

Short communication

Revision of the Cretaceous Proctotrupomorpha (Insecta: Hymenoptera) of Australia

Alexandr P. Rasnitsyn^{a, b, *}, Christoph Öhm-Kühnle^c^a A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, 117647 Moscow, Russia^b Natural History Museum, Cromwell Road, London SW7 5BD, UK^c Kirchgasse 11, 71083 Herrenberg, Germany

ARTICLE INFO

Article history:

Received 20 September 2018

Received in revised form

9 January 2019

Accepted in revised form 18 March 2019

Available online 22 March 2019

Keywords:

Koonwarra beds

Proctotrupomorpha

Australian insect fauna

Endemic distribution

Aptian

Hymenoptera

ABSTRACT

Based on new and better images of the fossils, we revise the known Cretaceous Proctotrupomorpha of Australia. The fossils were collected at the Koonwarra Fossil Bed, the only source of Cretaceous Proctotrupomorpha in Australia so far. The revision results in the following new taxa and new attributions: Cretacoformicidae fam. nov. in Proctotrupomorpha superfamily incertae sedis, including *Cretacoformica explicata* Jell & Duncan, 1986 from the Koonwarra Fossil Bed and *Iberapria perialla* Engel et al., 2013 from Lower Cretaceous Spanish amber, possibly related to Serphitoidea s.l. (including Mymarommatoidea and Yurapriidae) and Chalcidoidea, and *Koonwarrus katya* gen. et sp. nov. in Proctotrupomorpha incertae familiae from the Koonwarra Fossil Bed, possibly related to Proctotrupeoidea, Diaprioidea and/or Platygastroidea. Two other proctotrupomorph fossils from the Koonwarra Fossil Bed are confirmed to represent Proctotrupidae. Through the survey of Cretaceous Australian Proctotrupomorpha, which are preserved just in very few known fossils, the necessity of additional research on Australian Cretaceous Hymenoptera and continuing search for insect fossils in the Koonwarra Fossil Bed, as well as for additional research on known fossils and possible redescrptions is being emphasized.

© 2019 Elsevier Ltd. All rights reserved.

1. Introduction

Infraorder Proctotrupomorpha is one of the major subdivisions of the order Hymenoptera which includes superfamilies Proctotrupeoidea, Diaprioidea, Platygastroidea, Chalcidoidea and Serphitoidea (= Bipetiolarida *sensu* Engel, 2016). The earliest fossils of the infraorder are known from the Middle Jurassic and the infraorder has a rather rich fossil record. However, its Cretaceous fossils are poorly documented for Gondwana, with five families identified and three species described from Barremian Levantine ambers (Azar et al., 2010; Engel, 2016; Rasnitsyn et al., 2016), two families identified and one species described from the Aptian of Santana Formation in Brazil (Martill et al., 2007), two families identified and one species described from the Turonian of Orapa, Botswana (Brothers and Rasnitsyn, 2003; Rasnitsyn and Brothers, 2007), and 4 species in 3 families identifiable from the Aptian of Koonwarra in Australia (see below). We do not consider the rich mid-Cretaceous

fauna of Burmese amber as Gondwanan (or as Laurasian) for the reasons presented by Rasnitsyn and Öhm-Kühnle (2018) and Zhang et al. (2018). This is a further reason, why it was highly desirable to identify the exact taxonomic position of the only known Cretaceous proctotrupomorphs from Australia.

The Koonwarra Fossil Bed is located at the southernmost part of Australia, south of Melbourne, Victoria (38°34'03"S, 145°57'50"E according Tossolini et al., 2002; ca. 68°S paleolatitude, near the Southern Polar Ring, see Fig. 1), and it is dated as middle to late Aptian (118 ± 5–115 ± 6 Ma; *Cyclosporites hughesii* Zone palynomorphs), Lower Cretaceous, the climate most likely was temperate and wet (Poropat et al., 2018). The assemblage is famous for its rich and diverse fossils, including insects, which were described monographically by Jell and Duncan (1986; cf. also Jell, 2004). After correction of several initial misidentifications only seven hymenopteran fossils remain (all located in the collection of the Museum of Victoria, Melbourne), representing seven distinct morphospecies (only three described formally), three described genera, and five suggested families, all representing an informal group Parasitica, but not even a single fossil of Symphyta or Aculeata (Poropat et al., 2018, table 15). However, many of these

* Corresponding author. Paleontological Institute, Russian Academy of Sciences, 117647 Moscow, Russia.

E-mail address: alex.rasnitsyn@gmail.com (A.P. Rasnitsyn).

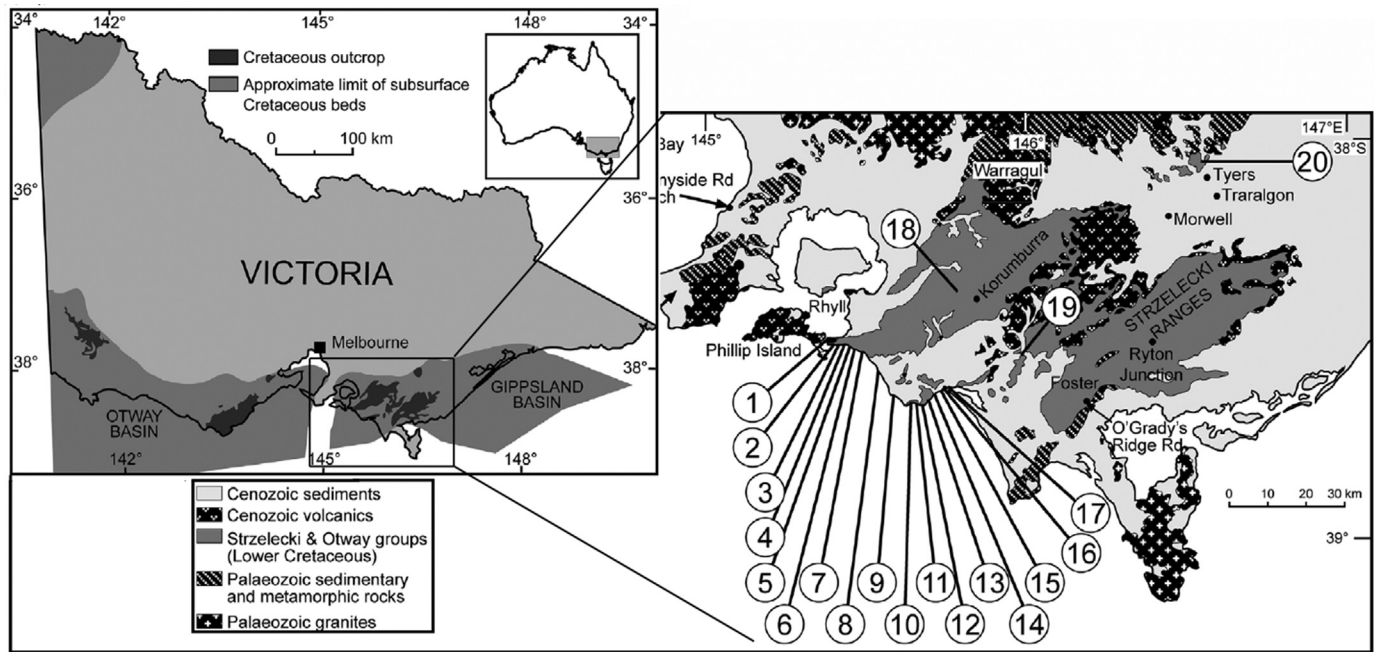


Fig. 1. Map of Victoria with the Cretaceous outcrop extent in the Otway and Gippsland basins (left map) and magnified view on the Victorian Early Cretaceous fossil locations of Gippsland, including the Koonwarra Fossil Bed (right map): 1 San Remo, 2 Potters Hill, 3 Rowells Beach, 4 Punchbowl, 5 The Arch, 6 Backhead, 7 Kilcunda, 8 Powlett River, 9 Harmers Haven, 10 Cape Paterson, 11 The Oaks, 12 Twin Reefs, 13 Shack Bay, 14 Eagles Nest (Gippsland), 15 The Caves, 16 Flat Rocks, 17 Inverloch, 18 Bena, **19 Koonwarra**, 20 Boola Boola Forrest (combined from two maps (Fig. 2 and 3) in Poropat et al., 2018, after Tosolini et al., 2002; reproduced with kind permission).

identifications are still raising questions and the collection needs to be studied again in detail, especially, because of the importance of the material for a better understanding of the Cretaceous fauna and the biogeography of Gondwana and Australia in particular, as well as for taxonomy and evolution of Hymenoptera. The research presented on hand, containing redescrptions of the Proctotrupomorpha, was made possible through recent photographs of the hymenopteran fossils, which were made at the Museum of Victoria (NMVP) by the late Dr Ekaterina Sidorchuk, in August 2018.

The new photographs allow the inference that three of four Koonwarra proctotrupomorphs have been initially misidentified (one, *Cretacoformica explicata* Jell & Duncan, 1986, as an ant, the other two as paratypes of *Westratia nana* Jell & Duncan, 1986, whose holotype was found to belong to the basal evanioid family Praeaulacidae; cf. Rasnitsyn, 1990; Naumann, 1993; Rasnitsyn et al., 1998). However, these new photographs additionally show, that the taxonomic placement of *Cretacoformica* in Diapriidae and one of the paratypes of *Westratia nana* in Monomachidae, as proposed by Rasnitsyn (1990) and Rasnitsyn et al. (1998), was incorrect as well, even though these two still are identified as Proctotrupomorpha, along with two fossils of Proctotrupidae identified as such either originally (Proctotrupid indet., NMVP 103106: Jell & Duncan, 1986), or newly (*Westratia nana* Jell & Duncan, 1986 male paratype NMVP103348: Rasnitsyn, 1990). These new insights made the present publication necessary.

2. Material and methods

The fossils presented and described herein are part of the collection of the Museum of Victoria, Melbourne, Australia (NMVP). These fossils were studied based on photographs made with Olympus E-M10 Mark II with a macro lens M. Zuiko Digital ED 60 mm 1:2.8. As illumination were used two scattered fluorescent light sources and one directed LED light source.

Some of the photographs were edited with FastStone Image Viewer 5.1 software. The drawings were made with CorelDraw X3 software.

3. Systematic paleontology

Order: Hymenoptera Linnaeus, 1758

Infraorder: Proctotrupomorpha Latreille, 1802

Superfamily: incertae sedis

Family: Cretacoformicidae Rasnitsyn & Öhm-Kühnle, fam. nov.

Type genus: *Cretacoformica* Jell & Duncan, 1986.

Diagnosis. Antenna oligomeric (14–15-segmented), not distinctly geniculate, with no clava, with scape moderately long or long, if the latter is the case, then attached far from clypeus on shelf (unknown and possibly different in type genus). Pronotum moderately short in its center, with dorsal lateral lobes not preserved but apparently reaching tegulae or nearly so. Notauli percurrent, no medial scutal suture present. Wing venation generally of usual proctotrupoid type, even though somewhat reduced, except that RS&M (basal vein) strongly arched and nearly aligned with base of Cu which is in turn angular to M+Cu. 1st metasomal segment forming distinct petiole, 2nd tergum not much elongate (at most ca. twice as long as 3rd).

Genera included. Type species and *Iberopria* Engel et al., 2013 from the Lower Cretaceous (Albian) amber of Spain (Engel et al., 2013).

Remarks. New family, which can easily be distinguished from other proctotrupomorphs through its wing venation, in the combination of the above described position of free Cu in respect to M+Cu and M (as a part of basal vein), particularly a strong bent Cu near M, and one-segmented tubular petiole. Very few Diapriidae, such as *Gaugainia electrogallica* Perrichot & Nel, 2008, and *Ismarus halidayi* Förster, 1850, show the slight similarity, that Cu is slightly bent back at its fork with M, however, they differ in having a disproportionately

long metasomal tergum 2, which is longer than terga 3–4 together, therefore the venation similarity most likely is not of taxonomic importance. The diagnostic characters of *Cretacoformica* suggest contradictory taxonomic placement affinities. One-segmented petiole and, in *Iberopria* only, head form, antennal attachment and length of scape, suggest affinity to Diapriidae, although the characteristic form of Cu suggests a closer relationship to Serphitidae, Jurapriidae and Khutelchalcididae. Of these three, Serphitidae represent the superfamily Serphitoidea (*sensu stricto* or *sensu lato*, the latter being equal to an informal taxon Bipetiolarida *sensu* Engel, 2016); Khutelchalcididae, Chalcidoidea (cf. Rasnitsyn et al., 2004; Rasnitsyn and Brothers, 2007 for details), and Jurapriidae are referred, although arbitrarily, to Serphitoidea (Rasnitsyn and Brothers, 2007). Among these three, Cretacoformicidae take an intermediate position between the less advanced Jurapriidae (with non-modified 1st metasomal segment and almost a ground plan-proctotrupomorph venation) and the other groups under comparison, with wing venation further reduced and metasomal base variously modified (bipetiolate in Serphitoidea, 1st metasomal segment not externally visible, probably much reduced in Khutelchalcididae).

That Chalcidoidea and Serphitoidea s.l. together could be the possible closest relatives of Cretacoformicidae is supported by recent phylogenetic analyses of living representatives of the above three superfamilies that suggest Serphitoidea s.l. (as represented by Mymaromatidae) and Chalcidoidea to be sister clades (Vilhelmsen and Tursi, 2010; Sharkey et al., 2012). However, this is of little help in seeking for a right place of Cretacoformicidae, which leaves us with morphological characters visible in the two unique fossils available thus far as only basis for our decision. For family attribution, we do tend to see a higher importance of the unique form of the Y-network of M+Cu&1M&1Cu characteristic of Chalcidoidea, Serphitoidea s.l., and Cretacoformicidae, as opposed to the characters that join Cretacoformicidae (and particularly *Iberopria*) with Diapriidae (listed above), which are prone to homoplasy. Yet this evidence is not very strong. Therefore, the new family is left to consider as Proctotrupomorpha incertae superfamiliae until more material is found and described and the taxonomic position of Cretacoformicidae is clearer. Unfortunately, our knowledge of the morphology of both *Cretacoformica* and *Iberopria* is insufficient in order to achieve a reliable result of a cladistic calculation.

Genus: *Cretacoformica* Jell & Duncan, 1986

Type species: *C. explicata* Jell & Duncan (1986) (by monotypy and original designation).

Diagnosis. Head short, transverse, apparently with no shelf bearing antennal attachments (although this is uncertain because of imperfect preservation). Antenna 15-segmented (teste Naumann, 1993: photographs available permit interpretation ranging 14 to 16 segments), short, not geniculate, with scape about twice as long as wide, flagellomeres mainly transverse. Forewing venation moderately reduced: pterostigma rather wide and sclerotized centrally, RS, M and Cu present at least as nebulous veins (RS almost reaching fore margin of the wing and tubular both basal and distal of 2r-rs). Legs short, hind tarsus shorter than hind tibia. Metasoma wide with wide petiole, triangular in upper view, terga 3–6 with basal transverse impression.

Remarks. The genus differs from *Iberopria* in lacking diapriid features characteristic of the latter (more elongate head with a shelf bearing antennal attachments, long scape and somewhat geniculate antenna), short legs, richer venation, wide triangular and not elongate tubular petiole, several metasomal terga impressed basally, and more robust stature.

Species included. Type only.

Cretacoformica explicata Jell & Duncan, 1986

Fig. 2.

Holotype. NMVP 102501 A and B; Australia, Victoria, Koonwarra Fossil Bed, PL425, Gippsland; Aptian; a part and counterpart of a complete fossil in upper view, with metasomal apex missing and legs incompletely preserved, sex unknown.

Description. Ground color dark, with antennal bases and legs possibly slightly paler. Wing veins distinctly paler. Head transverse with big, weakly elongate eyes, no visible antennal shelf, occipital carina forming rather narrow circle, possibly incomplete below. Scape almost twice as long as wide, pedicel of almost same length but much narrower, slightly more than twice as long as wide. Central 9 flagellomeres of subequal length and width, slightly transverse, basal and penultimate ones seemingly long, however each may represent two segments of same size, ultimate flagellomere longer and rounded apically. Mesosoma longer than wide, narrowing both forward and backward. Pronotum moderately narrow centrally, with posterolateral ends not preserved but apparently reaching wing base. Mesonotum moderately long, with notauli long, straight, diverging, well distant on transverse suture. Scutellum small, transverse. Otherwise structure of mesosoma unknown. Legs short, trochanter and trochantellus narrow cylindrical (unknown in fore leg), femora fusiform, fore and mid ones particularly short (fore one 0.7x, mid one 0.8x as long as hind one), fore and mid tibia scarcely longer than their femora, hind one almost 1.5x as long, fore tarsus 1.3x as long, hind one 0.7x so, basitarsus subequal to other segments together, terminal segment elongate, others short when discernible, claws short, weak. Forewing with pterostigma of moderate size, with tubular veins C, R, R₁, 1RS&1M (basal vein), 2r-rs, RS basal and distal of 2r-rs, M+Cu and short section of M distal of M + Cu fork, nebulous veins RS distal of tubular section and faded before R₁ (Naumann, 1993, shows RS reaching or almost reaching R₁), free M, Cu distal of tubular base, cu-a and A. Costal space wide at least distal (narrow in basal part but likely due to a deformation). 2r-rs placed at pterostigma near its middle, slightly longer than pterostigma width, RS incassate near 2r-rs, 1RS&1M strongly arching in its lower half, aligned with Cu at posterior end, Cu slightly bent at former junction with A ('2cu-a'), M, Cu and A far from reaching wing margin. Hind wing with R tubular, r-rs, 1r-m and M+Cu nebulous, with no distinct C. Metasoma with petiole 0.8x as long as wide at posterior end, 0.65x as long and 0.4x as wide as tergum 2, tergum 2 half-spherical, 0.33x as long as gaster (post-petiolar metasoma), terga III–V belt-like, narrow, impressed in basal half, tergum VI apparently conical and longer than previous ones, but precise form is unknown because of missing metasomal apex.

Measurements. Length of fossil 3.4 mm, lengths of parts: forewing 3.2 mm, mesosoma 1.2 mm, metasoma as preserved 1.7 mm, antenna 1.45 mm, fore tibia 0.4 mm, mid tibia 0.43 mm, hind tibia 0.8 mm, fore tarsus 0.55 mm, hind tarsus 0.55 mm.

Infraorder: Proctotrupomorpha Latreille, 1802

Superfamily: incertae sedis

Family: incertae sedis

Genus: *Koonwarrus* Rasnitsyn & Öhm-Kühnle, gen. nov.

Westratia Jell & Duncan, 1986 (p.p.: quoad *Westratia nana* Jell & Duncan, 1986, paratypus NMVP 103324).

Type species: *Koonwarrus katya* Rasnitsyn & Öhm-Kühnle, sp. nov.

Derivation of name. From Koonwarra Fossil Bed. Gender masculine.

Diagnosis. Forewing with usual proctotrupomorph venation (cell 3r triangular, r-m and 2m-cu crossveins lost, (M+)Cu straight throughout, or at least not bent backward distally of cu-a) except that RS+M and free M absent (preservation state is well enough in

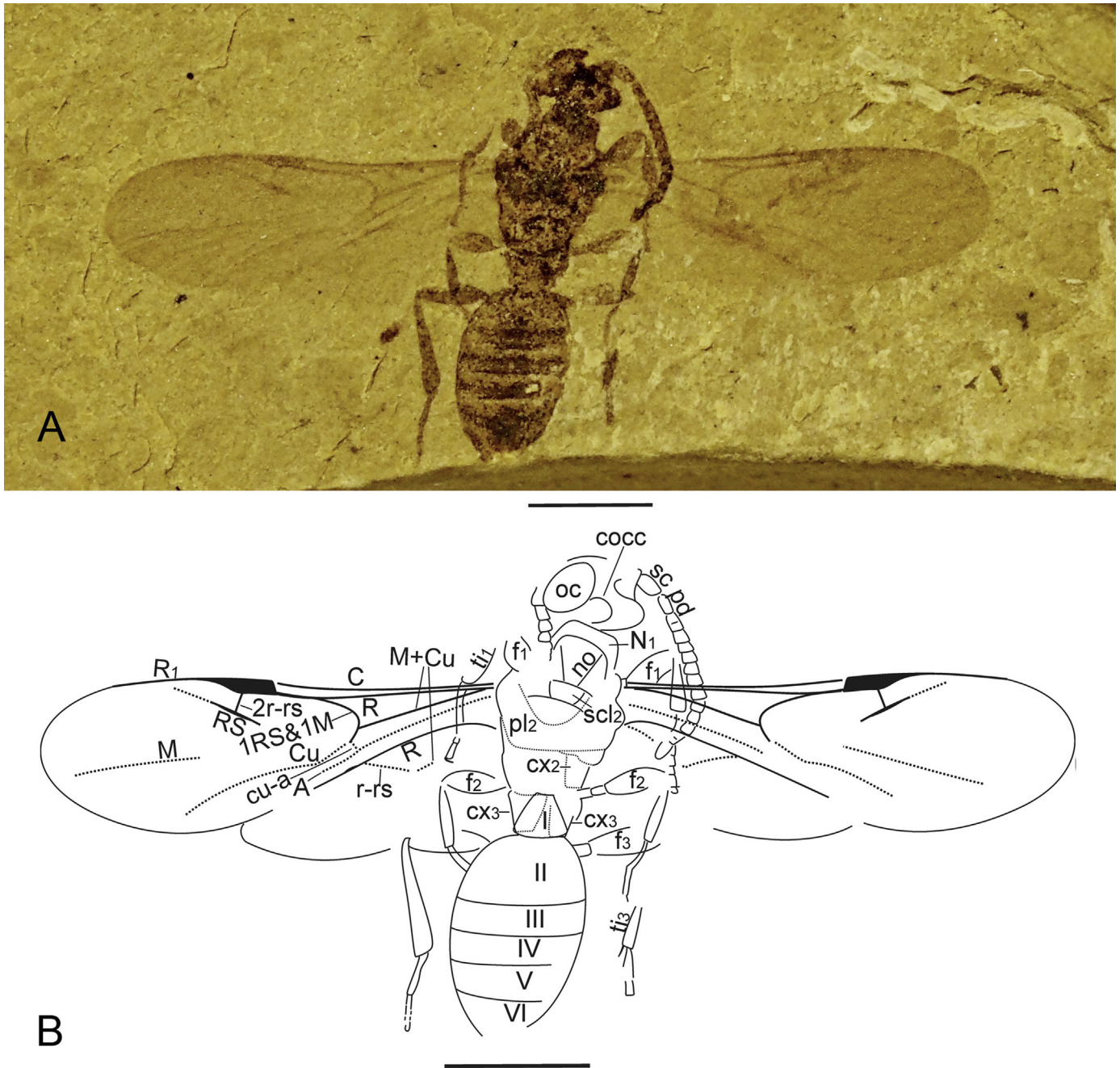


Fig. 2. *Cretacoformica explicata* [Jell & Duncan \(1986\)](#), holotype: A – upper view, B – interpretation. Scale bar equals 1 mm. Symbols: cocc – occipital carina, cx₂, cx₃ – mid and hind coxa, f₁, f₂, f₃ – fore, mid and hind femur, N₁ – pronotum, no – notaulus, oc – eye, pd – pedicel, pl₂ – mesoventropleuron, sc – scape, scl₂ – mesoscutellum, ti₁, ti₃ – fore and hind tibia, I–VI – metasomal tergites; forewing: 1RS&1M – basal vein (aligned first sections of RS and M), other venational symbols are standard.

order to consider the loss as real), straight fold present from posterior end of 2cu-a almost to wing margin.

Species included. Type only.

Remarks. Lost free M, combined with an otherwise just moderate vein reduction (only RS+M lost), is to our current knowledge unique in Proctotrupoidea, including Monomachidae (to which the fossil was erroneously ascribed, [Rasnitsyn, 1990](#)). Also, a longitudinal fold below free Cu is unusual in Proctotrupoidea. Unfortunately, only the incomplete forewing with limited set of characters is available for study. This renders a reliable attribution of the fossil to a particular family or superfamily impossible. It cannot be placed in Chalcidoidea (because of more complete

venation), Cynipoidea (because C is well developed), or Serphitoidea (including mymarommatoidea and jurapriids, because of Cu lacking posterior bent). However, Proctotrupoidea, Diaprioidea, and Platygastroidea cannot be rejected for the possible taxonomic placement of the new genus. Therefore, until in the future additional fossils reveal more details, the genus described herein is defined as *superfamilia et familia incertae sedis*.

Koonwarrus katya Rasnitsyn & Öhm-Kühnle, sp. nov.

[Fig. 3.](#)

Westratia nana [Jell & Duncan \(1986\)](#) (p.p., quoad paratypus NMVP 103324).

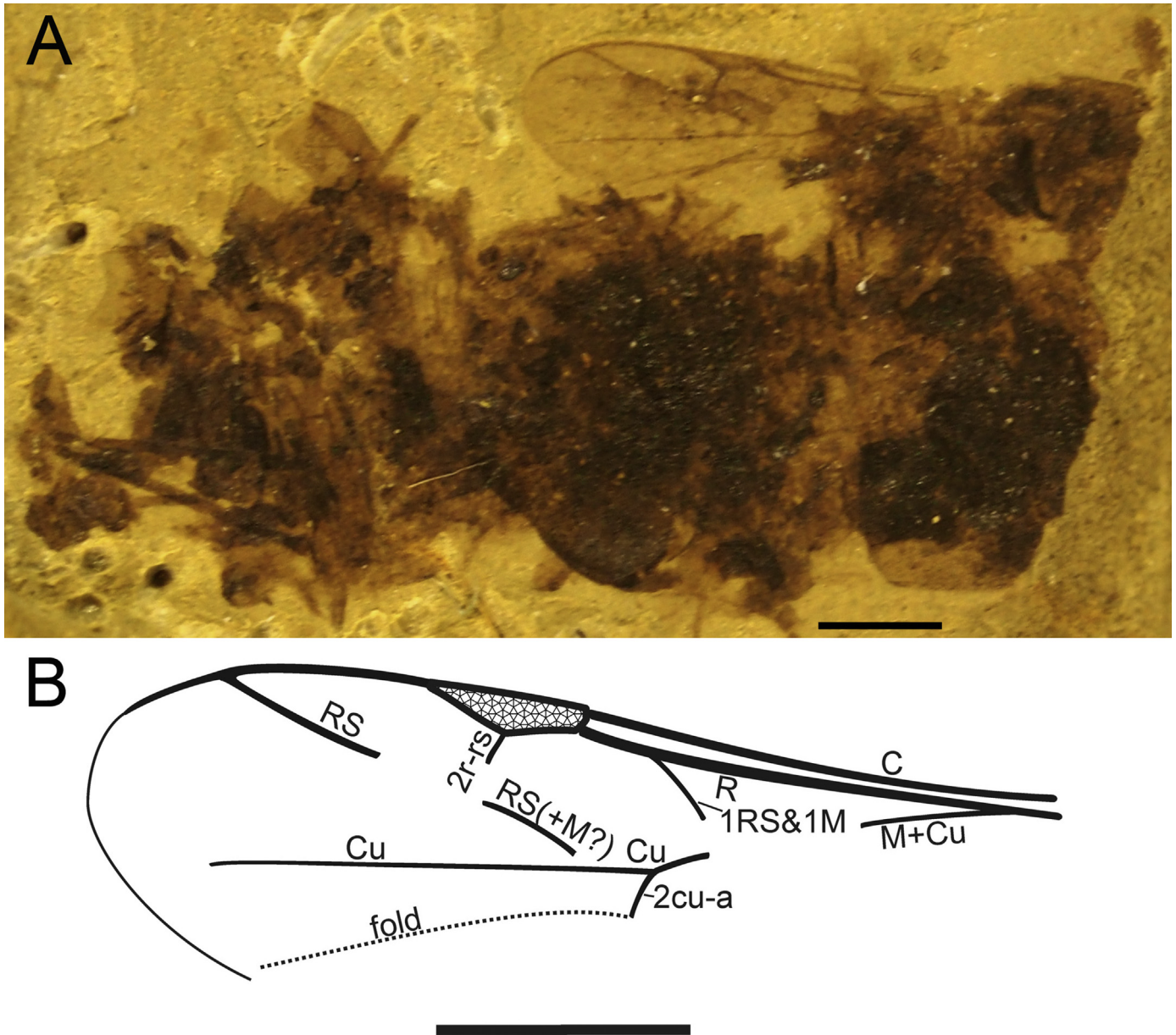


Fig. 3. *Koonwarrus katya* Rasnitsyn & Öhm-Kühnle, sp. nov., holotype: A – forewing, B – interpretation. The scale bar equals 1 mm. Symbols: 1RS&1M – basal vein (aligned first sections of RS and M), other venational symbols are standard.

Derivation of name. The species name is chosen in order to commemorate the untimely departure of brilliant acarologist and palaeontologist Ekaterina (Katya) Sidorchuk who had made the present work possible through preparing photographs of the types.

Holotype. NMVP 103324; Australia, Victoria, Koonwarra Fossil Bed, PL425, Gippsland; Aptian; just one forewing preserved, imbedded along with other arthropod fragments and organic mass, probably fish excrement; the forewing is well preserved, except that some wing details are obscured by dark fragments.

Description. Forewing with veins tubular except 2cu-a and upper part of basal vein (1RS&1M) pale and apparently nebulous. C well developed, pterostigma of medium size, just its margins strongly sclerotized, but less so in its interior, widened mid length at junction with 2r-rs, basal vein gently arching, as distant from pterostigmal base as 2r-rs, its junction with M+Cu obscured, RS+M lost, RS (+M?) forming posterodistal margin of central cell

(1r+2r+1mcu) and not connected to Cu, junction of 2r-rs with RS obscured, 3r cell (marginal) long, closed at wing margin, with R₁ running from its apex almost to wing apex, free M lost, Cu with 2cu-a near mid length of former 1mcu cell, slightly angular forward here, almost reaching wing margin, 1cu-a obscured, strong fold present, running from hind end of 2cu-a subparallel to Cu almost to wing margin, A obscured.

Measurements. Wing length 3.8 mm, width possibly 1.3 mm.

4. Conclusions

The composition of the small collection at the Museum of Victoria of Proctotrupomorpha from the Koonwarra Fossil Bed is noteworthy. Two of the four available fossils are still waiting for complete description, but do belong to the family Proctotrupidae, a family which is common in the Lower Cretaceous and particularly characteristic of the cooler environments of Eurasia and Australia,

so that fossil assemblages with abundant Proctotrupidae have been termed ‘proctotrupid subtype’ (Rasnitsyn et al., 1998). In contrast, two other proctotrupomorph fossils redescribed herein are very distinct and unique at the generic or (*Koonwarrus*) possibly at the family level. These highly interesting insects are probably either Australian endemics or at least rare in other regions. Although the material at hand is too limited to justify wider inferences, it is sufficiently informative to claim an urgent need to continuingly collect Koonwarra fossil insects and to restudy all further available fossils.

Acknowledgements

The authors are grateful for the important work of late Ekaterina Sidorchuk (formerly Palaeontological Institute RAS, Moscow) who prepared the excellent photographs of the fossils at the Museum of Victoria for the present article. In addition, they express their gratitude to the authorities of the Museum of Victoria for the permission to take photographs. Furthermore, the authors wish to thank the anonymous reviewers for their highly helpful comments.

References

- Azar, D., Gèze, R., Acra, F., 2010. Lebanese amber. In: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*, vol. 304. Siri Scientific Press, Manchester, pp. 271–298.
- Brothers, D.J., Rasnitsyn, A.P., 2003. Diversity of Hymenoptera and other insects in the Late Cretaceous (Turonian) deposits at Orapa, Botswana: a preliminary review. *African Entomology* 11 (2), 221–226.
- Engel, M.S., 2016. A new family of primitive serphitoid wasps in Lebanese amber (Hymenoptera, Serphitoidea). *Novitates Paleontologicae* 13, 1–22. <https://doi.org/10.17161/np.v0i13.5064>.
- Engel, M.S., Ortega-Blanco, J., Soriano, C., Grimaldi, D.A., Delclòs, X., 2013. A new lineage of enigmatic diapiroid wasps in Cretaceous amber (Hymenoptera: Diaprioidea). *American Museum Novitates* 3771, 1–23.
- Jell, P.A., 2004. Fossil insects of Australia. *Memoirs of the Queensland Museum* 50, 1–123. <https://www.researchgate.net/publication/268078349>.
- Jell, P.A., Duncan, P.M., 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Memoir of the Association of Australasian Palaeontologists* 3, 111–205.
- Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), 2007. *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge University Press, Cambridge, p. 625. <https://doi.org/10.1017/CBO9780511535512>.
- Naumann, I.D., 1993. The supposed Cretaceous ant *Cretacoformica explicata* Jell and Duncan (Hymenoptera). *Journal of the Australian Entomological Society* 32, 355–356. <https://doi.org/10.1111/j.1440-6055.1993.tb00601.x>.
- Poropat, S.F., Martin, S.K., Tosolini, A.M.P., Wagstaff, B.E., Bean, L.B., Kear, B.P., Vickers-Rich, P., Rich, T.H., 2018. Early Cretaceous polar biotas of Victoria, southeastern Australia – an overview of research to date. *Alcheringa: An Australasian Journal of Palaeontology* in press. <https://doi.org/10.1080/03115518.2018.1453085>.
- Rasnitsyn, A.P., 1990. New representatives of the hymenopterous family Praeaulacidae from the Early Cretaceous in Buriatia and Mongolia. *Vestnik Zoologii* 1990 (6), 27–31 in Russian.
- Rasnitsyn, A.P., Basibuyuk, H.H., Quicke, D.L.J., 2004. A basal chalcidoid (Insecta: Hymenoptera) from the earliest Cretaceous or latest Jurassic of Mongolia. *Insect Systematics and Evolution* 35 (2), 123–135. <https://doi.org/10.1163/187631204788912391>.
- Rasnitsyn, A.P., Jarzembowski, E.A., Ross, A.J., 1998. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and paleoenvironmental significance. *Cretaceous Research* 19 (3 & 4), 329–391. <https://doi.org/10.1006/cres.1997.0114>.
- Rasnitsyn, A.P., Bashkuev, A.S., Kopylov, D.S., Lukashevich, E.D., Ponomarenko, A.G., Popov, Yu.A., Rasnitsyn, D.A., Ryzhkova, O.V., Sidorchuk, E.A., Sukatsheva, I.D., Vorontsov, D.D., 2016. Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). *Cretaceous Research* 61, 234–255. <https://doi.org/10.1016/j.cretres.2015.12.025>.
- Rasnitsyn, A.P., Brothers, D.J., 2007. Two new hymenopteran fossils from the mid-Cretaceous of southern Africa (Hymenoptera: Jurapriidae, Evaniidae). *African Invertebrates* 47 (1), 193–202.
- Rasnitsyn, A.P., Öhm-Kühnle, Ch., 2018. Three new female *Aptenoperissus* from mid-Cretaceous Burmese amber (Hymenoptera, Stephanoidea, Aptenoperissidae): Unexpected diversity of paradoxical wasps suggests insular features of source biome. *Cretaceous Research* 91, 168–175. <https://doi.org/10.1016/j.cretres.2018.06.004>.
- Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J., Liljeblad, J., Dowling, A.P.G., Schulmeister, S., Murray, D., Deans, A.R., Ronquist, F., Krogmann, L., Wheeler, W.C., 2012. Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* 28, 80–112. <https://doi.org/10.1111/j.1096-0031.2011.00366.x>.
- Tosolini, A.-M.P., McLoughlin, S., Drinnan, A.N., 2002. Early Cretaceous megaspore assemblages from southeastern Australia. *Cretaceous Research* 23, 807–844. <https://doi.org/10.1006/cres.2002.1031>.
- Vilhelmsen, L., Turrisi, G.F., 2010. Per arborem ad astra: Morphological adaptations to exploiting the woody habitat in the early evolution of Hymenoptera. *Arthropod Structure & Development* 40, 2–20. <https://doi.org/10.1016/j.asd.2010.10.001>.
- Zhang, Q., Rasnitsyn, A.P., Wang, B., Zhang, H.C., 2018. Hymenoptera (wasps, bees and ants) in mid-Cretaceous Burmese amber: A review of the fauna. In: *Proceedings of the Geologists' Association* in press. <https://doi.org/10.1016/j.pgeola.2018.06.004>.