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A second genus of Progonocimicidae (Hemiptera: Coleorrhyncha) from the Early Toarcian of Luxembourg

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Abstract

Liassoprogonocimex bascharagensis **gen. et sp. nov.** of Progonocimicidae (Coleorrhyncha: Progonocimicomorpha) are described. It is one of two genera from the Early Jurassic of Luxembourg, the other being *Indutionomarus* Szwedo, 2011. This new occurrence increases the morphological diversity of Coleorrhyncha during the Mesozoic and helps us to discuss the systematics of extinct Coleorrhyncha as well as their evolutionary history.

Keywords: Insecta, Jurassic, moss bugs, fossil record, Progonocimicomorpha

Introduction

Coleorrhyncha Myers & China, 1929 or moss bugs is a hemipteran lineage considered as a relict group, represented nowadays by only one family (*i.e.*, Peloridiidae Breddin, 1897) with only 37 species in 17 genera, distributed only in the sub-Antarctic rainforests of the southern Hemisphere (Burckhardt, 2009). Ye *et al.* (2019) has linked the biogeographical pattern of these moss bugs to the successive break ups of Gondwana throughout the Late Cretaceous.

Although extant Coleorrhyncha are not especially diverse, their fossil record indicates that their past biodiversity was much greater, with numerous occurrences during the Mesozoic (Wang *et al.*, 2009). The current classification of Coleorrhyncha comprised two infra-orders. Firstly, the extinct Progonocimicomorpha Popov, 1980 and its unique family the Progonocimicidae Handlirsch, 1906 ranging from Permian to Late Cretaceous with two recent occurrences from the mid-Cretaceous Kachin amber (Jiang *et al.*, 2019; You *et al.*, 2024). Secondly, the extant Peloridiomorpha Popov, 1980 that encompassed two extinct families: Hoploridiidae Popov & Shcherbakov, 1991 and Karabasiidae Popov, 1985; and the extant family Peloridiidae. Recently, Burckhardt *et al.* (2023) described the earliest family of Coleorrhyncha with Permoridiidae Burckhardt *et al.* 2022 from Early Permian, pushing back the origin of moss bugs and trying to define putative synapomorphies for Coleorrhyncha, leaving the new family unranked within Coleorrhyncha systematics. According to recent phylogenomic analyses, moss bugs may well predate the Permian; they may have appeared during the Early Carboniferous [as is the case with all major hemipteran lineages, approx. 350 million years ago (Johnson *et al.*, 2018)].

The Progonocimicidae are known from the Permian to mid-Cretaceous (Popov & Shcherbakov, 1991; Dong *et al.*, 2014; Jiang *et al.*, 2019; You *et al.*, 2024) with more than 20 genera distributed within two subfamilies: Progonocimicinae Handlirsch, 1906 and Cicadocorinae Becker-Migdisova, 1958. The first subfamily is known from the Permian to the Jurassic, whereas Cicadocorinae are Jurassic to Cretaceous. In particular, eight Cretaceous genera and 11 species are described (see Jiang *et al.*, 2019: fig. 7). Several specimens of Progonocimicidae have been reported among the rich Crato Formation but have never been formally described (Bechly & Szwedo, 2007). They represent the first records of Coleorrhyncha in the New World. The presence of this lineage in the New World is crucial to undercover the biogeographical history of moss bugs. However, the Jurassic seems to be a linchpin point in the evolutionary history of the Coleorrhyncha with the

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decline of their representatives in Europe, probably linked to climate changes during this period. Subsequently, depicting the diversity of Coleorrhyncha in the Jurassic is important to better understand their decline. To this end, we describe the progonocimicid new genus and species *Liassoprogonocimex bascharagensis* gen. and **sp. nov.** from the Toarcian of Luxembourg, the second genus and species in this area after *Indutionomarus treveriorum* Szwedo, 2011. This new occurrence helps to discuss the general taxonomy and evolutionary history of Coleorrhyncha.

Material and methods

The new fossil was collected by one of us (MH) in the carbonate nodules in Bascharage, Grand-Duché-du-Luxembourg (see map in Ansorge, 2003: Fig. 1). The carbonate nodules are intercalated in the bituminous shales of the Elegantulum subzone, Lower Serpentinum Zone (Thuy *et al*., 2025). This outcrop has already provided many insects (Nel, 1989; Nel & Henrotay, 1992, 1994; Nel *et al*., 1993; Henrotay *et al*., 1997; 1998; Nel *et al*., 2003, Fleck *et al*., 2003; Szwedo, 2011).

The specimen was photographed with a Canon EOS 70D camera equipped with a Novoflex Micro-Tube M26 achromatic lens and a Mitutoyo M Plan Apo 5×/0.14 microscope lens. The camera was mounted on a semi-automatic Cognises Rail macro Stack Shot controlled by Helicon Remote software. We also conducted UV-a light imaging of the specimen following the setup and protocol described in Boderau *et al*. (2024).

Photographs were digitally stacked using Helicon Focus 6.7 software and were exported in TIF format. We used a camera lucida mounted on an Olympus SZX9 stereomicroscope to perform the drawing lines. Final images and original drawing lines were enhanced using Pixelmator Pro 3.6.12 Archipelago software.

We follow the systematic framework of Szwedo (2018) for the Coleorrhyncha higher ranks classification, the taxonomic attribution within Progonocimidae follows Popov & Shcherbakov (1991), Dong *et al*. (2014), and the Palaeobiology Database (https://paleobiodb.org/#/; last access on January, 7th 2025). The forewing venation nomenclature follows the general pattern for Acercaria proposed by Nel *et al*. (2012) modifying the interpretations of Popov & Shcherbakov (1991). We adopted the cell nomenclature of Bourgoin *et al*. (2015).

Forewing venation abbreviations are as follow: (CA) costa anterior; (CP) costa posterior; (Pc) praecosta; (bScP) basal portion of the subcosta posterior; (ScP) subcosta posterior; (RA) radius anterior; (RP) radius posterior; (M) media; (CuA) cubitus anterior; (CuP) cubitus posterior; (PCu) postcubitus vein; (A_1) first anal vein. Each crossvein between two main veins is written in lower case.

Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Coleorrhyncha Myers & China, 1929
Infraorder Progonocimicomorpha Popov, 1980
Superfamily Progonocimicoidea Handlirsch, 1906
Family Progonocimicidae Handlirsch, 1906
Subfamily uncertain

Genus *Liassoprogonocimex* gen. nov.

Type species. *Liassoprogonocimex bascharagensis* **sp. nov.**; by monotypy.

Etymology. The generic name is a combination of 'Liassic', other name for Lower Jurassic and '*Progonocimex*', the type genus of the family. Gender: masculine.

Diagnosis. Tegmen with ScP + RA_1 diverging before end of clavus; distance between ScP+RA_1 and RA_2 nearly the same as distance between RA_2 and RP at their bases; RA_2 not continuous with R-stem; *rp-m* crossvein very short; alignment of basal part of CuA_2, m-cua, and basal part of $M_{1+}2$; PCu strongly diverging from CuP before its fusion with A_1; PCu_2+A_1 very short, ending into posterior margin of wing well basal to apex of clavus; presence of a *m-cua* crossvein between M_{3+4} and CuA_1.

***Liassoprogonocimex bascharagensis* sp. nov.**

(Fig. 1)

Material. Holotype MNHN.F.C02460 housed in the collection of Palaeontology Department in the Muséum national d'Histoire naturelle (Paris, France).

Etymology. The specific epithet is referring to the type locality from where the specimen originated.

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

Locality and horizon. Bascharage; Grand-Duché-du-Luxembourg (Henrotay *et al*., 1998: Fig. 1); lower Toarcian; Lower Jurassic.

Description. Tegmen *ca*. 2.04 mm long, rounded apically; apex of clavus reaching roughly half of total tegmen length; postclaval area slightly wider than preclaval area; CP+PC long reaching end of clavus; basal cell closed apically by a long transverse *cua*-cup; basal portion of ScP (bScP) very weak, reaching R+M+CuA before basal half of clavus; ScP+R diverging from M+CuA and M diverging from CuA at level of basal half of clavus; ScP+R stem twice shorter than M-stem and CuA-stem; ScP+RA_1 nearly transverse and diverging from RA_2+RP slightly before level of end of clavus; RA_2 subparallel to

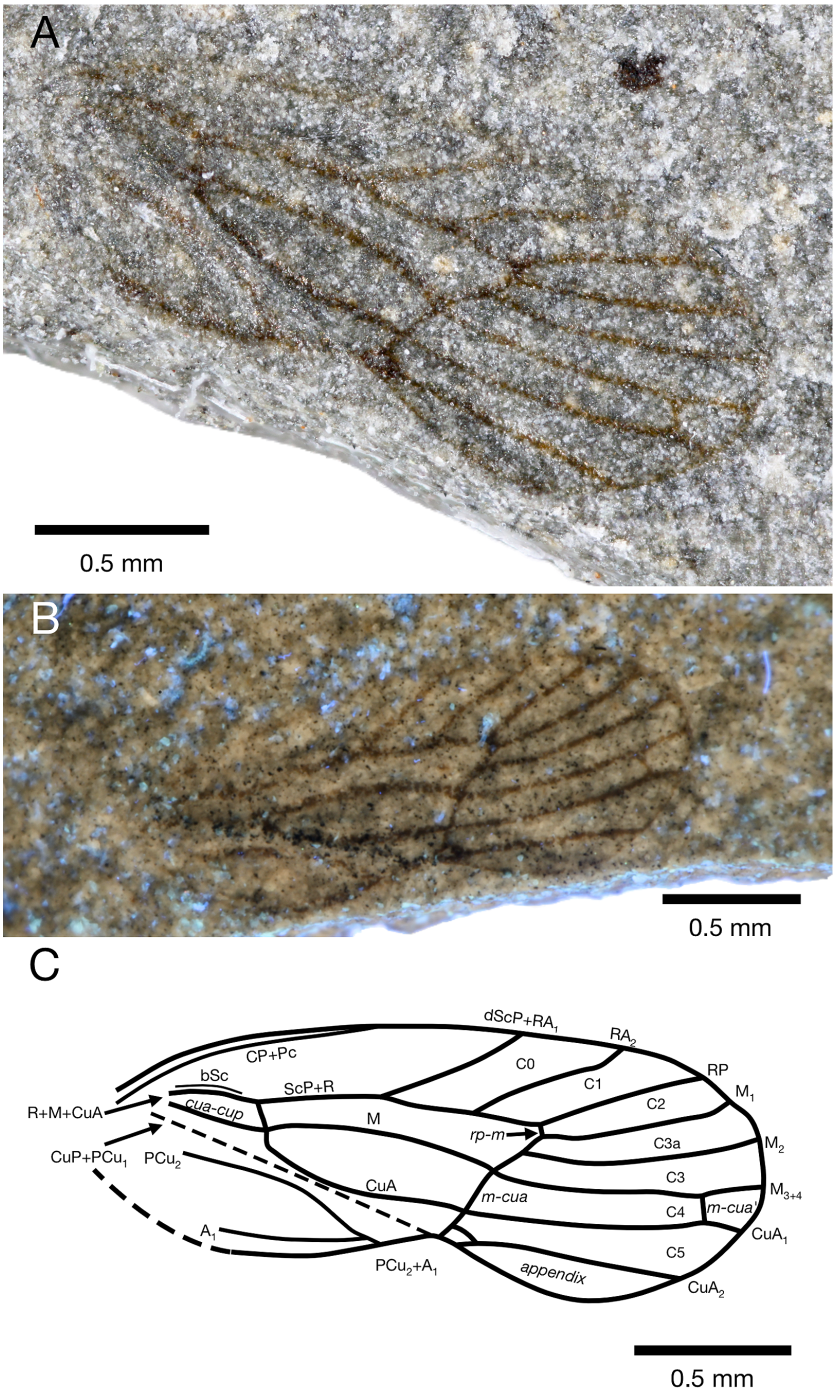

FIGURE 1. *Liassoprogonocimex bascharagensis* **gen. et sp. nov.** holotype MNHN.F.C02460. **A**, Photograph of forewing. **B**, Photograph of forewing under UV-light. **C**, Interpretive drawing line.

RP, diverging closer to ScP+RA_1 than to RP; M trifurcated, each fork parallel to each other, without a common stalk between M_{1+2} and M_{3+4} but with a common stalk of M_1 and M_2, *r-m* between RP and M_1 very short, *ca*. 0.005 mm; terminal M_{3+4} distinctly longer than terminals RP, M_1, and M_2, subequal in length to terminal CuA_1; terminals of M anteriorly curved apically; terminals of CuA slightly curved apically towards posterior margin of wing; M_{3+4} and CuA_1 separated by a short and thick crossvein; CuA_2 not parallel to appendix margin, this margin being medially curved; CuP+PCu_1 straight forming distinct claval suture, adpressed to CuA, distinctly thinner than other main veins; PCu_2 subparallel to CuP+PCu_1, strongly curved distally and fused with A_1 *ca*. 0.5 mm from wing base, distal vein PCu_2+A_1 extremely short, about ten times shorter than free portion of A_1, and ending well before apex of clavus; cell C0 elongate, subequal to cell C1; cells C3a to C5 subrectangular, with C5 the longest and the widest cell.

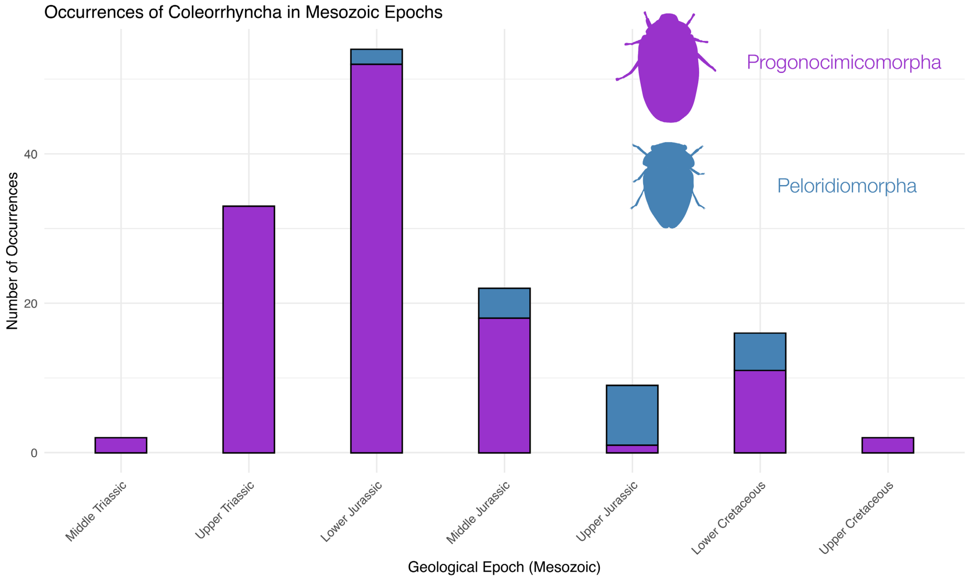

FIGURE 2. Diversity of Coleorrhyncha throughout Mesozoic. Data compiled from 'The Paleobiology Database' (https://paleobiodb.org/#/). Insect silhouettes drawn by M.B.

Discussion

The new fossil can be attributed within Progonocimicidae based on the tegmen with eight apical cells, without areolae and long ScP incorporated into R-stem (Popov & Shcherbakov, 1991; Wang *et al*., 2009). Progonocimicidae are divided into two subfamilies: Cicadocorinae Becker-Migdisova, 1958 and Progonocimicinae Handlirsch, 1906.

Popov & Shcherbakov (1991: 217) separated these two groups as follows: (1) A$_1$ not shorter than half of claval suture in Progonocimicinae *vs.* shorter in Cicadocorinae; (2) PCu$_2$ nearest to the suture before joining A$_1$ in Progonocimicinae *vs.* diverging from suture before joining A$_1$ in Cicadocorinae; (3) precostal carina [CP+Pc] deflected dorsad or obsolete in Progonocimicinae *vs.* horizontal or deflected ventrad (if dorsad, base of costal area narrow) in Cicadocorinae; (4) base of costal area not narrow in Progonocimicinae; (5) R-stem not continued by RP in Progonocimicinae *vs.* continued in Cicadocorinae; (6) and/or dScP+RA$_1$ at least partly curved anteriorly in Progonocimicinae *vs.* straight or curved posteriorly in Cicadocorinae.

Character (1) is not preserved in some taxa (*e.g.*, *Pelorisca* Popov & Shcherbakov, 1991 and *Woottonia* Popov & Shcherbakov, 1991); furthermore, its definition is ambiguous as A$_1$ is fused for a long distance with posterior margin of wing in its basal part in these wings. In the new fossil, its distal free part is half of claval suture, which is in-between the two states.

Character (2) is also not preserved in some taxa (*e.g.*, *Pelorisca* and *Woottonia*). In the genus *Cicadocoris* Becker-Migdisova, 1958 (type genus of the Cicadocorinae), PCu$_2$ is straight and, at most, very slightly diverging from the suture in its distal part (Becker-Migdisova, 1958; Dong *et al*., 2014; Jiang *et al*., 2016; Jiang & Huang, 2017; Xu & Huang, 2023). In the new fossil, it is strongly diverging from the suture.

Character (3) is quite difficult to determine whether it is deflected dorsal *vs*. ventral in compression fossils. Its state is unknown in the new fossil.

Character (4) can be present in both groups after Popov & Shcherbakov (1991).

Character (5) is also difficult to estimate because the angle between the radial stem and RP can be pronounced. In the new fossil, it is very weak, weaker than in the progonocimicine *Pelorisca*, suggesting an attribution to the Cicadocorinae.

Character (6): in the new fossil, dScP + RA$_1$ is distinctly curved anteriorly. This character would support an attribution to the Progonocimicinae. But in *Progonocimex* Handlirsch, 1906, dScP+RA$_1$ is as straight as in some species attributed to *Cicadocoris*, *e.g*., *C. henannensis* Xu & Huang, 2023 (Popov & Woottton, 1977: fig. 1, 2; Xu & Huang, 2023).

As a result, these characters have three defaults: one is not present in the type genus of the Cicadocorinae, some are ambiguous, and they are not polarized. Thus, the monophyly *vs.* paraphyly of these two groups of taxa are not demonstrated. The new fossil would be 'intermediate' between them. Therefore, we avoid putting it into a precise subfamily. These would need to be redefined after a phylogenetic analysis. This is confirmed by Dong *et al.*

(2014) who did not recover the monophyly of the two subfamilies in a partial phylogeny of the Coleorrhyncha.

Therefore, we need to compare it with all the genera of Progonocimicidae. The new fossil differs from *Progonocimex* in the distinctly curved PCu_2 *vs.* straight (Popov & Wootton, 1977). It differs from *Woottonia* and *Heterojassus* Evans, 1961 by the appendix separated by straight vein subparallel to CuA_1 (Popov & Shcherbakov, 1991) Affinities with *Pelorisca*, *Actinoscytina* Tillyard, 1926, *Triassodoecus* Evans, 1963, and *Heteroscytina* Evans, 1963 are excluded based on the imaginary continuation of R-stem closer to RP than RA_2. Unlike *Indutionomarus* Szwedo, 2011, the new specimen has the crossvein rp-m between RP and M_1 *vs.* between RP and M_{1+2} (Szwedo, 2011). The new fossil differs from *Platyscytinella* Evans, 1956 by lacking a common stalk formed by M_2 and M_{3+4} (Evans, 1956).

Mesoscytina Tillyard, 1919 and *Eocercopis* Handlirsch, 1939 differ from the new fossil in the M-stem and R-stem forming curved lines *vs.* straight (Lambkin, 2016; Zhang *et al.*, 2024). In *Mesocimex* Hong, 1983 and *Eocercopis*, PCu_2 is parallel to $CuP+PCu_1$ up to its apex (Wang *et al.*, 2009), *vs.* strongly diverging apically in the new fossil. Also *Mesocimex* has a longer PCu_2+A_1 than in the new fossil and ending at apex of the clavus (Szwedo, 2011). In *Onokhoia* Popov, 1988 and *Popovus* Özdikmen & Demir, 2007 (substitute name for *Progonus* Popov, 1986), PCu is less diverging from CuP than in the new fossil, and PCu_2+A_1 ends at apex of clavus *vs.* reaches posterior margin of wing basal of apex of clavus in the new fossil (Popov, 1986, 1988). *Archicercopis* Handlirsch, 1939 has PCu close to claval fracture, and M_{1+2}-forks beyond r-m. *Cicadocoris* also has PCu_2+A_1 ending at apex of clavus and PCu_2 straight. Its type species also strongly differs from the new fossil in the shape of the distal part of stem of M distal of m-cua and position of M_{3+4} (Becker-Migdisova, 1958: fig. 2), even if Dong *et al.* (2014) described another species with a pattern of M and CuA similar to that of the new fossil.

Hexascytina Wootton, 1963 is based on a small fragment of a forewing. It is supposed to have a RP making a very strong zigzag, and the crossvein rp-m very long (Wootton, 1963). *Microscytinella* Wootton, 1963 and *Platyscytinella* Wootton, 1963 also have a very long rp-m. *Popovigocimex* Martins-Neto & Gallego, 2003 strongly differs from the new fossil in the presence of five parallel anterior branches of ScP+R (Martins-Neto *et al.*, 2003). *Yurigocimex* Martins-Neto & Gallego, 2003 differs from the new fossil in the base of M + CuA opposite the base of $ScP+RA_1$, and very short r and m cells. *Ovicimex* Hong & Wang, 1990 has a forewing venation strongly different from those of the other Progonocimicidae and probably does not belong to this family (Hong & Wang, 1990: figs 66, 67). *Triscytina* Evans, 1956 strongly differs from the new fossil in the absence of alignment of the basal part of CuA_2, m-cua, and basal part of M_{1+2}, plus PCu closely parallel to CuP (Evans, 1956). *Triassodoecus* Evans, 1963 is based on an incomplete forewing. It differs from the new fossil in PCu parallel to CuP and PCu_2+A_1 ending at distal angle of clavus (Evans, 1963). *Heteronella* Evans, 1961 is based on an incomplete forewing, and its affinities are uncertain. It differs from the new fossil in the vein ScP+RA emerging at level of emergence of M + CuA (Evans, 1961).

Gakasha Jiang, Wang & Szwedo, 2019 strongly resembles the new fossil in the shape of PCu strongly diverging from CuP in its distal part, PCu_2+A_1 ending in posterior wing margin well basal to apex of clavus, pattern of the distal parts of veins RP, M, and CuA. It differs from the latter in distance between $ScP+RA_1$ and RA_2 much longer than distance between RA_2 and RP at their bases *vs.* of nearly the same, and PCu_2+A_1 much longer than in the latter (Jiang *et al.*, 2019).

Awanis You *et al.*, 2024 shares with our new fossil the short *rp-m* but differs from it based on R-stem not continued by RP; very short *cua-cup*. Additionally, the forking of M is strikingly different, in the new fossil M-stem is continuous with M_{3+4} branch whereas M-stem is between M_2 and M_{3+4} branches in *Awanis*. Furthermore, C5 is almost rectangular in *Awanis*, while C5 is enlarged distally in *Liassoprogonocimex* **gen. nov.**

In addition to the aforementioned differences, this new fossil exhibits unique features such as: a C0 cell more anterior than in any other Progonocimicidae genera with the division of $ScP+RA_1$ occurring before the end of the clavus; the *rp-m* crossvein is very short with the base of RP and M_1 very close to each other, and the presence of a distal crossvein between M_{3+4} and CuA_1, a feature never recorded in any Progonocimicidae. We considered that all these differences are sufficient to erect a new genus among Progonocimicidae with *Liassoprogonocimex* **gen. nov.**

Shcherbakov (1996) proposed that 'Progonocimicidae derive from the 'Ingruidae' (in the paraphyletic unit Ingruomorpha Szwedo, 2018). The Ingruidae putatively constitutes the 'ancestors' of Coleorrhyncha lineages (Popov & Shcherbakov, 1996). Such hypotheses of 'descendant' taxa in Coleorrhyncha are often cited but should be taken very carefully as a lineage cannot be derived from another, otherwise they are all paraphyletic. "Ingruomorpha" representatives are probably nested within Euhemiptera, with which they share the PCu fused with A_1, and the typical Y-shaped vein in the claval area. However, they strongly differ from the Progonocimicidae in the forking of the CuA vein, with two terminals very close to each other, whereas in Progonocimicidae the two branches of the CuA vein are very long and, in most cases, subparallel to each other.

Progonocimicidae are currently grouped with the Coleorrhyncha. However, as discussed by Burckhardt *et al.* (2023), there is no clear synapomorphy for moss bugs in wing venation. The Progonocimicidae do not share with Permoridiidae and Peloridiidae the ScA well separated from C with branches and an elongate and well-defined ScP. They also differ from Karabasiidae and Hoploridiidae by the ScP incorporated into R. Additionally, Popov & Shcherbakov (1996), and Shcherbakov & Popov (2002: 147, 148) proposed a list of 'putative synapomorphies' for Coleorrhyncha with: 'suprantennal ledge continuous below median ocellus; forewings overlapping in repose (left one uppermost); forewing with enlarged posterior apical cells, short transverse CuA_2 and broad appendix; coupling fold very short in forewing; fore and middle tarsi two-segmented; pygophore barrel-shaped, parameres protruding and elbowed'. These characters are very difficult to observe in most Progonocimicidae fossils or not preserved. However, the unique specimen described from mid-Cretaceous Kachin amber, *Gakasha calcaridentata* Jiang, Wang & Szwedo, 2019, definitely shows a suprantennal ledge continuous below median ocellus, and two-segmented fore and middle tarsi (but a feature present in numerous different acercarian lineages). The wing venation features proposed by Popov & Shcherbakov (1996) are not sufficient as they are present in other clades of Hemiptera. This highlights that a significant effort of systematics within Coleorrhyncha is required to delimit phylogenetically robust units.

The evolutionary history of Coleorrhyncha is complex. They originated more than 295 Myr ago (Burckhardt *et al.*, 2023) but they are quite uncommon in Late Paleozoic to Early Mesozoic outcrops, most notably because these periods are less documented (Schachat & Labandeira, 2021). The Coleorrhyncha are diverse in rocks of Upper Triassic to Middle Jurassic age (Fig. 2), corresponding to a high diversity of Progonocimicidae. The Progonocimicidae are widely spread between Triassic to Early Cretaceous, with occurrences in Australia, Eurasia, and South America (Martins-Neto *et al*., 2003). They strongly declined during the late Jurassic, in terms of occurrences. The Jurassic ones are currently restrained to Eurasia, but in the Cretaceous they are recorded in South America, Burmese paleo-island in the middle of the Tethys Ocean, and Eurasia. The last occurrence of Progonocimicidae is from the mid-Cretaceous Kachin amber, suggesting an extinction of the family related to the global floristic changes occurring during the late Cretaceous with the rise of the angiosperms and the subsequent decline of gymnosperms, their putative host-plants (Popov & Shcherbakov, 1996). But future discoveries in the latest Cretaceous could change this scenario.

The other main coleorrhynchan lineage is the Peloridiomorpha, known from the early Jurassic to the early Cretaceous (Fig. 2), their geographic distribution is limited to Asia, and they are morphologically closer to the only extant family of Coleorrhyncha (Peloridiidae). Recently, Ye *et al.* (2019) investigated the timing of diversification in Coleorrhyncha and the biogeographical history of Peloridiidae. However, their ingroup consists of the extant Peloridiidae, supposedly diverging from the outgroups (Heteroptera, Fulgoromorpha, Cicadomorpha, Sternorrhyncha) during the Carboniferous. This early divergence could strongly impact on the phylogenetic reconstruction and hamper molecular time divergence analyses. Additionally, the biogeographic analysis was only based on the Gondwanan distribution of Peloridiidae, but we illustrated that the Coleorrhyncha were widely spread throughout the Mesozoic. It would be interesting to have a total-evidence approach to study the diversification and biographical history of the Coleorrhyncha clade, by including the Progonocimicomorpha and the extinct Peloridiomorpha, to overcome the limitations due to their extant relict diversity. However, most of the extinct Coleorrhyncha are known by forewings, or poorly preserved bodies, which could lead to an issue of morphological data incompleteness between extant and extinct Coleorrhyncha.

Conclusion

We describe the second genus and species of Progonocimicidae of the Early Toarcian of Luxembourg. Intensive fieldwork in this locality has delivered interesting insect fossils, but this outcrop will need to be investigated, namely because a putative and particular entomofauna, linked to a short and fast period of global warming, occurring synchronously with the Toarcian-Oceanic Anoxic Event. Depicting the biogeographical history of Coleorrhyncha is challenging because of their relict diversity, hampered by their lacunar fossil record, which needs additional discoveries to propose enhanced hypotheses.

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References

Ansorge, J. (2003) Insects from the Lower Toarcian of Middle Europe and England. *Acta Zoologica Cracoviensia*, 46, 291–310.

Bechly, G. & Szwedo J. (2007) Coleorrhyncha: moss bugs. *In*: Martill, D.M., Bechly, G. & Loveridge, R.F. (Eds), *The Crato fossil beds of Brazil: window into an ancient world*. Cambridge University Press, Cambridge, pp. 313–317.

Becker-Migdisova, E.E. (1958) Novye iskopaemye ravnokrylye [New fossil Homoptera. Part 1. Homoptera from Kuznetzk basin]. Materialy k Osnovam Paleontologii. *Paleontologicheskogo Instituta Akademii nauk SSSR*, 2, 57–67.

Boderau, M., Aracheloff, C., Jouault, C., Ngô-Muller, V., Engel, M.S., Berthier, S., Schöllhorn, B., Huang, D., Nel, A. & Garrouste, R. (2024) Morphological and palaeoecological aspects of fossil insects unveiled by UV-A light. *MethodsX*, 13, 102794. https://doi.org/10.1016/j.mex.2024.102794

Bourgoin, T., Wang, R.R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroinski, A. & Szwedo, J. (2015) From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology*, 134, 63–77. https://doi.org/10.1007/s00435-014-0243-6

Breddin, G. (1897) Hemipteren. *In*: Michaelsen, W. (Ed.), *Ergebnisse der Hamburger magalhaensischen Sammelreise*, 1892/93, 2 (4), vols. 1–36, L. Friederichsen & Co, Hamburg, 2 pl.

Burckhardt, D. (2009) Taxonomy and phylogeny of the Gondwanan moss bugs or Peloridiidae (Hemiptera, Coleorrhyncha). *Deutsche Entomologische Zeitschrift*, 56 (2), 173–235. https://doi.org/10.1002/mmnd.200900019

Burckhardt, D., Nel, A., Raisch, M. & Poschmann, M.J. (2023) A new putative moss bug (Insecta: Hemiptera) from the lower Permian of the Saar-Nahe Basin, SW Germany, and the age of Coleorrhyncha. *Historical Biology*, 35 (6), 832–837. https://doi.org/10.1080/08912963.2022.2067759

Dong, Q., Yao, Y. & Ren, D. (2014) New fossil Progonocimicidae (Hemiptera: Coleorrhyncha: Progonocimicoidea) from the Upper Mesozoic of northeastern China, with a phylogeny of Coleorrhyncha. *Systematic Entomology*, 39 (4), 773–782. https://doi.org/10.1111/syen.12085

Evans, J.W. (1956) Palaeozoic and Mesozoic Hemiptera. *Australian Journal of Zoology*, 4 (2), 165–258. https://doi.org/10.1071/ZO9560165

Evans, J.W. (1961) Some Upper Triassic Hemiptera from Queensland. *Memoirs of the Queensland Museum*, 14 (1), 13–23.

Evans, J.W. (1963) The systematic position of the Ipsviciidae (Upper Triassic Hemiptera) and some new Upper Permian and Middle Triassic Hemiptera from Australia. *Journal of the Entomological Society of Queensland*, 2, 17–23. https://doi.org/10.1111/j.1440-6055.1963.tb00384.x

Fleck, G., Bechly, G., Martínez-Delclòs, X., Jarzembowski, E., Coram, R. & Nel, A. (2003) Phylogeny and classification of the Stenophlebioptera (Odonata: Epiproctophora). *Annales de la Société Entomologique de France (N.S.)*, 39 (1), 55–93. https://doi.org/10.1080/00379271.2003.10697363

Handlirsch, A. (1906–1908) Die fossilen Insekten und die Phylogenie der rezenten Formen. Verlag von Wilhelm Engelmann, Leipzig pp. ix+1430+51 plates (1906, 1–672; 1907, 673–1120; 1908, 1121–1430), 51 plates (1906, plates 1–36; 1907, plates 37–51).

Handlirsch, A. (1939) Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, paläogeographische und allgemeine biologische Probleme. Teil 2. *Annalen des Naturhistorischen Museums in Wien*, 49, 1–240.

Henrotay, M., Nel, A. & Jarzembowski, E.A. (1997) New protomyrmeleontid damselflies from the Triassic of Australia and the Liassic of Luxembourg, with the description of *Tillyardomyrmeleon petermilleri* gen. nov. & spec. nov. (Archizygoptera: Protomyrmeleontidae). *Odonatologica*, 26 (4), 395–404.

Henrotay, M., Marques, D., Paicheler, J.C., Gall, J.C. & Nel, A. (1998) Le Toarcian inférieur des régions de Bascharage et de Bettembourg (Grand-Duché du Luxembourg): évidence paléontologiques et sédimentologiques d'environnements restreints proches de l´émersion. *Geodiversitas*, 20 (2), 263–284.

Hong, Y.C. & Wang, W.L. (1990) [Fossil insects from the Laiyang basin, Shandong province]. pp. 44–189. *In*: Regional Geological Surveying Team, Shandong Bureau of Geology and Mineral Resources (Ed.), *The stratigraphy and palaeontology of Laiyang Basin, Shandong province*. Geological Publishing House, Beijing, 1–255. [In Chinese with English summary]

Jiang, J.Q. & Huang, D.Y. (2017) New species of *Cicadocoris* (Hemiptera: Coleorrhyncha: Progonocimicidae) from mid-Jurassic deposits in northeastern China. *European Journal of Entomology*, 114, 355–364. https://doi.org/10.14411/eje.2017.045

Jiang, J.Q., Cai, C.Y. & Huang, D.Y. (2016) Progonocimicids (Hemiptera, Coleorrhyncha) from the Middle Jurassic Haifanggou Formation, western Liaoning, northeast China support stratigraphic correlation with the Daohugou beds. *Alcheringa*, 40, 53–61. https://doi.org/10.1080/03115518.2015.1086053

Jiang, T., Wang, B. & Szwedo, J. (2019) The first representative of Progonocimicidae (Hemiptera: Coleorrhyncha) from mid-

Cretaceous Burmese amber. *Cretaceous Research*, 93, 346–359.
https://doi.org/10.1016/j.cretres.2018.09.018

Johnson, K.P., Dietrich, C.H., Friedrich, F., Beutel, R.G., Wipfler, B., Peters, R.S., Allen, J.M., Petersen, M., Donath, A., Walden, K.K.O., Kozlov, A.M., Podsiadlowski, L., Mayer, C., Meusemann, K., Vasilikopoulos, A., Waterhouse, R.M., Cameron, S.L., Weirauch, C., Swanson, D.R., Percy, D.M., Hardy, N.B., Terry, I., Liu, S., Zhou, X., Misof, B., Robertson, H.M. & Yoshizawa, K. (2018) Phylogenomics and the evolution of hemipteroid insects. *Proceedings of the National Academy of Sciences of the United States of America*, 115 (50), 12775–12780.
https://doi.org/10.1073/pnas.1815820115

Lambkin, K.J. (2016) Revision of the Scytinopteridae (Hemiptera: Cicadomorpha: Scytinopteroidea) of the Queensland Triassic. *Zootaxa*, 4117 (4), 580–590. https://doi.org/10.11646/zootaxa.4117.4.9

Linnaeus, C. (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10 th revise. Holmiae, Stockholm, Laurentius Salvius, 824 pp.
https://doi.org/10.5962/bhl.title.542

Martins-Neto, R.G., Gallego, O.F. & Melchor, R.N. (2003) The Triassic insect fauna from South America (Argentina, Brazil and Chile): a checklist (except Blattoptera and Coleoptera) and descriptions of new taxa. *Acta Zoologica Cracoviensia*, 46, 229–256.

Myers, J.G. & China, W.E. (1929) The systematic position of the Peloridiidae as elucidated by a further study of the external anatomy of *Hemiodoecus leai* China. *Annals and Magazine of Natural History, (10)*, 3 (15), 282–294.
https://doi.org/10.1080/00222932908672971

Nel, A. (1989) Les Gyrinidae fossiles de France (Coleoptera). *Annales de la Société Entomologique de France (N.S.)*, 25 (3), 321–330.
https://doi.org/10.1080/21686351.1989.12277593

Nel, A. & Henrotay, M. (1992) Les Protomyrmeleontidae (Odonatoptera, Odonata, Archizygoptera stat. rest.): État actuel des connaissances. *Annales de Paléontologie*, 78 (1), 1–47.

Nel, A. & Henrotay, M. (1994) Les Chrysopidae mésozoïques. État Actuel des connaissances. description d'un nouveau genre et nouvelle espèce dans le Jurassique inférieur (Lias) (Insecta: Neuroptera). *Annales de la Société entomologique de France (N.S)*, 30 (3), 293–310.
https://doi.org/10.1080/21686351.1994.12277709

Nel, A., Prokop, J., Nel, P., Grandcolas, P., Huang, D., Roques, P., Guilbert, E., Dostál, O. & Szwedo, J. (2012) Traits and evolution of wing venation pattern in paraneopteran insects. *Journal of Morphology*, 273, 480–506.
https://doi.org/10.1002/jmor.11036

Özdikmen, H. & Demir, E. (2007) New substitute names for three preoccupied homopteran genera: *Deltometopus* Williams, 1977, *Mariaella* Szelegiewicz, 1961 and *Progonus* Popov, 1986 (Homoptera). *Munis Entomology & Zoology*, 2, 436–438.

Popov, Y.A. (1980) Nadotryad Cimicidea Laicharting, 1781. Otryad Cimicina Laicharting, 1781. Poluzhestorylye, ili khobotnye [Superorder Cimicidea Laicharting, 1781. Order Cimicina Laicharting, 1781. Hemipterans, or rhynchotans]. *In*: Rohdendorf, B. B. & Rasnitsyn, A.P. (Eds), Istoricheskoe razvitye klassa nasekomykh [Historical development of the class Insecta]. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, 175, 58–69.

Popov, Y.A. (1985) Yurskie klopy i peloridiinovye Yuzhnoï Sibiri i zapadnoï Mongolii [Jurassic bugs and Coleorrhyncha of southern Siberia and western Mongolia]. *Trudy Paleontologicheskogo Instituta AN SSSR*, 211, 28–47.

Popov, Y.A. (1986) [Insects in the Early Cretaceous ecosystems of the West Mongolia. Description of fossils (Cicadoidea, Hemiptera)]. *In*: Rasnitsyn, A.P. (Ed.), *Nasekomye v rannemelovykh ekosistemakh Zapadnoy Mongolii [Insects in Early Cretaceous Ecosystems of Western Mongolia]*. Trudy Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ehkspeditsiya, 28, 50–83.

Popov, Y.A. (1988) New Mesozoic peloridiinians and true bugs (Hemiptera: Coleorrhyncha et Heteroptera) from Eastern Transbaikalia. *Paleontological Journal*, 22 (4), 67–77.

Popov, Y.A. & Shcherbakov, D.E. (1991) Mesozoic Peloridioidea and their ancestors (Hemiptera, Coleorrhyncha). *Geologica et Palaeontologica*, 25, 215–235.

Popov. Y.A. & Wootton, R.J. (1977) The Upper Liassic Heteroptera of Mecklenburg and Saxony. *Systematic Entomology*, 2, 333–351.
https://doi.org/10.1111/j.1365-3113.1977.tb00382.x

Schachat, S. & Labandeira, C.C. (2021) Are insects heading toward their first mass extinction? Distinguishing turnover from crises in their fossil record. *Annals of the Entomological Society of America*, 114 (2), 99–118.
https://doi.org/10.1093/aesa/saaa042

Shcherbakov, D.Y. (1996) Origin and evolution of the Auchenorrhyncha as shown by the fossil record. *In*: Schaefer, C.W. (Ed.), *Studies in the hemipteran phylogeny*. Proceedings of the Thomas Say Publications in Entomology. Entomological Society of America, Lanham, Maryland, 31–45.

Shcherbakov, D.Y. & Popov, Y.A. (2002) Superorder Cimicidea Laicharting, 1781 order Hemiptera Linné, 1758. *In*: Rasnitsyn, A.P. & Quicke, D.L.J. (Eds), *History of insects*. Kluwer Academic Publishers, Dordrecht, Boston, London, 143–157.

Szwedo, J. (2011) The Coleorrhyncha (Insecta: Hemiptera) of the European Jurassic, with a description of a new genus from the Toarcian of Luxembourg. *Volumina Jurassica*, 9, 3–20.

Szwedo, J. (2018) The unity, diversity and conformity of bugs (Hemiptera) through time. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 107, 109–128.
https://doi.org/10.1017/S175569101700038X

Thuy, B., Korte, C., Delsate, D., Di Cencio, A., Garbay, L., Hellemond, A., Numberger-Thuy, L.D., Rollinger, C., Steen, J.C. & Weis, R. (2025) The Bascharage Konservat Lagerstätte in Luxembourg: stratigraphy and palaeontology of a Lower Toarcian near-shore environment. *Newsletters on Stratigraphy*, 58 (3), 373–395.
https://doi.org/10.1127/nos/2025/0875

Tillyard, R.J. (1919) Mesozoic insects of Queensland. 7. Hemiptera, Homoptera. *Proceedings of the Linnean Society of New South Wales*, 44, 857–896.

Tillyard, R.J. (1926) Upper Permian insects of New South Wales. 1. Introduction and the order Hemiptera. *Proceedings of the Linnean Society of New South Wales*, 51, 1–30.

Wang, B., Szwedo, J. & Zhang, H.C. (2009) Jurassic Progonocimicidae (Hemiptera) from China and phylogenetic evolution of Coleorrhyncha. *Science in China Series D: Earth Sciences*, 52 (12), 1953–1961.
https://doi.org/10.1007/s11430-009-0160-6

Wootton, R.J. (1963) Actinoscytinidae (Hemiptera: Heteroptera) from the Upper Triassic of Queensland. *Annals and Magazine of Natural History, (13)*, 6 (64), 249–255.
https://doi.org/10.1080/00222936308651349

Xu, M.M. & Huang, D.Y. (2023) A new species of Cicadocoris (Hemiptera, Coleorrhyncha, Progonocimicidae) from the Middle Jurassic of the Jiyuan Basin, China. *Zootaxa*, 5396 (1), 35–40.
https://doi.org/10.11646/zootaxa.5396.1.8

Ye, Z., Damgaard, J., Burckhardt, D., Gibbs, G., Yuan, J., Yang, H. & Bu, W. (2019) Phylogeny and historical biogeography of Gondwanan moss-bugs (Insecta: Hemiptera: Coleorrhyncha: Peloridiidae). *Cladistics*, 35 (2), 135–149.
https://doi.org/10.1111/cla.12237

You, Y.J., Jiang, T., Guan, X.E., Bieszczad, B. & Szwedo, J. (2024) A second progonocimicid (Hemiptera: Coleorrhyncha) from the Middle Cretaceous Kachin amber of Myanmar. *Palaeoworld*, 34 (4), 200904.
https://doi.org/10.1016/j.palwor.2024.200904

Zhang, Q., Du, X., Zhu, X. & Zhang, H. (2024) First record of *Mesoscytina* (Hemiptera, Scytinopteroidea, Scytinopteridae) from the Middle Triassic Tongchuan Entomofauna of China. *ZooKeys*, 1219, 99–104.
https://doi.org/10.3897/zookeys.1219.135654