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ORIGINAL PAPER

The revision of fossil big-eyed bugs suggests a peculiar evolutionary history of a peculiar true bug family (Heteroptera: Lygaeoidea: Geocoridae)

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Abstract

The fossil record of the lygaeoid true bug family, Geocoridae so far consisted of a compression fossil from the Florissant Formation, *Geocoris infernorum*, and a mould fossil from the Izarra Formation, *G. monserrati*. Here, we report the third taxon, *Protogeocoris arcanus* gen. et sp. nov. from Cenomanian Burmese amber along with revision of the two previously mentioned species. The study of the specimens resulted in erecting a new genus, *Eocenogeocoris* gen. nov. to accommodate *G. infernorum* [= Eocenogeocoris infernorum (Sudder, 1890) comb. nov.], because of its unique combination of characters compared to extant geocorine true bugs. Furthermore, the interpretation of the novel morphological data acquired from the study of the fossil geocorids in the context of the knowledge on extant representatives of the family suggests that characteristic groups of the family may have been evolved until the mid-Cretaceous, whilst the species-level diversity of the nominotypical genus, *Geocoris* Fallén, 1814, and closely allied genera is possibly resulted by quick radiation event after a climatic changes at the Eocene-Oligocene boundary.

Keywords Evolution · Phylogeny · Morphology · Big-eyed bugs · Heteroptera · Geocoridae

Introduction

The family Geocoridae (Heteroptera: Pentatomomopha: Lygaeoidea), or commonly known as big-eyed bugs, is a peculiar lygaeoid true bug family in terms both morphological and ecological aspects. Representatives of the family display a series of highly specialised exoskeletal morphological features that are unique among lygaeoid true bugs, e.g. enlarged, reniform, often stylate eyes and medially curved sutures of abdominal tergites 4/6 and 5/6 (Henry, 1997). Furthermore, omnivorous feeding with a preference on predaceous behaviour is also unusual within the superfamily Lygaeoidea (lygaeoids are mostly seed and sap feeding except the hematophagous tribe Cleradini), which has consequently made some of the species promising candidates for biocontrol research (Sweet 2000; Kóbor 2020). However, taxonomy, phylogenetic relationships between and within taxon groups, and evolution of the representatives of the family are not well understood and virtually unstudied.

Controversially, these deficiencies are resulted by the peculiar appearance of these insects. Diagnoses of taxa were mostly based on colouration patterns and easy-to-observe exoskeletal characters, e.g. arrangement of head and eyes or shape of pronotum. This resulted in taxonomic confusions and misconceptions, especially in the nominotypical genus, *Geocoris* Fallén, 1814 which is considered as non-monophyletic in its current sense as suggested by more recent revisionary works (Readio and Sweet, 1982; Malipatil, 1994).

The examination of fossils provides useful information regarding the phylogenies and evolution of the studied groups and the interpretation of the results in context of recent taxa (e.g. including fossil taxa in phylogenetic reconstructions of extant groups) is momentous in solving systematic problems. As for geocorid true bugs, such data is relatively scarce. In

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total two fossil representatives of the family are known so far: *Geocoris infernorum* Scudder, 1890 from the Eocene (Florissant Formation, approximately 34 Ma.); and *Geocoris monserrati* Ortuño and Arillo, 1997 from the Oligocene (Izarra Formation, approximately 33.9 to 23.03 Ma.). Furthermore, the taxonomic placement of *G. infernorum* is precarious as stated by the author himself in the original description (Scudder 1890).

In this study, we present the description of the oldest known taxon belonging to this family from mid-Cretaceous Burmese amber. Furthermore, we review and revise the knowledge on the previously described fossil representatives of big-eyed bugs, discuss their placement within the family based on the morphological data available on recent taxa and form hypotheses on their evolutionary significance.

Materials and methods

The amber piece containing the studied fossil originated from Noije Bum, near Tanai Village Hukawng Valley, Kachin State, northern Myanmar (26–21°33.41′N, 96–43°11.88′E) (Grimaldi et al. 2002: fig. 1, Cruickshank and Ko 2003: fig. 1; Bai et al. 2016). The studied piece of amber was purchased by and deposited in the collection of Paleoentomological Collection, Instituto de la Patagonia, Universidad de Magallanes in good faith for educational and research purposes and the authors of present study have no knowledge on unethical origin.

Observations, photomicrographs, and measurement for *Protogeocoris arcanus* gen. et sp. nov. were done with the use of Japan Optical Co. XLT-2310 stereoscopic microscope with Ricoh WG-50 digital camera adapted. Incident and transmitted lighting were used, mostly simultaneously.

Morphological terminologies were adapted from Tsai et al. (2011), Malipatil and Blackett (2013), and Kóbor (2019).

Instutional abbreviations: MCNA, Museo de Ciencias Naturales de Álava, Vitória, Spain; MCZC, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; PCIP, Paleoentomological Collection, Instituto de la Patagonia, Universidad de Magallanes, Punta Arenas, Chile.

Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Heteroptera Latreille, 1810
Infraorder Pentatomomorpha Leston, Pendergrast and Southwood, 1954
Superfamily Lygaeoidea Schilling, 1829
Family Geocoridae Baerensprung, 1860
Subfamily Geocorinae Baerensprung, 1860

A key to fossil Geocorinae

1. Eyes projected. Pronotum with a narrow, but distinct collar. Corium with R-M branching in apical third. … *Protogeocoris arcanus* gen. et sp. nov.
- Eyes not projected. Pronotum without distinct collar. R-M of corium appear to be fused at entire length. … 2.
2. Head pentagonal, eyes touching anterior edges of pronotum. Pronotum trapeziform. … *Geocoris monserrati* Ortuño and Arillo, 1997
- Head lunular, eyes encompassing anterior edges of pronotum. Pronotum conspicuously widened. … *Eocenogeocoris infernorum* (Scudder, 1890) comb. nov.

Genus *Protogeocoris* nov.
(Figures 1-3)

Type species: *Protogeocoris arcanus* sp. nov.; by present designation and monotypy; gender: masculine.
Etymology: Generic name is derived from the name of genus *Geocoris* Fallén, 1814 (nominotypical genus of family Geocoridae) adding the prefix "proto-" (Latin, meaning: "first of its kind") which refers to the fact that this genus is the oldest known representative of the geocorid true bugs.
Differential diagnosis: Pronotum bilobate with narrow, but distinct collar and posterior margin concave (bilobate pronotum and distinct prothoracic collar can be observed in some representatives of Pamphantinae, but posterior margin is never concave); R-M of hemelytron basally fused, branching at 2/3 of length (basally fused, branching R-M can be observed in e.g. Engistus Fieber, 1864, *Umbrageocoris* Kóbor, 2019, but in these taxa pronotum always unilobed with straight or convex posterior margin); sutures between abdominal tergites 4/5-5/6 slightly and evenly curved posteriad at entire length (sutures of abdominal tergites 4/5-5/6 curved moderately to strongly medially in other geocorine genera; see Fig. 6a-b).

Description

Head pentagonal with vertex broad; eyes large, reniform, moderately stylate. Ocelli present, situated at middle of vertex, near base of eye stalks. Clypeus slightly pointed, appearing to exceed the mandibular plates. Antenniferous tubercles developed, but not visible is dorsal view. Antennomere I shortest, granuliform; antennomere II longest, cylindrical; antennomeres III and IV subequal in length; antennomere III cylindrical, antennomere IV fusiform. Labial trough non-observable. Labiomere I shortest, labiomeres II-IV subequal in length; apex of labium reaching mesocoxae.
Thorax: Pronotum bilobate, trapeziform with narrow, but distinct collar; lateral margins moderately carinate and slightly constricted medially; posterior margin concave; pronotal callosities furrow-like, separated. Scutellum subequilateral,

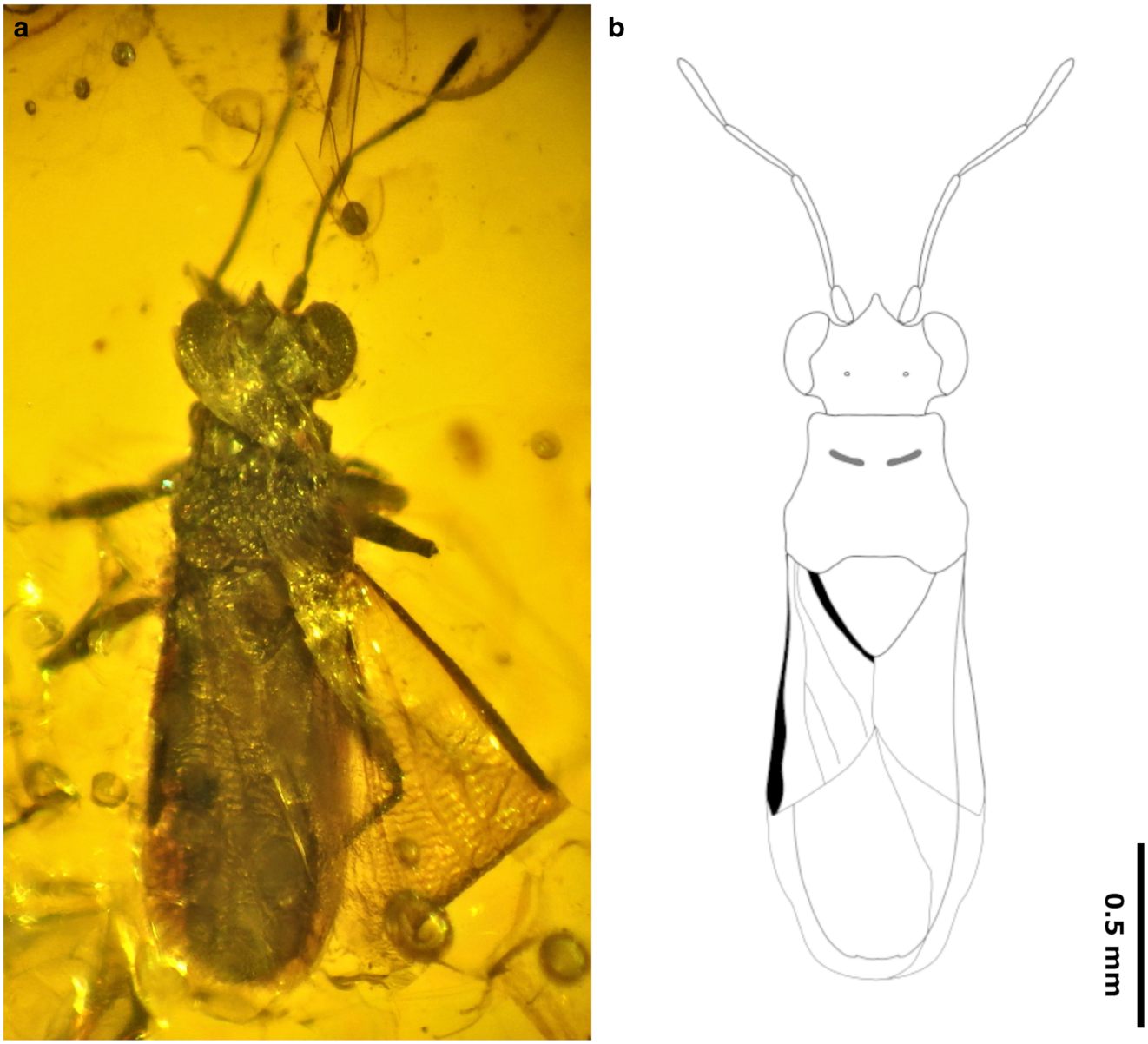


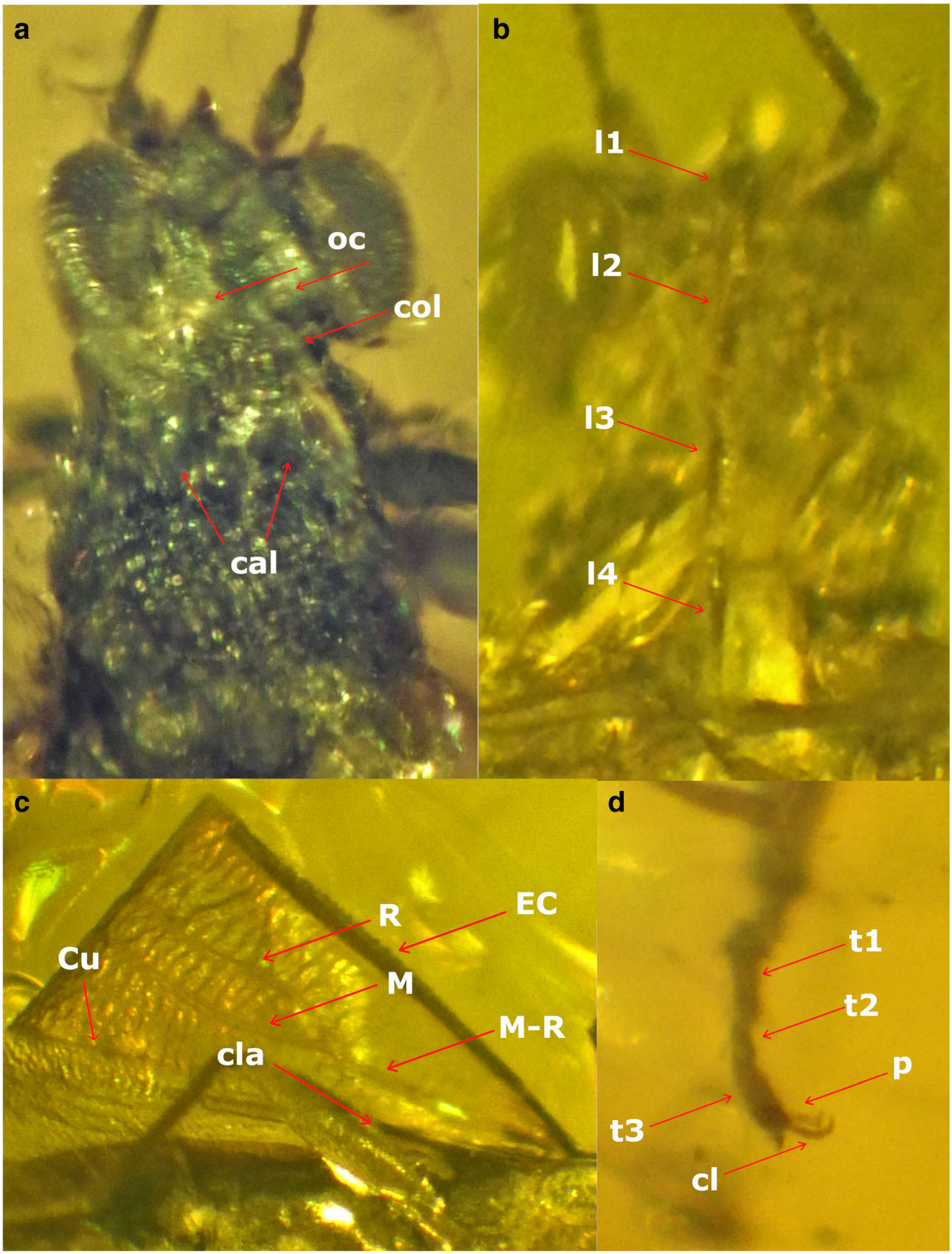
Fig. 1. *Protogeocoris arcanus* gen. et sp. nov.: **a** dorsal habitus; **b** reconstruction (scale bar = 0.50 mm for both images).

triangular with lateral margins slightly curved. Hemelytron appears to be membranous with clavus and exocorium more sclerotized than the rest of the hemelytron. Margins of clavus subparallel; claval commissure short, but distinct. Integument of corium appears to be wrinkled with simplified venation; Cu running near claval furrow; R-M basally fused, branching at approximately 2/3 of length; exocorium widening apically. Membrane with simplified, slightly visible venation lacking closed cells. Peritreme of metathoracic scent efferent apparatus bulbous without dorsal supportive process; orifice appears to be rounded; evaporatorium fine, matte, covering most of the metapleurite. Femora incrassate, fusiform; tibiae subcylindrical, slightly widened at apex. Tarsomere I longest, tarsomere II and III subequal in length; tarsomeres I and II cylindrical, tarsomere III fusiform. Claws simple, thin, evenly curved with thin parempodia-like appendages.

Abomen: Abdominal dorsum mostly obscured by wings. Sutures between abdominal sternites 4/5-5/6 appear to be slightly, evenly curved posteriad. Outer genital characters, e.g. posterior opening of pygophore, parameres in situ, not observable.

Protogeocoris arcanus sp. nov.
(Figures 1, 2 and 3)

Material: Holotype, PCIP: curatorial number: type n° 0003.
Locality and horizon: Noije Bum, near Tanai Village Hukawng Valley, Kachin State, northern Myanmar; lowermost Cenomanian, mid-Cretaceous.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◀ **Fig. 2.** *Protogeocoris arcanus* gen. et sp. nov.: **a** head and pronotum in dorsal view (image not to scale; lettering: *cal* pronotal callosities, *col* prothoracic collar, *oc* ocelli); **b** labiomeres (image not to scale; lettering: l1-4 – labimeres I-IV); **c** hemelytron (image not to scale; lettering: *cla* clavus, *Cu* cubitus, *EC* exocorium, *M* Media, *R-M* fused Media and Radius, *R* radius); **d** tarsus and pretarsal structures (image not to scale; *cl* tarsal claw, *p* parempodia-like pretarsal appendage, t1-3 – tarsomeres I-III).

Etymology: Species epithet "arcanus" (Latin, meaning: mysterious) refers to the evolutionary importance of the species in terms of the family Geocoridae.

Differential diagnosis: Small insect (> 2mm) with characteristic pentagonal head, and slightly stylate reniform eyes. Hemelytra with clavus and exocorium more sclerotized and darker than rest of the hemelytron. Abdominal dorsum with a pair of dark longitudinal bands sublaterally. Other characteristics as in generic diagnosis.

Description: Almost complete male individual in amber piece, left hind leg missing; characters obscured by syninclusions and air bubbles denoted in description respectively.

Colouration: Vertex, eye stalks and thoracic dorsum with irregular darker markings, partly obscured by air bubbles. Antennomere I with irregular brownish spots and brownish annulation apically, antennomeres II-III with darker annulation apically, antennomere IV entirely darker (Fig. 1a). Hemelytra with clavus and exocorium entirely darker than rest of the hemelytron. Femora with irregular brownish spots. Abdominal dorsum with a pair of longitudinal, subparallel darker bands sublaterally. Abdominal sternites darker dorsolaterally.

Structure: General habitus moderately elongate, slightly flattened dorsoventrally.

Head: Eye stalks slightly projected, posterior edge of eyes not encompassing, nor touching anterior edges pronotum; ocular sulcus unobservable. Ratio of antennomeres: 1: 5.5: 5.0: 4.0. Ratio of labiomeres: 1: 6.5: 5.25: 0.30.

Thorax: Integument of thoracic dorsum densely punctate except at pronotal callosities. Anterior edges of pronotum angulate, slightly rounded; humeral angles acute anteriorly and rounded posteriorly. Median trifurcate carina not observable, obscured by air bubbles. Thoracic pleurites and sternites densely punctate. Femora appear to be maculate.

Measurements (in mm): total length of body**:** 1.85; length of head: 0.27; antennomeres I-IV: 0.02-0.11-0.10-0.8; labiomeres: 0.08-0.52-0.42-0.24; length of pronotum: 0.48; width of pronotum: 0.57; length of scutellum: 0.22; width of scutellum: 0.40; length of hemelytron: 1.10.

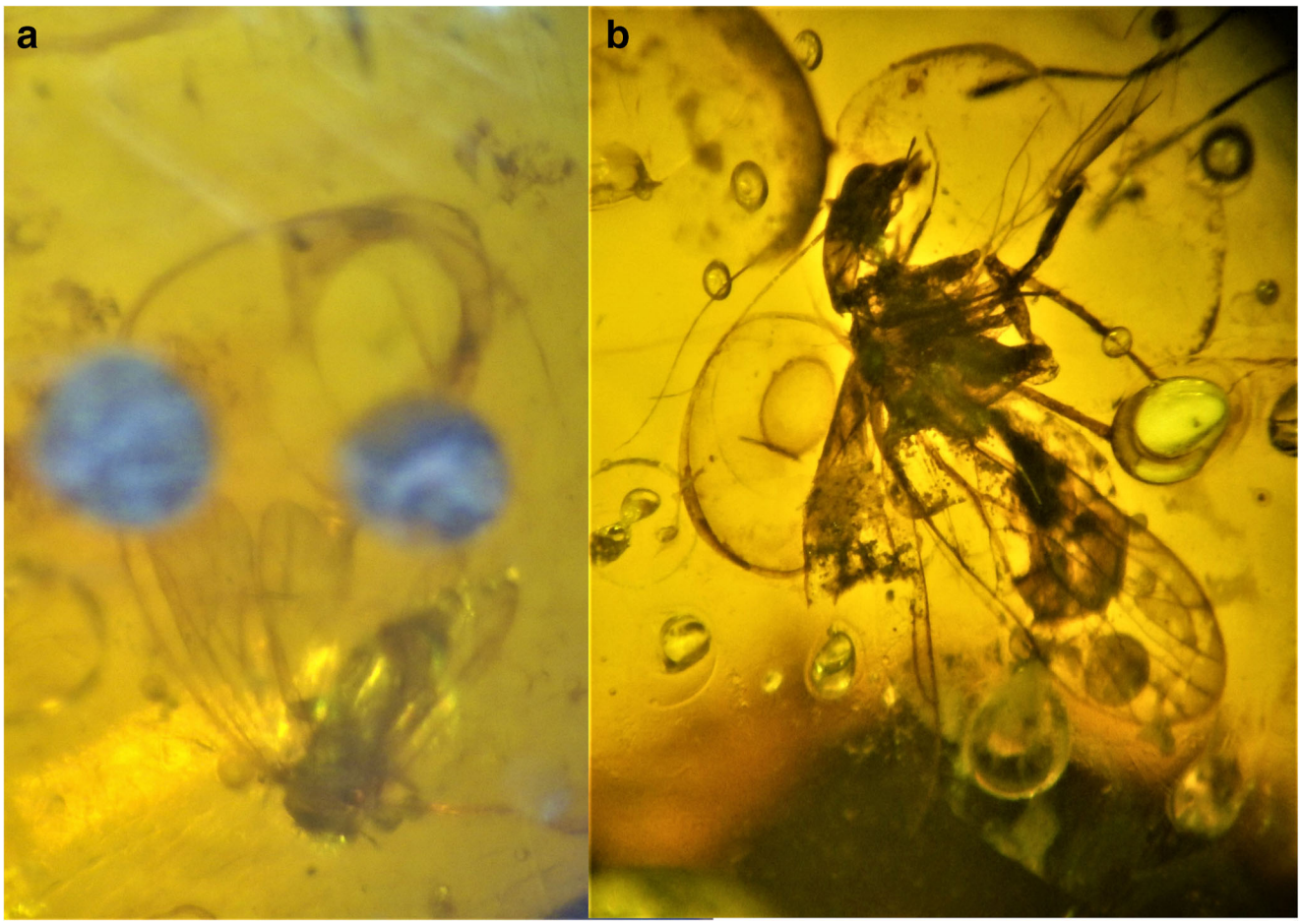


Fig. 3. Syninclusion of the holotype of *P. arcanus*: **a** Psocoptera gen. sp.; **b** Nanoraphidiini gen.sp. (images not to scale).

Remarks on palaeohabitat: The amber piece containing multiple syninclusions, mostly soil and plant debris, remains of other insects and a piece of skin suspected to be originating from an avian leg. The most notable syninclusions are three complete insects: two barklice (Psocoptera gen. sp.) and a snakefly (Nanoraphidiini gen.sp.). Considering the results of Christiansen and Nascimbene (2006), Lis et al. (2018, 2020) and Jiang et al. (2019) we suggest that the palaeohabitat of the insect was part of an abundant geophilous-arboreal environment in an amber forest. The preference of geophilous-arboreal habitats is similar to those of the extant representatives of the family Geocoridae (Slater 1977).

Genus *Eocenogeocoris* Kóbor nov.
(Figure 4)

Type species: *Geocoris infernorum* Scudder, 1890 by present designation; gender masculine
Etymology: Generic name is derived from the name of genus *Geocoris* Fallén, 1814, adding the prefix "eoceno-" referring to that the genus is known exclusively from the Eocene epoch.
Differential diagnosis: *Eocenogeocoris* Kóbor gen. nov. possesses a combination of characters as in the representatives of subgenus *Piocoris* Stål, 1872 and some *Geocoris* species e.g. *G. flaviceps* (Burmeister, 1834) or *G. willey* Kirkaldy, 1905: habitus ovoid; head lunular, compound eyes slightly stylate with posterior edge of eyes encompassing the anterior edges of pronotum; pronotum widened; ccutellum elongate triangular. However, margins of clavus subparallel; claval commissure short, but complete in *Eocenogeocoris* (margins of clavus converging in Geocoris sensu lato and allies; synapomorphy with Geocorinae incertae sedis, see Table 1). Fore femora strongly incrassate (autapomorphy; fore femora is moderately incrassate in other Geocorinae). Sutures between abdominal tergites 4/5-5/6 appear to be at most moderately curved posteriad medially (sutures between abdominal tergites 4/5-5/6 curved strongly in Geocoris sensu lato as in Fig. 6b; suspected synapomorphy with genus *Germalus* and allies).

Eocenogeocoris infernorum (Scudder, 1890) comb. nov.
(Fig. 4)

Material examined: Holotype, MCZC: PALE-4411; paratypes, MCZC: PALE-4412, PALE-4413, PALE-4414, PALE-4415, PALE-4416.
Locality and horizon: Florissant Fossil Beds National Monument, Colorado, USA; uppermost Priabonian, late Eocene (approximately 34 Ma).

Redescription

Head lunular with vertex strongly widened; posterior edge of eyes encompassing anterior edges of pronotum. Eyes appear to

Table 1. Diagnostic characters of the suspected infrasubfamilial groups in Geocorinae (asterisk indicates characters observed by senior author).

Characters	"Geocorine lineage"	"Germaline lineage"	Geocorinae incertae sedis	*Protogeocoris* gen. nov.
Head and eyes (adapted from Montandon, 1913)	eye stalks short, never projected; ocular sulcus at least partly reduced	eye stalks moderate, sometimes projected; ocular sulcus developed, conspicuous	eye stalks moderate, not projected; ocular sulcus shallow or partly reduced	eye stalks short, projected; ocular sulcus not observable
Scutellum (Montandon, 1913)	elongate	subequilateral	subequilateral	subequilateral
Clavus of hemelytron (Montandon, 1913)	margins converging towards apex, claval commissure reduced	margins subparallel, claval commissure developed, length of claval commissure to length of scutellum: ≥ 1: 2.0	margins subparallel, claval commissure developed, length of claval commissure to length of scutellum: ≤ 1: 2.0	margins subparallel, claval commissure developed, length of claval commissure to length of scutellum: ≤ 1: 2.0
Metathoracic wing (Slater and Hurlbutt, 1957)	hamus and intervannals reduced	hamus present, intervannals basally fused	hamus present, intervannal basally fused	not observable
Metathoracic scent efferent apparatus*	peritreme bulbous, evaporatorium reduced to surroundings of peritreme	peritreme auricular, with dorsal supportive process; evaporatorium covering entirely metapleurite and posterior half of mesopleurite	peritreme auricular without dorsal supportive process, evaporatorium covering at least half of the metapleurite	peritreme appears to be bulbous, evaporatorium covering most of the metapleurite

be reniform, slightly stylate; ocelli present, situated near base of eye stalks. Antennomere I shortest, granuliform; antennomere II longest, cylindrical; antennomeres III and IV subequal in length; antennomere III cylindrical, antennomere IV fusiform.
Thorax: Pronotum conspicuously widened with anterior edges strongly rounded. Scutellum appears to be elongate triangular. Clavus, surroundings of venation and exocorium appear to be more sclerotized than the rest of the hemelytron. Clavus with margins subparallel; claval commissure complete, developed. Femora fusiform, fore femora appear to be strongly incrassated.
Abdomen. Abdominal tergites with sutures appear to be straight.
Remarks: The original description (Scudder, 1890) denotes that the identity and generic assignment of the species is problematic. This uncertainty stems from the nature of compression fossil (Azar et al., 2011; Chen et al., 2016) which can be distorted and mostly lacking detail. However, in case of *G. infernorum* there are characteristics to be observed based on which a diagnosis can be formulated. The convex general habitus, conspicuously lunular head and widened pronotum resembles to representatives of subgenus *Piocoris* Stål, 1872 and *Geocoris* s. str. species e.g. *G. flaviceps* (Burmeister, 1834) or *G. willey* Kirkaldy, 1905. However, these taxa are characterised by moderately incrassate fore femora, clavus with margins converging and claval commissure reduced, and sutures of abdominal tergites 4/5-5/6 strongly curved posteriad. In *G. infernorum* the fore femora are strongly incrassate, margins of clavus subparallel with a complete claval commissure and sutures of abdominal tergites 4/5-5/6 appear to be at most moderately curved. Similar arrangement of clavus and abdominal tergites can be found in *Germalus* and allies. Summarising, this species displays an amalgamation of characters present in various geocorine genera combined with the unusually strongly incrassate fore femora which is to be considered as autapomorphy in terms of the subfamily, thus its placement in *Geocoris* s. str. is not justified. Considering the above it is to be concluded that the species represents an extinct lineage of geocorine true bugs which lived during the Eocene epoch thus, the genus *Eocenogeocoris* Kóbor gen. nov. is suggested to be erected to accommodate the species.

Genus *Geocoris* Fallén, 1814

Type species: *Cimex grylloides* Linnaeus, 1761 (= *Geocoris grylloides grylloides*), fixed by Oshanin, 1912.

Subgenus *Geocoris* Fallén, 1814
Type species: As for genus.

Geocoris (*Geocoris*) *monserrati* Ortuño and Arillo, 1997
(Fig. 5)

Material examined: Holotype, MCNA: IZA-017, MCNA-5361.

Locality and horizon: Upper clayey member of the Izarra Formation, central part of the Basque-Cantabrian Basin, Spain; Oligocene epoch (33.9 – 23 Ma).

Redescription

Head pentagonal, eyes reniform, slightly stylate; ocular sulcus appears to be complete, but slightly defined; posterior edge of eyes touching anterior edges of pronotum. Ocelli situated near ocular sulcus, at base of vertex. Clypeus rounded, appearing to be exceeding the mandibular plates; margins of clypeus converging basally. Vertex with median longitudinal furrow extending from the middle of vertex to apex of clypeus. Antenniferous tubercle appears to be well-developed. Antennae tetramerous with antennomere I granuliform, shortest; antennomere II cylindrical, longest (but incomplete); antennomeres III and IV subequal; antennomere III cylindrical, antennomere IV fusiform. Labial furrow appears to be closed; labiomere I present but appears to be incomplete.
Thorax: Pronotum trapeziform, integument appears to be densely punctate except callosities, humeral angles and posterior margin. Pronotal callosities separated by punctures. Scutellum elongate triangular, integument punctate except well-developed median trifurcate carina. Clavus of hemelytron with margins converging towards apex; punctuation visible basally. Corium suspectedly macropterous or submacropterous (claval furrow present, clavus separable) with puctures along claval furrow and Cu. Thoracic pleurites desenly punctate except supracoxal lobes and surroundings of peritreme. Peritreme bulbous; orifice appears to be rounded. Femora of legs fusiform, fore femora slightly incrassate.
Abdomen: Characters of abdominal dorsum not observable. Ovipositor bisecting abdominal sternite VII.
Remarks: Ortuño and Arillo (1997) assigned the taxon to genus *Geocoris* and suggested a close relationship to *G. ater* (Fabricius, 1787), a species of subgenus *Geocoris*. According to our findings the genus assignment and the suspected relationship is established, thus *G. monserrati* is the first known representative of "modern geocorids", i.e. *Geocoris* sensu lato and allied mono- and oligotypic genera.

Discussion

Superfamilial placement of *Protogeocoris* gen. nov.
(Fig. 5)

The studied fossil possesses four-segmented piercing-sucking mouthpart i.e. rostrum and heteronomous forewing i.e. hemelytron consisting of clavus + corium and membrane, such characteristics are placing this insect in suborder Heteroptera (Schuh and Weirauch, 2020). The general appearance of the

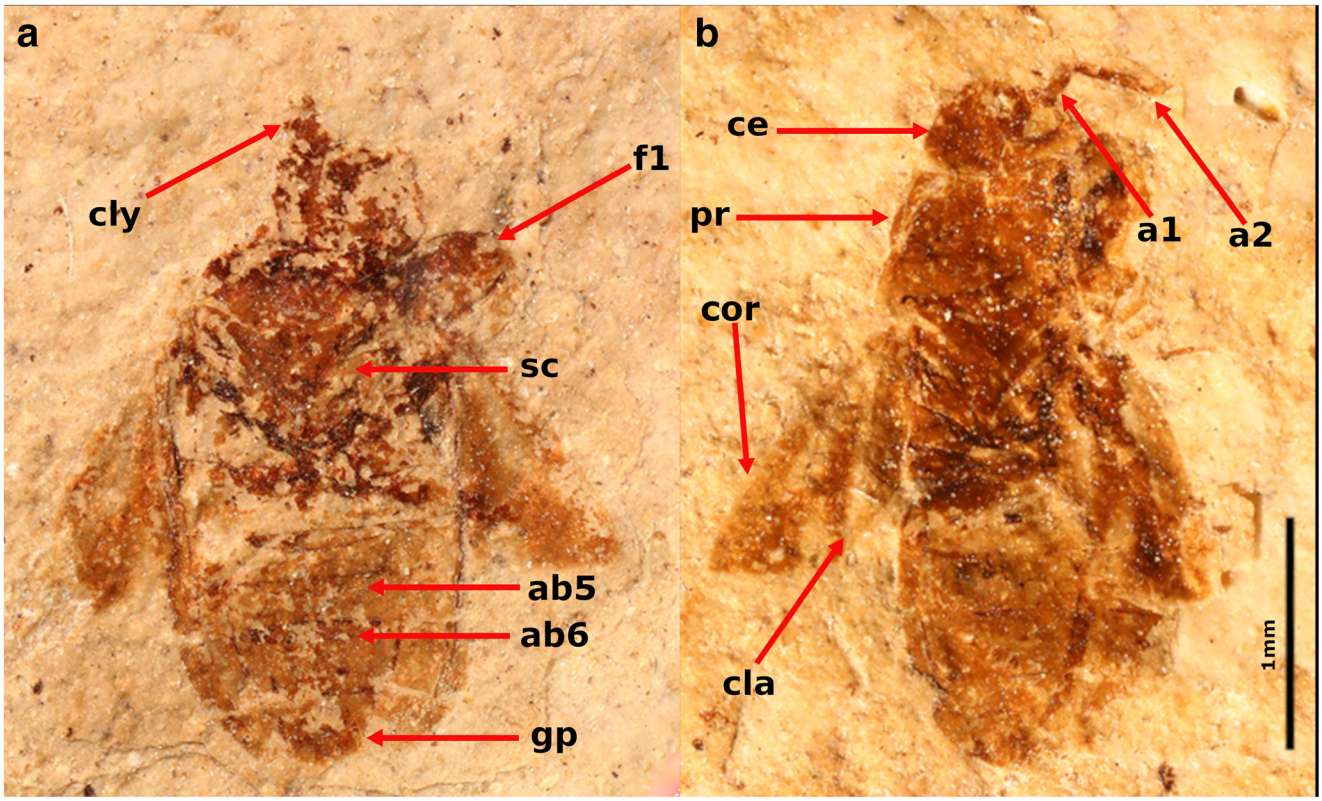


Fig. 4. *Eocenogeocoris infernorum* (Scudder, 1890): **a** holotype; **b** paratype (scale bar = 1 mm for both images; lettering: a1-2: antennomeres I-II, abd5-6 – abdominal tergites V-VI; *ce* compound eye, *cla* clavus of hemelytron, *cly* clypeus, *cor* corium of hemelytron; *fl* fore femora, *gp* genital plate; *pr* pronotum, *sc* scutellum).

insect, especially the large and stylate compound eyes resemble to the representatives of Yuripopovinidae Azar et al., 2011 e. g. *Caulisoculus* Zhang and Chen, 2020 or *Pseudocaulisoculus* Kóbor and Roca-Cusachs, 2021. However, the venation of hind consists of three veins from which M-R are basally fused and venation of membrane is simplified, i.e. lacking closed cells. Contrastingly, hemelytron of the representatives of Yuripopovinidae possess three separate, longitudinal veins forming two closed cells, venation of membrane with closed cells. Furthermore, eyes unequivocally appear to be reniform, not rounded as in Yuripopovinidae. The presence of ocelli, incrassate fore femora and simplified venation of hemelytron with membrane lacking closed cells are shared synapomorphies of superfamily Lygaeoidea (Henry 1997). The studied fossil possesses all three of these characteristics, thus we ascribe this taxon to superfamily Lygaeoidea.

Placement of *Protogeocoris* gen. nov. within Lygaeoidea

This lygaeoid bug has pentagonal head with wide vertex and large, reniform, moderately stylate compound eyes which are characteristic to the family Geocoridae. Besides the arrangement of head and eyes, this peculiar true bug family is characterised by the dorsally situated abdominal spiracles II-IV and medially curved sutures between abdominal tergites 4/5-5/6 (Henry 1997) Abdominal sutures 4/5-5/6 appear to be slightly curved in *Protogeocoris* gen. nov. The degree of curvature of abdominal sutures considerably varies among geocorid taxa as demonstrated in Fig. 6a-b. Though abdominal spiracles are obscured in case of the specimen, supportive characters are to be observed which are displayed by various representatives of Geocoridae, e.g. placement of ocelli or trapeziform pronotum with furrow-like callosities (similar as in *Unicageocoris* Malipatil, 2013 and *Nannogermalus* Kóbor and Kondorosy, 2020).

The proportion of diameter of compound eyes to head length is similar as in subfamily Geocorinae Baerensprung, 1860. This similarity is supported by the arrangement of head which resembles to genus *Germalus* Stål, 1862 and allied genera. Furthermore, these geocorine taxa are characterised with subequilateral triangular scutellum and clavus with margins parallel and claval commissure present. Prothoracic collar as separate structure can be observed in genus *Epipolops* Herrich-Schaeffer, 1850 of subfamily Pamphantinae Barber and Bruner, 1933 (Rengifo-Correa et al. 2014). However, traces of such structure can be found in form of slightly elevated, impunctate region near the anterior margin of pronotum and prosternum in several species of subfamily Geocorinae

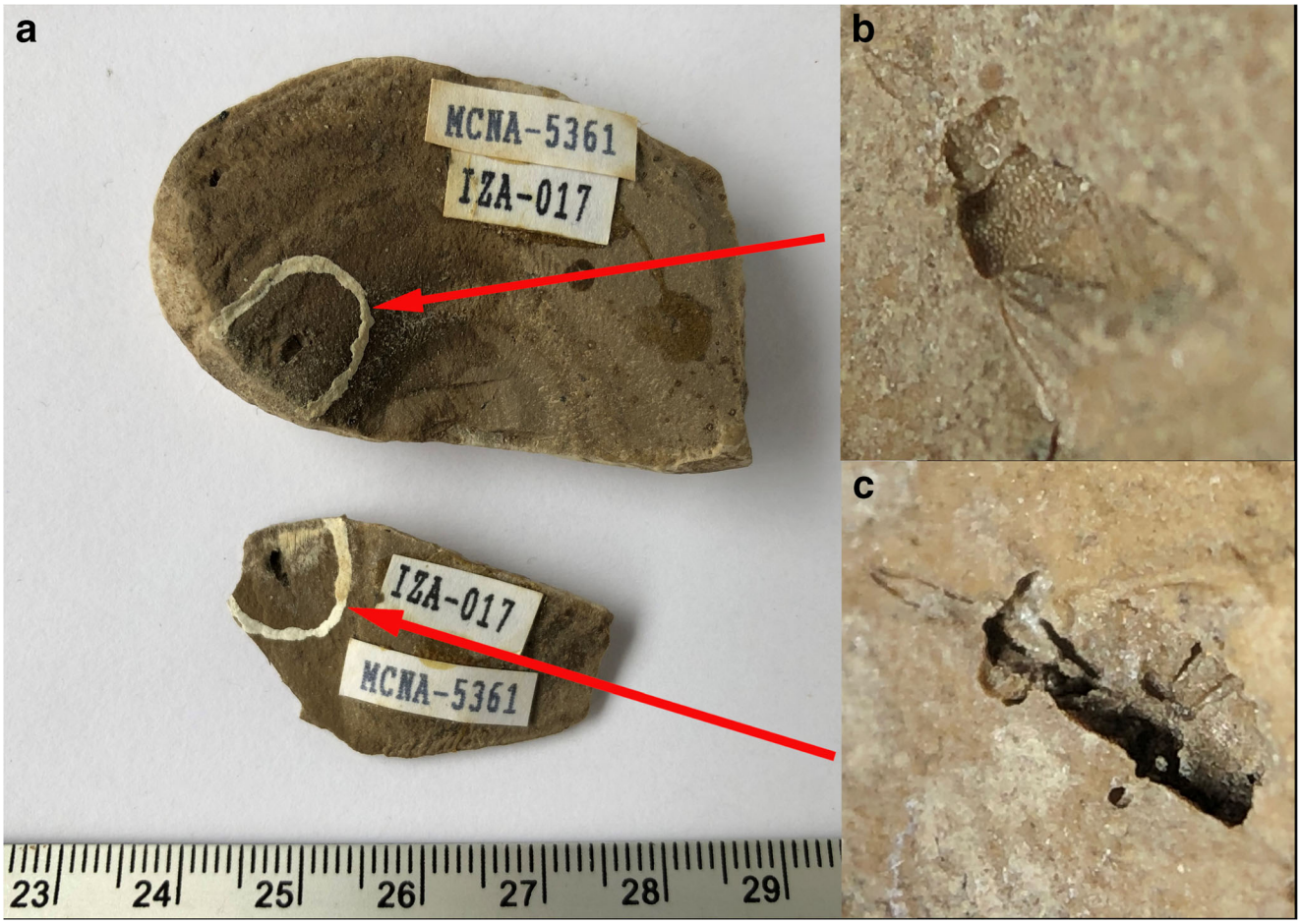


Fig. 5. *Geocoris* (*Geocoris*) *monserrati* Ortuño and Arillo, 1997 (holotype): **a** overview of fossil; **b** dorsal half; **c** ventral half (scale bar = 1 mm for images **b** and **c**).

(senior author's unpublished notes, Fig. 6c-d). Based on the above discussed evidence we suggest ascribing this new true bug taxon in subfamily Geocorinae.

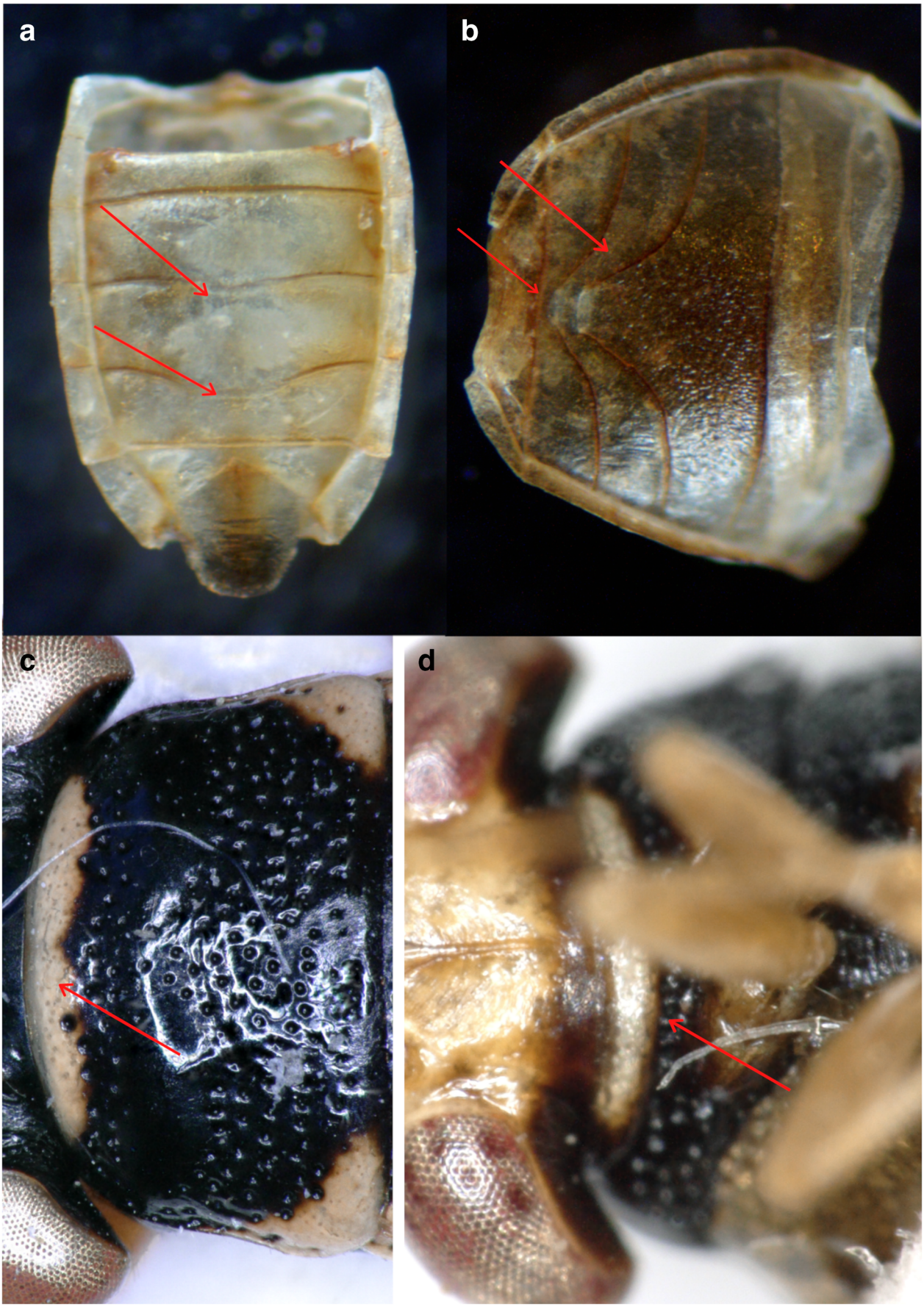
Relationship of *Protogeocoris* gen. nov. to other representatives of Geocorinae

The tribal classification of Geocorinae was proposed and later elaborated by Montandon (1907, 1913). Further improvement of the classification was later suggested by Parshley (1921); however, no revised classification was proposed subsequently. Though Montandon's concept gained no further acceptance by the community, the additional evidence provided by the study of Slater and Hurlbutt (1957) on the morphology of the metathoracic wing of Lygaeoidea, along with the senior author's unpublished findings suggests that two distinct major lineages are to be recognised within Geocorinae which are partly consonant with Montandon's tribes. However, there are genera which display transitions or unique states of characters, thus cannot be classified in these two groups e.g. *Apennocoris* Montandon, 1907; *Stylogeocoris* Montandon, 1913 or *Nannogermalus* Kóbor and Kondorosy, 2020. Based on the comparison of diagnostic characters of these groups (Table 1) and the unique character state of prothorax with distinct collar it is to be assumed that *Protogeocoris* represents a separate, extinct lineage within the subfamily. The basally fused and apically branching R-M of hemelytron can be observed in multiple geocorid genera e.g. *Engistus* Fieber, 1864 (Henestarinae) or *Umbrageocoris* Kóbor, 2019 (Geocorinae) and the exact systematic importance of the characteristics of the hemelytron is subject of further comparative study.

Evolutionary significance of fossil big-eyed bugs

According to Ross (2019, 2022), *Protogeocoris* is the first representative of the superfamily Lygaeoidea reported from mid-Creatceous Burmese amber and the oldest known taxon of family Geocoridae. Until now, only two extinct representatives of the family were known from compression and mould fossils: *Eocenogeocoris infernorum* (Scudder, 1890) from the Eocene (Florissant formation, approximately 34 Ma.); and *Geocoris monserrati* Ortuño and Arillo, 1997 from the Oligocene (Izarra formation, approximately 33.9 to 23.03 Ma.).

The original description of *E. infernorum* is cursory and the illustrations are lacking detail. It must be noted that


a
b
c
d

◀ **Fig. 6.** Morphological characteristics of extant representatives of subfamily Geocorinae discussed in present study (indicated by arrow): **a-b** sutures of abdominal tergites 4/5-5/6 in *Germalus victoriae* Bergroth, 1895 (**a**) and *Geocoris willeyi* Kirkaldy, 1905 (**b**); **c-d** remnants of prothoracic collar (col) in *Geocoris* sp. in dorsal (**c**) and lateral view (**d**) (images not to scale).

characterisation and diagnosis of compression fossils is problematic in most cases (Azar et al. 2011; Chen et al. 2016). The examination of the available photo documentation of the fossils suggest that the species clearly identifies as a representative of family Geocorinae and can be considered as a representative of an extinct of lineage displaying a combination of characteristics of various geocorine genera and possessing a suspected autapomorphy, strongly incrassate fore femora, thus *Eocenogeocoris* gen. nov. is erected to accommodate the species. *G. monserrati* is described and illustrated accurately and it is to be confirmed that the placement suggested by Ortuño and Arillo (1997), i.e. the species is closely related to the extant species, *Geocoris ater* (Fabricius, 1787) and its Mediterranean and Palaearctic relatives, is justified.

The fossil record of big-eyed bugs currently consists of three distinct taxa from three different geographic era: *Protogeocoris arcanus* from the mid-Cretaceous, *Eocenogeocoris infernorum* from the late Eocene and *Geocoris monserrati* from the Oligocene. The two oldest of them, *P. arcanus* and *E. infernorum*, represent extinct lineages whilst *G. monserrati* is unambiguously displaying characteristics of the "modern" representatives of the subfamily Geocorinae, more specifically the genus *Geocoris* sensu stricto. This suggests that the major synapomorphies characterising the family Geocoridae, e.g. the pentagonal head with variably stylate, reniform eyes have been evolved until the lowermost-Cenomanian age of the mid-Cretaceous, thus the origin of geocorid subfamilies and characteristic lineages can be dated back to this epoch. Other character states e.g. the reduction of claval commissure or the variability in the degree of curvature of the sutures of abdominal sutures 4/5-5/6 (Fig. 6a-b), have been developed more recently and the taxa displaying character states which are suspectedly derived, i.e. the "geocorine lineage" (*Geocoris* sensu lato and closely allied mono- and oligotypic genera) appear latest in the Oligocene. The majority of geocorid species are representing this lineage. The species-level delimitation of these taxa is often problematic because the species can be diagnosed by a set of minor characters, which often display intraspecific variability of various degree (senior author's unpublished findings). The Eocene-Oligocene boundary witnessed a cooling event, which resulted significant changes in the taxonomic composition, richness, and abundance distribution of insect groups (Smith et al. 2014). Taking the above into account it is to be assumed that the diversity of the "geocorine lineage" is resulted by a quick radiation event that can be dated back to the Oligocene epoch and the "uniform heterogeneity" can be attributed to the relatively young age (< 33.9 Ma) of these taxa. However, it must be noted that this hypothesis is based on indirect evidence and its proof requires further investigations. A promising method of proof is performing morphology-based phylogenetic reconstructions involving both extant and fossil taxa. Including fossil records in morphological phylogenies of extant taxa is considered to improve the accuracy of reconstructions and to test evolutionary hypotheses even if the data acquired from the study of fossils is incomplete or partly incorrect (Edgecombe 2010; Mongiardino Koch et al. 2021).

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Author contribution All authors contributed to the study conception and design. The specimens studied were examined by Péter Kóbor and Eudardo I. Faúndez. Photomicrographs were done by Eudardo I. Faúndez, line drawings were done by Marcos Roca-Cusachs. The first draft of the manuscript was written by Péter Kóbor and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest

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