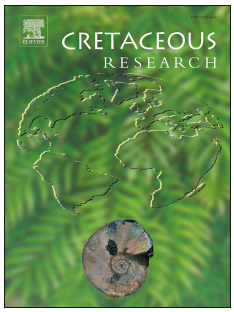
Accepted Manuscript



Chilamnestocoris mixtus gen. et spec. nov., the first burrower bug (Hemiptera: Pentatomoidea: Cydnidae) in Upper Cretaceous Burmese amber

Jerzy A. Lis, Barbara Lis, Ernst Heiss

PII: S0195-6671(18)30067-3

DOI: 10.1016/j.cretres.2018.06.017

Reference: YCRES 3910

To appear in: *Cretaceous Research*

Received Date: 16 February 2018

Revised Date: 27 May 2018

Accepted Date: 22 June 2018

Please cite this article as: Lis, J.A., Lis, B., Heiss, E., *Chilamnestocoris mixtus* gen. et spec. nov., the first burrower bug (Hemiptera: Pentatomoidea: Cydnidae) in Upper Cretaceous Burmese amber, *Cretaceous Research* (2018), doi: 10.1016/j.cretres.2018.06.017.

Short communication

Chilamnestocoris mixtus gen. et spec. nov., the first burrower bug (Hemiptera: Pentatomoidea: Cydnidae) in Upper Cretaceous Burmese amber

Jerzy A. Lis [a*], Barbara Lis [a], Ernst Heiss [b]

[a] Department of Biosystematics, Opole University, Oleska 22, 45-052 Opole, Poland

[b] Tiroler Landesmuseum Ferdinandeum, Josef-Schraffl-Strasse 2a, 6020, Innsbruck, Austria

*Corresponding author. Department of Biosystematics, Opole University, 45-052 Opole, Poland. E-mail address: cydnus@uni.opole.pl (J.A. Lis).

ABSTRACT

A new genus and species of burrower bug, *Chilamnestocoris mixtus* gen. et sp. nov. (Hemiptera: Cydnidae), is described from Upper Cretaceous Myanmar amber. The new genus is characterized by a very long claval commissure and, therefore, is classified within the extant subfamily Amnestinae. It presents a mixture of generic characters relevant to the genus *Chilocoris* Mayr (Cydninae) and the genus *Amnestus* Dallas (Amnestinae), but also has its own autapomorphies, i.e., each cephalic marginal setigerous puncture arises from its own well-developed tubercle, and the middle and posterior tibiae are strongly compressed and flattened.

Keywords:

Cydnidae

Amnestinae

Chilamnestocoris mixtus gen. et sp. nov.

Myanmar amber

Upper Cretaceous

Burrower bug fossil

1. Introduction

The Cydnidae, commonly known as Burrower Bugs or Burrowing Bugs, is a pentatomoid family, the monophyly of which is constantly being questioned (Grazia et al., 2008; Pluot-Sigwalt & Lis, 2008; Lis, 2010; Lis et al., 2017). The family includes more than 750 species known from tropical, warm, and temperate regions of the world (Cassis & Gross, 2002; Schwertner & Nardi, 2015; Lis et al., 2017), and is, at present, divided into six subfamilies, i.e., Amaurocorinae, Amnestinae, Cephalocteinae, Cydninae, Garsauriinae, and Sehirinae (Pluot-Sigwalt & Lis, 2008; Lis et al., 2017).

The oldest fossil records of Cydnidae are known from the Late Jurassic to Early Cretaceous Yixian Formation of China (Yao et al., 2007, 2010). Fossils of the family Cydnidae are represented by 70 species (Vršanský et al., 2015; palaeobiology database [URL: paleobiodb.org; accessed 7 January 2018]), including only nine species in seven genera of the subfamily Amnestinae (Pinto & Ornellas, 1974; Popov, 1986, 1990; Thomas, 1988, 1994; Popov & Pinto, 2000; Shcherbakov & Popov, 2002; Yao et al., 2007, 2010). Among these, only three species, i.e. *Amnestus guapinolinus* Thomas, 1988, *A. electricus* Thomas, 1994, and *A. priscus* Thomas, 1994, have been described from amber (*A. guapinolinus* from the Oligo-Miocene of Chiapas, Mexico; the remaining two species are from the Dominican Republic).

Although 53 species of Hemiptera have been described from Burmese amber (Guo et al., 2017; Ross, 2018), no representative of the family Cydnidae was reported among the Burmite inclusions. In this paper we describe a new genus and species of the subfamily Amnestinae, which is the first Burmite inclusion not only for the family Cydnidae, but also the entire superfamily Pentatomoidea.

2. Material and methods

Burmese amber is of Upper Cretaceous age, probably from the Turonian or Cenomanian (90–100 Ma) (Grimaldi et al., 2002). No particular locality of origin in Kachin State in Northern Myanmar is known, and therefore no further stratigraphic information is available, as is the case for Aradidae inclusions described recently in amber pieces originating from the same source (Heiss & Poinar, 2012; Heiss, 2016). However, according to Guo et al. (2017), most known Burmite arthropod inclusions came from the Hukawng Valley, Kachin State in northern Myanmar, where the mining locality is at Noije Bum, near Tanai Village (26°21′33.41″N, 96°43′11.88″E) (Cruickshank & Ko, 2003; Grimaldi et al., 2002; Bai et al., 2016). The map of Myanmar showing the position of the Hukawng Valley was provided by Dunlop et al. (2015). Detailed investigation of these deposits (Cruickshank & Ko, 2003; Shi et al., 2012) dated them as 97 to 110 Ma (the late Albian of the Early Cretaceous) or 98.8 ± 0.6 Ma old (Cenomanian, earliest Late Cretaceous), respectively.

This study is based on material permanently deposited in the Tiroler Landesmuseum (CEHI Collection Ernst Heiss), Innsbruck, Austria. All photos were captured with a Moticam 1000 digital camera mounted to an Olympus SZX10 microscope using Images Plus 2.0 software (Motic Asia, Hong Kong). Multiple focal planes were merged using Helicon Focus 6.3.0 software (Helicon Soft Ltd.).

The terminology for cephalic chaetotaxy follows that used by Lis & Pluot-Sigwalt (2002), for mesothoracic wing venation that used by Lis (2002), and for pretarsal structures that used by Lis & Ziaja (2010).

3. Systematic palaeontology

Order: Hemiptera Linnaeus, 1758

Suborder: Heteroptera Latreille, 1810

Infraorder: Pentatomomorpha Leston, Pendergast et Southwood, 1954

Superfamily: Pentatomoidea Leach, 1815

Family: Cydnidae Billberg, 1820

Subfamily: Amnestinae Hart, 1919

Genus ***Chilamnestocoris*** gen. nov.

LSID urn: lsid:zoobank.org:act:CDCF292B-2478-4F57-A0ED-4BF6E6D44D61

Type species: *Chilamnestocoris mixtus* sp. nov.

Diagnosis. Head margins bearing both peg-like and hair-like setae; each marginal setigerous puncture arising from its own well-developed tubercle; clypeal submargin with four peg-like setae; eyes large, each with an apical seta; ocelli present; antennae five-segmented, second segment minute. Pronotum almost parallel-sided; pronotal disc with an anterior submarginal line clearly visible, pronotal umbones slightly swollen, not concealing the postero-lateral margins of pronotal disc; lateral margins with setigerous punctures bearing long hair-like setae. Scutellum triangular. Corium with very broad clavus, bearing four rows of coarse punctures; claval commissure present, very long. Costal margins with setigerous punctures bearing hair-like setae. Meso- and metapleuron with large evaporatoria, metapleural peritreme very long and strongly recurved. Tibiae of middle and posterior legs flattened. The coxal combs unseen due to the poor visibility of characters on the ventral side of the specimen.

Etymology. The name is a compilation of two generic names, i.e. *Chilocoris* Mayr, 1865 and *Amnestus* Dallas, 1851, in reference to the fact that several characters are intermediate between these two genera (*Chil-amnest-ocoris*).

Chilamnestocoris mixtus Lis J.A., Lis B. & Heiss, sp. nov.

(Figs. 1–3)

LSID urn:lsid:zoobank.org:act:5CD2C8A8-E94C-4E39-9E7E-5E4EA760F5D7

Etymology. The specific epithet refers to a mixture of generic characters relevant to the genus *Chilocoris* (Cydninae) and the genus *Amnestus* (Amnestinae).

Holotype female. The specimen belongs to and is deposited as BUR-CYD-01 in the collection of the second author (EH) at the Tiroler Landesmuseum, Innsbruck, Austria.

Type locality. No particular locality of origin in Kachin State in Northern Myanmar is known for this taxon of the Cydnidae (however, see also the section: “Material and methods”).

Diagnosis. As for the new genus.

Description. Completely preserved female specimen (Figs. 1A–D). Body almost unicolorous, its dorsal side slightly polished; head, pronotum and scutellum dark castaneous; antennae, rostrum, tibiae and tibial spines, costal margins, exocorium and mesocorium, and lateral parts of pronotum brown; the ventral body side castaneous.

Head (Figs. 2A–B). Dorsally with clearly visible small punctures, and with slightly developed oblique striae in the posterior part of paraclypei; clypeus as long as paraclypei, broadened in its apical part; clypeal submargin with four (three cleraly visible and one torn out) blackish brown, apically more or less sharpened peg-like setae; paraclypei each with a submarginal row of five more or less sharply ended peg-like setae, and three hair-like setae; each marginal setigerous puncture arising from its own well-developed tubercle; eyes large,

brown with a silver tinge, each with an apical seta, ocular index about 2.8; ocelli yellowish, interocellar distance about four times greater than a distance between the ocellus and the eye; antennae five segmented with the second segment minute and hardly visible, about nine times shorter than the third (Fig. 2B), the fifth segment longest; rostrum reaching the midcoxae.

Thorax. Pronotum (Fig. 1C) almost parallel-sided; pronotal disc with an anterior submarginal line cleraly visible, calli impunctate, the area behind calli with a short row of large punctures laterally on each side; anterior lobe almost impunctate, except for setigerous punctures and a few punctures anteriorly and laterally; posterior lobe with clearly visible punctures; pronotal umbones slightly swollen and impunctate, not concealing the postero-lateral margins of the pronotal disc; lateral margins with seven (right side) and eight (left side) setigerous punctures bearing long hair-like setae, two setae present also on the lateral part of the anterior submarginal line on each side; moreover, two additional setae occur on lateral parts of the anterior lobe of the pronotal disc. Propleuron alutaceous; its anterior and posterior convexities impunctate, a median depression with punctures close to the coxae. Scutellum triangular; scutellar disc evenly punctured with large coarse punctures; scutellar tip narrow, elongated. Clavus (Fig. 1D) very broad, with three rows of coarse punctures parallel to scutellum, and a single row of large punctures close to mesocorium; the latter with two rows of coarse punctures paralleling the clavo-corial suture (one complete row, and the second incomplete, visible only basally) and with several well-spaced punctures forming two hardly visible rows; exocorium almost evenly punctured with large shallow punctures; claval commissure present, very long (Fig. 1D). Costal margins paler than the remaining part of the corium, bearing setigerous punctures (two hair-like setae visible on left hemelytron, and several hair-like seta visible close to the costal margin of right hemelytron); membrane almost translucent, slightly embrowned, distinctly surpassing the tip of the abdomen. Mesopleuron and metapleuron with evaporatorium similar to that of the genus *Chilocoris*, with very long

and strongly recurved peritreme. Legs brown, tibial spines only a little darker; anterior tibia broadened apically, with four spines at the apical margin; mid- and posterior tibiae strongly flattened, only slightly broadened apically, each bearing numerous long spines at the outer margin and only a few at the inner margin; tarsus of posterior legs with 1st and 2nd segments altogether longer than the third; pretarsal claws long and narrow, pulvilli narrow, slightly recurved and apically somewhat capitate (Fig. 2C–D).

Abdomen. Sterna dark brown, alutaceous, laterally with numerous distinct small punctures and whitish shiny semierect hairs; 4th, 5th and 6th visible segments medially with numerous long whitish semierect hairs.

Measurements. Female holotype (in mm): body length (from the head apex to the apex of membrane): 2.85; body width (at the widest part of hemelytra): 1.38; head length: 0.46; head width: 0.70; pronotum length: 0.89; pronotum width: 1.30; scutellum length: 0.41; scutellum width: 0.47; antennal segments: 0.17, 0.03, 0.25, 0.26, 0.28.

4. Remarks on the palaeohabitat of the new species

Burrower bugs, as suggested by their common family name, mostly live underground and feed on plant roots, although some of them inhabit aboveground plant parts, some may be mycetophagous or cavernicolous, and some are associated with ants (e.g., Froeschner, 1975; Schaefer, 1988; Linnavuori, 1993; Lis, 1994; Lis et al., 2000; Kłys & Lis, 2013; Lis, 2015; Lis & Lis, 2016; Schwertner & Nardi, 2015). Extant species of the subfamily Amnestinae are mostly litter inhabitants in various types of humid forests, but have sometimes been found belowground or in guano in bat caves (Froeschner, 1960; Mayorga & Cervantes, 2001; Eger, 2008; Mayorga & Brailovsky, 2012; Mayorga & Cervantes, 2005, 2014; Schwertner & Nardi, 2015).

Nevertheless, no one has ever attampted to reconstruct the habitat in which species of fossil Amnestinae lived, since no accompanying plant fossils have been described along with amnestine fossil remnants. Fortunately, in the piece of amber studied herein, we noticed several plant syninclusions that can be classified into two groups, i.e., branched hairs (Figs. 3A–D) and star-shaped structures (Figs. 3E–F).

The star-shaped structures found in the studied amber piece (Figs. 3E–F) are similar to the structure described by Grimaldi et al. (2002) as an isolated archegoniophore of a *Marchantia*-like liverwort (Hepatopsida: Marchantiaceae) in Burmese amber (Fig. 3F), and by Schmidt et al. (2010) as "stellate hairs" in Cretaceous African amber, resembling those of modern representatives of the tree-fern family Cyatheaceae (Fig. 3E). Several branched hairs (Figs. 3A–D) accompanying our amnestine specimen are known to be quite common in Burmese amber (Heinrichs et al., 2017). The same branched hairs were also recorded in Cretaceous amber from New Jersey and Lebanon, and in Tertiary Baltic amber (Gifford and Foster, 1987; Hall and Burke, 1974; Jones, 1998; Peñalver et al., 2007), and were regarded as originating possibly from a fern or conifer. Similar hairs in Early Cretaceous amber from Spain have been assigned to the fern family Gleicheniaceae (Pérez de la Fuente et al., 2012). Recently, this type of branched hair was found as syninclusions to *Frullania pinnata*, the newly described mid-Cretaceous Burmese amber species of leafy liverwort (Heinrichs et al., 2017). Because, "stellate hairs" occur in various amber sites, but are characteristic mainly of the Baltic amber, and regarded as belonging to Fagaceae (Weitschat and Wichard, 2002), their botanical origin in burmites can't be precisely defined.

Taking all the above into account, especially the environmental conditions in which the species of *Frullania* lived (Grimaldi et al., 2002; Heinrichs et al., 2017), we conclude that *C. mixtus* most probably inhabited areas surrounding the conifer tree trunks where ferns and liverwort grew. We are aware that our hypothesis is highly speculative and the presence of the

202 described trichomes can simply show that the habitat could have been arboreal. However, it is
203 consistent with the biology of some extant species of the subfamily Amnestinae, which live in
204 the litter of various types of humid forests (Mayorga & Cervantes, 2001; Eger, 2008;
205 Mayorga & Cervantes, 2014; Schwertner & Nardi, 2015).
206
207 **5. Discussion**
208 The new genus was placed in the family Cydnidae based on the following characters: (1) the
209 presence of cephalic chaetotaxy, including peg-like setae (Figs. 1C, 2A–B), (2) spinose tibiae
210 (Figs. 1A–B, 2C), and (3) margins of pronotum and costal margins of hemelytra with hair-like
211 setae (Figs. 1B–C). It can easily be classified within the subfamily Amnestinae due to the
212 presence of the claval commissure (Figs. 1A–B, D), which is a diagnostic feature of this
213 burrower bug subfamily.
214 This new genus possesses the same characters as those occurring in species of the
215 genus *Amnestus* Dallas, 1851, i.e., clypeus with four apical peg-like setae (Fig. 2A), pretarsal
216 structures with long, slender claws and narrow, slightly recurved and apically somewhat
217 capitate pulvilli (Fig. 2D), and mesothoracic wing venation bearing the vein R entirely
218 coalescent with M, and the vein 2A present and clearly visible (Fig. 1B).
219 However, the new genus also has several characters in common with species of the genus
220 *Chilocoris* Mayr, 1865 (representing tribe Cydnini of the subfamily Cydninae), i.e., clypeus as
221 long as paraclypei and apically bearing peg-like setae similar to those occurring in many
222 species of *Chilocoris* (Fig. 2A) (in Amnestinae the clypeus is distinctly longer than the
223 paraclypei, and usually bears pegs on the clypeus apical margins), metapleural peritreme long
224 and strongly recurved (in Amnestinae it is not as long, and never as strongly apically
225 recurved), and the membranal suture almost straight (Fig. 1B) (in species of *Amnestus* it is
226 deeply emarginated on the inner half, and in species of *Lattinestus* it is almost straight, but

this character is connected with the coleopterous form of the hemelytra in all species of the genus).

Beside the fact that *Chilamnestocoris mixtus* displays a mixture of characters found in *Chilocoris* and *Amnestus*, it also has its own two autapomorphies, i.e., (1) strongly compressed and flattened middle and posterior tibiae (Fig. 2C) (the middle and posterior tibiae in *Chilocoris* and species of Amnestinae are more or less semicircular in diameter), and (2) each cephalic marginal setigerous puncture arises from its own well-developed tubercle (Fig. 2B). What is most important is that the latter character is unknown elsewhere in the family Cydnidae.

6. Concluding remarks

Burrower bugs (Cydnidae) recorded in fossil amber are extremely rare. *Chilamnestocoris mixtus* gen. et sp. nov. is the first Burmite inclusion not only for the family Cydnidae, but also the entire superfamily Pentatomoidea. The presence of a very long claval commissure enables to classify this new taxon within the subfamily Amnestinae. However, it presents also several generic characters relevant to the genus *Chilocoris* of the subfamily Cydninae, but also has its own autapomorphies. *C. mixtus* most probably inhabited areas surrounding the conifer tree trunks where ferns and liverwort grew, what is consistent with the biology of some extant species of the subfamily Amnestinae.

Acknowledgements

We thank the anonymous reviewers whose comments have improved this manuscript.

References

Bai, M., Beutel, R.G., Klass, K.D., Zhang, W.W., Yang, X.K., Wipfler, B., 2016. †Alienoptera – a new insect order in the roach - mantodean twilight zone. Gondwana Research 39, 317–26.

Cassis, G., Gross, G.F., 2002. Hemiptera: Heteroptera (Pentatomorpha). In: Houston, W.W.K., Wells, A., (Eds.) Zoological Catalogue of Australia. Vol. 27.3B. Melbourne, CSIRO Publishing, Australia. XIV + 737 pp.

Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21, 441–455.

Dunlop, J.A., Bird, Th.L., Brookhart, J.O., Bechly, G., 2015. A camel spider from Cretaceous Burmese amber. Cretaceous Research 56, 265–273.Eger, J.E., 2008. A new genus and three new species of burrowing bugs (Hemiptera: Heteroptera Cydnidae: Amnestinae). Proceedings of the Entomological Society of Washington 110, 940–947.

Froeschner, R.C., 1960. Cydnidae of the Western Hemisphere. Proceedings of the United States National Museum 111, 337–680.

Froeschner, R.C., 1975. Three new species of burrowing bugs found in associations with ants in Brazil (Hemiptera: Cydnidae). Journal of the Kansas Entomological Society 48, 105–110.

Gifford, E.M., Foster, A.S., 1987. Morphology and Evolution of Vascular Plants, Third Edition. W.H. Freeman and Co., New York, 626 pp.

Grazia, J., Schuh, R.T., Wheeler, W.C., 2008. Phylogenetic relationships of family groups in Pentatomoidea based on morphology and DNA sequences (Insecta: Heteroptera). Cladistics 24, 1–45.

Grimaldi, D., Engel, M.S., Nascimbene, P.C., 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates 3361, 1−71.

Guo, M., Xing, L., Wang, W., Zhang, W., Wang, S., Shi, A., Bai, M., 2017. A catalogue of Burmite inclusions. Zoological Systematics 42, 249–379.

Hall, D.M., Burke, W., 1974. Wettability of leaves of a selection of New Zealand plants. New Zealand Journal of Botany 12, 283–298.

Heinrichs, J., Feldberg, K., Müller, P., Schëfer-Verwimp, A., von Konrat, M., Ilsemann, B., Krings, M,, 2017. *Frullania pinnata* spec. nov. (Frullaniaceae, Porellales), a new leafy liverwort in mid-Cretaceous Burmese amber from Myanmar. Cretaceous Research 78, 56–60.

Heiss, E., 2016. New genera and species of Aradidae in Cretaceous Burmese Amber (Hemiptera: Heteroptera). Linzer biologische Beiträge 48, 419–429.

Heiss, E., Poinar Jr., O., 2012. New Aradidae in Mesozoic Burmese Amber (Hemiptera, Heteroptera). Annalen des Naturhistorischen Museums Wien, Serie A 114, 307–316.

Jones, D.L., 1998. Encyclopaedia of Ferns. An introduction to Ferns, their structure, biology, economic importance, cultivation and propagation. Timber Press, Portland, Oregon. 433 pp.

Kłys, G., Lis, J.A., 2013. First cave records for Palearctic burrower bugs (Hemiptera: Heteroptera: Cydnidae) from Tajikistan, with a checklist of the World Cydnidae associated with caves. Zootaxa 3686, 493–496.

Linnavuori, R.E., 1993. Cydnidae of West, Central and North-East Africa (Heteroptera). Acta Zoologica Fennica 192, 1–148.

Lis, J.A., 1994. A revision of Oriental burrower bugs (Heteroptera: Cydnidae). Upper Silesian Museum, Bytom, Poland. 349 pp.

Lis, J.A., 2002. The mesothoracic wing and its phylogenetic significance in Cydnidae (Hemiptera: Heteroptera: Pentatomoidea). Polish Journal of Entomology 71, 43–71.

Lis, J.A., 2010. Coxal combs in the Cydnidae *sensu lato* and three other related "cydnoid" families – Parastrachiidae, Thaumastellidae, Thyreocoridae (Hemiptera: Heteroptera): functional, taxonomic, and phylogenetic significance. Zootaxa 2476, 53–64.

Lis, J.A., 2015. *Chilocoris quadraticollis* Linnavuori, 1993 (Hemiptera: Heteroptera: Cydnidae): first records from the Democratic Republic of Congo with first data on its biology. Heteroptera Poloniae – Acta Faunistica 9, 43–44.

Lis, J.A., Lis, B., 2016. *Chilocoris serratus* n. sp., the first burrower bug species (Hemiptera: Heteroptera: Cydnidae) recorded in Guinea-Bissau with an annotated checklist of the Afrotropical species of the genus *Chilocoris* Mayr, 1865. Zootaxa 4103, 383–389.

Lis, J.A., Pluot-Sigwalt, D., 2002. Nymphal and adult cephalic chaetotaxy of the Cydnidae (Hemiptera: Heteroptera), and its adaptive, taxonomic and phylogenetic significance. European Journal of Entomology 99, 99–109.

Lis, J.A. & Ziaja, D.J., 2010**.** Pretarsal structures in the family Cydnidae sensu lato (Hemiptera: Heteroptera: Pentatomoidea). Zootaxa 2545, 23–32.

Lis, J.A., Becker, M., Schaefer, C.W., 2000. Chapter 12. Burrower Bugs (Cydnidae). In: Schaefer, C.W., Panizzi, A.R. (Eds.), Heteroptera of Economic Importance. CRC Press, Boca Raton, London, New York, Washington D.C. pp. 405–419.

Lis, J.A., Ziaja, D.J., Lis, B., Gradowska, P., 2017. Non-monophyly of the "cydnoid" complex within Pentatomoidea (Hemiptera: Heteroptera) revealed by Bayesian phylogenetic analysis of nuclear rDNA sequences. Arthropod Systematics & Phylogeny 75, 481–496.

Mayorga, C.M., Brailovsky, H. 2012. Four new species of *Lattinestus* (Hemiptera: Heteroptera: Cydnidae: Amnestinae). Revista Mexicana de Biodiversidad 83, 1013–1024.

Mayorga, C.M., Cervantes, L.P., 2001. Life cycle and description of a new species of Amnestus Dallas (Hemiptera-Heteroptera: Cydnidae) associated with the fruits of several

species of Ficus (Moraceae) in Mexico. Journal of the New York Entomological Society 109, 392–402.

Mayorga, C.M., Cervantes, L.P., 2005. Description of six new species of *Amnestus* Dallas (Hemiptera: Heteroptera: Cydnidae) from Mexico. Journal of the New York Entomological Society 113, 159–173.

Mayorga, C.M., Cervantes, L.P., 2014. The genus *Amnestus* Dallas (Hemiptera: Heteroptera: Cydnidae: Amnestinae) in Mexico, with the description of eleven new species from Chiapas. Zootaxa 3779, 401–432.

Peñalver, E., Delclòs, X., Soriano C., 2007. A new rich amber outcrop with palaeobiological inclusions in the Lower Cretaceous of Spain. Cretaceous Research 28, 791–802.

Pérez de la Fuente, R., Delclòs, X., Peñalver, E., Engel, M.S., 2012. A defensive behavior and plant-insect interaction in Early Cretaceous amber – The case of the immature lacewing *Hallucinochrysa diogenesi*. Arthropod Structure & Development 45, 133–139.

Pinto, I.D., Ornellas, L.P. 1974. New Cretaceous Hemiptera (Insects) from Codo Formation – Northern Brazil. Anais 28th Congresso Sociedade Brasileira de Geologia, Porto Alegre 3, 289–304.

Pluot-Sigwalt, D., Lis, J.A., 2008. Morphology of the spermatheca in the Cydnidae (Hemiptera: Heteroptera): bearing of its diversity on classification and phylogeny. European Journal of Entomology 105, 279–312.

Popov, Y.A., 1986. Peloridiina (= Coleorrhyncha) and Cimicina (= Heteroptera). In: Rasnitsyn, A.P. (Ed.) Nasekomye v rannemelovykh ekosistemakh zapadnoy Mongolii. The Joint Soviet-Mongolian Palaeontological Expedition 28, 50–83.

Popov, Y.A., 1990. Bugs, Cimicina. In: Pozdne-Mezozoyskie Nasekomye Vostochnogo Zabaykal'ya. Akademiya Nauk SSSR. Rasnitsyn, A.P. (Ed.) Trudy Paleontologicheskogo Instituta 239, 20–39.

Popov, Y.A., Pinto, I.D., 2000. On some Mesozoic burrower bugs (Heteroptera: Cydnidae). Paleontological Journal 34 (Suppl. 3), 298–302.

Ross, A.J., 2018. *Burmese (Myanmar) amber taxa, on-line checklist v.2017.4*. 88pp. http://www.nms.ac.uk/explore/stories/natural-world/burmese-amber/

Schaefer, C.W., 1988. The food plants of some "primitive" Pentatomoidea (Hemiptera: Heteroptera). Phytophaga 2, 19–45.

Schmidt, A.R., Perrichot, V., Svojtka, M., Anderson, K.B., Belete, K.H., Bussert, R., Dörfelt, H., Jancke, S., Mohr, B., Mohrmann, E., Nascimbene, P.C., Nel, A., Nel, P., Ragazzi, E., Roghi, G., Saupe, E.E., Schmidt, K., Schneider, H., Selden, P.A., Vávra, N. 2010. Cretaceous African life captured in amber. Proceedings of the National Academy of Sciences of the United States of America 107, 7329–7334.

Schwertner, C.F., Nardi, C., 2015. Chapter 21. Burrower Bugs (Cydnidae). In: Panizzi, A.R., Grazia, J. (Eds.) True Bugs (Heteroptera) of the Neotropics. Dordrecht-Heidelberg-New York-London: Springer Netherland. XXII + 901.

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J.Y.M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163.

Thomas, D.B., 1988. Fossil Cydnidae (Heteroptera) From the Oligo-Miocene Amber of Chiapas, Mexico. Journal of the New York Entomological Society 96, 26–29.

Thomas, D.B., 1994. Fossil Cydnidae (Heteroptera) in the Dominican Amber. Journal of the New York Entomological Society 102, 303–309.

Vršanský, P., Lis, J.A., Schlögl, J., Guldan, M., Mlynský, T., Barna, T., Štys, P., 2015. Partially disarticulated new Miocene burrower bug (Hemiptera: Heteroptera: Cydnidae) from Cerová (Slovakia) documents occasional preservation of terrestrial arthropods in deep-marine sediments. European Journal of Entomology 112, 844–854.

Weitschat, W., Wichard, W., 2002. Atlas of Plants and Animals in Baltic Amber. Verlag Dr. Friedrich Pfeil, München. 256 pp.

Yao,Y., Cai, W., Ren, D., 2007. The first fossil Cydnidae (Hemiptera: Pentatomoidea) from the Late Mesozoic of China. Zootaxa 1388, 59–68.

Yao, Y., Ren, D., Shih, C., Zhang, W., 2010. Chapter 15. Heteroptera – smelly defence or piercing offense. In: Ren, D., Shih, C., Gao, T., Yao, Y., Zhao, Y. (Eds.) Silent Stories. Insect fossil treasures from dinosaur era of the northeastern China. Science Press, Beijing. pp. 139–157.

FIGURE CAPTIONS

Fig. 1. Holotype female of *Chilamnestocoris mixtus* gen. et sp. nov. in Burmese amber. A. Dorsal view of entire specimen. Scale bar: 1 mm. B. Reconstruction of specimen. Scale bar = 1 mm. C. Head and pronotum. Scale bar: 1 mm. D. Scutellum, clavus and claval commissure (c – clavus, cc – claval commissure, s – scutellum). Scale bar: 0.1 mm.

Fig. 2. Holotype female of *Chilamnestocoris mixtus* gen. et sp. nov. in Burmese amber. A. Dorsal view of entire head. B. Head dorsal view showing the first three antennal segments and the paraclypeal margin (s – second antennal segment, t – setigerous punctures tubercles). C. Tibia and tarsus of the posterior leg (ps – pretarsal structure). D. Pretarsal structure (cl – claw, pv – pulvillus). Scale bars: 0.1 mm.

Fig. 3. Plant syninclusions. A–D. Branched hairs. E. Stellate hairs. F. Star-shaped structure. Scale bars: 0.1 mm.