1 Umenocoleidae (Insecta: Dictyoptera) from Turonian sediments of Kzyl-Zhar,

2 Kazakhstan and Cenomanian northern Myanmar amber

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- 25 Phylogenetically annotated character list (numbers 1-58 modified after Bai et al. (2016), numbers
- 26 **59-130** from Vršanský et al. (2018); numbers 131-206 from Vršanský et al. (2021), others originals
- 27 based on referenced sources; none of the character is weighted in the present analysis weight
- refer to original character definitions by Bai et al. (2016)). 0- plesiomorphy, 1- apomorphy)
- 29
- 30 1. Orientation of head (0) hypognathous; (1) orthognathous ((0) orthognathous; (1) prognathous or
- 31 subprognathous (slightly inclined) according to Bai et al. (2016)). Hypognathous is an original state in
- 32 Blattaria including some Umenocoleidae in all lineages, Vitisma, Cratovitisma, Jantaropterix, and also
- 33 some Umenocoleinae s.str. specimens of *Ponopterix* (Lee 2016 fig. 3m); orthognathous in
- 34 *Alienopterus* like in living cockroach *Melyroidea*, Mantodea (Grimaldi 2003; Wieland 2013), most
- 35 Ponopterix (Lee 2016), Manipulator (Vršanský and Bechly 2015); homoplastically in
- 36 Mantophasmatodea (Baum et al. 2007), and most other groups of Polyneoptera (Wipfler et al. 2011).
- 37 Derived prognathous state in some other orders but also in predatory Raphidiomimidae (Vishniakova
- 38 1973) is not present in the present lineage and is disregarded herein.
- 39 2. Parietal ridge s.str. (0) absent, (1) present. Such a ridge is present in certain Umenocoleoidea,
- 40 extant Mantodea (Leverault 1936; Wipfler et al. 2011, 2012), and Grylloblattodea (Walker 1931; KDK
- 41 pers. Observation in Bai et al. (2016)). It does not occur in other groups of Polyneopterea (Wipfler et
- 42 al. 2011) such as *Manipulator*. The condition in *Santanmantis* (although new specimens seems to
- 43 possess it Hörning et al. in press) and most extinct mantises (e.g., Grimaldi 2003; Vršanský 2003;
- 44 Wieland 2013; Vršanský and Bechly 2015) is uncertain.
- 45 3. **Ocelli** (0) present, (1) absent ((0) absent, (1) present according to Bai et al. (2016)). Ocelli are
- 46 present in stem cockroaches (Vršanský 2008; Anisyutkin and Gorokhov 2008) including all sufficiently
- 47 studied Umenocoleidae and also in the most primitive mantodeans (Vršanský 2002; Delclós et al.
- 48 (2016); Grimaldi 2003: Fig. 3), but not in other known predatory cockroaches. The reverse polarity
- 49 would be correct regarding the more distant derivation (from Palaeozoic cockroaches), which is not
- 50 the case (Alienopteridae were derived in the Mesozoic).
- 4. Number of ocelli (0) three, (1) two. See above (3). *Vitisma, Jantaropterix* and *Ponopterix* preserved
 in Myanmar amber possess central ocellus (unpublished).
- 53 5. Interantennal ridge (0) present, (1) absent ((0) absent, (1) present according to Bai et al. (2016)).
- 54 The interantennal ridge connects the antennal sockets of the two sides. It is present in certain
- 55 Alienopteridae, in extant Mantodea (Wieland 2013; see also Leverault 1936; Grimaldi 2003; Wipfler
- 56 et al. 2011, 2012), in Ambermantis (Grimaldi 2003), in Jantaromantis (Vršanský 2002), and in
- 57 Odonata (Blanke et al. 2012). The reverse polarity is due to the plesiomorphic presence in
- 58 Umenocoleoidea and stem Liberiblattinidae and in higher level it would be correct.
- 59 6. X-shaped median apodeme of frontal region (0) absent, (1) present. Absent in Mantodea (Wipfler
- 60 et al. 2012; Wieland 2013: Figs. 68-70, 74-77) and also in most other groups of Polyneoptera (Wipfler
- et al. 2011). Present in Mantophasmatodea (Baum et al. 2007). Disregarded due to absence in adult
- 62 fossils, although an alienopterid immature (Fig. SI6a) seem to have it indicated. All other unpublished
- 63 adults of Alienopteridae and Umenocoleidae (including the most primitive *Vitisma* and *Jantaropterix*)
- 64 do not have it.

- 65 7. Gula (0) absent, (1) present. Absent in Alienopterus like in extinct and extant Mantodea (Wipfler et
- 66 al. 2012; Wieland 2013) and most other groups of Polyneoptera (Wipfler et al. 2011). Present in
- 67 Embioptera, Dermaptera and Zoraptera (Rähle 1970; Beutel and Gorb 2006; Matsumura et al. 2015).
- 68 Disregarded due to absence of evidence and presence on all Blattaria.
- 69 8. Antennal flagellum (0) not separated into basi- and distiflagellum, (1) separated in basi- and
- 70 distiflagellum. Unlike in Mantophasmatodea (Drilling and Klass 2010; Hockmann et al. 2009) a
- 71 distinct differentiation between a basi- and distiflagellum is absent in other groups of Polyneoptera;
- 72 ambiguous in Alienopterus. Disregarded – the state is absent in cockroaches.
- 73 9. Antennal length (0) of comparable length than body, (1) shorter than body ((0) distinctly longer
- 74 than head, (1) shorter than head (bristle-like) according to Bai et al. (2016)). Long in all cockroaches
- including Umenocoleidae, Alienopterus and Vcelesvab, like in most other groups of Polyneoptera 75
- 76 (e.g., Wipfler et al. 2011; Beutel et al. 2014). The original length consideration (very short in
- 77 Ephemeroptera and Odonata) is modified here as the stem group Umenocoleidae has already a very
- 78 long antenna identically as in primitive alienopterids Alienopterus and Vcelesvab.
- 79 10. Secondary (anterior) mandibular joint (0) gliding device, (1) ball-and-socket joint. A secondary 80 mandibular articulation is present as a ball-and socket joint in Odonata and neopteran groups with 81 normally developed mandibles. This condition is invisible in Alienopterus
- 82 11. Number of maxillary palpomeres (0) five, (1) less than five ((0) more than five, (1) five, (2) less
- 83 than five according to Bai et al. (2016)). Four are present in Alienopterus (see Fig. 4a, Bai et al.
- 84 (2016)), unlike in other groups of Polyneoptera (e.g., Wipfler et al. 2011, 2012) including extant
- 85 Mantodea (Wieland 2013), Manipulator (Vršanský and Bechly 2015) and Ambermantis (Grimaldi
- 86 2003; condition in Ambermantis unclear; in Burmantis 5-state was validated in Delclós et al. (2016)).
- 87 Palps are four-segmented in Ponopterix (clearly visible in a single specimen, which might be a
- 88 developmental error or incomplete regeneration after damage) and Jantaropterix (Vršanský 2003 –
- 89 and in many unpublished amber records of this genus). Five-segmented palp is present in stem
- 90 cockroaches.
- 91 12. Angle between submentum and mentum (0) less than 60° or absent, (1) more than 60°. Very
- 92 small or absent in Alienopterus like in most other groups of Polyneoptera (e.g., Walker 1931; Klass
- 93 and Ehrmann 2003). More than 60° in Mantophasmatodea and Grylloblattodea (Wipfler et al. 2011).
- 94 Unknown in *Ponopterix* and other fossil taxa included here (scored as ?). Disregarded because of
- 95 traced origin within Blattaria
- 96 13. Glossa (0) present, (1) partly or completely reduced. Even though the glossae and paraglossae
- 97 cannot be very clearly distinguished, it is obvious that the endite lobes of Alienopterus are well-
- 98 developed like in most other groups of Polyneoptera (e.g., Leverault 1936; Rähle 1970; Wipfler et al.
- 99 2011; Friedemann et al. 2012). The glossa is reduced in Dermaptera (Wipfler et al. 2011) and
- 100 Macroxyela (Beutel and Vilhelmsen 2007). Disregarded due to absence of evidence.
- 101 14. Origin of Musculus tentorioparaglossalis Disregarded herein due to absence of evidence in the
- 102 presently analysed taxa (and condition in fossil taxa is unknown according to Bai et. al (2016)
- 103 confirmed.

- 104 15. Accessory anterior tentorial bridge (leading to "perforated corpotentorium") (0) absent, (1)
- 105 present. The presence of an accessory anterior tentorial bridge is a characteristic feature of
- 106 Dictyoptera (Hudson 1945; Klass and Eulitz 2007). Disregarded due to absence of evidence on fossils.
- 16. Paired lateral cervical sclerites (0) absent, (1) present. These sclerites are distinctly developed in
 Alienopterus like in most other groups of Polyneoptera (e.g., Walker 1931; Klass and Ehrmann 2003;
 Wieland 2006).
- 110 17. Length of prothorax (Grimaldi, 2003: char. 23) (0) less than 2x as long as wide; (1) at least 2x as
- long as wide. At most slightly longer than wide in *Alienopterus* and other fossils considered here
- 112 (Grimaldi et al. 2003; Vršanský 2003; Vršanský and Bechly 2015). State (0) in Mantophasmatodea
- 113 (Klass et al. 2003: table 2; Wipfler et al. 2014). It is a derived state of some of the modern (Cenozoic-
- living, not Mesozoic) Mantodea and homoplasically for generally elongated *Teyia* (as autopomorphyin the present matrix).
- 116 18. Prothoracic paracoxal process (0) absent, (1) present. This complex prothoracic configuration is
- present in Mantophasmatodea and Grylloblattodea, but missing in other extant groups of insects
- 118 (Wipfler et al. 2015). Disregarded due to absence of evidence in fossil Dictyoptera.
- 19. Prothoracic defensive glands (0) absent, (1) present. Prothoracic defensive glands are present in
 Phasmatodea (e.g., Bradler 2009) but absent in other groups of Polyneoptera (Beutel et al. 2014).
- 121 Disregarded to to absence in Dictyoptera and obscure identification in fossils.
- 122 20. Mesoscutellum (0) not present as a defined part of the mesonotum, (1) present as a defined part
- of the mesonotum. Present as all Aienopteridae but missing in Mantophasmatodea and
- 124 Grylloblattodea (Beutel and Gorb 2006).
- 21. Profemoral brush (Grimaldi 2003: char. 12): (0) absent, (1) present. Present in extant and extinct
 Mantodea (except *Jersimantis*) and also visible in *Alienopterus*. Data for sedimentary fossils are not
 available, although the forelegs of *Ponopterix axelrodi* are cursorial and similar to those of early
 mantises (Vršanský 2003).
- 129 22. Shape of distal half of dorsal edge of protibia (0) straight or concave, (1) at least slightly convex. 130 In most Mantodea, including *Chaeteessa* and *Mantoida* (and thus most likely in the ground plan of 131 the group), the distal half is at least slightly convex throughout (e.g., Wieland 2013); the lack of this 132 tibial curvature in some Mantodea (e.g., Toxoderinae) is likely an apomorphic condition developed 133 within the order. The curvature is also absent in Alienopteridae, predaceous roaches (e.g., Grimaldi 134 and Ross 2004: fig. 3; Vršanský 2003; Vršanský and Bechly 2015) and their stem Liberiblattinidae 135 (with already achieved raptorial forelegs), and in representatives of other polyneopteran orders
- 136 examined.
- 137 23. Size of anterior terminal tibial spine of protibia (Tt1) relative to Tt1 spine of mesotibia (Grimaldi
- 138 2003: char. 17) (1) subequal, (0) distinctly smaller ((0) subequal, (1) distinctly larger, (2) distinctly
- 139 smaller according to Bai et al. (2016)). The spines are subequal in size in most Polyneoptera including
- 140 Blattodea, *Manipulator* (Vršanský and Bechly 2015: Fig. 1D) and *Alienopterus*. In the known
- 141 Mantodea, including most fossil taxa (Grimaldi 2003), the protibial Tt1 is larger, only in *Chaeteessa* it
- 142 is distinctly smaller (Wieland 2013: Fig. 278, arrow in Figs. 418–422). The character is unclear in
- 143 Santanmantis (Grimaldi 2003; Hörnig et al. 2013). Also subequal in Mantophasmatodea and

- Grylloblattodea. The reverse polarity is used due to early derivation of *Vitisma* and *Jantaropterix*(visible in new samples) and ancestral (outgroup) Liberiblattina (with shorter protibial Tt1).
- 146 24. **Orientation of ultimate tarsomere** (0) not distinctly bent upwards, (1) distinctly bent upwards.
- 147 Distinctly bent upwards in most Alienopteridae like in Mantophasmatodea (Beutel and Gorb 2008).
- 148 Unclear in *Santanmantis* (reconstructed as bent by Horning et al. in press).
- 149 25. Number of tarsomeres (0) five, (1) less than five. Character disregarded herein due to standard
 150 occurrence of 5-segmented tarsi in all cockroaches including aleinopterids and standard occurrence
 151 of 4-segmented tarsi in damaged individuals (Vršanský 2002).
- 152 26. Euplantulae (0) absent, (1) present. Tarsal euplantulae are present in all studied Umenocoleoidea
 and also stem Liberiblattinidae, like in most groups of Polyneoptera (Beutel and Gorb 2006), but it is
 unclear whether they are present in *Manipulator with* slender tarsomeres (Vršanský and Bechly
 2015: Fig. 1d and unpublished). Unclear in *Santanmantis, Jersimantis, Burmantis* and *Ambermantis,*
- 156 *but present in Jantarimantidae* (Vršanský 2002) and Juramantidae.
- 157 27. **Arolium** (0) absent, (1) present. Present in most cockroaches (absent only in some extremely
- derived Mesozoic and living cockroaches), in Mantophasmatodea (Beutel and Gorb 2008) and most
- 159 other polyneopteran groups (e.g., Beutel and Gorb 2006). Absent in extant Mantodea (Beutel and
- 160 Gorb 2006; Wieland 2013), Jantarimantis (Vršanský 2002) and Santanmantis (Grimaldi 2003; Grimaldi
- and Engel 2005: Fig. 7.98). Unclear in *Juramantis, Jersimantis, Burmantis* and *Ambermantis*.
- 162 28. Size of arolium (0) not enlarged and not pan-shaped, (1) enlarged and pan-shaped. Enlarged and
- 163 pan-shaped in Mantophasmatodea and Phasmatodea-Timematidae (Beutel and Gorb 2006, 2008)
- and homoplasically in some Alienopteridae and Umenocoleidae. *Teyia* immatures have extremely
- 165 large arolia, while adult has comparatively more standard (even though still large). This character
- 166 might be related to contact with ants, sometimes even regarded for related to their phoresis
- 167 (referenced below).
- 168 29. Jumping legs (0) absent, (1) present. Jumping hindlegs with enlarged femora are characteristic for
- 169 Orthoptera. This condition does not occur in other investigated taxa including *Alienopterus*,
- 170 Ponopterix (Vršanský 2003; Lee 2016) and extant and extinct members of Mantodea (Grimaldi 2003;
- 171 Wieland 2013). disregarded
- 172 30. **Resting position of wings** (0) not folded back over the abdomen, (1) folded back over the
- abdomen. The wings of *Alienopterus* and other winged fossils under consideration (Grimaldi 2003;
- 174 Vršanský 2003; Lee 2016; Vršanský and Bechly 2015) are folded back over the abdomen as in other
- 175 groups of Neoptera. Disregarded due to presence in all Dictyoptera.
- 176 31. Middle plate of wing base (0) undivided, (1) divided. Generally divided in neopteran insects with177 developed wings.
- 178 32. Connection between axillary sclerites and the main longitudinal veins (0) present, (1) absent.
- 179 The main longitudinal veins are separated from the axillary sclerites in neopteran insects with
- 180 developed wings.

- 33. Forewings, length relative to length of hindwings (in unfolded condition) (0) of similar length or
 longer, (1) at most half as long as the hindwing. Short in most Alienopteridae (unique autapomorphy
 within Mesozoic cockroaches; a single collected Mesozoic (and none Palaeozoic) cockroach other
- 184 than Alienopteridae (none Umenocoleidae) has reduced forewing length although forewing
- 185 reduction is common in living cockroaches). This state is homoplasically common in Dermaptera
- 186 (Haas 2006; Giles 1963), Phasmatodea (Bradler 2003: Fig. 16.1b) (and very common in e.g., beetles).
- 187 34. Callous stigma (pseudovein) (Grimaldi 2003: char. 9) (0) absent, (1) present. The callous stigma of
 188 the forewing, also called pseudovein in Grimaldi (2003: Figs. 4, 5, 6), is present in *Ambermantis* and
 189 Santanmantis (Grimaldi 2003). It is apparently absent in *Manipulator* (Vršanský and Bechly 2015: Fig.
 190 1d). Absent in all studied Umenocoleoidea.
- 191 35. **Hindwings** (0) well-developed, (1) absent. Well developed in *Alienopterus* and most other groups 192 under consideration (Grimaldi 2003; Vršanský 2003; Lee 2016; Vršanský and Bechly 2015). Absent in
- 193 Grylloblattodea and Mantophasmatodea. Disregarded due to presence in all Mesozoic Dictyoptera.
- 194 36. Transverse hindwing folding (0) absent, (1) present. Transverse hindwing folding is a
- 195 characteristic feature of Dermaptera and some Blattodea (Kleinow 1966; Haas and Kukalová-Peck

196 2001). This condition is missing in *Alienopterus* and other groups of Polyneoptera. Disregarded due

- 197 to presence in all Mesozoic Dictyoptera.
- 37. Hindwing vannus (0) large, (1) small ((0) small, (1) large according to Bai et al. (2016)). Large in all
 Mesozoic cockroaches including stem Umenocoleidae, *Alienopterus* and most Alienopteridae. (small
 in derived genus *Mimimio*) like in most other groups of Polyneoptera with developed wings (Bai et al.
 2016). Reverse polarity would work in earlier, Palaeozoic derivation of the family.
- 38. Precostal field of hindwing (0) small, (1) enlarged. Small in *Alienopterus* and other winged fossils
 included here (Vršanský 2003: Figs. 15, 79). A distinctly enlarged precostal field is a characteristic of
 Orthoptera. Disregarded due to presence in all Dictyoptera.
- 39. Anal filament (0) a long segmented process, (1) a short unsegmented process or absent. Among
 the taxa here sampled, a long segmented filament is only found in *Thermobia* and *Oniscigaster*, but
 not in *Alienopterus* and the remaining pterygote taxa (e.g., Beutel and Gorb 2006). Disregarded due
 to absence in all Dictyoptera.
- 40. **Cerci** (0) present, (1) absent. Cerci are distinctly developed in *Alienopterus* and *Ponopterix* (e.g.,

210 Vršanský 2003: Fig. 15), as in Mantodea (Klass and Ehrmann 2003) and other groups of Polyneoptera

211 (e.g., Wipfler et al. 2011). Absent in *Stenopsocus* and *Macroxyela*. Disregarded due to presence in all

- 212 Dictyoptera.
- 213 41. Cerci: (0) segmented, (1) unsegemented. The cerci are segmented in all cockroaches except
- 214 Attaphilidae, in Mantodea, Grylloblattodea and other polyneopteran groups. They are one-
- 215 segmented in Mantophasmatodea, Orthoptera, Phasmatodea, Odonata, Dermaptera and Zoraptera
- 216 (Klass and Ehrmann 2003; Beutel et al. 2014).
- 42. Shape of cerci in females (0) straight, (1) curved. Curved cerci in females are a characteristic
- 218 feature of Dermaptera even though this derived condition is not found in Arixenina and Hemimerina
- 219 (e.g., Haas 2006). Clasping cerci also occur in cockroaches of the family Fuziidae (Vršanský et al.

- 2009). Disregarded here as cerci are modified, but not hardened in Umenocoleoidea (and allDictyoptera).
- 43. Ventromedian drumming process on the male subgenital plate (0) absent, (1) present. This
- 223 structural modificiation of the male abdominal coxosternite IX is a characteristic feature of
- 224 Mantophasmatodea but it also occurs in many Plecoptera (Zwick 1980: p. 53; with much structural
- variation). It is missing in *Alienopterus* and other groups of Polyneoptera. Disregarded due to
- absence in all Dictyoptera. Neverteheless, some unidentified process at coxosternite IX (and coevally
- at other coxosternites) is presence in an undescribed immature of Alienopteridae (Fig. SI6b).
- 44. Insemination (0) indirect, (1) direct with secondary copulatory organ on abdominal venters II and
- 229 III; (2) direct, with phallic organ of abdominal venter IX. The insemination is direct with an
- anteroabdominal copulatory organ in Odonata and a postabdominal one in Neoptera (e.g., Beutel et
- al. 2014). This very likely also applies to the extinct taxa included in this study considering the
- structure of the postabdomen (scored as 2). Disregarded due to presence in all Dictyoptera and
- absence of evidence in fossils.

45. Chambered ootheca formed by asymmetrical accessory glands IX (0) absent, (1) present. The
presence is characteristic for Dictyoptera (e.g., Hennig 1969; Nalepa and Lenz 2000; Wieland 2010).
Disregarded due to absence in all Umenocoleoidea (possessing ovipositor).

46. Micropylar plate system at the dorsal surface (0) absent, (1) present. Eggs with a micropylar
plate system on the dorsal surface are characteristic for Embioptera and Phasmatodea. Disregarded
due to absence of evidence in Umenocoleoidea.

240 47. Anterior terminal tibial spine of protibia (Tt1) placed on a projection of the apical tibial margin

241 (formation of tibial claw) (0) present, (1) absent ((0) absent, (1) present according to Bai et al.

242 (2016)). In most Polyneoptera the Tt1 spines of the protibia (as far as Tt1 spines can be identified) are

- 243 placed on a part of the apical tibial margin that projects not at all or only a little the same condition
- as for the Tt1 of the meso- and metatibiae. This condition has also been documented for *Burmantis*
- and *Jersimantis* (Grimaldi 2003: Figs. 8, 14, 15) and is also present in *Alienopterus*. Only in all extant
 mantodeans (Wieland 2013) and at least in *Ambermantis, Burmantis* and *Jantarimantis* among the
- fossil ones (Grimaldi 2003: Fig. 3b,c) the part of the tibial apex that bears Tt1 forms an elongate
- projection; the projection and spine Tt1 form the tibial claw. Also indicated in *Santanmantis*
- (Grimaldi 2003; Hörnig et al. 2013, 2016). Due to the presence of this structure in certain
- 250 Alienopteridae, basal Umenocoleidae (*Vitisma*) and also in stem Liberiblattinidae, the polarity is
- 251 reversed.
- 48. Abdominal sternite VII of female strongly expanded posteriorly (0) absent, (1) present. Present
- in all extant Dictyoptera and Dermaptera, and also visible in *Ponopterix* (Lee 2016: Fig. 13);
- 254 unknown for most fossil taxa. Absent in the other sampled extant taxa. Disregarded due to presence
- 255 in all Mesozoic Dictyoptera.

49. Discoidal spines ventromedially on proximal part of profemur (0) absent, (1) present ((0) absent,

- 257 (1) present according to Bai et al. (2016)). Absent in all non-dictyopteran Polyneoptera, all extant
- 258 Blattodea, and in the fossil Mantodea *Jersimantis*, *Burmantis*, and *Ambermantis* (Grimaldi 2003).
- Present in all extant Mantodea including *Chaeteessa* and *Metallyticus* (Wieland 2013: section 4.6.4.).

- 260 Unknown for *Santanmantis* (scored as ?; though presence may appear likely based on Hörnig et al.
- 261 2013: Fig. 2) and remaining fossils (scored as ?). This character was meanwhile proved for
- 262 Santanmantis (Hörnig (in press)) and also recorded in Mesozoic mantodeans (Bo et al. 2015, cover of
- the book), Manipulatoridae and numerous other Mesozoic cockroaches of diverse families (such as
- 264 Mesoblattinidae Hörnig et al. (2016) corrected interpretation by Lee (2016) and also *Liberiblattina*
- 265 (used here as an outgroup which results in a reverse polarity in a more wide taxonomic study the
- 266 former polarity would work).
- 267 50. Mandibular postmola (0) absent, (1) present. A membranous postmola on the mandible is
- 268 present in extant Dictyoptera (Wipfler et al. 2011) but absent in all other studied species.
- 269 Disregarded due to unclear situation in the fossils.
- 270 51. Posterior part of apical mesotibial margin with a notch and an accessory lobe adjoining it
- ventrad (0) absent, (1) present. This character is poorly documented across insects; detailed data are
- 272 only available for Dictyoptera and selected members of some other polyneopteran orders (Klass et
- al. 2009). Among the taxa here sampled, the presence of a notch and an accessory lobe is
- documented for *Chaeteessa* and *Metallyticus* (Klass et al. 2009) and likely for the early fossil taxon
- 275 Burmantis (Grimaldi 2003: Fig. 9e). Some Alienopteridae show the notch. Absence is known for the
- 276 blattodeans Periplaneta and Ectobius (Klass et al. 2009) and for the Orthoptera, Mantophasmatodea,
- and Grylloblattodea here sampled (Klass et al. 2009, Bai et al. 2016).
- 278 52. **Presence of intertibiotarsal sclerite (itts) on midlegs** (0) absent, (1) present. The occurrence of
- this sclerite, which is located anteroventrally in the membrane between the distal tibial and the basal
- 280 tarsal margins was found only (autapomorphy) in all extant dictyopterans so far studied (except for
- 281 Isoptera; Klass et al. 2009), in extinct *Alienopterus, Jantaripterix, Vitisma, Cratovitisma* and
- 282 *Manipulator* (only sufficiently studied amber cockroaches to date) and Mesozoic mantodeans.
- 283 53. Lacinial incisivi (0) present, (1) absent. Lacinial incisivi are present in all studied species with the
 284 exception of *Macroxyela* and *Stenopsocus* (Wipfler et al., 2011). Disregarded due to unclear situation
- 285 in the fossils and presence in all Dictyoptera.
- 54. Stipital ridge on maxillary stipes (0) present, (1) absent. In all studied species with the exception
 of *Macroxyela* and *Stenopsocus* the stipes has a stipital ridge (Wipfler et al. 2011).
- 55. Lacinia (0) free, (1) in galeal cavity. Autapomorphy of dictyopterans (Wipfler et al. 2012). The
 state in amber fossils proved except for *Alienopterus*.
- 290 56. Proximal part of antennal vessel wall (0) one-layered, (1) two-layered. In Dictyoptera and
- 291 Mantophasmatodea the antennal vessel wall is two-layered with an inner transport epithelium, while
- in all other studied species that have antennal vessels it is one-layered (Pass et al. 2006). Disregarded
- 293 due to unclear situation in the fossils.
- 294 57. **Musculus interampullaris** (0ah1) (0) absent, (1) present. *M. interampullaris* connects the
- antennal ampullae of the two sides, thus dilating them. It is present in Dictyoptera, Orthoptera,
- 296 Phasmatodea and Zoraptera (Pass et al. 2006; Wipfler and Pass 2014. Disregarded due to unclear
- 297 situation in the fossils.

- 58. Detachable operculum at the anterior pole of the egg (0) absent, (1) present. Such an operculum
 is only found in Plecoptera, Embioptera and Phasmatodea. Disregarded due to unclear situation in
 the fossils.
- 59. Head oval/globular (1) absent, (0) present. Head is globular in most stem LIberiblattinidae and
 also in most primitive *Vitisma* and primitive *Jantaripterix* (Vršanský 1999, 2002, 2009) and thus is
 regarded as plesiomorphic at the level of Umenocoleoidea.
- 60. Head (0) standard, (1) prognathous. Head is prognathous only (homoplasically) in unrelated
 (Caloblattinoidea) Raphidiomimidae (Vishniakova 1973; Liang et al. 2009, 2012) and in *Grant* it is
- 306 regarded for autapomorphy.
- 307 61. **Head** (0) standard, (1) modified. Head is extremely conservative in living cockroaches
- 308 (exceptionally orthognathous in *Melyroidea*) and little variability, except for predatory
- 309 Manipulatoridae, Eadiidae and Raphidiomimidae (and Mantodeans) (Vishniakova 1973; Liang et al.
- 2011, 2012; Vršanský 2009; Vršanský and Bechly 2015), is characteristic also for Mesozoic
- 311 cockroaches. The head underwent drastic changes (to-orthognathy) in the transition to beetle-like
- habits (while no such change occurred in other beetle-like lineages like Diplopteridae or
- Anaplectidae)(Vršanský et al. 2016; Barna et al. submitted) and further in certain Alienopteridae (up
- to prognathous state in *Grant*) in seriously modified unlike in any other Dictyoptera.
- 62. Antenna (0) filiform, (1) other. Antenna is filiform and filamentous in all cockroaches including
- 316 type Alienopterus (see Bai et al. 2016). Nevertheless, in most of the species of the family (and also in
- some Umenocoleidae Vršanský 2003) it is modified and regarded for apomorphic.
- 318 63. Antenna with numerous small homogenic sensilla (1) present, (0) absent. Autapomorphy of
- 319 certain Umenocoleoidea. NB! Sensillar apparatus on antenna is family-specific in cockroaches
- 320 (Vršanský et al. 2001).
- 64. Antenna (1) diversified not straight, (0) straight. Autapomorphy of undescribed specimen at fig
 SI3.
- 323 65. Antenna (0) thin, (1) truncate. Autapomorphy of certain Umenocoleoidea.
- 66. Palp (0) elongate, (1) short. Plesiomorphy at the level of order. Palp reduces only among
 Mesozoic Umenocoleoidea and some stem Liberiblattinidae.
- 326 67. **Ocelli** (1) in one line, (0) in triangle. Autapomorhy of advanced Alienopteridae.
- 327 68. **Ocelli** (1) lentiform, (0) diffuse or plain. Ocelli are primitively structured in standard cockroaches
- 328 (Vršanský 2008). Autapomorphy of Umenocoleoidea, homoplasic with Mantodeans.
- 329 69. **Ocelli very large** (1) present, (0) absent. Autapomorphy of some Umenocoleoidea.
- 330 Homoplasically can occur in certain mantodeans. Ocelli of Mesozoic standard cockroaches (including
- Blattulidae, Caloblattinidae, Mesoblattinidae and Raphidiomimidae) are small (Vršanský 2008).
- 332 70. **Ocelli directed** (1) laterally, (0) forwards. Autapomorhy of *Caputoraptor*.
- 333 71. **Eyes protruding laterally** (1) present, (0) absent. Eyes slightly protruding from the head outline
- are characteristic for advanced cockroaches including Mesozoic groups (validated for Fuziidae,

- 335 Vršanský 2009). Significant protrusion is autapomorphy of advanced Umenocoleoidea (see character
- matrix). While this character is absent in most primitive Umenocoleoidea, synapomorphy with
- 337 mantodean is excluded, instead a homoplasy is proposed. Slight lateral protrusion is characteristic for
- all studied umenocoleoids.
- 339 72. Eyes modified and white with structured surface (1) present, (0) absent. Autapomorhy of *Meilia*.
- 340 73. **Glossa.** Disregarded to the lack of evidence in fossils.
- 341 74. **Neck** (1) elongate, (0) short. Autapomorphy of *Teyia*.
- 342 75. Antenna directed (1) to sides, (0) forewards. Autapomorhy of advanced Umenocoleoidea.
- 343 76. **Pronotum strongly 3D** (1) present, (0) absent. Autapomorhy of advanced Umenocoleoidea.
- 344 77. Paranotalia (1) partially reduced, (0) fully developed. Paranotalia are plesiomorphically well
 345 developed (at the level of the order).
- 346 78. **Paranotalia** (1) totally reduced, (0) present. Autapomorhy of advanced Umenocoleoidea.
- 347 79. **Pronotum with sharp teeth** (1) present, (0) absent. Autapomorhy of *Caputoraptor*.
- 348 80. **Pronotum with lateral extensions** (1) present, (0) absent. Autapomorhy of *Caputoraptor*.
- 349 81. **Pronotum with basal separation sutura and tubercle** (1) present, (0) absent. Plesiomorphically
- this state is absent in stem Liberiblattina and Jantaropterix (Vršanský 2003, 2008); occurs in most of
- the Umenocoleidae (Vršanský 2003) and Alienopteridae (Bai et al. 2016 and character matrix).
- 352 82. **Pronotum with color fields** (1) present, (0) absent. Autapomorhy of *Meilia*.
- 353 83. Prothoracic posterior gland (1) present, (0) absent. Autapomorhy of *Teyia*.
- 84. Scale FW large (0) present, (1) absent. Alienopterid scale originated from the modified but hard
 Umenocoleoid forewing. It is still completely developed in a group of species at Figs. SI2.
- 356 85. **Scale** (0) standard, (1) carved. Autapomorphy of certain Alienopteridae.
- 357 86. **Hindwing membrane** (0) transparent, (1) dark. Hindwing membrane is plesiomorphically
- transparent in fossil cockroaches (and very rarely locally dark). Autapomorphy of certainAlienopteridae.
- 360 87. FW venation (0) traceable, (1) absent. Plesiomorphy at the level of order. Tend to reduce with361 degree of elytrization.
- 362 88. Clavus (0) distinct, (1) indistinct. Plesiomorphy at the level of order. Tend to reduce with degree363 of elytrization.
- 89. Clavus sigmoidal (1) present, (0) absent. Synapomorphy of *Umenocoleus* and *Umenopterix*.
 Homoplasically present in *Anaplecta* sp. from Mexican amber (Barna et al., submitted).
- 366 90. Bunky (1) present, (0) absent. Autapomorhy of most Umenololeoidea. In modified form
 367 homoplasically present in some Anaplectidae, some Diplopteridae, *Oulopterix* and some others.

- 368 91. Bunky distributed (1) everywhere, (0) locally. Synapomorphy of advanced Umenocoleoidea
 369 (except the most basal undescribed taxa and *Vitisma*).
- 92. FW posterior margin with bunky (1) present, (0) absent. Bunky are synapomorphically present
 throughout the FW surface also in some Umenocoleoidea , such as *Jantaropterix* (without delimited
 margin Vršanský 2003).
- 93. FW posteriorly with margin (1) narrow, (0) wide. FW posterior margin is wide in primitive (in this
 respect) or standard cockroaches due to wing overlap. Margin becomes narrow with the
 specialization.
- 94. Legs (1) short, (0) standard. Legs are of normal length in stem Liberiblattinidae and primitive *Vitisma* (Vršanský 1999, 2002).
- 378 95. Legs extremely short (1) present, (0) absent. Autapomorhy of *Chimaeroblattina*.
- 379 96. **Smaller claw adjacent to big arolium** (1) present, (0) absent. Autapomorhy of Alienopteridae.
- 380 Homoplasically rarely present in living lineages but in a different combination of characters (no big
- arolia). This charater become less obvious with the immature stages (in early instar extremely well
- developed possibly due to phoresis (see analogical character and function in living ant nest
- 383 parasitizing Attaphilidae Gurney 1937).
- 97. Carination (1) reduced, (0) present. Most cockroaches plesiomorphically possess rich carination
 of legs. This character is autapomorphically reduced in Umenocoleoidea except *Jantaropterix*-group
 (Vršanský 2003).
- 387 98. Carination (1) entirely reduced, (0) locally present. Autapomorhy of Umenocoleoidea (except
 388 Jantaropterix lineage Vršanský 2003).
- 100. HW (1) fenestrate, (0) standard. Autapomorhy of certain Umenocoleoidea (probably due to
 aerodynamics replacing the forewings stroke). Homoplasically present in Diplopteridae (see Vršanský
 et al. 2016).
- 101. HW wide intercalary present (0) present, (1) absent. Plesiomorphy at the level of orderm
 present in all Phyloblattoidea, Caloblattinoidea and stem Liberiblattinidae (Schneider 1973; Vršanský
 2000, 2002; Martin 2010). Character tends to reduce within Umenocoleoidea.
- 102. HW pterostigma (0) present, (1) absent. Plesiomorphy at the level of stem Liberiblattinidae.
 Nevertheless, this character might rarely vary among right and left wing (*Petropterix, Ponopterix* Vršanský 2003).
- 398 103. HW venation extremely simplified (1) present, (0) absent. Autapomorhy of certain
 399 Umenocoleoidea.
- 400 104. **RS dense** (1) present, (0) absent. Autapomorhy of fully elytrised *Alienopterix*.
- 401 105. **R1** (0) present, (1) reduced to few veins. R1 is rich in stem cockroaches (if differentiated; see
- 402 Paleozoic Schneider 1973 and Mesozic Martin 2010 groups) and also in stem Liberiblattinidae (in
- some it tends to reduce with narrowing of the corresponding field). It tends to reduce with
- 404 decreasing size as in miniature Liberiblattinidae (Vršanský 2002).

- 405 106. **R1 sigmoidal and rich** (1) present, (0) absent. Autapomorphy of certain Umenocoleoidea.
- 406 107. HW with numerous large distinct sensilla (mostly in form of sensillar pitts) (1) present, (0)
- 407 absent. Most cockroaches have membrane covered with number of small sensilla from both sides
- 408 (varying from total cover like in Blattulidae up to very sporadic or totally absent in some of the
- 409 present fossils). Big sensilla are autapomorphic for certain Umenocoleoidea, while absence if
- 410 characteristic for others (Alienopteridae).
- 411 108. **Pterostigma with dense sensilla chaetica** (1) present, (0) absent. Autapomorphy of *Teyia*.
- 412 109. **Body** (0) fat, (1) reduced. Plesiomorphy at the level of order. Body in N-fixing cockroaches loses
- 413 fat (and *Blattabacterium*) only during changed diet such as in Nocticolidae (but surprisingly remain
- fixed in predatory Eadiidae and Raphidiomimidae, and in somewhat transitional form also in
- 415 Manipulatoridae and Mantodea). Autapomorphy of advanced pollen-feeding Alienopteridae.
- 416 110. **Body extremely narrow** (1) present, (0) absent. Synapomorphy of *Alienopterus* and *Grant*.
- 417 111. **Cercus short** (0) absent, (1) present. Autapomorphy of Alienopteridae. Cercus can be shortened
- also in other ant-related taxa such as in immatures of Cryptocercidae (the hidden state in adults
- results from fixation, and is not the living state) and Attaphilidae (Scudder 1862; Wheeler 1900).
- 420 112. Cercus extremely short (0) absent, (1) present. Autapomorphy of certain Alienopteridae.
- 421 113. Cercus extremely long (0) absent, (1) present. Autapomorphy of certain Umenocoleoidea.
 422 Homoplasically present also in some *Macrocerca* Hanitsch, 1930.
- 423 114. Antenna sensilla (1) fine, (0) normal. Autapomorphy of certain Umenocoleoidea. NB! Sensillar
 424 apparatus on antenna is family-specific in cockroaches (Vršanský et al. 2001).
- 425 115. Whole body densely covered with fine sensilla (0) absent, (1) present. Autapomorphy of426 Alienopteridae.
- 427 116. Subapical tarsomere with ventral processus (0) absent, (1) present. Autapomorphy of428 Alienopteridae.
- 429 117. Posterior RS (1) transparent, (0) coloured as other veins. Autapomorphy of certain
 430 Alienopteridae.
- 431 118. Legs coloured (0 absent, 1 present). Although the wings are frequently coloured in stem
- 432 Liberiblattinidae (including the type), legs are coloured only in form of stripes (including Blattulidae –
- 433 see Vršanský et al. 2013). Sophisticated coloration in considered for autapomorphy within
- 434 cockroaches (present homoplasically in certain Mantodea see Grimaldi 2003).
- 435 119. Pronotum widest at base (0) present, (1) absent. This state is ancestral for Umenocoleoidea and
 436 pronota widest in the center are present only in strongly derived taxa.
- 437 120. **Hind wing coloured** (0 absent, 1 present). Coloration of hindwing except for pterostigma and
- 438 terminal darkening is extraordinary rare among Mesozoic cockroaches and among described species
- 439 occur only in *Mesoblattina zirkelli* Handlirsh, 1906 (Vršanský and Ansorge 2007).

- 440 121. Hind wing distinctly overlapping body (1) absent, (0) present. HW overlaps body in most
 441 cockroaches including stem Liberiblattinidae and also primitive Umenocoleoidea.
- 442 122. **R1 reduced to 2 veins** (0) absent, (1) present. Reduction in R1 is present in some
- 443 Umenocoleidae and Alienopteridae, but is never present in other groups including stem444 Liberiblattinidae.
- 445 123. Ovipositor laterally compressed (0) absent, (1) present. Ovipositor is round in section in all
 446 cockroaches including ancestral Liberiblattinidae, Umenocoleidae and basal Alienopteridae.
- 447 Ovipositor is elongated horizontally only in *Teyia* (autapomorphy).
- 448 124. Cerci elongated (1) present, (0) absent. Cerci are not elongated in stem Liberiblattinidae and
 449 other Corydioid cockroaches. This character is primarily present in Caloblattinoidea (Vršanský 2002,
 450 2003).
- 451 125. Forewing extremely hard (1) present, (0) absent. Autapomorphy of *Elytropterix*.
- 452 126. Forewing with coloration pattern (0) present, (1) absent. All known representatives of the stem
- 453 family Liberiblattinidae are coloured, similarly as most Umenocoleoidea (Vršanský 2002, 2003;
- 454 Martin 2010), thus this character is regarded for plesiomorphic at the level of stem Liberiblattinidae
- 455 (including all Umenocoleoidea including most Alienopteridae even the totally black species like
- 456 *Teyia* possess rudiments of FW coloration).
- 457 127. **Pronotum with coloration** (0) present, (1) absent. Pronotum is colored in all known
- representatives of the stem family Liberiblattinidae and homoplastically in representaitves of mostlineages. In Umenocoleoidea it is thus regarded for ancestral state.
- 460 128. Pronotum with distinct total ridge (around pronotum) (1) present, (0) absent. This state is
 461 unique autapomorphy of *Umenopterix*, although in modified form it occurs also in *Teyia*.
- 462 129. Eyes significantly protruding laterally (1) present, (0) absent. Eyes slightly protruding from the
 463 head outline are characteristic for advanced cockroaches including Mesozoic groups (validated for
 464 Fuziidae, Vršanský 2009). Significant protrusion is autapomorphy of advanced Umenocoleoidea (see
 465 character matrix). While this character is absent in most primitive Umenocoleoidea, synapomorphy
 466 with mantodean is excluded, instead a homoplasy is proposed.
- 467 130. Antenna differentiated (1) present, (0) absent. Autapomorphy of undescribed specimen at fig468 SI3
- 469 131. Body elongated- autapomorphy (1) of certain Umenocoloidea (particularly Alienopteridae).
- 470 132. Body dark in color- plesiomorphy (0) at the level of Alienopteridae, with *Teyia*, background is
 471 black also in *Caputoraptor* and *Meilia*.
- 472 133. Head triangular- plesiomorphy (0) at the level of Umenocoleoidea.
- 473 134. Sensilla on head small- plesiomorphy (0) at the level of Umenocoleoidea.
- 135. Sensilla on head sparsely distributed plesiomorphy (0) at the level of Umenocoleoidea.

- 475 136. Eye facets small- plesiomorphy (0) at the level of superfamily Umenocoleoidea.
- 476 137. **Eye facets silver in color** autapomorphy (1) of *Formicamendax*.
- 477 138. Area between eyes wide- plesiomorphy (0) at the level of Umenocoleoidea.
- 478 139. Segments of maxillary palp of different length, terminal palpomere hook shaped-
- 479 autapomorphy (1) of *Formicamendax*.
- 480 140. Antenna short- plesiomorphy (0) of Umenocoleoidea except Jantaropterix.
- 481 141. 24 antennal segments- autapomorphy (1) of Formicamendax.
- 482 142. Antennal sensilla small- plesiomorphy (0) at the level of Umenocoleoidea.
- 483 143. Anntenal sensilla dense- plesiomorphy (0) at the level of Umenocoleoidea.
- 484 144. **Proximal anntenal segments conical** plesiomorphy (0) at the level of order.
- 485 145. Distal antennal segments elongated- plesiomorphy (0) at the level of order.
- 486 146. Antennal segments 12-14 curved- autapomorphy (1) of Formicamendax.
- 487 147. Antennal segments 12-14 forming elbow- autapomorphy (1) of *Formicamendax*.
- 488 148. **Neck short** plesiomorphy (0) at the level of order.
- 489 149. **Pronotum elongated** synapomorphy (1) of *Formicamendax, Teyia* and *Aethiocarenus*.
- 490 150. Pronotum with toothed extension- synapomorphy (1) of *Formicamendax, Laticephalana* and
 491 *Caputoraptor*.
- 492 151. Head and Pronotum toothed extension small- plesiomorphy (0) at the level of genus
- 493 *Formicamendax*. (unless reduced from the state in *Caputoraptor*).
- 494 152. **Supracoxal furrow strong** plesiomorphy (0) at the level of order.
- 495 153. Supracoxal furrow ring shaped- autapomorphy (1) of Formicamendax.
- 496 155. Forewings with sensillary holes- plesiomorphy (0) of Umenocoleoidea.
- 497 156. Forewing sensillary holes densely distributed- plesiomorphy (0) of Umenocoleoidea other than
 498 Jantaropterix.
- 499 157. Hindwing extending beyond abdomen- plesiomorphy (0) of order Blattaria.
- 500 158. Hindwing transparent- plesiomorphy (0) of order Blattaria.
- 501 159. Veins thick- autapomorphy (1) of Umenocoleoidea.
- 502 160. **Crossveins present** plesiomorphy (0) at the level of Necymylacrididae.
- 503 161. Venation simple- autapomorphy (1) of Umenocoleoidea.

- 504 162. Venation forming fenestrate structure- autapomorphy (1) of Alienopteridae.
- 505 163. Veins dark- plesiomorphy (0) of Blattaria.
- 506 164. Pterostigma dark- plesiomorphy (0) of Corydioidea.
- 507 165. Pterostigma brown in color- autapomorphy (1) of *Formicamendax* and *Enervipraela*.
- 508 166. **CuP dichotomized-** autapomorphy (1) of *Formicamendax* and *Vzrkadlenie*.
- 509 167. Sensillary holes densely distributed- autapomorphy (1) of Alienopteridae.
- 510 168. Sensillary holes regulary distributed- autapomorphy (1) of Alienopteridae.
- 511 169. Fore femur strong- plesiomorphy (0) of Umenocoleoidea.
- 512 170. Fore femur saddle-shape- plesiomorphy (0) of Umenocoleoidea.
- 513 171. Mid femur elongated- synapomorphy (1) of *Formicamendax, Teyia* and *Aethiocarenus*.
- 514 172. Hind femur longest- plesiomorphy (0) of order Blattaria.
- 515 173. **Hind femur narrow** autapomorphy (1) of *Formicamendax*.
- 516 174. Femur with small sensilla- autapomorphy (1) of Alienopteridae.
- 517 175. Femur sensilla dense- autapomorphy (1) of Alienopteridae.
- 518 176. **Curved sensilla on femoral surface** autapomorphy (1) of *Formicamendax*.
- 519 177. **Hind tibia slender** synapomorphy (1) with *Teyia* and *Aethiocarenus*.
- 520 178. Tibia with dense sensilla- autapomorphy (1) of several Umenocoleoidea.
- 521 179. Tarsi elongated- synapomorphy (1) of Formicamendax, Teyia and Aethiocarenus.
- 522 180. Tarsi strong and well developed- plesiomorphy (0) at the level of order Blattaria.
- 523 181. Tarsal claw asymmetric- synapomorphic (1) with several genera of Umenocoleoidea, such as
- 524 *Alienopterix* (rarely original state occurs).
- 525 182. Cerci with 7 segments- synapomorphic (1) with Alienopteridae.
- 526 183. **Cercal sensilla long** plesiomorphy (0) at the level of Umenocoleoidea.
- 527 184. Cercal sensilla curved- synapomorphy (1) of Formicamendax and Vzrkadlenie.
- 528 185. **Ovipositor asymmetric** synapomorphy (1) of *Formicamendax* and *Vzrkadlenie*.
- 529 186. **Ovipositor segmented** plesiomorphy (0) at the level of the order Blattaria.
- 530 187. **Ovipositor 5 segmented** synapomorphy (1) of *Formicamendax* and *Vzrkadlenie*.

- 188. **Ovipositor terminal end pointed** plesiomorphy (0) at the level of Umenocoleoidea (present
 also in *Alienopterix*).
- 189. **R1 reduced to two strong veins** autapomorphy (1) of Alienopteridae (in Umenocoleidae this
 character might vary among respective wings).
- 535 190. **Rs long** plesiomorphy (0) at the level of Umenocoleoidea.
- 536 191. **M straight** synapomorphy (1) of Alienopteridae and advanced Umenocoleoidae.
- 537 192. **CuA reduced to 4 branches** synapomorphy (1) with Alienopteridae and some Umenocoleoidae.
- 538 193. **CuP simple** plesiomorphy (0) at the level of Corydioidea (Liberiblattinidae, Blattulidae).
- 539 194. Forewings densely covered with hair ("fur") autapomorphy (1) of Antophiloblatta;
- 540 Jantaropterix has not densely covered sensilla on its wings; this character homoplasically occurs in
- 541 some living desert cockroaches and also parasitic species (see Vršanský et al. 2019).
- 542 195. Forewing sensilla modified into scales autapomorphy (1) of *Lepidopterix;* this character
- 543 homoplasically occurs in Collembola, Archaeognatha, Zygentoma, Psocodea, Coleoptera,
- 544 Diptera, Trichoptera and Lepidoptera
- 545 196. **Body ventrally sophistically coloured –** synapomorphy (1) of *Antophiloblatta* and *Lepidopterix*.
- 546 197. Body segments densely approximated, trunk becomes compact *s*ynapomorphy (1) of
- 547 *Antophiloblatta* and *Lepidopterix*; this character homoplasically occurs in Latiblattidae.
- 548 198. Forewing sensilla are with structures synapomorphy (1) with *Antophiloblatta* and
 549 *Lepidopterix.*
- 550 199. **Subcosta richly branched on forewing –** plesiomorphy (0) at the level of order.
- 551 200. First and second tarsomeres subequal symnapomorphy (1) of *Lepidopterix* and *Jantaropterix*.
- 201. **R overlapping apex on forewing** synapomorphy (1) of Umenocoleoidea except some
 Vitisminae.
- 554 202. **R1 tertiary branched on forewing –** autapomorphy (1) of *Lepidopterix* this character as a
- plesiomorphy occurs in lineages with rich venation, whose are not ancestral for present taxa .
- 556 203. Cubital vein reduced to 2 veins on forewing synapomorphy (1) of *Lepidopterix* with
 557 *Blattapterix* and *Elytropterix*.
- 558 204. Forewing strongly vaulted synapomorphy (1) of *Antophiloblatta* with *Elytropterix*.
- 559 205. Subgenital plate strongly sigmoidally curved and vaulted autapomorphy (1) of *Lepidopterix*.
- 560 206. **Ovipositor fine -** synapomorphy (1) of *Antophiloblatta* and *Vzrkadlenie*.
- 561 207. Pronotum disc-like with flattenede paranotalia and small spikes autapomorphy (1) of
- 562 Archaeospinapteryx

563	208. Pronotum elevated	and widest proximally	– autapomorphy (1)	of Trapezionotum
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- 209. Pronotum with triangularly shaped with circle-like colouration autapomorphy (1) of
 Poikiloprosopon
- 566 210. Forewings with 5 translucent fields autapomorphy (1) of V. miso
- 567 211. Forewings with 4 translucent fields synapomorphy (1) of *Vzrkadlenie octomaculata* and *V.* 568 saintgermaini
- 569 212. Forewings with 4 translucent fields not vertically arranged autapomorphy (1) of *V*.
 570 saintgermaini
- 570 Suntgernum
- 571 213. Forewings with translucent fields autapomorphy (1) of *Vzrkadlenie*
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577 References

- 578
- Anisyutkin LN, Gorochov AV (2008) A new genus and species of the cockroach family Blattulidae from
 Lebanese amber (Dictyoptera, Blattina). Paleontol J 42(1):43–46[a1].
- 581 Baum JA, Bogaert T, Clinton W, Heck GR, Feldmann P, Ilagan O, Johnson S, Plaetinck G, Munyikwa T,
- 582Pleau M, Vaughn T, Roberts J (2007) Control of coleopteran insect pests through RNA interference.
- 583 Nature Biotechnology 25:1322–1326.
- Beutel RG, Friedrich F, Ge SG, Yang XK (2014) Insect Morphology and Phylogeny. Walter De Gruyter,Berlin, Germany.
- Beutel RG, Gorb SN (2006) A Revised Interpretation of the Evolution of Attachment Strucutres in
 Hexapoda with Special Emphasis on Mantophasmatodea. Arthropod Syst Phyl 64(1):3–25.
- Beutel RG, Vilhelmsen L (2007) Head anatomy of Xyelidae (Hexapoda: Hymenoptera) and
 phylogenetic implications. Org Divers Evol 7(3):207–230.
- 590 Blanke A, Wipfler B, Letsch H, Koch H, Beckmann F, Beutel R, Misof B (2012) Revival of Palaeoptera –
- head characters support a monophyletic origin of Odonata and Ephemeroptera (Insecta). Cladistics
 28(6):560–581.
- Bradler S (2003) Phasmatodea, Gespenstschrecken. In: Dathe HH (ed) Lehrbuch der peziellen
 ZoologieSpektrum Akademischer Verlag, Gustav Fischer, Hamburg, pp 251–261
- Bradler S (2009) Phylogenie der Stab- und Gespenstschrecken (Phasmatodea). Species, Phylogeny
 and Evolution 2(1):3–139.
- 597 Drilling K, Klass KD (2010) Surface structures of the antenna of Mantophasmatodea (Insecta). Zool
 598 Anz 249(3–4):121–137.
- 599 Friedemann K, Wipfler B, Bradler S, Beutel RG (2012) On the head morphology of *Phyllium* and the 600 phylogenetic relationships of Phasmatodea (Insecta). Acta 93(2):184-199.
- Giles ET (1963) The comparative external morphology and affinities of the Dermaptera. Transactions
 of the Royal Entomological Society, London 115(4):95–164.
- Grimaldi DA (2003) A revision of Cretaceous mantises and their relationships, including new taxa
 (Insecta: Dictyoptera: Mantodea). Am Mus Novit 3410:1–47.
- Haas F, Kukalova-Peck J (2001) Dermaptera hindwing structure and folding: new evidence for
- 606 familial, ordinal and superordinal relationships within Neoptera (Insecta). Eur J Entomol 98:445-509.
- Hennig W (1969) Die Stammesgeschichte der Insekten, Senckenberg- Buch 49, W. Kramer, Frankfurtam Main, 436 pp.
- 609 Hockmann D, Picker MD, Klass KD, Pretorius L (2009) Postembryonic development of the unique
- antenna of Mantophasmatodea (Insecta). Arthropod Structure & Development 38(2):125–133.

- Hörnig MK, Haug JT, Haug C (2013) New details of *Santanmantis axelrodi* and the evolution of the
 mantodean morphotype. Palaeodiversity **6**:157–168.
- 613 Hörnig MK, Sombke A, Haug C, Harzsch S, Haug JT (2016) What nymphal morphology can tell us
- about parental investment a group of cockroach hatchlings in Baltic amber documented by a multi-
- 615 method approach. Paleontol Electron 19(1):1–20.
- Hudson G B (1945) A study of the tentorium in some orthopteroid Hexapoda. J EntomolSoc South Afr8(2):71-90.
- 618 Klass KD, Ehrmann R (2003) 13. Ordnung Mantodea, Fangschrecken, Gottesanbeterinnen. In: Dathe,
- H.H. (ed) Lehrbuch der Speziellen Zoologie, Band I: Wirbellose Tiere, 5. Teil: Insecta. Heidelberg,
 Berlin, pp Pp. 182-197.
- 621 Klass KD, Eulitz U (2007) The tentorium and anterior head sulci in Dictyoptera and
- 622 Mantophasmatodea (Insecta). Zool Anz 246(3):205–234.
- Klass KD, Eulitz U, Schmidt C, Barton A (2009) The tibiotarsal articulation and antertibiotarsal leg
 sclerite in Dictyoptera (Insecta). Ins Syst Evol 40(4):361–387.
- 625 Kleinow W (1966) Untersuchungen zum Flügelmechanismus der Dermapteren. Z Morphol Ökol Tiere 626 56(4):363–416.
- Lee SW (2016) Taxonomic diversity of cockroach assemblages (Blattaria, Insecta) of the Aptian Crato
 Formation (Cretaceous, NE Brazil). Geol Carpath 67(5):433 450.
- 629 Leverault P (1936) The morphology of the *Carolina mantis*. Univ Kans Sci Bull 14:205 –259.
- 630 Liang JH, Shih CG, Ren D (2018) New Jurassic predatory cockroaches (Blattaria: Raphidiomimidae)
- 631 from Daohugou, China and Karatau, Kazakhstan. Alcheringa 42(1):101–109.
- Liang JH, Vršanský P, Ren D (2012) Variability and symmetry of a Jurassic nocturnal predatory
 cockroach (Blattida: Raphidiomimidae). Rev Mex Cienc Geol 29(2):411–421.
- Liang JH, Vršanský P, Ren D, Shih CC (2009) A new Jurassic carnivorous cockroach (Insecta, Blattaria,
 Raphidiomimidae) from the Inner Mongolia in China. Zootaxa 1974:17–30.
- Luo C, Xu C, Jarzembowski AE (2020) *Enervipraeala nigra* gen. et sp. nov., a umenocoleid
 dictyopteran (Insecta) from mid-Cretaceous Kachin amber. Cretac Res 119:104702.
- 638 Loveridge RF (2007) The Crato fossil beds of Brazil. Window into an ancient world. Cambridge639 University Press, Cambridge.
- 640 Matsumura Y, Wipfler B, Pohl H, Dallai R, Machida R, Mashimo Y, Câmara JT, Rafael JA, Beutel RG
- (2015) Cephalic anatomy of *Zorotypus weidneri* New, 1978: new evidence for a placement of
 Zoraptera. Arthropod Systematics & Phylogeny 73(1):85–105.
- Martin S (2010) Early Jurassic cockroaches (Blattodea) from the Mintaja insect locality, Western
 Australia. Alavesia 3:55–72.

- 645 Nalepa CA, Lenz M (2000). The ootheca of *Mastotermes darwiniensis* Frogatt (Isoptera:
- 646 Mastotermitidae): homology with cockroaches oothecae. Proc Roy Soc B 267(1454):1809–1813.
- 647 Pass G, Gereben-Krenn BA, Merl M, Plant J, Szucsich NU, Tögel M (2006) Phylogenetic Relationships
- of the Orders of Hexapoda: Contributions from the Circulatory Organs for a Morphological Data
 Matrix. Arthropod Systematics & Phylogeny 64(2):165–203.
- Rähle W (1970) Untersuchungen am Kopf und Prothorax von Embia ramburi Rimsky-Korsakow 1906
 (Embioptera, Embiidae). Zool Jahrb Abt Anat Ontogenie Tiere 87:248–30.
- Schneider JW (1983) Die Blattodea (Insecta) des Palaozoikums, Teil 1: Systematik, Ökologie und
 Biostratigraphie. Freiberger Forschungshefte C 382:107–146.
- 654 Scudder SH (1862) Materials for a monograph of the North American Orthoptera including a
- catalogue of the known New England species. Boston J Nat Hist 7(3):409–480.
- 656 Sendi H, Hinkelman J, Vršanská L et al (2020a) Roach nectarivory, gymnosperm and earliest flower
- 657 pollination evidence from Cretaceous ambers. Biologia 75:1613–1630.
- 658 https://doi.org/10.2478/s11756-019-00412-x
- 659 Vishniakova VN (1973) New cockroaches (Insecta: Blattodea) from the Upper Jurassic deposits of
- 660 Karatau. In Narchuk EP (ed) Voprosy paleontologii nasekomykh. Doklady na 24-m Ezhegodnom
- 661 chtenii pamyati N.A.Kholodkovskogo, 1971. [Problems of the Insect Palaeontology. Lectures on the
- 662 XXIV Annual Readings in Memory of N.A. Kholodkovsky (1–2 April, 1971)]. Nauka, Leningrad, pp 64–
- 663 77 [in Russian].
- Vršanský P (1999) Two new species of Blattaria (Insecta) from the Lower Creataceous of Asia with
 comments on the origin and phylogenetic position of families Polypagidae and Blattulidae (Insecta,
 Blattaria). Entomol Probl 30(2):85–91.
- 667 Vršanský P (2002) Origin and the early evolution of mantises. AMBA projekty **6**(1):1–16.
- 668 Vršanský P (2008) Central ocellus of extinct cockraoches (Blattida: Caloblattinidae). *Zootaxa* 1958:41–
 669 50.
- 670 Vršanský P (2009) Albian cockroaches (Insecta, Blattida) from French amber of Archingeay.
 671 Geodiversitas 31(1):73–98.
- 672 Vršanský P, Ansorge J (2007). Lower Jurassic cockroaches (Insecta: Blattaria) from Germany and
 673 England. Afr Invertebr 48(1):103–126.
- 674 Vršanský P Liang J-H, Ren D (2009) Advanced morphology and behaviour of extinct earwig-like
 675 cockroaches (Blattida: Fuziidae). Geol Carpath 60(6):449–462.
- 676 Vršanský P Quicke DLJ, Rasnitsyn AP, Basibuyuk H, Ross A, Fitton M, Vidlička Ľ (2001) The oldest fossil
 677 insect sensilla.AMBA projekty 4(1):1–12.
- 678 Vršanský P., Van de Kamp T, Azar D, Prokin A, Vidlička L, Vagovič P (2013) Cockroaches probably
 679 cleaned up after dinosaurs. PLoS ONE 0080560.

- 680 Vršanský P, Sendi H, Hinkelman J, Hain M (2021) Alienopterix Mlynský et al., 2018 complex in North
 681 Myanmar amber supports Umenocoleoidea/ae status. Biologia 76(8): 2207-2224.
- Walker EM (1931) On the anatomy of *Grylloblatta campodeiformis* Walker. 1. Exoskeleton and
 musculature of the head. Ann Entomol Soc Am 24(3):519–536.
- 684 Wheeler WM (1900) The female of *Eciton sumichrasti* Norton, with some notes on the habits of
 685 Texan Ecitons. Am Nat 34(403):563–574.
- 686 Wieland F (2006) The cervical sclerites of Mantodea discussed in the context of dictyopteran
 687 phylogeny (Insecta: Dictyoptera). Entomol Abh 63(1-2):51–76.
- 688 Wipfler B, Machida R, Müller B, Beutel RG (2011) On the head morphology of Grylloblattodea
- 689 (Insecta) and the systematic position of the order, with a new nomenclature for the head muscles of
 690 Dicondylia. Syst Entomol 36(2):241–266.
- Wipfler B, Pass G (2014) Antennal heart morphology supports relationship of *Zoraptera* with
 polyneopteran insects. Syst Entomol 39(4):800–805.
- Wipfler B, Wieland F, DeCarlo F, Hörnschemeyer T (2012) Cephalic morphology of *Hymenopus coronatus* (Insecta: Mantodea) and its phylogenetic implications. Arthropod Struct Dev 41(1):87–100.
- 695 Wipfler B, Klug R, Ge SQ, Bai M, Göbbels J, Yang XK, Hörnschemeyer T (2015) The thorax of
- 696 Mantophasmatodea, the morphology of flightlessness, and the evolution of the neopteran insects.697 Cladistics 31(1) 50–70.
- 698 Zwick P (1980) Plecoptera (Steinfliegen). In Helmcke JG, Stark D, Wermuth H (Eds) Handbuch der
- 699 Zoologie.Berlin, de Gruyter pp 1-115.

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