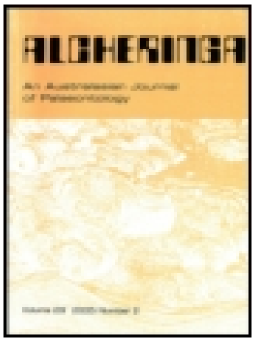

Alcheringa: An Australasian Journal of Palaeontology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/talc20

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To cite this article: Russell D.C. Bicknell, Patrick M. Smith & Julien Kimmig (2023): Novel coprolitic records from the Silurian (Přídolí) Wallace Shale of New South Wales, Alcheringa: An Australasian Journal of Palaeontology, DOI: 10.1080/03115518.2023.2185679

To link to this article: https://doi.org/10.1080/03115518.2023.2185679

Published online: 21 Mar 2023.

ALCHERINGA: AN AUSTRALASIAN JOURNAL OF PALAEONTOLOGY
https://doi.org/10.1080/03115518.2023.2185679

Novel coprolitic records from the Silurian (Přídolí) Wallace Shale of New South Wales

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ABSTRACT
Evidence of successful predation or scavenging in the fossil record represents important palaeobiological data to more thoroughly understanding extinct ecosystems. Shelly coprolites are particularly useful indications of durophagous predation in deposits, as they can have a higher preservational potential than their producers. Here we present a new shelly coprolite from the Silurian (Přídolí) Wallace Shale of New South Wales, Australia. This specimen contains abundant fragments of the trilobite *Denckmannites rutherfordi* Sherwin, 1968 that show limited disarticulation across exoskeletal sections. We propose that a pterygotid eurypterid was the most likely producer of this coprolite, although trilobites and fishes are not completely excluded as possible trace-makers. In documenting this specimen, we highlight that the Wallace Shale likely preserves a more complex palaeoecosystem than previously thought and renewed efforts to understand this deposit are needed in light of this new insight.

ARTICLE HISTORY
Received 12 January 2023
Revised 22 February 2023
Accepted 24 February 2023

KEYWORDS
Coprolite; predation; durophagy; Wallace Shale; Australia; Silurian

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RECORDS of predation within the fossil record present important information regarding predator–prey dynamics in palaeoecosystems (Brett 1990, 2003, Kowalewski 2002, Klompmaker *et al.* 2019). Injured specimens (Babcock 1993, 2003, Vinn 2009, 2017, 2018, Bicknell & Paterson 2018, Bicknell & Pates 2020, Bicknell *et al.* 2018b, 2023), drill holes (Kowalewski *et al.* 2000, Hoffmeister 2002, Amano 2003, Hoffmeister *et al.* 2004, Vinn *et al.* 2021), gut contents (Richter 1992, Sues 1993, Jago *et al.* 2016, Zacaï *et al.* 2016), and coprolites (Häntzschel *et al.* 1968, Hunt 1992, Toom et al. 2020, Kimmig & Strotz 2017, Kimmig & Pratt 2018, Knaust 2020, Hunt & Lucas 2021) all represent useful evidence of predation. These different records present varying degrees of insight into possible trophic interactions, with the rarer specimens (such as prey within gut contents) presenting much more palaeoecological information (Babcock 1993, Zacaï *et al.* 2016, Bicknell & Paterson 2018).

Coprolites containing fragmentary animal parts record predation or scavenging and are very useful for reconstructing trophic interactions. Shelly coprolites often reflect shell crushing (durophagous) activity and have a higher preservation potential than their producers (Vannier & Chen 2005). Shelly coprolites are well-documented in early to middle Paleozoic deposits (e.g., Vannier & Chen 2005, Klompmaker *et al.* 2019) and such examples are usually attributed to activity by durophagous animals, such as trilobites and other euarthropods (e.g., Vannier & Chen 2005, Bicknell & Paterson 2018, Bicknell *et al.* 2022a), with few examples possibly being produced by early vertebrates (Hunt *et al.* 2012). While the Cambrian coprolite record is excellent (e.g., Vannier & Chen 2005, Kimmig & Strotz 2017, Kimmig & Pratt 2018, Knaust 2020), the Ordovician and Silurian records are comparatively poor (Hunt *et al.* 2012). The identification of shelly coprolites within deposits of these time periods therefore presents new evidence for possible durophagous animals. To expand the record of Silurian coprolites (e.g., Rolfe 1973, Bischoff 1990, Gilmore 1992, Edwards *et al.* 1995), and demonstrate novel examples of durophagous predation within late Silurian deposits of Australia, we report a shelly aggregation from the Silurian (Přídolí)-aged Wallace Shale.

Materials and methods

The specimen (AM F158002) reported herein was collected by PMS from near Mirrabooka 'homestead' along a tributary of Wattle Creek, at approximately 33°12′27.00″S, 148°51′48.72″E (originally collected by Sherwin 1968) within the Wallace Shale (Figure 1). This location is slightly north of the old township of Cheesemans Creek (near Orange), at the midpoint between Bathurst and Parkes, central New South Wales (NSW), Australia. The specimen was collected from a single bedding plane that contained numerous *Denckmannites rutherfordi* Sherwin, 1968 (Figure 1D), preserved in articulation, or in the Salterian moulting

Published online 21 Mar 2023

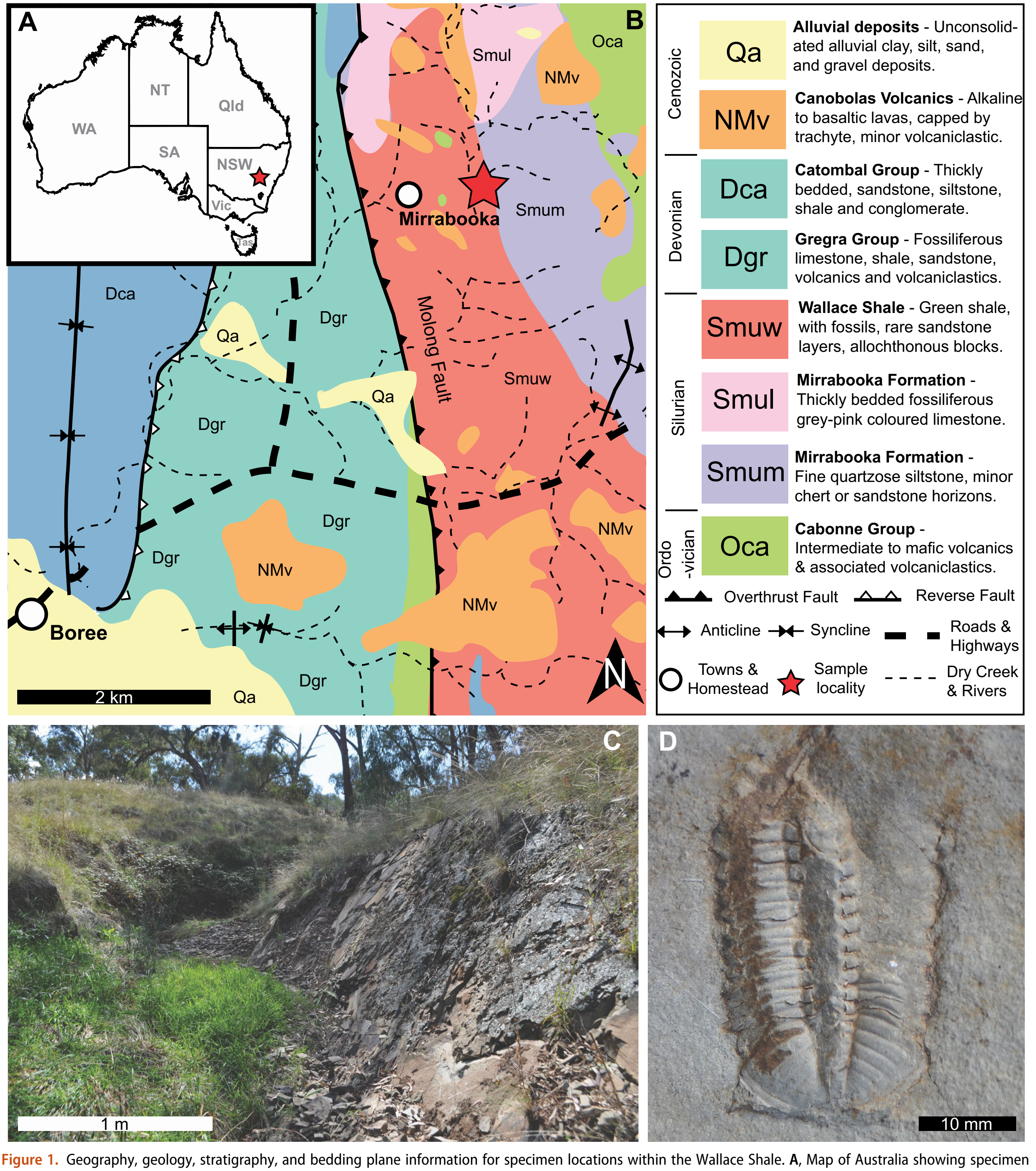

Figure 1. Geography, geology, stratigraphy, and bedding plane information for specimen locations within the Wallace Shale. **A**, Map of Australia showing specimen location (red star) in New South Wales. **B**, Geological map showing rocks proximal to Mirrabooka 'homestead'. Red stars indicate specimen location. A simplified stratigraphic column is shown on the right. **C**, Panoramic view of located where specimens were collected, from exposure of left creek bank – small tributary running east of Wattle Creek. **D**, Typical specimen of *Denckmannites rutherfordi* Sherwin, 1968 found at the specimen site with Salterian moulting arrangement. Hundreds of individuals comparable to this specimen are uncovered on bedding surfaces.

arrangement. Hence, this specimen was somewhat aberrant for having been crushed, disarticulated, and containing multiple individuals within a constrained region (compare Figure 2 to typical specimens from the same horizon, such as Figure 1D and Sherwin 1968, pl. 133). The specimen was coated in magnesium oxide and photographed under low angle LED light with a Canon EOS 5DS. Images were stacked using Helicon Focus 7 (Helicon Soft Limited) stacking software.

Geological and geographical context

The geological context of this Wallace Shale site was discussed in Sherwin & Rickards (2002, p. 87); hence, a summary is provided here. The unit at the considered site outcrops primarily as a green-grey to olive shale that occasionally splits along bedding planes, although more often splits conchoidally along cleavage planes (Wood 1955, Tuckerson 1966, Partridge 1967). The shale is medium to thickly bedded, with internal laminations only apparent in distinct marker horizons (typically containing course, angular volcanic feldspar and quartz grains). The unit also appears to be enriched in heavy minerals like rutile, zircon, and tourmaline compared to the underlying sequences (Pickett 1982). Near Mirrabooka 'homestead', and in the surrounding Cheesemans Creek-Spring Creek area, the Wallace Shale conformably overlies the Mirrabooka Formation. Slightly northeast of this, the shale also interfingers with (and may conformably overly) the Borenore and Molong limestones. The unit is conformably overlain by the Bulls Camp Volcanics and disconformably overlain in local patches by Miocene basaltic volcanics (Pogson & Watkins 1998).

The Wallace Shale generally hosts boulder beds representing slump deposits. These range in size from relatively small to extremely large (3–450 m) and of various different ages (although locally derived blocks tend to be of a similar age). Most are contemporaneous with the Wallace Shale. However, four outcrops near Mirrabooka 'homestead' appear to be Ordovician, hosting conodonts, graptolites, brachiopods, and trilobites similar to those of the basal Malongulli Formation (Sherwin 1966, Percival 1978, 1979, and observations by PMS). The upper part of the unit near Mirrabooka 'homestead' also hosts a turbiditic sandstone with subordinate interbeds of shale. This sandstone is reddish-brown or greenish-grey in colour and contains flute casts and invertebrate trails on the bedding surfaces. This upper sandstone sequences was termed the Nyrang Sandstone Member by Sherwin (1971a), who expanded on work by Wood (1955). Presence of turbidites, major slumping, and allochthonous blocks in the unit, along with common planktonic graptolites and small-eyed *Denckmannites rutherfordi*, suggest that the environment was a relatively deep marine basin. This is further supported by a rather depauperate benthic fauna consisting of *Batocara* cf. *robustus* (Mitchell, 1924) and an unidentified odontopleurid trilobite, as well as several species of dendroidal graptolites, molluscs, brachiopods, conularids, and corals (Sherwin 1968, 1971b, 1976, Strusz 1980, Pickett 1982, see Pogson & Watkins 1998, table A1.18 for an overview).

Graptolites from the site sampled in the Wallace Shale near Mirrabrook 'homestead' give a definitive Přídolí age (Sherwin & Rickards 2002). The shale contains a fauna, mainly dominated by monograptid species, that are very similar to those described from the Rosebank Shale and Cowridge Siltstone at Yass, NSW (Jenkins 1982, Rickards & Wright 1999) and the Humevale Formation, Ghin Ghin, Victoria (Rickards & Garratt 1990, Rickards 2000, Packham *et al.* 2001). The conodont species *Belodella anomalis* Cooper, 1974 described from an allochthonous (likely contemporaneous) block within the unit at Boree Creek, NSW (Cockle 1999) supports a Přídolí age (Farrell 2004) for the Wallace Shale. Finally, the upper portion of the unit potentially extends into the Early Devonian further along Wattle Creek, as indicated by the presence of *Monograptus* cf. *uniformis* (Tuckerson 1966, Sherwin 1976).

Description

The shelly aggregation is elongated, 28.9 mm long and 15.1 mm wide (Figure 2). The edge of AM F158002 is sharp and defined by the dense aggregation of tens of trilobite sections. Due to the shelly composition, the specimen has at least 2 mm relief. Identifiable trilobite sections include pygidia, thoracic segments, and cephala. All fragments belong to *Denckmannites rutherfordi*. No soft-tissue is preserved.

Discussion

Shelly aggregates within the invertebrate fossil record are typically considered examples of cololite and coprolite bromalites. Comparing AM F158002 with the most recent systematic work on bromalites (Knaust 2020), we conclude that the specimen does not completely conform with diagnoses of the described ichnospecies. This has limited our ability to present a formal taxonomic assessment of AM F158002 and we have therefore chosen to leave the specimen in open nomenclature. However, the lack of any evidence for a gut tract surrounding the specimen excludes AM F158002 from the cololite category. Furthermore, the specimen is morphologically comparable to other trilobite-rich aggregates considered coprolites (see Babcock 2003, Daley *et al.* 2013, Ding *et al.* 2020, Bicknell *et al.* 2022a). As such, we suggest AM F158002 is likely a coprolite, illustrating the presence of a durophagous predator or scavenger within the Wallace Shale.

Previous examples of eurypterid and fish-rich shelly coprolites have been noted from Silurian-aged deposits (Caster & Kjellesvig-Waering 1964, Rolfe 1973). Further, Silurian-aged coprolites that show primarily eurypterid fragments also contain trilobite fragments (Caster & Kjellesvig-Waering 1964) and are up to four times longer than AM F158002. Both eurypterid and fish-rich shelly coprolites have been attributed to predation by large

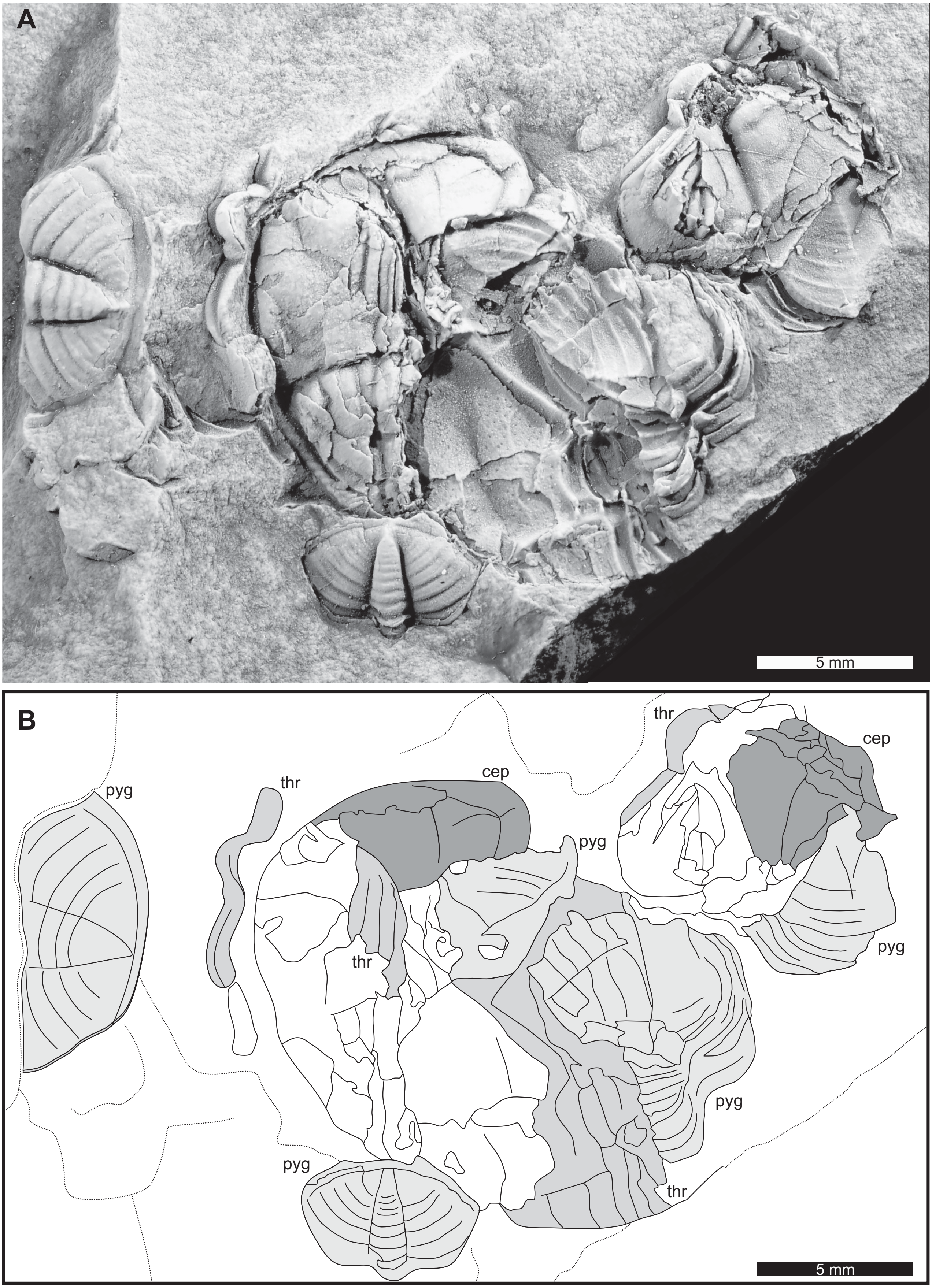

Figure 2. Coprolite from the Wallace Shale. **A**, Complete specimen. AM F158002. **B**, Line drawing of **A** showing edges of the fragmented sections. Identifiable structures coloured grey. Acronyms: cep: cephalon; pyg: pygidial section; thr: thoracic fragment.

eurypterids (Caster & Kjellesvig-Waering 1964, Rolfe 1973, Selden 1984, Schmidt *et al.* 2022), based on the co-occurrence of sea scorpions with the coprolites. Large pterygotid eurypterids are known from other Silurian deposits of Australia (McCoy 1899, Bicknell *et al.* 2020) and would have been capable of capturing prey with hypertrophied chelicerae (Bicknell *et al.* 2022b) for subsequent shell crushing with re-enforced gnathobasic spines on the large coxal regions of swimming legs (Clarke & Ruedemann 1912, Miller 2007, Poschmann *et al.* 2017, Haug 2020). This contrasts the structurally weaker gnathobasic spines of smaller eurypterid genera that were likely limited to shredding soft prey (Selden 1981, Bicknell *et al.* 2018a). Eurypterid fossils have not been identified within the Wallace Shale to date. However, this likely reflects a preservational bias towards biomineralized structures within the formation and a notable lack of soft-bodied fauna. An alternative to eurypterids as producers of this coprolite could be trilobites. The trilobites of the Wallace Shale may have consumed each other, likely targeting smaller individuals, using gnathobasic spines on walking legs (Bicknell *et al.* 2021). However, coprolites produced by Cambrian-aged trilobites show marked disarticulation along exoskeletal sections (Daley *et al.* 2013, Bicknell *et al.* 2022) and AM F158002 lacks this degree of breakage. As such, a trilobite producer is less likely when compared to the eurypterid explanation.

One final possibility is that AM F158002 represents a fish coprolite. Fishes, while rare in Silurian deposits of Australia, have been recorded from some localities (Burrow & Young 1999, Burrow & Turner 2000), and possible Přídolí-aged ancanthodians and thelodontidid scales are known from the so-called 'Carribuddy' Formation (Turner 1993). However, ancanthodians may not have been effective at consuming trilobites and antiarch placoderm fishes are not known from Gondwana until the Emsian (Lebedev *et al.* 2022). As such, it is unlikely that fishes produced the coprolite.

Taken together, the most likely coprolite producer was a pterygotid eurypterid. This presents important insight into the fauna that may not be preserved within the formation. This palaeoecosystem was more complex than previously thought and we suggest that additional sampling from other sections of the shale may yield novel fossil material to expand the known palaeodiversity of the deposit.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This research was funded by a University of New England Postdoctoral Fellowship (to R.D.C.B.) and an Australian Museum AMF/AMRI Visiting Research Fellowship (to R.D.C.B.). Finally, we thank two anonymous referees for their comments that improved the direction and scope of the text.

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