, ~350 µm long, probably surrounding ocelli (the latter not discernible).
278 *Thorax.* Pronotum with long bristles, ~300–350 µm long; only one right foreleg partially
279 preserved, elongate, rather delicate, bearing microsetae on its entire length; femur bearing
280 ventral bristles; tibiae with a few whorls of spike-like setae arranged in whorls and bearing
281 two long spurs distally. *Wings.* Only right wings fully preserved. Wings elongate and narrow,
282 almost 4× longer than wide, 6.5 mm long, 1.7 mm wide; C covered with setae, longer and
283 thinner in anal region. *Forewing* (Figure 4A). Costal area narrow, with Sc unbranched and
284 long, reaching wing margin opposite tip of M₄; R₁ faint, its two branches surrounding
285 pterostigmal area; radial sector with four branches; Rs₁₊₂ almost twice as long as Rs₃₊₄; M₁₊₂
286 almost 7× longer than M₃₊₄; Cu₁ and Cu₂ fused at base; three anal veins present, A₁ reaching
287 the wing margin beyond fork of Rs; short spines along anal veins and wing membrane on anal
288 area; jugal area with few long bristles. *Hind wing* (Figure 4B). Venation mostly similar to that
289 of forewing, except short Sc, not reaching beyond the level of end of Cu₁; R₁ forking at the
290 level of end of Cu₁; Mb fused with Cu₁; A₁ proximally fused with Cu₂ and reaching wing
291 margin only slightly beyond fork of Rs; one crossvein between Cu₂ and A₂; crossveins hardly
292 visible. *Abdomen* (Figure 4C). Significantly longer than wings; tergite III not visible dorsally,
293 notal organ not discernible, but (if present) not long, (otherwise it would be visible above
294 tergite IV); small postnotal organ present on tergite IV; long bristles on sternites IV–V;
295 abdominal segments VI to VIII elongate and narrow, segment VI (1.8 mm long) 7× longer
296 than wide, segment VII (1.4 mm) 6× longer than wide, segment VIII (1.5 mm) 10× longer than
297 wide; segment VI most probably with a fusing seam; segments VII and VIII with tergites and
298 sternites fused. *Genitalia* (Figure 3F and G, 4C and D). Genital bulb elongate, hypovalves
299 probably broad, not extending to apex of gonocoxites; gonostyli (1 mm) longer than
300 gonocoxites (700 µm), slender, inwardly curved at apex, without median tooth, and with
301 rounded and relatively small basal processes; inner margin of gonostylus with at least eight
302 short triangular denticles in a row along median and basal parts; basal processes of parameres
303 long and curved ventrally, with their basal branch rounded, covered with dense microsetae
304 reaching apex of gonocoxite, hypovalve probably broad.

305

306 **DISCUSSION**

307 A series of clamping devices used to seize and hold different body parts of the female
308 during courtship and copulation exist in panorpid males. These structures ensure the eventual
309 genital connection and sperm transfer; and extend copulation time (Zhong and Hua, 2013;
310 Zhong et al., 2014). The latter is critical for males, as the more prolonged the copulation, the
311 more sperm can be transferred and, thus, the greater the number of potentially fertilised eggs
312 (Engqvist and Sauer, 2001; Kullmann and Sauer, 2005). Aside from genital clamping
313 structures (among which the most conspicuous is a pair of pincer-like gonostyli), panorpid
314 present non-genital clamping systems on their abdomens. These are notal and postnotal
315 organs, as well as anal horns which are used to catch and immobilize female during mating.
316 Based on the size, shape and interlocking mechanism of these clamping structures, the grasp
317 on the body of female becomes more or less secure, therefore facilitating a greater degree of
318 coercion during mating, which has been associated with less investment in costly nuptial gifts
319 (Tong and Hua, 2019).

320

321 **Notal and postnotal organs**

322 The notal organ (NO) is a process on abdominal tergite III. The postnotal organ (PO)
323 typically consists of a small process on abdominal tergite IV (Crampton, 1931; Mickoleit,
324 1971b). In extant scorpionflies, both structures are present in most Panorpidae, in one and the
325 only recent species from the Eomeropidae (the ‘living fossil’ *Notiothauma reedi* MacLachlan,
326 1877; Crampton, 1931), and can be vestigial, if present, in the Panorpididae (Tong et al.,
327 2017; Wang and Hua, 2018a). Both NOs and POs act jointly by typically creating a clamping
328 structure that grasps the female forewing before and during copulation; in panorpid
329 organs allow to achieve and maintain the typical V-shaped mating position (Figure 6A and B)
330 (Byers and Thornhill, 1983). Moreover, the NO and the PO bear specialised setae,
331 cephalically directed and thinned terminally, which interlace and/or electrostatically interact
332 with both venational setae and membrane microtrichia from the female’s wing (Zhong and
333 Hua, 2013). Observations on three species of *Neopanorpa* van der Weele, 1909 bearing NOs
334 of different lengths have shown different mating strategies in these species (Zhong and Hua,
335 2013; Tong and Hua, 2019). Males of two species with short and medium-sized NO (i.e., *N.*
336 *lui* Chou and Ran, 1981 and *N. carpenteri* Cheng, 1957, respectively) indirectly transfer a
337 nuptial gift of a salivary secretion prior to copulation. The short NO of *N. lui* ends at the base

of the PO, and the medium sized NO in *N. carpenteri* reaches the end of the abdominal segment IV; both stabilize the female wings only partially and apparently play an auxiliary role during copulation. Contrarily, *N. longiprocessa* Hua and Chou, 1997, with a long NO capable to cover and keep the entire wing width of the female, exclusively relies on coercive copulation, and does not offer nuptial gifts. Short NOs and POs pinch only the anterior margin of female forewings, and both processes are spatially suited to fit the latter. In *Panorpa amurensis* MacLachlan, 1872 (Figures 5A and B), the space created by the clasped NO and PO matches the space of the anterior valley fold of the female wing delimited by the convex costal vein (C), the concave subcostal vein (Sc), and the convex radial vein (R_1), clamping together with the PO before or at the latter vein. Our measurements of these distances in this and other panorpid species with various NOs indicate that this seems to be an effective arrangement to grip the anterior wing fold of the female (see Supplementary File 1 for measurements). As the C, Sc, and R_1 run almost parallel over a long stretch, the female forewing may be gripped more anteriorly or posteriorly, usually by its half or basal third, as can be observed in photographs of mating panorpid (Zhong and Hua, 2013; Zhong et al., 2014; Tong and Hua, 2019).

A short NO of the type similar to that in Recent panorpid was already present among the Late Jurassic panorpoids, as evidenced by *Orthophlebia heidemariae* Willmann and Novokschonov, 1998 (Figure 6C and D). This species is currently classified in Orthophlebiidae, a Mesozoic polyphyletic panorpid assemblage ancestral to Panorpidae (Soszyńska-Maj et al., 2020). In *Burmorthophlebia multiprocessa* gen. et sp. nov. the NO, although also short, differs from all the hitherto known in Mecoptera, extinct or extant. The NO is distinctly raised over abdomen but poorly pronounced, not reaching any process to form a clamp with. The PO is here replaced by two elevated areas on tergite IV, the postnotal areas 1 and 2 (PA1 and PA2; Figure 5E). The former is mound-like, located after an anterior depression on tergite IV and at a distance from the NO comparable to that of C to R_1 . The PA2 is sharply elevated, and measurements show that it contacted the female wing just at or slightly beyond the concave radial sector vein (R_s). Both PAs were involved in adhering the female's wing as indicated by their location and specialised setation, consisting of short and dense tufts of hairs different from other abdominal bristles. Apparently, only the costal vein and a brief anterior wing membrane portion were covered by the NO in *B. multiprocessa*, and so the remaining portion of the female wing was to a certain degree immobilised by the setation of both PAs. Among the extant panorpid the hirsute PAs, more flattened than those of *Burmorthophlebia* and situated on three consecutive tergites, have been described in

Neopanorpa setigera Wang and Hua, 2018 and *N. luojishana* Wang and Hua, 2019 (Wang and Hua, 2018b, 2019b), and also exist in *N. longistipitata*. However, in these species the NO is long and able to keep the entire wing of a female pressed against the male's abdomen to a lesser or greater extent, so the hirsute PAs are probably only of auxiliary importance (Figures 6A-D). This contrasts with the armature in *B. multiprocessa* gen. et sp. nov., where it was the interaction between NO-PO setae and the integumentary structures of the female's wing that kept a larger portion of the latter in place, although the fixing must have been weaker. Recent panorpids with a short NO (and anal horns) adopt a mixed mating strategy (Neff and Svenson, 2013). After a courtship ritual, males present nuptial gifts to the female, but if they are not able to get one ready (including if they have been stolen by other males) or the gift is deemed as unsatisfactory by the female (e.g., small salivary secretions due to poor condition of the male), they resort to attempt coercive copulation (Thornhill and Sauer, 1991). *Baltipanorpa multiprocessa*, with its short NO and no other armature to immobilize the female's wing, probably had a similar approach when mating.

As introduced above, long NOs differ mechanically from short NOs. They are present in a small group of species classified in the genera *Panorpa* and *Neopanorpa* (Hu et al., 2015; Tong and Hua, 2019; Wang and Hua, 2018a). Instead of a pincer-like clamp composed by a PO and NO, the long NO covers the entire female's wing across its full width and immobilizes it more or less pressed against the abdomen. As the mating couple of *N. longistipitata* shows (Figures 6A-D), the leading edge of the female wing is also accommodated in a small depression of tergite IV under the base of the NO. As can be deduced from measured distances, of the three hirsute PAs on tergites IV-VI the first one supports the wing fold by the convex R₁; the more distal part of the wing is pressed against the abdomen by the long NO with the help of special muscles (Thornhill, 1990). The tip of the NO is locked between the genital hypovalvae. Although this conformation fully encloses the female wing during mating, the resulting grip is likely not particularly tight. In any case, nuptial gifts are not offered prior or during the mating of *Neopanorpa* species with a long NO, such as *N. longiprocessa* (Zhong and Hua, 2013), which would suggest that such process enables highly coercive mating behaviour.

Among extinct mecopterans, an extremely long NO was hitherto only known in *Baltipanorpa damzeni* from Baltic amber (Krzemiński and Soszyńska-Maj, 2012). In this species, the NO forms together with an unusually elongate PO a clip-like structure able to reach beyond the full width of the female's wing during mating (Figures 6E). Both NO and PO possess short tooth-like bristles, which would have increased their holding power. The PO

is bent anteriorly, partially securing the clip in this way. *Baltipanorpa oppressiva* sp. nov has a similarly characteristic NO-PO clip bearing inner tooth-like bristles, but its NO is terminally forked in two prongs bent posteriorly at an almost right angle, which embrace the tip of PO (Figure 1B and E, Figure 6F). The interaction of these structures in the new species results in a full clasp-like mechanism. The female wing enclosed in this remarkable clamp was likely fully immobilised, a withdrawal attempt probably causing risk of tearing the wing membrane. A similar function, although less effective than that in *B. oppressiva* sp. nov, must have been accomplished in *B. damzeni* by a few pairs of elongate bristles on the posterior side of the NO (Figure 6E). Furthermore, the NO-PO clamp in *Baltipanorpa* is raised at angle of about 50° from the abdomen, and so the captured female's forewing was also kept raised and separated from the male's abdomen. This position is deemed as genuine (not preservational) as it is now known from two different species (Figure 6E and F) and is unique to this genus. In extant panorpids with very long NOs (*Neopanorpa*), this process is placed at a much lower angle and keeps the female wing rather flat against the abdomen, having no other counterpart such as the long PO in the two fossil *Baltipanorpa* species discussed herein (Figure 6A and D).

Anal horns

The anal horns are distal processes directed posteriorly on abdominal tergite VI. Among extant panorpids, anal horns are single (in *Cerapanorpa* Gao, Ma and Hua, 2016, *Megapanorpa* Wang and Hua, 2018, and some species of *Panorpa* Linnaeus, 1758) or paired (*Dicerapanorpa* Zhong and Hua, 2013), and arise at different angles from the dorsal end of tergite VI (Zhong et al., 2014; Tong et al., 2018; Wang and Hua, 2019a). Aside from panorpids, anal horns are also known in *Notiothauma reedi* (Eomeropidae; Crampton, 1931; Mickoleit, 1971). In conjunction with tergite VII, which is proximally narrowed and/or depressed, the anal horns create a clamping system to accommodate and hold the female's terminal abdomen into the strained copulatory position necessary for sperm transmission. It has been demonstrated that anal horns play an important role at initiating copulation and in prolonging its duration in the absence of nuptial gifts and under female resistance, and that the lack of anal horns is correlated with the inability to prolong copulation after gift provisioning (Zhong et al., 2014).

Burmorthophlebia multiprocessa gen et sp. nov. bears a pair of anal horns raised at a 45° angle (Figure 2E and F, Figure 5E). By comparison with extant species, these processes must have been involved in manipulating and holding the female abdomen during mating. Paired anal horns in other fossil species are known in *Orthophlebia longicauda* Willmann &

Novokshonov 1998 (Orthophlebiidae; Late Jurassic of Karatau in Kazakhstan) and in two species of *Holcorpa* (Holcorpidae) from two Eocene localities (Florissant, Colorado, USA, and the Okanagan Highlands, British Columbia, Canada) (Willmann and Novokshonov, 1998; Archibald, 2010).

Other mating-related modifications in males

Aside from notal-postnotal organs and anal horns, other male abdominal processes involved in the physical interaction with the female during mating are occasionally present in scorpionflies. Among extant panorpids these are positioned on the ventral side, such as a long process on abdominal sternite III (*Neopanorpa furcata* (Hardwicke, 1825)) and a ‘ventral hook’ on sternite VI (*Leptopanorpa linyejiei*, Wang and Hua, 2020). In fossil panorpids, other male abdominal structures with assumed clamping function occurred in the Late Jurassic species *Orthophlebia heidemariae* Willmann and Novokshonov, 1998. This was the case of a large medial horn-like process on tergite V (Figure 5C and D). Such process has been referred to as “tergal spine”, “unpaired median tergal process (monocornus)”, or a “median tergal horn” (Crampton, 1931; Mickoleit, 1971; Willmann and Novokshonov, 1998, respectively). It is probable that this process was also used to fix the female abdomen during mating in conjunction with other more distal structures from the male dorsal abdomen. The abdomen of *O. heidemariae* is preserved in an upturned position and forming a full circle (Figure 5C), which is a frequent mating position among panorpid males. The large horn-like process is opposite to a small putative process and notch on tergite VII (Figure 5D); both structures likely interlocked with one another to facilitate a strained copulatory position (Willmann and Novokshonov, 1998). In *Baltipanorpa oppressiva* sp. nov. the horn-like process on tergite V is strongly recurved, and the subsequent tergite VI has an anterior depression and a greatly expanded end, resulting in a notched shape. Both specialised shapes strongly suggest that this horn and the tergite VI were engaged in holding the female abdomen during mating (Figure 6F). Such conformation was enabled to a certain extent by the position of the female’s wings (at least a forewing) which was raised high (56°) over the male’s abdomen and secured in this position by the extremely long notal-postnotal clip unique to *Baltipanorpa*. Moreover, *Burmorthophlebia multiprocessa* gen. et sp. nov. bears paired processes directed posteriorly at 45° angle on tergite VII, similar to the paired anal horns present on tergite VI, but smaller. Alleged homologous structures have been formerly referred to as “paired tergal processes (bicornua)” or “lateral tergal horns” (Crampton, 1931;

Mickoleit, 1971). The most plausible function for these processes in this new species was also holding the female terminal abdomen during mating.

Cantabra soplao gen et sp. nov. has greatly elongate abdominal segments VI–VIII. Among extant panorpids, such development is present in species of *Leptopanorpa* MacLachlan, endemic to Indonesia, and also in a few *Neopanorpa* species (Wang and Hua, 2020). Although biology of these taxa remains unknown, the greatly elongate abdomens are considered to be influenced by sexual selection, in displays to females and competition among male rivals. Extremely elongate abdomens were also present among other extinct panorpoid lineages: the Orthophlebiidae (Willmann and Novokschonov, 1998), the Holcorpidae (Archibald, 2010; Li et al., 2017; Zhang et al., 2021), and in taxa of uncertain relationships from the Middle Jurassic of China, where abdomen elongation was extreme (Wang et al., 2013). Great abdominal elongation is regarded as a result of convergence (Wang and Hua, 2020). Additionally, in the Holcorpidae and Orthophlebiidae swellings on the first tarsomeres of the hind legs in males were most probably used in sexual display; the size and shape of these swellings was likely species specific (Zhang et al., 2021). In the mecopterans presented herein the tarsomeres were not modified (yet in *Cantabra soplao* gen. et sp. nov. the shape of legs is unknown). Tarsal swellings do not occur in Recent Panorpoidea.

CONCLUSIONS

The morphology of the male's abdomen in extant scorpionflies represents a good approximation to the mating strategy used toward a female. Thus, the abdominal structures of fossil specimens have the ability to convey information on the likely reproductive strategies of extinct scorpionflies and, to some extent, on their evolution. Based on the disparate male abdominal shapes of the three fossil taxa described herein, these almost certainly had different mating strategies along a nuptial gifting-coercive gradient as observed among their extant panorpid relatives. Firstly, the Cretaceous species *Cantabra soplao* gen. et sp. nov., currently the only known member of its lineage, bears a small PO, with the absence of other posterior abdominal processes. This suggests that its mating behaviour was devoid of coercion and that nuptial gifting must have played an important role in these scorpionflies. Extant panorpid species which NO-PO system is very small or even absent and lack posterior abdominal processes ('horns') either rely on nuptial edible gifts or on mouth-to-mouth feeding during copulation adopting an O-shaped position instead of the typical V-position (Fig. 6; Zhong et al., 2015). It is plausible that the mating in *C. soplao* was similar. Regardless, the great degree

of elongation of the abdomen in this species was probably involved in sexual selection dynamics.

Secondly, the Cretaceous *Burmorthophlebia multiprocessa* gen. et sp. nov., the only orthophlebiid specimen described from amber to date, likely exhibited a mixed mating strategy involving both nuptial gifting and coercive behaviour, as observed in some extant Panorpidae species. This inference is based on a weak notal-postnotal clamping system and two sets of paired processes on the abdomen, which likely ensured female restraint and probably extended copulation beyond any possible nuptial gift stages. Noteworthy, abdominal processes are exceptionally abundant in this species, on the dorsal and ventral sides. Such armature is unknown among extant Panorpidae, and can be compared only with that of *Nothiotrauma reedi* of the relict family Eomeropidae.

Lastly, in the Eocene *Baltipanorpa oppressiva* sp. nov. the NO-PO wing clamp, which resembled a sealing clip, was able to tightly grasp the full wing width of the female. Unlike its previously known congeneric relative *B. damzeni*, this structure bore a sophisticated terminal clasp. Together with a highly recurved abdominal horn in this new species, these traits represent the most extreme set of female clamping devices known among scorpionflies, both extinct or extant. Consequently, a fully coercive mating strategy was likely dominant, even exclusive, in this species. During copulation, the female wings (at least the forewings) were likely kept in the notal-postnotal clamp well raised over the male abdomen, this way being separated from the male's anal horn, which is positioned more proximally in this species (i.e., on tergite V vs. in tergite VI in other panorpids). This inclined position of the female's wing(s) enabled the entrapment of her abdomen by the male's anal horn during mating. In evolutionary terms, the fitness costs of such organs and the resulting coercive mating behaviour might have been too high for *Baltipanorpa*. The very long notal and postnotal processes (Figure 6E and F) raised over the male's body might have hindered flight ability; moreover, because of their size (and perhaps their permanently raised position) these processes were likely prone to injury and thus they might entailed a risk for their bearers. These factors might have contributed to the extinction of *Baltipanorpa* and its singular morphology, so that the evolution of this extreme clamping device resulted in a blind alley. Moreover, the biology of the female could have also contributed to this extinction if the mating became too oppressive or dangerous, related to the risk of tearing the wing membrane with the teeth and hard bristles of the male's notal organ.

The remarkable diversity of abdominal configurations shown herein suggests that panorpoid mecopterans had accordingly disparate mating strategies and behaviours in the

past. Data based on fossil and extant species suggest that the coercive mating behaviour in this group is secondary (derived) from the habit of nuptial gifting. According to the current fossil record, long notal organs did not evolve prior to the Eocene (Fig. 7; Supplementary File 2). Data from extant mecopterans point at the Choristidae as the sister group of Panorpoidea (Willmann, 1989; Wang and Hua, 2021), which lack notal organs or other abdominal modifications (including elongate distal segments) and adopt an O-shaped mating position while the male transfers mouth-to mouth salivary secretion to the female (Zhong et al., 2015). Hence, it is assumed that the latter condition is likely plesiotypic for Panorpoidea.

Our data provide first steps towards gaining a deep-time perspective able to inform discussions on the evolution of mating-related sexual conflict in Mecoptera and in insects more generally. Extant fauna show that extreme female holding mechanisms such as those from *Baltipanorpa* did not survive until today among scorpionflies (Wang, 2020). In fact, mating strategies involving gift provisioning appear to have been evolutionarily favored among mecopterans contrary to forced mating, and likely more prone to promote the species' genetic diversity. In order to start formulating hypotheses about when mating strategies – including those fully coercive– and associated anatomical structures of scorpionflies appeared throughout evolutionary history, it will be necessary to keep discovering fossil males with good abdominal preservation. The latter will in turn necessitate from improving the knowledge on the currently contentious phylogenetic relationships among mecopteran groups.

MATERIALS AND METHODS

Geological context

The geographical provenance of the amber samples used in this study is marked on the map provided (Figure 8). The Spanish amber sample was gathered in official excavations with the participation of one of us (RPF) taking place between 2008 and 2010 in the El Soplao outcrop (near Rábago village, Cantabria, northern Spain) (Najarro et al., 2009; Najarro et al., 2010), and is dated as middle Albian, Early Cretaceous (ca. 105 Ma) (Barrón, pers. comm.). The Myanmar amber sample comes from Kachin, near Tanai town, Hukawng Valley, Kachin State, Myanmar, and is dated as earliest Cenomanian (98.8 ± 0.62 Ma), Late Cretaceous (Shi et al., 2012). It was acquired in 2016, prior to the armed conflict and the escalation of the ethnic strife in the area (Haug et al., 2020; Szwedo et al., 2020). The age of Baltic amber is estimated as Lutetian, middle Eocene (ca. 45 Ma) (Grimaldi and Ross, 2017), or as late Eocene (Kasiński et al., 2020).

573

574 **Specimen repository**

575 All the studied specimens are deposited in public institutions. Holotype CES-437 is deposited
576 at the Institutional Collection from the El Soplao Cave (Government of Cantabria), Celis,
577 Cantabria, N Spain. The specimen is partly preserved, the amber piece was polished and
578 included in Epoxy resin for visibility and protection. Holotype MP/3721 is housed at the
579 collection from the Museum of the Institute of Systematics and Evolution of Animals, Polish
580 Academy of Sciences, Kraków, Poland (ISEA PAS). The specimen is almost complete,
581 several cracks cut the specimen. Holotype MP/2711 is housed at the collection of the Museum
582 of the ISEA PAS, Kraków, Poland. The specimen is well preserved but incomplete, a
583 neuropteran and a cecidomyiid dipteran are present as syninclusions.

584

585 **Methods**

586 Photographs of amber inclusions were taken with a Leica M205C stereomicroscope and an
587 attached Leica DFC295 camera, under a Nikon Eclipse E100 compound microscope with an
588 attached Nikon DS F11 camera at the University of Łódź, and with a Nikon SMZ25
589 stereomicroscope equipped with a Nikon DS-Ri2 digital camera at the ISEA (PAS). In most
590 instances, incident and transmitted light were used simultaneously. Stacks of photographs
591 were processed using NIS-Elements Imaging Software. Drawings were obtained based on the
592 photographs but corroborating the morphological details under the optic equipment, and then
593 digitally processed in CorelDraw X10.

594 Adult extant scorpionflies were caught by one of us (J.W.) with a collecting net and
595 then preserved in 95% ethanol or pinned. These specimens are deposited at the Biological
596 Science Museum, Dali University (DALU), Yunnan Province, China. Photographs of the
597 insects were taken with a Nikon D7000 digital camera with a Nikkor AF-S Micro 105 mm
598 f/2.8 lens. The figured specimens of *Panorpa amurensis* were collected by Sigita Podenas in
599 South Korea in 2014, and are deposited at the collection of the Department of the Invertebrate
600 Zoology and Hydrobiology, University of Lodz, Poland.

601 Maps were built using the app Maps-For-Free (<https://maps-for-free.com>) and
602 modified with the software programs Corel Draw and Corel Photopaint X7.

603 Wing venation terminology follows that of Tillyard (Tillyard, 1933), with minor
604 modifications after Soszyńska-Maj *et al.* (Soszyńska-Maj *et al.*, 2018). Wing vein
605 abbreviations: A, anal vein; C, costal vein; Cu, cubital vein, M, medial vein; R, radial vein;

R1, first radial vein; Rs, radial sector vein; Sc, subcostal vein. Other abbreviations used in figures appear in their respective captions.

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REFERENCES

- Archibald B. 2010. Revision of the scorpionfly family Holcorpidae (Mecoptera), with description of a new species from Early Eocene McAbee, British Columbia, Canada. *Annales de la Société entomologique de France* **46**: 173–182. DOI: <http://dx.doi.org/10.1080/00379271.2010.10697654>
- Arnqvist G, Rowe L. 2002. Correlated evolution of male and female morphologies in water striders. *Evolution* **56**: 936–947. DOI: <http://dx.doi.org/10.1111/j.0014-3820.2002.tb01406.x>.
- Arnqvist G, Rowe L. 2005. *Sexual conflict*. Princeton University Press.
- Bergsten J, Toy A, Nilsson AN. 2001. Intraspecific variation and intersexual correlation in secondary sexual characters of three diving beetles (Coleoptera: Dytiscidae) *Biological Journal of the Linnean Society* **73**: 221–232. DOI: <https://doi.org/10.1006/GJbpls.2001.054>
- Bicha W. 2018. Biodiversity of Mecoptera: Science and Society. Footit R, Adler PH (Eds). *Insect Biodiversity: Science and Society*, II. John Wiley & Sons, Hoboken. p. 705–720.

636 Bockwinkel G, Sauer KP. 1994. Resource dependence of male mating tactics in the
 637 scorpionfly, *Panorpa vulgaris* (Mecoptera, Panorpidae). *Animal Behaviour* **47**: 203–209.
 638 DOI: <https://doi.org/10.1006/anbe.1994.1023>

639 Brennan PRL, Prum RO. 2012. The limits of sexual conflict in the narrow sense: new insights
 640 from waterfowl biology. *Philosophical Transactions of The Royal Society B: Biological*
 641 *Sciences* **367**: 2324–2338. DOI: <http://dx.doi.org/10.1098/rstb.2011.0284>

642 Bussière LF, Basit HA, Gwynne DT. 2005. Preferred males are not always good providers:
 643 female choice and male investment in tree crickets. *Behavioral Ecology* **16**: 223–231.

644 Byers GW, Thornhill R. 1983. Biology of the Mecoptera. *Annual Review of Entomology* **28**:
 645 203–228. DOI: <https://doi.org/10.1146/annurev.en.28.010183.001223>

646 Cheng FY. 1957. Descriptions of new Panorpidae (Mecoptera) in the collection of the
 647 California Academy of Sciences. *Memoirs of the College of Agriculture* **5**: 27–33.

648 Chou I, Ran RB, Wang SM. 1981. Studies on the classification of Chinese Mecoptera (I, II).
 649 *Entomotaxonomia* **3**: 1–18.

650 Cordero A., Andrés JA. 2002. Male coercion and convenience polyandry in a calopterygid
 651 damselfly. *Journal of Insect Science*, 2: 14. DOI: <http://dx.doi.org/10.1093/jis/2.1.14>

652 Crampton GC. 1931. The Genitalia and Terminal Structures of the Male of the Archaic
 653 Mecopteran *Notiothauma reedi*, compared with related Holometabola from the standpoint of
 654 Phylogeny. *Psyche* **38**: 1–21. DOI: <http://dx.doi.org/10.1155/1931/28135>

655 Ding H, Shih C, Bashkuev A, Zhao Y, Ren D. 2014. The earliest fossil record of Panorpidae
 656 (Mecoptera) from the Middle Jurassic of China. *ZooKeys* **431**: 79–92. DOI:
 657 <https://doi.org/10.3897/zookeys.431.7561>

658 Eberhard WG. 2002. Physical Restraint or Stimulation? The Function(s) of the Modified
 659 Front Legs of Male *Archiseopsis diversiformis* (Diptera, Sepsidae). *Journal of Insect Behavior*
 660 **15**: 831–850.

661 Eggert AK, Sakaluk SK. 1994. Sexual cannibalism and its relation to male mating success in
 662 sagebrush crickets, *Cyphoderris strepitans* (Haglidae: Orthoptera). *Animal Behaviour* **47**:
 663 1171–1177.

664 Engqvist L, Sauer KP. 2001. A life-history perspective on strategic mating effort in male
 665 scorpionflies. *Behavioral Ecology* **13**: 632–636. DOI: <https://doi.org/10.1093/beheco/13.5.632>

666 Gao C, Ma NA, Hua BZ. 2016. *Cerapanorpa*, a new genus of Panorpidae (Insecta:
667 Mecoptera) with descriptions of three new species. *Zootaxa* **4158**: 93–104.
668 <http://doi.org/10.11646/zootaxa.4158.1.5>

669 Ghislandi PG, Beyer M, Velado P, Tuni C. 2017. Silk wrapping of nuptial gifts aids cheating
670 behaviour in male spiders. *Behavioral Ecology* **28**: 744–749. DOI:
671 <https://doi.org/10.1093/beheco/arx028>

672 Grimaldi DA, Engel MS. 2005. *Evolution of the Insects*. Cambridge University Press.

673 Grimaldi DA, Ross AJ. 2017. Extraordinary Lagerstätten in amber, with particular reference
674 to the Cretaceous of Burma. Fraser NC, Suess HD (Eds). *Terrestrial Conservation*
675 *Lagerstätten: Windows into the Evolution of Life on Land*. Dunedin Academic Press,
676 Edinburgh. p. 287–342.

677 Gwynne DT. 1984. Nuptial feeding behaviour and female choice of mates in *Harpobittacus*
678 *similis* (Mecoptera: Bittacidae). *Journal of Australian Entomological Society* **23**: 271–276.

679 Han CS, Jablonski P. 2010. Male water striders attract predators to intimidate females into
680 copulation. *Nature Communications* **1**: 52. <https://doi.org/10.1038/ncomms1051>

681 Handlirsch A. 1906-1908. Die fossilen Insecten und die Phylogenie der rezenten Formen.
682 Leipzig, Engelmann.

683 Hardwicke T. 1825. Description of the *Cermatia longieornis* and of three new insects from
684 Nepal. *Transactions of the Linnean Society of London* **14**: 131–136.

685 Haug JT, Azar D, Ross A, Szwedo J, Wang B, Arillo A, Baranov V, Bechteler J, Beutel R,
686 Blagoderov V, Delclòs X, Dunlop J, Feldberg K, Feldmann R, Foth C, Fraaije RHB, Gehler
687 A, Harms D, Hedenäs L, Hyžný M, Jagt JWM, Jagt-Yazykova EA, Jarzembowski E, Kerp H,
688 Khine PK, Kirejtshuk AG, Klug C, Kopylov DS, Kotthoff U, Kriwet J, McKellar RC, Nel A,
689 Neumann C, Nützel A, Peñalver E, Perrichot V, Pint A, Ragazzi E, Regalado L, Reich M,
690 Rikkinen J, Sadowski EM, Schmidt AR, Schneider H, Schram FR, Schweigert G, Selden P,
691 Seyfullah LJ, Solórzano-Kraemer MM, Stilwell JD, van Bakel BWM, Vega FJ, Wang Y,
692 Xing L, Haug C. 2020. Comment on the letter of the Society of Vertebrate Paleontology
693 (SVP) dated April 21, 2020 regarding "Fossils from conflict zones and reproducibility of
694 fossil-based scientific data": Myanmar amber. *Paläontologische Zeitschrift* **94**: 431–
695 437. DOI: <https://doi.org/10.1007/s12542-020-00524-9>

696 Hrušková-Martišová M, Pekár S, Bilde T. 2010. Coercive copulation in two sexually
697 cannibalistic camel-spider species (Arachnida: Solifugae). *Journal of Zoology* **282**: 91–99.
698 DOI: <https://doi.org/10.1111/j.1469-7998.2010.00718.x>

699 Hu GL, Yan G, Xu H, Hua BZ. 2015. Molecular phylogeny of Panorpidae (Insecta: Mecop-
700 tera) based on mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* **85**:
701 22–31. DOI: <https://doi.org/10.1016/j.ympev.2015.01.009>

702 Hua BZ, Chou I. 1997. The Panorpidae (Mecoptera) of Funiu Mountain in Henan Province.
703 *Entomotaxonomia* **19**: 273–278.

704 Kasiński JR, Kramarska R, Słodkowska B, Sivkov V, Piwocki M. 2020. Paleocene and
705 Eocene deposits on the eastern margin of the Gulf of Gdańsk (Yantarny P-1 bore hole,
706 Kaliningrad region, Russia). *Geological Quarterly* **64**: 29–53. DOI:
707 <http://dx.doi.org/10.7306/gq.1513>

708 Kimura K, Chiba S. 2015. The direct cost of traumatic secretion transfer in hermaphroditic
709 land snails: individuals stabbed with a love dart decrease lifetime fecundity. *Proceedings of*
710 *the Royal Society B* **282**: 20143063. DOI: <http://dx.doi.org/10.1098/rspb.2014.3063>

711 Kock D, Engels S, Fritsche C, Sauer KP. 2009. Sexual coercion in *Panorpa* scorpionflies? –
712 The function of the notal organ reconsidered. *Behavioral Ecology* **20**: 639–643. DOI:
713 <https://doi.org/10.1093/beheco/arp043>

714 Krzemiński W, Soszyńska-Maj A. 2012. A new genus and species of scorpionfly (Mecoptera)
715 from Baltic amber, with an unusually developed postnotal organ. *Systematic Entomology* **37**:
716 223–228. DOI: <https://doi.org/10.1111/j.1365-3113.2011.00602.x>

717 Kullmann H, Sauer KP. 2005. Life histories and mating system aspects of two Caucasian
718 scorpionfly species: *Panorpa similis* Esben-Petersen and *Panorpa connexa* Mac
719 Lachlan. *Zoologischer Anzeiger* **244**: 1–9. DOI: <https://doi.org/10.1016/j.jcz.2004.12.003>

720 Latreille PA. 1805. Historie naturelle, générale et particulière, des Crustacés et des Insectes,
721 13e. Paris.

722 LeBas N, Hockham LR. 2005: An invasion of cheats: the evolution of worthless nuptial gifts.
723 *Current Biology* **15**: 64–67. DOI: [https://doi.org/10.1016/S0960-9822\(04\)01021-8](https://doi.org/10.1016/S0960-9822(04)01021-8)

724 Lehmann GUC. 2012. Weighing costs and benefits of mating in bushcrickets (Insecta:
725 Orthoptera: Tettigoniidae), with an emphasis on nuptial gifts, protandry and mate density.
726 *Frontiers in Zoology* **9**: 19. DOI: <https://doi.org/10.1186/1742-9994-9-19>

727 Li L, Shih C, Wang C, Ren D. 2017. A new fossil scorpionfly (Insecta: Mecoptera:
728 Holcorpidae) with extremely elongate male genitalia from northeastern China. *Acta*
729 *Geologica Sinica - English Edition* **91**: 797–805. DOI: [https://doi.org/10.1111/1755-](https://doi.org/10.1111/1755-6724.13310)
730 6724.13310

731 Liu X, Hayashi F, Lavine LC, Yang D. 2015. Is diversification in male reproductive traits
732 driven by evolutionary trade-offs between weapons and nuptial gifts? *Proceedings of the*
733 *Royal Society B* 282: 20150247. DOI: <http://dx.doi.org/10.1098/rspb.2015.0247>

734 McCartney J, Potter MA, Robertson AW, Heller KG, Gwynne DT. 2013. Chapter 2. Evidence
735 of natural and sexual selection shaping the size of nuptial gifts among a single bush-cricket
736 genus (Poecilimon; Tettigoniidae): An analysis of sperm transfer patterns. Geldani R, Davin
737 M *Sexual Selection*. Nova Science Publishers, Inc. p. 45–68.

738 MacLachlan R. 1877. *Monographic Revision and Synopsis of the Trichoptera of the European*
739 *Fauna* (1874–1880). London, John van Voorst.

740 Martynov, A. 1937. Liassic insects from Shurab and Kisyl-Kiya. Part 1. Various orders except
741 Blattodea and Coleoptera. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* **7**: 1–
742 232.

743 Miao Y, Wang JS, Hua BZ. 2018. Molecular phylogeny of the scorpionflies Panorpidae
744 (Insecta: Mecoptera) and chromosomal evolution. *Cladistics* **35**: 1–16. DOI:
745 <http://dx.doi.org/10.1111/cla.12357>

746 Mickoleit G. 1971. Das Exoskelet von *Notiothauma reedi* MacLachlan, ein Beitrag zur
747 Morphologie und Phylogenie der Mecoptera (Insecta). *Zeitschrift für Morphologie und*
748 *Ökologie der Tiere* **69**: 318–362.

749 Najarro M, Peñalver E, Pérez-de la Fuente R, Ortega-Blanco J, Menor-Salván C, Barrón E,
750 Soriano C, Rosales I, López del Valle R, Velasco F, Tornos F, Daviero-Gomez V, Gomez B,
751 Delclòs X. 2010. A review of the El Soplao amber outcrop, early Cretaceous of Cantabria
752 (Spain). *Acta Geologica Sinica, English Edition* **84**: 959–976. DOI: [https://doi.org/](https://doi.org/10.1111/j.1755-6724.2010.00258.x)
753 10.1111/j.1755-6724.2010.00258.x

754 Najarro M, Peñalver E, Rosales I, Pérez-de la Fuente R, Daviero-Gomez V, Gomez B,
755 Delclòs X. 2009. Unusual concentration of Early Albian arthropod-bearing amber in the
756 Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain): palaeoenvironmental and

757 palaeobiological implications. *Geologica Acta* **7**: 363–387. DOI: <https://doi.org/10.1344>
758 /105.000001443

759 Neff BD, Svensson EI. 2013. Polyandry and alternative mating tactics. *Philosophical*
760 *Transactions of the Royal Society B: Biological Sciences* **368**: 20120045. DOI:
761 <https://doi.org/10.1098/rstb.2012.0045>

762 Packard AS. 1886. A new arrangement of the orders of insects. *American Naturalist* **17**: 932–
763 945.

764 Parker GA. 1979. Sexual selection and sexual conflict. Blum MA, Blum NA (Eds). *Sexual*
765 *selection and reproductive competition in insects*. London: Academic Press. p. 123–166.

766 Petrulėvičius J, Ren D. 2012. A new species of "orthophlebiidae" (Insecta: Mecoptera) from
767 the Middle Jurassic of Inner Mongolia, China. *Revue de Paléobiologie* **31**: 311–315.

768 Preston-Mafham KG. 1999. Courtship and mating in *Empis* (*Xanthempis*) *trigramma* Meig.,
769 *E. tessellate* F. and *E. (Polyblepharis) opaca* F. (Diptera: Empididae) and the possible
770 implications of 'cheating' behavior. *Journal of Zoology* **247**: 239–246. DOI:
771 <http://dx.doi.org/10.1111/J.1469-7998.1999.TB00987.X>

772 Rostant WG, Fowler EK, Chapman T. 2020. Sexual Conflict Theory: Concepts and Empirical
773 Tests. Shackelford TK (Eds). *The Sage Handbook of Evolutionary Psychology: Foundations*
774 *of Evolutionary Psychology*. SAGE Publications. p. 241–259.

775 Sadowski JA, Moore AJ, Brodie ED. 1999. The evolution of empty nuptial gifts in a dance
776 fly, (Diptera: Empididae): bigger isn't always better. *Behavioral Ecology and Sociobiology*
777 **45**: 161–166. DOI: <https://doi.org/10.1007/s002650050549>

778 Sakaluk SK, Campbell MTH, Clark AP, Chadwick-Johnson J, Keorpes PA. 2004.
779 Hemolymph loss during nuptial feeding constrains male mating success in sagebrush crickets.
780 *Behavioral Ecology* **15**: 845–849.

781 Shi G, Grimaldi DA, Harlow GE, Wang J, Yang M, Lei W, Li Q, Li X. 2012. Age constraint
782 on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* **37**: 155–163. DOI:
783 <http://dx.doi.org/10.1016/j.cretres.2012.03.014>

784 Siva-Jothy MT 2006. Trauma, disease and collateral damage: conflict in cimicids.
785 *Philosophical transactions of the Royal Society B* **361**: 269–275.
786 DOI:<https://doi.org/10.1098/rstb.2005.1789>

787 Soszyńska-Maj A, Krzemiński W, Kopeć K, Cao Y, Ren D. 2018. Large Jurassic
 788 scorpionflies – belonging to a new subfamily of the family Orthophlebiidae (Mecoptera).
 789 *Annales Zoologici* **68**: 85–92. DOI: <http://dx.doi.org/10.1080/08912963.2018.1564747>

790 Soszyńska-Maj A, Krzemiński W, Kopeć K, Cao Y, Ren D. 2020. New Middle Jurassic
 791 fossils shed light on the relationship of recent Panorpoidea (Insecta, Mecoptera). *Historical*
 792 *Biology* **32**: 1081–1097. DOI: <https://doi.org/10.1080/08912963.2018.1564747>

793 Stålhandske P. 2001. Nuptial gift in the spider *Pisaura mirabilis* maintained by sexual
 794 selection. *Behavioral Ecology* **12**: 691–697. DOI: <https://doi.org/10.1093/beheco/12.6.691>

795 Szwedo J, Wang B, Soszyńska-Maj A, Azar D, Ross A. 2020. International
 796 Palaeoentomological Society Statement. *Palaeoentomology* **3**: 221–222. DOI:
 797 <https://doi.org/10.11646/palaeoentomology.3.3.1>

798 Tillyard RJ. 1933. *The Panorpid Complex in the British Rhaetic and Lias*. Britain Museum Fossil
 799 Insects 3, 1-79.

800 Thornhill R. 1976. Sexual selection and nuptial feeding behaviour in *Bittacus apicalis*
 801 (Insecta: Mecoptera). *American Naturalist* **110**: 529–548.

802 Thornhill R. 1979. Male and female sexual selection and the evolution of mating strategies in
 803 insects. Blum MS, Blum NA (Eds). *Sexual Selection and Reproductive Competition in*
 804 *Insects*. Academic Press, New York. p. 81–121.

805 Thornhill R. 1980. Rape in *Panorpa* scorpionflies and a general rape hypothesis. *Animal*
 806 *Behaviour* **28**: 52–59. DOI: [https://psycnet.apa.org/doi/10.1016/S0003-3472\(80\)80007-8](https://psycnet.apa.org/doi/10.1016/S0003-3472(80)80007-8)

807 Thornhill R. 1990. The study of adaptation. Bekoff M, Jamieson D (Eds). *Adaptation*
 808 *Interpretation and Explanation in the Study of Behaviour*. Boulder: Westview Press, vol 2,
 809 chap. 2.

810 Tong X, Hua BZ. 2019. Nuptial feeding and genital coupling of *Neopanorpa* scorpionflies
 811 (Insecta: Mecoptera: Panorpidae) with notal organs of various lengths. *Contributions to*
 812 *Zoology* **88**: 498–512. DOI: <https://doi.org/10.1163/18759866-20191409>

813 Thornhill R, Sauer KP. 1991. The notal organ of the scorpionfly (*Panorpa vulgaris*): an
 814 adaptation to coerce mating duration. *Behavioral Ecology* **2**: 156–164. DOI:
 815 <https://doi.org/10.1093/beheco/2.2.156>

816 Tong X, Jiang L, Hua BZ. 2017. A unique mating pattern of *Panorpodes kuandianensis*
817 (Mecoptera: Panorpididae). *Contributions to Zoology* **86**: 229–237. DOI: 10.1163/18759866-
818 08603003

819 Tong X, Zhong W, Hua BZ. 2018. Copulatory mechanism and functional morphology of
820 genitalia and anal horn of the scorpionfly *Cerapanorpa dubia* (Mecoptera:
821 Panorpididae). *Journal of Morphology* **279**:1532–1539. DOI: [https://doi.org/10.1002/](https://doi.org/10.1002/jmor.20903)
822 [jmor.20903](https://doi.org/10.1002/jmor.20903)

823 Wang JS. 2020. *Phylogeny and Taxonomy of the World Panorpidae (Mecoptera)*.
824 Dissertation. College of Plant Protection Northwest A&F University, Shaanxi, China.

825 Wang JS, Hua BZ. 2018a. *A Color Atlas of the Chinese Mecoptera*. Henan Science and Tech-
826 nology Press, Zhengzhou.

827 Wang M, Hua BZ. 2018b. A new species of *Neopanorpa* with an extremely long notal organ
828 from Sichuan, China (Mecoptera, Panorpididae). *ZooKeys* **750**: 131–140. DOI:
829 <https://doi.org/10.3897/zookeys.750.23486>

830 Wang JS, Hua BZ. 2019a. *Megapanorpa*, a new genus with a single anal horn in males from
831 Oriental China (Mecoptera: Panorpididae). *Entomological Science* **22**: 64–79. DOI:
832 <https://doi.org/10.1111/ens.12336>

833 Wang JS, Hua BZ. 2019b. Taxonomy of the genus *Neopanorpa* van der Weele, 1909
834 (Mecoptera, Panorpididae) from the Oriental Region, with the description of two new species.
835 *European Journal of Taxonomy* **543**: 1–17. DOI: <http://dx.doi.org/10.5852/ejt.2019.543>

836 Wang JS, Hua BZ. 2020. Taxonomic revision and phylogenetic analysis of the enigmatic
837 scorpionfly genus *Leptopanorpa* MacLachlan (Mecoptera: Panorpididae). *Journal of Zoological*
838 *Systematics and Evolutionary Research* **58**: 900–928. DOI: <https://doi.org/10.1111/jzs.12363>

839 Wang JS, Hua BZ. 2021. Morphological phylogeny of Panorpidae (Mecoptera: Panorpoidea).
840 *Systematic Entomology* **43**: 526–557. DOI: <https://doi.org/10.1111/syen.12474>

841 Wang Q, Shih C, Ren D. 2013. The Earliest Case of Extreme Sexual Display with
842 Exaggerated Male Organs by Two Middle Jurassic Mecopterans. *PLoS ONE* **8**,e71378. DOI:
843 <https://doi.org/10.1371/journal.pone.0071378>

844 van der Weele HW. 1909. Mecoptera and Planipennia of Insulinde with biological notes from
845 Edw. Jacobson. *Notes Leyden Museum* **31**: 1–100.

- 846 Willmann R. 1989. Evolution und phylogenetisches System der Mecoptera. *Abhandlungen*
847 *der Senckenberg Gesellschaft für Naturforschung* **544**: 1–153.
- 848 Willmann R, Novokschonov V. 1998. Neue Mecopteren aus dem oberen Jura von Karatau
849 (Kazachstan) (Insecta: ‘Orthophlebiidae’). *Paläontologische Zeitschrift* **72**: 281–298.
- 850 Yamane T, Okada K, Nakayama S, Miyatake T. 2011. Dispersal and ejaculatory strategies
851 associated with exaggeration of weapon in an armed beetle. *Proceedings of the Royal Society*
852 *B* **277**: 1705–1710. DOI: <https://doi.org/10.1098/rspb.2009.2017>
- 853 Zhang Y, Shih PJM, Wang Y, McNamara ME, Shih C, Dong R, Gao T. 2021. Jurassic
854 scorpionflies (Mecoptera) with swollen first metatarsal segments suggesting sexual
855 dimorphism. *BMC Ecology and Evolution* **21**: 47. DOI: [https://doi.org/10.1186/s12862-021-](https://doi.org/10.1186/s12862-021-01771-3)
856 [01771-3](https://doi.org/10.1186/s12862-021-01771-3)
- 857 Zhong W, Hua BZ. 2013. Mating behaviour and copulatory mechanism in the scorpionfly
858 *Neopanorpa longiprocessa* (Mecoptera: Panorpidae). *PLoS ONE* **8**: e74781. DOI:
859 <https://doi.org/10.1371/journal.pone.0074781>
- 860 Zhong W, Ding G, Hua BZ. 2014. The role of male’s anal horns in copulation of a scorpion-
861 fly. *Journal of Zoology* **295**: 170–177. DOI: <https://doi.org/10.1111/jzo.12194>
- 862 Zhong W, Qi ZY, Hua BZ. 2015. Atypical mating in a scorpionfly without a notal organ.
863 *Contributions to Zoology* **84**: 305–315. DOI: <http://dx.doi.org/10.1163/18759866-08404003>
864
- 865 Figure captions
- 866 **Figure 1.** *Baltipanorpa oppressiva* sp. nov. (Panorpidae) from Baltic amber (middle Eocene),
867 holotype MP/2711. A-B, habitus, photograph of preserved portion (A) and explanatory
868 drawing (B), with genital bulb in ventrolateral view magnified; C-E, notal organ: fully-
869 clasped clamp formed by notal and postnotal organs (C), teeth inside the notal-postnotal
870 clamp (D), detail of terminal clasp (E); F, life reconstruction of entire specimen (head and
871 thorax, missing in this species, based on habitus of congeneric *Baltipanorpa damzeni*). G,
872 forewing. H, hind wing (same scale in both wings). Abbreviations: Ep, epandrium; HP, horn-
873 like process; Hv, hypovalve; NO, notal process; PO, postnotal process; Gs, gonostylus; Gcx,
874 gonocoxite. Red colour: notal process.
- 875
- 876 **Figure 2.** *Burmorthophlebia multiprocessa* gen. et sp. nov. (Orthophlebiidae) from Kachin
877 amber, Myanmar (Late Cretaceous), holotype MP/3721. A, amber piece with habitus in lateral

view; B, life reconstruction; C, forewing; D, hind wing, partially reconstructed; E-F, abdomen in lateral view, explanatory drawing (E) and photograph (F); G, detail of head in lateral view, antennae and rostrum; H, notal process and postnotal areas (on tergites III and IV, respectively). Abbreviations: AH, anal horns; PA1, PA2, postnotal areas 1, 2; other symbols as in Fig. 1.

Figure 3. Photomicrographs of *Cantabra soplao* gen. et sp. nov. (Cantabridae fam. nov.), from El Soplao amber, Spain (Early Cretaceous), holotype CES-437. A, ventral and lateral habitus, respectively; B-C, head, frontoventral view (B), lateral view (C); D, setae on anal area of forewing; E, postnotal organ seen in ventrolateral view (head is to the left), morphology distorted due to the skewed view; F, genital bulb in ventral view; G, detail of gonostylus, showing its inner denticles. Abbreviations: OB, ocellar bristles; PO, postnotal organ.

Figure 4. Explanatory drawings of *Cantabra soplao* gen. et sp. nov. (Cantabridae fam. nov.) from El Soplao amber, Spain (Early Cretaceous), holotype CES-437. A, right forewing; B, right hind wing (same scale for both wings); C-D, reconstruction of abdomen in lateral view, with genital bulb shown in ventral view (C); inset (arrow) shows the genital bulb expanded, with elements tagged (D); E, life reconstruction, in resting position. Notal organ not visible in holotype and thus not depicted for caution. Length of antennae and rostrum are conjectural; morphology of legs is based on the preserved left foreleg, which is mostly complete. Abbreviations: Bp, basal process; Pm, parameres; other symbols as in Fig. 1.

Figure 5. Spatial coupling between short male notal organs and female (fore)wings during mating in extant and extinct Mecoptera. A–B, *Panorpa amurensis* MacLachlan, 1872 (Recent): A, photograph of notal organ in male, and diagram cross section through the notal and postnotal processes with anterior fold of female forewing entrapped; B, photograph and diagram of anterior fold in female forewing; C–D, *Orthophlebia heidemariae* Willmann and Novokschonov, 1998 (Late Jurassic): habitus (C) and explanatory drawing (D; inset showing notal-postnotal system magnified); E, *Burmorthophlebia multiprocessa*, gen. et sp. nov. (Late Cretaceous): diagram of abdominal modifications (bottom) and hypothetical spatial coupling between male notal organ and female wing (top). Abbreviations: SP, small process (tergite VII); other as in Figs 1, 2. Colour legend of cross section through veins: black circle, C (Costa); blue circle, Sc (Subcosta); red circle, R1 (1st radial vein); red line, wing membrane.

912

913 **Figure 6.** Spatial coupling between long male notal organs and female (fore)wings during
914 mating in extant and extinct Mecoptera. A–D, *Neopanorpa longistipitata* Wang and Hua,
915 2018 (Recent): A, photograph of mating couple; inset (arrow) shows notal and hypovalves
916 connection magnified; B, diagram of mating couple (notal organ depicted in red); C,
917 photograph of male abdomen in lateral view; D, diagram of coupling mechanism between
918 male notal organ and genital bulb; E, F, spatial coupling diagram between male notal-
919 postnotal clip clasping the female wing in two species of *Baltipanorpa* (Eocene): *B. damzeni*
920 (E); *B. oppressiva* sp. nov. (F). Abbreviations as in Figs 1, 2, 4, 5.

921

922 **Figure 7.** Male abdominal modifications in extinct and extant Panorpoidea on a time scale: A,
923 *Orthophlebia heidemariae* Willmann and Novokschonov, 1998 (Orthophlebiidae); B,
924 *Cantabra soplao* gen et sp. nov. (Cantabridae fam. nov.); C, *Burmorthophlebia multiprocessa*
925 gen. et sp. nov. (Orthophlebiidae); D, *Baltipanorpa damzeni* Krzemiński and Soszyńska-Maj,
926 2012 (Panorpidae); E, *Baltipanorpa oppressiva* sp. nov. (Panorpidae); F–I, some examples of
927 extant Panorpidae species: F, *Leptopanorpa linyejiei* Wang and Hua, 2018; G, *Leptopanorpa*
928 *jacobsoni* (van der Weele, 1909); H, *Neopanorpa longistipitata* Wang and Hua, 2018; I,
929 *Panorpa jinhuaensis* Wang, Gao and Hua, 2019. Notal processes depicted in red. Drawings
930 not at same scale.

931

932 **Figure 8.** Geographical provenance of amber specimens studied herein. The two white stars
933 represent Cretaceous localities (El Soplao amber, Spain; Kachin amber, Myanmar); the
934 yellow star an Eocene deposit (Baltic amber).

935

936 **Supplementary File 1.** Spatial match between the space created by the clasped notal and
937 postnotal processes (NO-PO) and the anterior valley fold (from Costa to R1, measured across
938 wing) of the wing in some recent panorpids. T5, T6, tergites 5, 6. Measurements are
939 approximate, based on scale bars in published figures as specified.

940

941 **Supplementary File 2.** Remarks on the abdomen of fossil Panorpoidea. AH, anal horn; NO,
942 notal organ; PA, postnotal area; PO, postnotal organ; A5, A6, abdominal segments 5, 6.

943

A

B

C

D

E

F

Legend:

Cross section
through wing

C R1 wing ♀
Sc

SPAIN

1000 km

MYANMAR