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## The first beetle species described from Oligocene New Zealand amber (Coleoptera: Scirtidae)

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### Abstract

Previously reported beetle inclusions from New Zealand amber have preserved insufficient morphological details for an identification beyond family-level. Here, we describe the first beetle species from New Zealand amber, *Contacyphon pomahakaensis* Ruta **sp. nov.**, based on a newly discovered, well-preserved inclusion from the late Oligocene Pomahaka Formation in southern New Zealand. *C. pomahakaensis* Ruta **sp. nov.** is the first fossil record of marsh beetles (Scirtidae) described from New Zealand. The worldwide genus *Contacyphon* is well diversified with exclusively endemic species in New Zealand, suggesting a long presence and independent evolution in the region, which is confirmed by the new Oligocene amber fossil. A coastal swamp forest environment reconstructed for the formation of Pomahaka amber is in agreement with wet forest habitats of extant marsh beetles. Fourier transform infrared (FTIR) analysis of late Oligocene Pomahaka amber indicates that it originates from an Araucariaceae parent plant of *Agathis* affinity and has undergone comparatively little maturation.

**Keywords:** marsh beetle, araucarian resin, Oligocene, Pomahaka Formation, Zealandia

### Introduction

The long geographically isolated islands of New Zealand harbour a diverse beetle fauna of 82 families with some 1,090 genera and approximately 5,500 species plus many more undescribed species (Klimaszewski & Watt, 1997; Leschen *et al.*, 2003). Some groups that are diverse elsewhere are absent or poorly represented in the New Zealand fauna (*e.g.*, suborders Archostemata and Myxophaga) whereas several families and subfamilies

include endemic forms that are highly diverse compared to other parts of the world (*e.g.*, Byrrhidae, Zopheridae (Colydiinae), Hydraenidae, Melandryidae, Ptiliidae, Scirtidae and Scydmaeninae) (Klimaszewski & Watt, 1997; Leschen *et al.*, 2003). Overall the New Zealand beetle fauna is a composite of ancient forms that existed long before the break-up of Gondwana and more derived lineages introduced by dispersal mainly from Australia, Pacific Islands, Asia and Indonesia (Klimaszewski & Watt, 1997; Leschen *et al.*, 2003). Other factors responsible for the composition of the present-day beetle fauna are the long geographic isolation of New Zealand of ~80 mya, resulting in an extraordinarily high level of endemism (~90%) of species (plus many endemic genera, some endemic tribes and subfamilies and three endemic families, Agapythidae, Chalcodryidae, Cyclaxyridae), a complex geologic and climatic history through time and the absence of mammals and other biota that are present in ecosystems elsewhere (Klimaszewski & Watt, 1997; Leschen *et al.*, 2005; Gimmel *et al.*, 2009).

The published fossil (pre-Quaternary) record of beetles from New Zealand is extremely scarce with few specimens identified beyond family-level, thus providing little information on past diversity, habitats and possible extinctions of lineages through geological time. The Mesozoic record comprises a few beetle fragments of uncertain family assignment, including a probable elytron fragment from the Triassic (Grant-Mackie, 1958), two elytra and an abdominal fragment tentatively identified as Buprestidae(?) and Carabidae(?) from the mid-Cretaceous (Cenomanian–lowermost Turonian) of Chatham Islands (Stilwell *et al.*, 2016) and an unidentified elytron from the Upper Cretaceous (Campanian–Maastrichtian) (Craw & Watt, 1987).

From the Cenozoic Era numerous articulated beetles have been reported from various lake deposits and amber but only a few specimens have been described in detail. Articulated beetles of families Cerambycidae, Chrysomelidae, Curculionidae (Cossoninae and Curculioninae), Hydrophilidae and Staphylinidae (Osoriinae and Pselaphinae) have been reported from the Early Miocene (Aquitainian) lacustrine diatomites at Foulden Maar (Kaulfuss *et al.*, 2015) and one staphylinid species, *Sphingoquedius meto* Jenkins Shaw, Solodovnikov, Bai & Kaulfuss (Staphylinae, Amblyopinini), has so far been described from this site (Jenkins Shaw *et al.*, 2020). A species of straight-snouted weevil, *Perroudia manuharikia* Brown & Kaulfuss is the sole beetle published so far from the Early Miocene fluvial-lacustrine Dunstan Formation (Kaulfuss *et al.*, 2018). The mid-Miocene (Langhian) lacustrine deposits of the Hindon Maar Complex have yielded representatives of families Hydrophilidae, Buprestidae, Elateridae, Chrysomelidae(?) and Curculionidae, with the latter particularly common and including Apioninae, Cryptorhynchinae and Curculioninae, but detailed specimen descriptions are not yet available (Kaulfuss *et al.*, 2018).

The first beetles preserved as inclusions in New Zealand amber were reported by Schmidt *et al.* (2018). Among these, a complete but poorly preserved specimen was assigned to Chrysomelidae and a further specimen bearing hairs typical of Dermestidae was identified as *Trogoderma*-like larva, both from early Miocene amber. Other partially preserved amber beetles were not identifiable (Schmidt *et al.*, 2018).

In this contribution, we describe the first beetle species from New Zealand amber, based on a well-preserved specimen from the late Oligocene Pomahaka Formation in southern New Zealand. The new species is the first New Zealand fossil of the family Scirtidae (marsh beetles). The oldest unambiguous fossils of Scirtidae are larvae from the Lower Cretaceous deposits of Koonwarra Fossil Bed in Victoria, Australia (Watts & Hamon, 2023). Marsh beetles are rare in the mid-Cretaceous Kachin amber from Myanmar (Li *et al.*, 2022), in contrast to the Eocene Baltic amber, where Scirtidae are common—more than 10% of Coleoptera inclusions in Baltic amber are marsh beetles (Kulicka & Ślipiński, 1996). We provide a brief outline of the geological setting of the amber-bearing strata and discuss a FTIR spectrum of fossiliferous Pomahaka amber.

## Material and methods

About 1 kg of amber from locality G45/f0107 was processed and microscopically screened for inclusions

at the Department of Geobiology and the Department of Animal Evolution and Biodiversity at the University of Göttingen. No biological inclusions were found in blocky, angular pieces, whereas layered amber pieces formed by successive resin flows typically contained one or multiple arthropod inclusions (Fig. 1C).

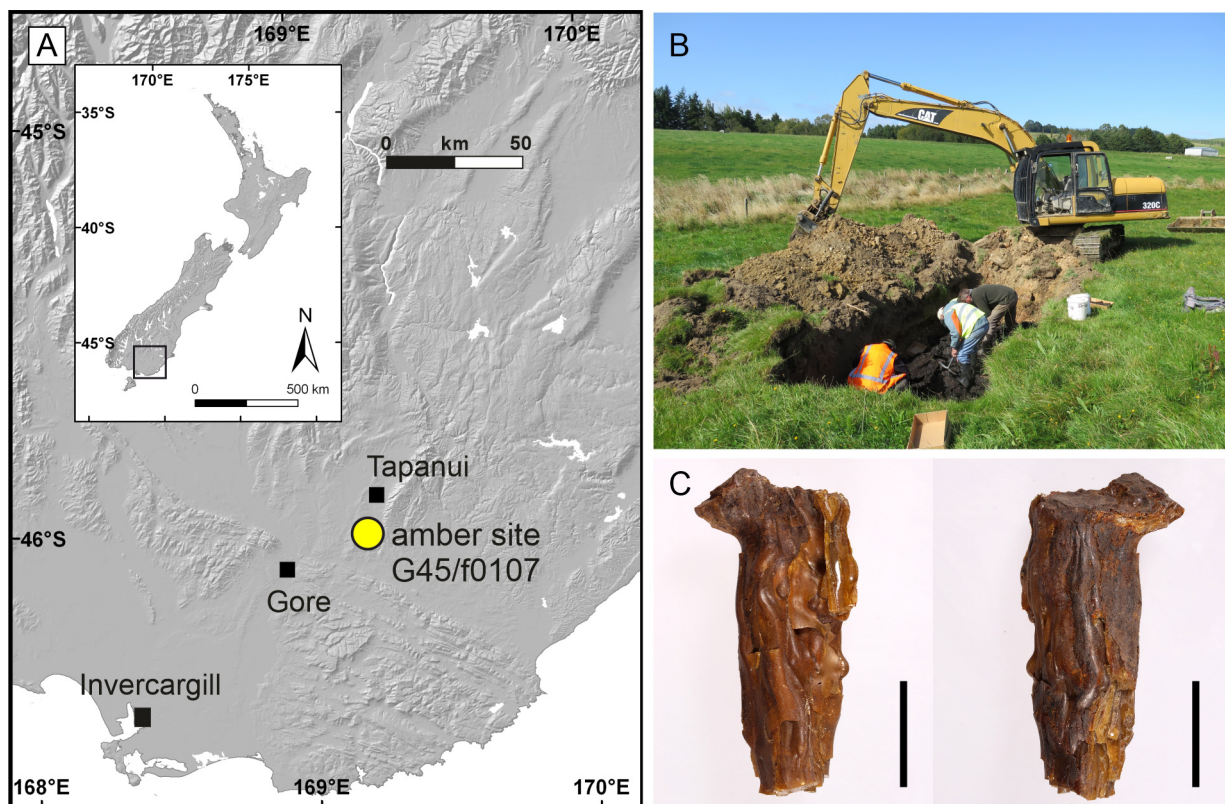
The amber piece containing specimen OU47547 was ground and polished manually to allow views of the dorsal and ventral sides of the beetle, using wet silicone carbide abrasive papers (FEPA P #220–4000). To stabilize the brittle amber and to improve its optical properties, the piece was embedded in epoxy resin. To this end, the piece was fixed to an ice cube compartment with a drop of epoxy-minute adhesive (Weicon), submerged in high-grade two-component epoxy resin (EPO-TEK 301-2, Epoxy Technology) and placed in a vacuum (50 mbar) for five minutes to remove air bubbles from the epoxy resin. After curing for 72 hours, the embedded amber piece was polished with a Buehler Eco-Met 250 grinder-polisher machine and CarbiMet silicone carbide abrasive papers (Buehler).

The specimen was observed with a Carl Zeiss AxioScope A1 compound microscope and a Nikon SMZ1500 stereomicroscope, and photographs were taken with Canon 5D and Nikon D5100 digital cameras. Final figures were generated with Helicon Focus (8.2.0) software and enhanced using Adobe® Photoshop CC. Total length is measured from anterior edge of pronotum to elytral apices. The nomenclature of male genitalia follows that of Nyholm (2000). Abbreviations: TL—total length, EW—elytral width.

Fourier transform infrared spectra (FTIR) were obtained for the amber samples containing the beetle specimen described here. Analyses were performed at the laboratory Amber Experts in Gdańsk, Poland with a Nicolet 380 FTIR spectrometer with an attenuated total reflectance accessory. The spectrum of Pomahaka amber was compared to previously published FTIR spectra of modern and fossil resins (Lyons *et al.*, 2009; Wolfe *et al.*, 2009; Tappert *et al.*, 2011; Seyfullah *et al.*, 2015).

## Geological setting

The beetle specimen described herein is deposited in the Geology Museum, Geology Department, University of Otago, under catalogue number OU47547. It is embedded in a piece of amber from the late Oligocene Pomahaka Formation, which is exposed along the banks of the Pomahaka River and its tributaries near Tapanui, South Otago, New Zealand (Fig. 1A). Interbedded sandstones/mudstones, shell beds, carbonaceous mudstones and lignite of the Pomahaka Formation represent repeated



**FIGURE 1.** Late Oligocene amber from the Pomahaka Formation in southern New Zealand. **A**, Locality map of amber site G45/f0107 near Pomahaka River south of Tapanui (Otago). **B**, Temporary outcrop of amber-bearing lignite. **C**, Piece of layered, fossiliferous Pomahaka amber. Scale bars = 2 cm.

depositional cycles within an estuarine to coastal swamp forest environment (Lindqvist *et al.*, 2016). The late Oligocene age (Chattian, New Zealand stage: Duntroonian, 27.3–25.3 Ma) of Pomahaka Formation is based on palynomorph and molluscan biostratigraphy (summarized in Lindqvist *et al.*, 2016).

The numerous lignite beds, often forming resistant banks in Pomahaka River, are 5 to <150 cm thick and typically contain large amounts of fossilized resin (amber). Peat accumulation occurred from *in situ* growth (as evidenced by rootlets and upright tree stumps in the lignite) and decomposition of wetland forest trees and litter in domed forest swamps protected from seawater incursion or overbank sedimentation (Lindqvist *et al.*, 2016). The palynoflora of trees and herbaceous plants from the lignite indicates that the forest trees included abundant Araucariaceae and several Podocarpaceae taxa, together with *Casuarina* Linnaeus (Casuarinaceae), palms (Arecaceae) and southern beech (Nothofagaceae), with the latter probably growing further inland (Pocknall, 1982; D.C. Mildenhall, pers. comm., 2014). Carbonaceous mudstones at the base of lignite seams also frequently contain amber and likely accumulated in areas of brackish mire or saltmarsh shoreward of peat-forming forests (Lindqvist *et al.*, 2016).

Specimen OU47547 originates from an amber-bearing lignite bed that was temporarily exposed in a small prospecting pit on private farmland, near Pomahaka River, 12 km south of the township of Tapanui (46.0445°S, 169.22292°E) in 2014 and 2024 (Fig. 1B). The locality is registered as G45/f0107 in the New Zealand Fossil Record File (GNS Science & Geological Society of New Zealand, 2024).

### Systematic palaeontology

#### Family Scirtidae Fleming, 1821

#### Subfamily Scirtinae Fleming, 1821

#### Genus *Contacyphon* des Gozis, 1886

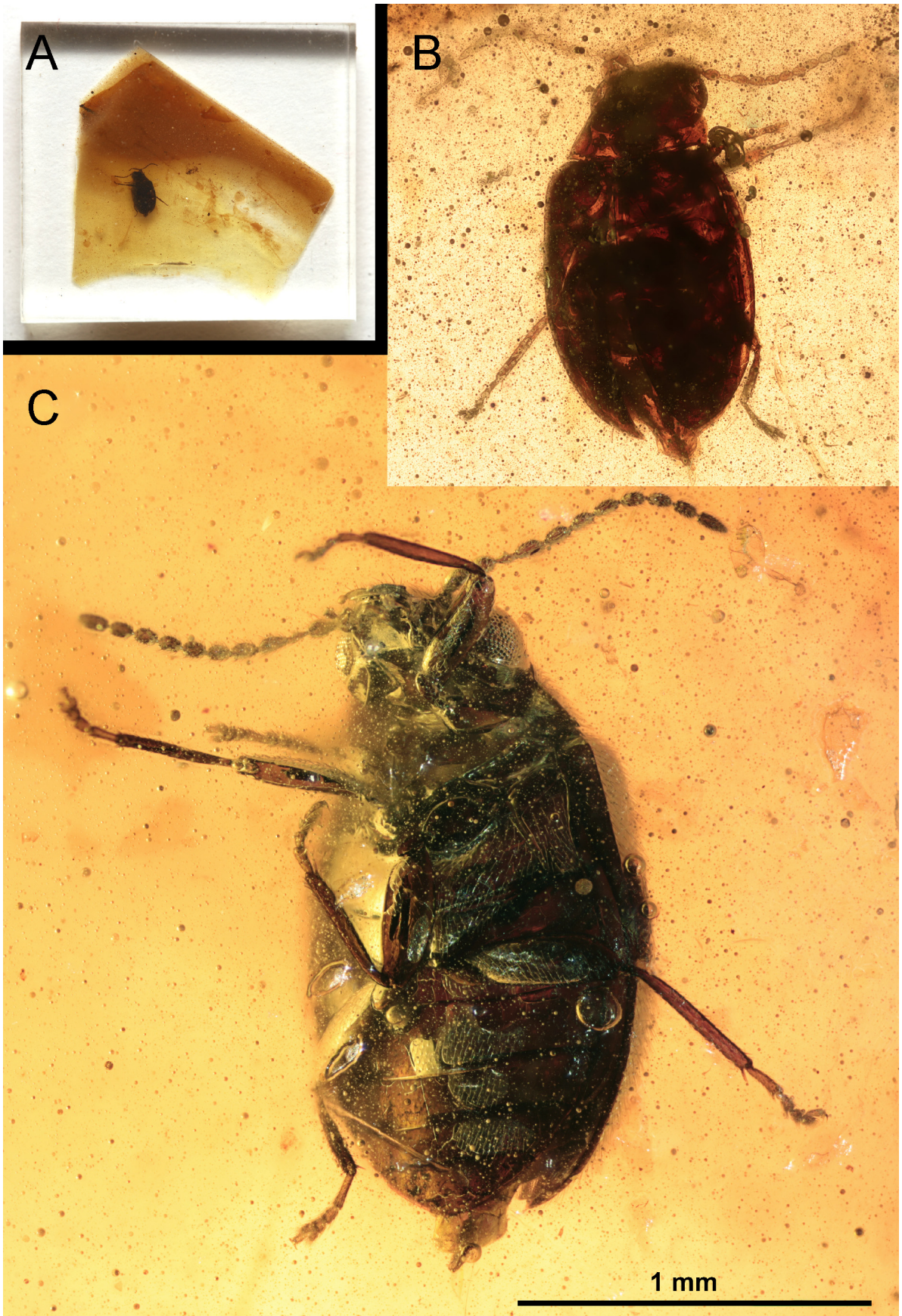
**Type species.** *Cantharis variabilis* Thunberg, 1787; by original designation.

#### *Contacyphon pomahakaensis* Ruta, sp. nov.

(Figs 2–4)

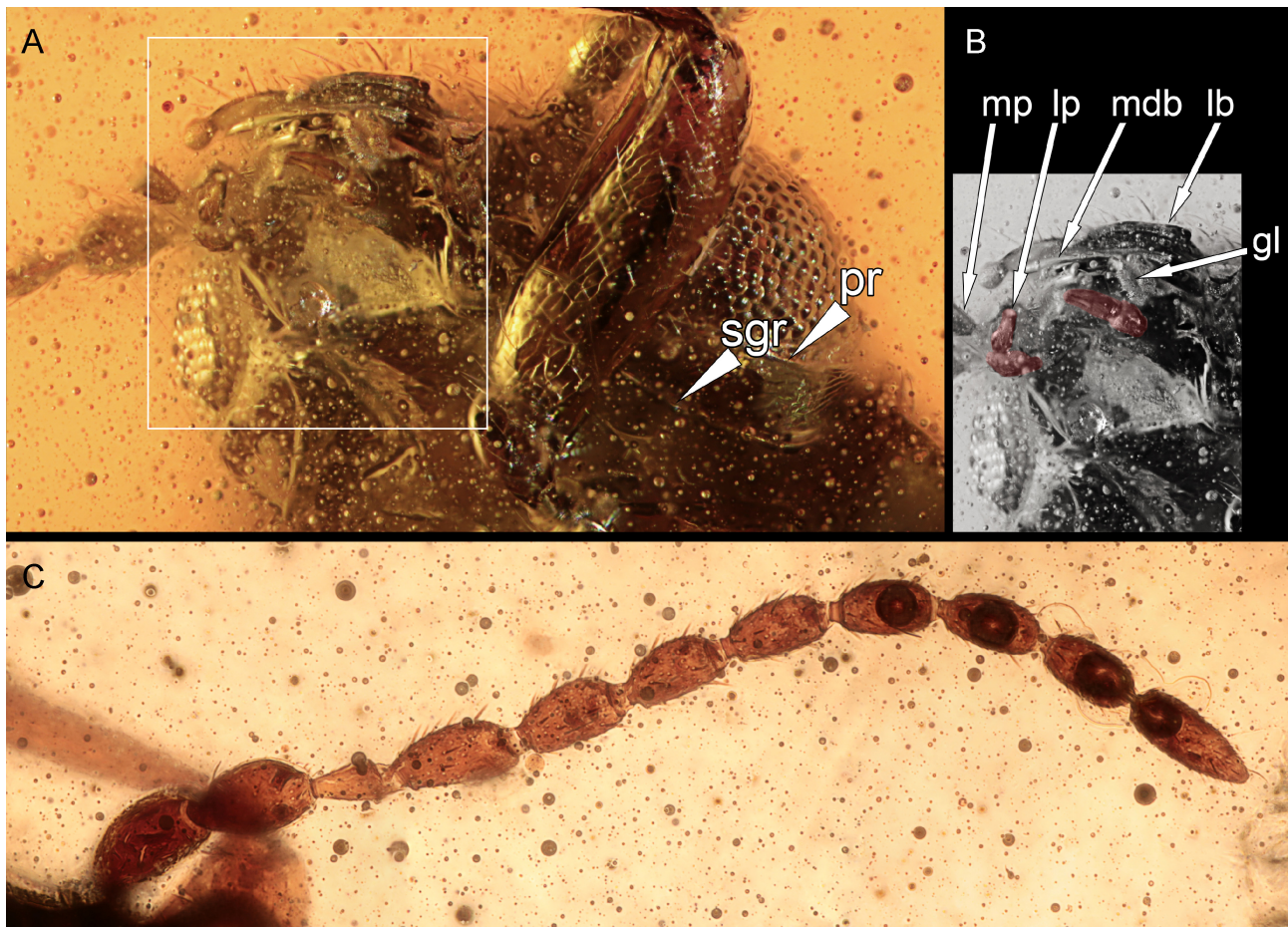
**Type material.** Holotype OU47547 deposited in the Geology Museum, Department of Geology, University of Otago, New Zealand.





**FIGURE 2.** *Contacyphon pomahakaensis* Ruta, **sp. nov.** **A**, General view of the specimen embedded in resin. **B**, Habitus, dorsal view. **C**, Habitus, ventral view.





**FIGURE 3.** *Contacyphon pomahakaensis* Ruta, **sp. nov.** **A**, Head, ventral view, white frame marks the portion shown in **B**. **B**, Mouthparts, labial palpi marked in red. **C**, Antenna. Abbreviations: gl, galea; lb, labium; lp, labial palpus; mdb, mandible; mp, maxillary palpus; pr, postocular ridge; sgr, subgenal ridge.

**Etymology.** The specific epithet refers to Pomahaka River in southern New Zealand, where the new species was discovered.

**Diagnosis.** The species externally resembles other small members of the genus. Identification is possible on the basis of male genitalic characters: apices of parameroids rounded, trigonium bifid, pointed at apices. This combination of characters is unknown in extant members of the genus recorded in New Zealand.

**Type locality and horizon.** Temporary excavation in lignite, locality G45/f0170, 12 km south of Tapanui, New Zealand; Pomahaka Formation, late Oligocene (Chattian; New Zealand stage Duntroonian).

**Description.** Holotype, male. Body small (TL 1.7 mm, EW 0.96 mm), oblong oval, TL/EW 1.8, slightly depressed, covered with semi-erect, brownish, setae. Body dark brown, head and pronotum appear slightly lighter than elytra.

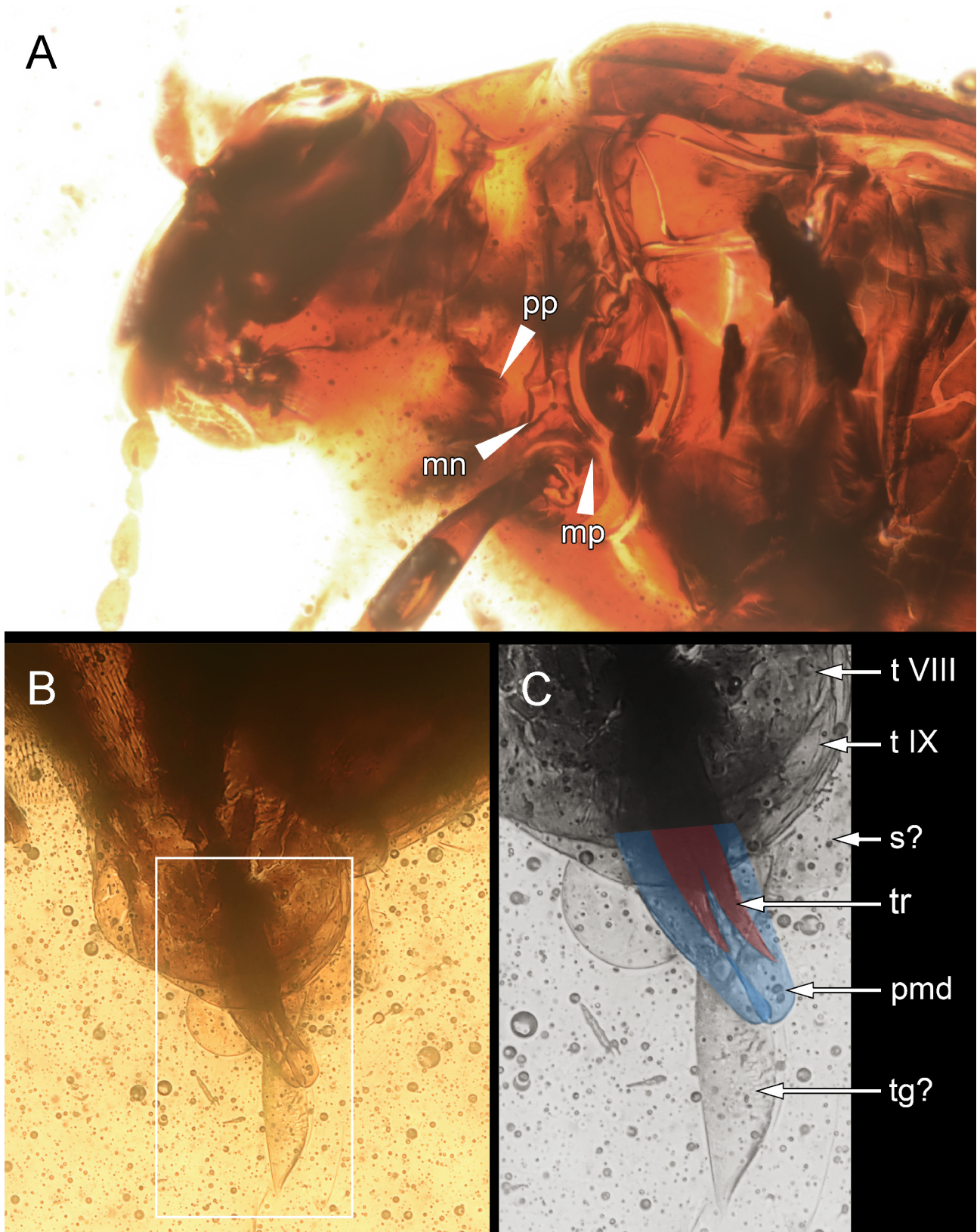
Head 1.6× as wide as interocular space, eyes moderately big, slightly protuberant; tempora short, converging posteriorly. Clypeus transverse, with distinct

emargination in the middle of anterior margin, apical maxillary palpomeres missing in the examined specimen, apical labial palpomeres arising from the apices of preapical palpomeres, mandibles with acute, narrow apices. Scape cylindrical without ridge on anterior portion, antennomere 2 globular, 3 subconical, short, very narrow, antennomeres 4–5 elongated, subconical, antennomeres 6–10 subcylindrical, antennomere 11 with pointed apical portion. Length ratio of antennomeres: 1.7 : 1.5 : 1.0 : 1.5 : 1.2 : 1.2 : 1.2 : 1.1 : 1.1 : 1.1 : 1.7. Subgenal ridge well marked, buttonhole not visible in the studied specimen; postocular ridge present.

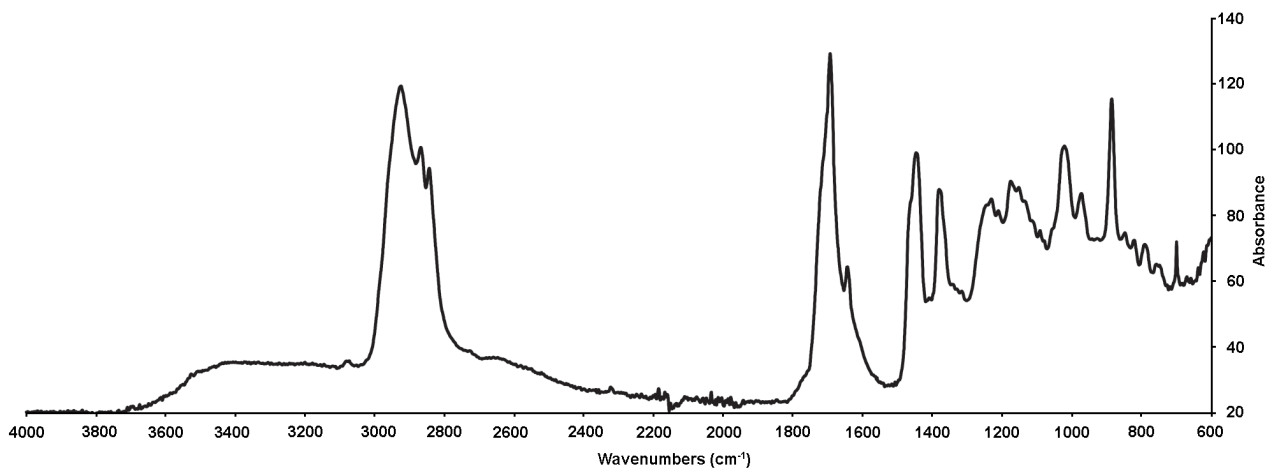
Pronotum transverse, widest at posterior angles, anterolateral angles not produced, posterior angles almost right-angled, sides of pronotum short, straight, slightly converging anteriorly.

Scutellar shield equilaterally triangular. Angle between pronotum and elytra well marked in dorsal outline. Elytra without traces of longitudinal ridges, sides rounded, regularly converging to apex in posterior half. Humeri subtly marked. Punctuation of elytra normal (not





**FIGURE 4.** *Contacyphon pomahakaensis* Ruta, **sp. nov.** **A**, Ventrolateral view. **B**, Exposed genitalia, white frame marks the area shown in **C**. **C**, Details of genitalia, apical portions of trigonum marked in red, apical portions of parameroide marked in blue. Abbreviations: mn, mesoventral notch; mp, mesoventral process; pmd, parameroide; pp, prosternal process; s, sternite; t VIII, tergite VIII; t IX, tergite IX; tg, tegmen; tr, trigonum.



**FIGURE 5.** Fourier-Transform infrared (FTIR) spectrum of amber from locality G45/f0107, late Oligocene Pomahaka Formation.

granulate), rather coarse, punctures separated by *ca.* 0.5 diameter. Metatibial spur as long as width of tibia.

Prosternal process tear-shaped, *ca.* 2.0× as long as wide. Mesoventral notch subtriangular. Mesocoxae separated by short process with emarginated apex, mesocoxal cavities not contiguous. Ventrites of similar lengths, ventrite 5 regularly rounded, truncate at apex.

Genitalia exposed, symmetrical. Sternites indistinct, probably membranous. Tergites VIII and IX with transverse, subrectangular apical plates. Penis slightly distorted, narrow, trigonium bifid, divided into two sharp spines, parameroids rounded at apices. Structure interpreted here as part of tegmen (paramere?) elongate, pointed at apex.

**Remarks.** Some of important morphological features of *Contacyphon*, like the buttonhole configuration of the subgenal ridge, are not visible in the studied specimen or are poorly visible, like the mesoventral notch that seems to be triangular rather than pentagonal and elevated, like in contemporary *Contacyphon*. On the other hand, the general body shape and the presence of the postocular ridge strongly resemble New Zealand species classified as members of *Contacyphon* and there is little doubt that the new species belongs to this genus.

## Results

### FTIR analysis

The FTIR spectrum of Pomahaka amber is shown in Figure 5. Following the characterisation of modern and fossil gymnosperm exudates by Tappert *et al.* (2011), the Pomahaka sample is identified as a “cupressaceous resin” type based on distinct peaks at 2848 cm<sup>-1</sup> (absent or poorly expressed peak in pinaceous resins) and 1448

cm<sup>-1</sup> (weak peak or shoulder in pinaceous resins), and the absence of a peak at 1460 cm<sup>-1</sup> (peak in pinaceous resins). This is further supported by distinctive absorption features below 1100 cm<sup>-1</sup>, that is, peaks at 1091, 1030, 887 and 791 cm<sup>-1</sup>, which characterize cupressaceous resins and are absent in pinaceous resins (Tappert *et al.*, 2011). Cupressaceous resins are mainly produced by members of the Cupressaceae and Araucariaceae, and, to a lesser extent, by members of the Podocarpaceae and Sciadopityaceae. The cupressaceous resins analysed by Tappert *et al.* (2011: figs 1, 2) include four members of Cupressaceae (*Cupressus sempervirens* L., *Chamaecyparis lawsonia* (A. Murray) Parl., *Juniperus chinensis* L. and *Widdringtonia dracomontana* (L.) Powrie) and three members of Araucariaceae (*Agathis australis* (D. Don) Lindl., *Araucaria laubenfelsii* Corbasson and *Wollemia nobilis* W.G. Jones, K.D. Hill & J.M. Allen). Compared to these, the spectrum of Pomahaka amber is most similar to *A. australis*, particularly in the region of highest variability of spectra between 1200–1300 cm<sup>-1</sup>.

Among other published FTIR spectra of modern araucarian resins and fossil resins from New Zealand (Lyons *et al.*, 2009; Wolfe *et al.*, 2009; Seyfullah *et al.*, 2015), our sample is again most similar to *A. australis* but differs slightly in intensities and absorbance features that are most likely related to oxidation and maturation of the resin. Seyfullah *et al.* (2015) compared FTIR spectra of seven modern Araucariaceae exudates and one Miocene amber sample from New Zealand and provided 12 key distinguishing features for sample differentiation. Applying their distinguishing features, the Pomahaka amber corresponds most closely to *A. australis* and the Miocene amber (of *Agathis* affinity) and has less similarity to other araucarian species (*Agathis lanceolata* Warb., *A. ovata* Moore ex Vieill. Warb., *Araucaria heterophylla*



(Salisb.) Franco, *A. humboldtensis* Buchh., *A. nemorosa* de Laub. and *Wollemia nobilis*) sampled by Seyfullah *et al.* (2015). All modern araucarian resins analysed by Seyfullah *et al.* (2015) were interpreted as having peaks at 1385 cm<sup>-1</sup> and the absence of such a peak in the Miocene amber sample was explained by possibly different oxidation histories. In this regard, the Pomahaka amber is more similar to modern resins than to the Miocene amber, as a peak is clearly present at 1385 cm<sup>-1</sup>. The spectrum of Pomahaka amber also differs from that of Miocene amber (Seyfullah *et al.*, 2015) in having a shoulder at 1234 cm<sup>-1</sup> (not featured in Miocene amber) and peaks at 1178 cm<sup>-1</sup> and 1091 cm<sup>-1</sup> (not featured in Miocene amber). If the suggestion that the lack of clear peaks between about 1265–1091 cm<sup>-1</sup> might reflect effects of maturation is correct (Seyfullah *et al.*, 2015), the presence of peaks in this region in Pomahaka amber would indicate a comparatively immature amber.

Compared with FTIR spectra of modern *A. australis* resin and Miocene and Eocene Australasian resins in Lyons *et al.* (2009), our sample of Pomahaka amber shows high similarity with *A. australis* and Eocene New Zealand resins and less similarity with Miocene Australian resins, which are thought to represent a different botanical source. In terms of exomethylene groups, which are very distinct in modern resins, become less distinct in older resins and disappear in resins from high volatile C bituminous coal, our sample is more similar to the modern *A. australis* resin than to the Eocene New Zealand resins (resinites) analysed by Lyons *et al.* (2009), as is evident from distinct (albeit somewhat weaker than in the modern resin) peaks at 3082, 1644 and 887 cm<sup>-1</sup>, again implying a relatively immature amber.

## Discussion

*Contacyphon pomahakaensis* Ruta, **sp. nov.** is the first beetle species described from New Zealand amber and the first fossil marsh beetle (Scirtidae) reported from this country. Scirtidae of New Zealand are diverse, species-rich and highly endemic, with 12 genera (10 of them endemic) and 129 species (all endemic) known to date (Kiałka & Ruta, 2017, 2018, 2022). Little is known about the biology and biogeography of these taxa and many more New Zealand Scirtidae remain to be described (*e.g.*, Klimaszewski & Watt, 1997; Kiałka & Ruta, 2017). In general, most larvae are filter-feeding detritivores in shallow stagnant waters but may also occur ponds, stream microhabitats, groundwater, phytotelmata or wet soil, whereas adults are found on riparian vegetation, on flowers, shrubs or on trees in wet forest areas (Klimaszewski & Watt, 1997; Kiałka & Ruta, 2017; Libonatti & Ruta, 2018). One of the non-endemic genera in New Zealand

is the worldwide distributed *Contacyphon* des Gozis, formerly known under the invalid name *Cyphon* Paykull (Zwick *et al.*, 2013). There are 50 species of *Contacyphon* recorded from New Zealand, and a larger number that are still undescribed. The only modern review was published by Nyholm (2000), but it covered only a fraction of New Zealand species. The presence of exclusively endemic species of *Contacyphon* in New Zealand may indicate an isolated evolution on the islands over geological time scales. This view is supported by the find of *Contacyphon pomahakaensis* **sp. nov.** as an inclusion in amber from a coastal swamp forest environment of late Oligocene age (~26 Ma).

Our FTIR analysis suggests an araucarian origin for fossiliferous Pomahaka amber, most likely from a species of *Agathis* since the amber spectrum has the highest similarity to that of *Agathis australis* and Miocene amber of *Agathis* affinity. This result is in agreement with previous studies, which suggested *Agathis* as the parent plant of most or all New Zealand amber (Lambert *et al.*, 1993, 1999; Lyons *et al.*, 2009; Seyfullah *et al.*, 2015). A parent plant in Araucariaceae is further supported by the presence of araucarian wood (either *Agathis* or *Araucaria*) (Lee *et al.*, 2009) and locally frequent pollen of *Araucariacites australis* Cookson (Pocknall, 1982; D.C. Mildenhall, pers. comm., 2014) in Pomahaka Formation. *Araucariacites australis* is known in New Zealand since the Cretaceous but its parent plant has not been determined; it probably represents an extinct species of either *Agathis* or *Araucaria* (Raine *et al.*, 2011).

Compared to Eocene resins from bituminous coal in New Zealand (Lyons *et al.*, 2009), the Pomahaka amber is less matured, as would be expected from a much younger amber from lignite. However, our sample of Pomahaka amber also appears to be less matured than the slightly younger, early Miocene New Zealand amber analysed by Seyfullah *et al.* (2015). This may reflect minimal burial and diagenetic alteration of Pomahaka Formation, which can also be inferred from the exceptional preservation of molluscs with carbonised ligament and periostracal tissue (Lindqvist *et al.*, 2016), leaves with cuticle preservation (Lee *et al.*, 2009) and iridescent colours in beetle elytra (pers. observation) in Pomahaka Formation mudstones.

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## References

- Craw, R.C. & Watt, J.C. (1987) An Upper Cretaceous beetle (Coleoptera) from Hawkes Bay, New Zealand. *Journal of the Royal Society of New Zealand*, 17 (4), 395–398.  
<https://doi.org/10.1080/03036758.1987.10426480>
- Gimmel, M.L., Leschen, R.A.B. & Ślipiński, A. (2009) Review of the New Zealand endemic family Cyclaxyridae, new family (Coleoptera: Polyphaga). *Acta Entomologica Musei Nationalis Pragae*, 49 (2), 511–528.
- GNS Science & Geological Society of New Zealand. (2024) New Zealand Fossil Record File [G43/f8500, G45/f0107]. GNS Science.  
<https://doi.org/10.21420/JQQB-NK89>
- Grant-Mackie, J.A. (1958) *The stratigraphy and paleontology of rocks of the Hokonui System, Awakino-Mahoenui area, Southwest Auckland*. Unpublished MSc thesis, University of Auckland, New Zealand, 186 pp.  
<https://doi.org/10.1080/00288306.1959.10422769>
- Jenkins Shaw, J., Solodovnikov, A., Bai, M. & Kaulfuss, U. (2020) An amblyopinine rove beetle (Coleoptera, Staphylinidae, Staphylininae, Amblyopinini) from the earliest Miocene Foulden Maar fossil-Lagerstätte, New Zealand. *Journal of Paleontology*, 94 (6), 1082–1088.  
<https://doi.org/10.1017/jpa.2020.35>
- Kaulfuss, U., Brown, S.D.J., Henderson, I.M., Szewo, J. & Lee, D.E. (2018) First insects from the Manuherikia Group, early Miocene, New Zealand. *Journal of the Royal Society of New Zealand*, 49 (4), 494–507.  
<https://doi.org/10.1080/03036758.2018.1477054>
- Kaulfuss, U., Lee, D.E., Barratt, B.I.P., Leschen, R.A.B., Larivière, M.-C., Dlussky, G.M., Henderson, I.M. & Harris, A.C. (2015) A diverse fossil terrestrial arthropod fauna from New Zealand: evidence from the early Miocene Foulden Maar fossil Lagerstätte. *Lethaia*, 48, 299–308.  
<https://doi.org/10.1111/let.12106>
- Kiałka, A. & Ruta, R. (2017) An illustrated catalogue of the New Zealand marsh beetles (Coleoptera: Scirtidae). *Zootaxa*, 4366 (1), 1–76.  
<https://doi.org/10.11646/zootaxa.4366.1.1>
- Kiałka, A. & Ruta, R. (2018) *Meatopida* gen. nov., a new genus to accommodate two species originally described in *Atopida* White, 1846 (Coleoptera: Scirtoidea: Scirtidae). *Zootaxa*, 4382 (2), 242–260.  
<https://doi.org/10.11646/zootaxa.4382.2.2>
- Kiałka, A. & Ruta, R. (2022) Revision of *Atopida* White, 1846 (Coleoptera: Scirtoidea: Scirtidae). *Zootaxa*, 5174 (4), 401–443.  
<https://doi.org/10.11646/zootaxa.5174.4.6>
- Klimaszewski, J. & Watt, J.C. (1997) *Coleoptera: family-group review and keys to identification*. Landcare Research, Lincoln, New Zealand, 197 pp.
- Kulicka, R. & Ślipiński, S. (1996) A review of the Coleoptera inclusions in the Baltic amber. *Prace Muzeum Ziemi*, 44, 5–11.
- Lambert, J.B., Shaul, C.E., Poinar, G.O., Jr & Santiago-Blay, J.A. (1999) Classification of modern resins by solid nuclear magnetic resonance spectroscopy. *Bioorganic Chemistry*, 27, 409–433.  
<https://doi.org/10.1006/bioo.1999.1147>
- Lambert, J.B., Johnson, S.C., Poinar, G.O., Jr & Frye, J.S. (1993) Recent and fossil resins from New Zealand. *Geoarchaeology*, 8, 141–155.  
<https://doi.org/10.1002/gea.3340080206>
- Lee, D., Lindqvist, J., Mildenhall, D., Bannister, J. & Kaulfuss, U. (2009) Paleobotany, palynology and sedimentology of Late Cretaceous—Miocene sequences in Otago and Southland. In: Turnbull, I.M. (Ed.), Field trip guides, Geosciences 09 Conference, Oamaru, New Zealand. *Geological Society of New Zealand Miscellaneous Publication*, 128B, 39 pp.
- Leschen, R.A.B., Lawrence, J.F. & Ślipiński, A. (2005) Classification of basal Cucujoidea (Coleoptera: Polyphaga): cladistic analysis, keys and review of new families. *Invertebrate Systematics*, 19 (1), 17–73.  
<https://doi.org/10.1071/IS04007>
- Leschen, A.B., Lawrence, J.F., Kuschel, G., Thorpe, S. & Wang, Q. (2003) Coleoptera genera of New Zealand. *New Zealand Entomologist*, 26, 15–28.  
<https://doi.org/10.1080/00779962.2003.9722105>
- Li, Y.D., Ruta, R., Tihelka, E., Liu, Z.H., Huang, D.Y. & Cai, C.Y. (2022) A new marsh beetle from mid-Cretaceous amber of northern Myanmar (Coleoptera: Scirtidae). *Scientific Reports*, (2022) 12, 13403.  
<https://doi.org/10.1038/s41598-022-16822-y>
- Libonatti, M.L. & Ruta, R. (2018) Family Scirtidae. In: Hamada, N., Thorp, H. & Rogers, D.C. (Eds), *Thorp and Covich's Freshwater Invertebrates*. 4<sup>th</sup> Edition. Vol. 3. Keys to Neotropical Hexapoda. Academic Press, Cambridge, pp. 599–603.  
<https://doi.org/10.1016/B978-0-12-804223-6.00028-7>
- Lindqvist, J.K., Gard, H.J.L. & Lee, D.E. (2016) Geological setting, sedimentology and biota of the estuarine late Oligocene Pomahaka Formation, New Zealand. *New Zealand Journal of Geology and Geophysics*, 59 (2), 352–365.  
<https://doi.org/10.1080/00288306.2016.1150862>

- Lyons, P.C., Mastalerz, M. & Orem, W.H. (2009) Organic geochemistry of resins from modern *Agathis australis* and Eocene resins from New Zealand: Diagenetic and taxonomic implications. *International Journal of Coal Geology*, 80, 51–62.  
<https://doi.org/10.1016/j.coal.2009.07.015>
- Nyholm, T. (2000) New species, taxonomic notes, and genitalia of New Zealand *Cyphon* (Coleoptera, Scirtidae). *New Zealand Entomologist*, 22, 45–67.  
<https://doi.org/10.1080/00779962.1999.9722054>
- Pocknall, D.T. (1982) Palynology of late Oligocene Pomahaka Estuarine Bed sediments, Waikoikoi, Southland, New Zealand. *New Zealand Journal of Botany*, 20, 263–287.  
<https://doi.org/10.1080/0028825X.1982.10428495>
- Raine, J.I., Mildenhall, D.C. & Kennedy, E.M. (2011) New Zealand fossil spores and pollen: an illustrated catalogue. 4<sup>th</sup> edition. GNS Science miscellaneous series no. 4. Available from: <http://data.gns.cri.nz/sporepollen/index.htm> (accessed 6 May 2024).
- Schmidt, A.R., Kaulfuss, U., Bannister, J.M., Baranov, V., Beimforde, C., Bleile, N., Borkent, A., Busch, A., Conran, J.G., Engel, M.S., Harvey, M., Kennedy, E.M., Kerr, P.H., Kettunen, E., Kiecksee, A.P., Lengeling, F., Lindqvist, J.K., Maraun, M., Mildenhall, D.C., Perrichot, V., Rikkinen, J., Sadowski, E.-M., Seyfullah, L.J., Stebner, F., Szewedo, J., Ulbrich, P. & Lee, D.E. (2018) Amber inclusions from New Zealand. *Gondwana Research*, 56, 135–146.  
<https://doi.org/10.1016/j.gr.2017.12.003>
- Seyfullah, L.J., Sadowski, E.-M. & Schmidt, A.R. (2015) Species-level determination of closely related araucarian resins using FTIR spectroscopy and its implications for the provenance of New Zealand amber. *PeerJ*, 3, e1067.  
<https://doi.org/10.7717/peerj.1067>
- Stilwell, J.D., Vitacca, J. & Mays, C. (2016) South Polar greenhouse insects (Arthropoda: Insecta: Coleoptera) from the mid-Cretaceous Tupuangi Formation, Chatham Islands, eastern Zealandia). *Alcheringa*, 40, 502–508.  
<https://doi.org/10.1080/03115518.2016.1144385>
- Tappert, R., Wolfe, A.P., McKellar, R.C., Tappert, M.C. & Muehlenbachs, K. (2011) Characterizing modern and fossil gymnosperm exudates using micro-Fourier transform infrared spectroscopy. *International Journal of Plant Sciences*, 172 (1), 120–138.  
<https://doi.org/10.1086/657277>
- Watts, C.H.S. & Hamon, H. (2023) Fossil marsh beetle larvae (Scirtidae: Coleoptera) from the Lower Cretaceous (Aptian) Koonwarra Fossil Bed of Victoria, Australia. *Alcheringa: An Australasian Journal of Palaeontology*, 47 (1), 122–126.  
<https://doi.org/10.1080/03115518.2023.2184493>
- Wolfe, A.P., Tappert, R., Muehlenbachs, K., Boudreau, M., McKellar, R.C., Basinger, J.F. & Garrett, A. (2009) A new proposal concerning the botanical origin of Baltic amber. *Proceedings of the Royal Society B*, 276, 3403–3412.  
<https://doi.org/10.1098/rspb.2009.0806>
- Zwick, P., Klausnitzer, B. & Ruta, R. (2013) *Contacyphon* Gozis, 1886 removed from synonymy (Coleoptera: Scirtidae) to accommodate species so far combined with the invalid name, *Cyphon* Paykull, 1799. *Entomologische Blätter und Coleoptera*, 109, 337–353.