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# Novel information on *Caryosyntrips* based on new appendages from China and the USA



RTHROPOD TRUCTURE & EVELOPMENT

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#### ABSTRACT

*Caryosyntrips* is a relatively rare but long-lived and geographically widespread radiodont genus with specimens reported from Cambrian Stage 4 to the Drumian of Gondwana and Laurentia. Most of the currently known specimens are from the Wulian to Drumian deposits of North America and only one specimen is known from Stage 4 of Gondwana. Here, two new specimens are reported. The first one is a C. cf. *Caryosyntrips serratus* appendage from the Malong Biota of China (Cambrian, Series 2, Stage 3), which also represents the first reported occurrence of *Caryosyntrips* from China. The second appendage is from the Spence Shale Member (Cambrian, Miaolingian, Wuliuan) of Utah, USA and shares characters with both *Caryosyntrips camurus* and *Caryosyntrips durus*. This new specimen indicates that characters previously used to diagnose species might instead reflect intraspecific variation, however confirmation of this depends on discovery of new material. These new finds increase the temporal range of the genus into Cambrian Stage 3 and the specimen from the Malong Biota significantly increases the geographical range of the genus, with its first occurrence in China. In addition to the description of the new material we also discuss the function of the appendages in *Caryosyntrips* and the ecology of the genus.

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#### 1. Introduction

Exceptionally preserved fossils from Fossil-Lagerstätten (*sensu* Kimmig and Schiffbauer, 2024) are key for understanding the evolution of life. In the Cambrian these deposits are especially abundant (Muscente et al., 2017), and the abundance of panar-thropods makes Fossil-Lagerstätten from this time interval particularly interesting in the study of their early evolution. Among the earliest panarthropods to appear in the fossil record are radiodonts

(Daley et al., 2018). These animals are some of the largest and best known animals from Cambrian Fossil-Lagerstätten, with over 25 formally described genera (Wu et al., 2021; Potin and Daley, 2023; and references therein), and are the earliest diverging euarthropods with arthropodized appendages (e.g., Daley et al., 2009; Legg et al., 2013; Vinther et al., 2014; Ortega-Hernández, 2016; Zeng et al., 2020; O'Flynn et al., 2023). Radiodonts are extremely diverse and represent a large set of feeding ecologies, from apex-predators, sediment sifters to filter feeders (e.g., Daley and Budd, 2010; Daley et al., 2013; Vinther et al., 2014; Lerosey-Aubril and Pates, 2018; Moysiuk and Caron, 2019; De Vivo et al., 2021; Potin and Daley, 2023).

One radiodont taxon that has been considered an apex predator based on its frontal appendage morphology and size is *Caryosyntrips* (Daley and Budd, 2010; Pates and Daley, 2017). This taxon, which is only known from its appendages and some fragmentary carapace material, has been reported from the major Wuliuan and Drumian assemblages of Laurentia (Spence Shale, Burgess Shale,

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Wheeler Formation, and Marjum Formation) and in Gondwana from the Stage 4 Valdemiedes Formation of Spain. The most complete specimen is a connected pair of Caryosyntrips serratus appendages attached to partial carapace material from the Burgess Shale (Daley and Budd, 2010). However, specimens are relatively rare, and no material posterior to the appendages and partial carapace have vet been described. The incomplete nature of the material, and distinct nature of the appendages means that Caryosyntrips has not been assigned to any of the four radiodont families (Pates and Daley, 2017; Potin and Daley, 2023), and in some phylogenetic analyses has not been recovered within monophyletic Radiodonta (Moysiuk and Caron, 2021; Zeng et al., 2022). Confirmation that Caryosyntrips is indeed a radiodont requires the discovery and description of the rest of the body, especially in light of recent descriptions of deuteropods with radiodont-like feeding appendages (e.g., O'Flynn et al., 2020, 2024; Zeng et al., 2020).

Here, we describe two new *Caryosyntrips* appendages. The first one is a *C*. cf. *C. serratus* appendage from the Malong Biota of China (Cambrian, Series 2, Stage 3), which also represents the first reported occurrence of *Caryosyntrips* from China. The second appendage is from the Spence Shale Member (Cambrian, Miaolingian, Wuliuan) of Utah, USA, and shares characters with both *Caryosyntrips camurus* and *Caryosyntrips durus*. These specimens provide fresh insights into the distribution of the genus, more information on the diversity of two important Cambrian fossil deposits, and additional information on the ecology and systematics of *Caryosyntrips*.

#### 2. Material and methods

#### 2.1. Geological setting

#### 2.1.1. Malong Biota

The specimen from the Malong Biota was collected by Xianfeng Yang from the lower part of the upper Hongjiangshao Formation (Cambrian, Series 2, Stage 3, Yiliangella-Zhangshania Biozone) at the Langzan locality (GPS: 25.317, 103.436), Yunnan Province, China (Fig. 1A). The Malong Biota is slightly younger than the Chengjiang Biota, but also preserves exquisite 2D compression fossils (Luo et al., 2008; Ding et al., 2020). The exposure at the new locality is approximately 20 m thick, consisting mainly of greyish-black mudstones in the lower to middle part and interbedded siltstones and mudstones in the upper part. The top of the section is missing at this locality and the bottom is not exposed. The specimen was collected from the lower part of the exposure in the greyish-black mudstones (Fig. 1B). The Hongjiangshao Formation has been interpreted as a nearshore, supralittoral to subtidal zone, sand mudflat to inner shelf environment (Luo et al., 2008; Wu et al., 2021). The lithology of the rock hosting the Caryosyntrips specimen, indicates that it was likely deposited on the inner shelf.

#### 2.1.2. Spence Shale

The *Caryosyntrips* appendage from the Spence Shale was collected by Paul Jamison from the lower cycle 3 (Liddell et al., 1997; Kimmig et al., 2019) of the Spence Shale Member (Cambrian, Miaolingian, Wuliuan, *Glossopleura walcotti* Biozone), Langston Formation, at the Miners Hollow locality (GPS: 41.602, -112.033), Box Elder County, Utah (Fig. 1C).

At the Miners Hollow location, on the west flank of the Wellsville Mountains north of Brigham City, Utah, the Spence Shale is a dark grey to brown calcareous shale with interlayered lime mudstone units, the exposure is about 59 m thick (Fig. 1D). The Spence Shale overlies the Naomi Peak Limestone Member and is itself overlain by the High Creek Limestone Member (Maxey, 1958; Liddell et al., 1997; Kimmig et al., 2019). The Spence Shale is interpreted as a shelf environment of a rimmed carbonate platform (Kimmig et al., 2019).

#### 2.2. Photography

At the YKLP (Yunnan Key Lab for Palaeobiology, Yunnan University, Kunming, China) the fossil was photographed immersed in ethanol, under polarized or cross-polarized illumination, using a Canon EOS 5D digital SLR camera mounted with a Canon 50 mm macro lens. Close-ups were captured using a Leica DFC 500 digital camera mounted on a Leica M205-C stereoscope.

At the SMNK the fossil was photographed immersed in ethanol, under polarized or cross-polarized illumination, using a Canon EOS R5 digital camera mounted with a Canon EF 100 f/2.8 Macro IS USM lens. Close-ups were captured using a Keyence VHX 7000 digital microscope.

The color, contrast, and brightness of the images were adjusted using Adobe Photoshop. Line drawings were made with Adobe Illustrator. Specimen measurements were made from photographs in ImageJ (Schneider et al., 2012).

#### 2.3. Terminology

The terminology used in our descriptions broadly follows Guo et al. (2019) and Lerosey-Aubril et al. (2020) for frontal appendages. Additional terminology relating to *Caryosyntrips* frontal appendages follows Pates and Daley (2017) and Pates et al. (2021b).

#### 2.4. Repositories and institutional abbreviations

BPM, Back to the Past Museum, Cancún, Mexico; KUMIP, Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas, Lawrence, USA; MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza, Spain; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; SMNK-PAL, Division of Palaeontology, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; UMNH, Natural History Museum of Utah, University of Utah, Salt Lake City, Utah, USA; YKLP, Yunnan Key Lab for Palaeobiology, Yunnan University, Kunming, China.

#### 3. Results

Superphylum PANARTHROPODA Nielsen (1995). Order RADIODONTA Collins (1996). Family uncertain. Genus *Caryosyntrips* Daley and Budd, 2010. *Type species. C. serratus* Daley and Budd (2010), from the

Wuliuan Burgess Shale, British Columbia, Canada.

**Diagnosis.** A radiodont with 14 podomeres per frontal appendage, which are elongated and tapering in outline. A pair of endites extends from the ventral surface of each podomere. Appendages have a convex bell-shaped proximal margin, a terminal spine protrudes from the distal end in some species (Pates and Daley, 2017).

**Occurrence.** Hongjiangshao Formation, South China (Cambrian Series 2, Stage 3); Valdemiedes Formation, Spain (Cambrian, Series 2, Stage 4); Spence Shale Member, Langston Formation, Utah, USA (Cambrian, Miaolingian, Wuliuan); 'Thick' Stephen (Burgess Shale) Formation, British Columbia, Canada (Cambrian, Miaolingian, Wuliuan); Wheeler Formation, Utah, USA (Cambrian, Miaolingian, Drumian); and Marjum Formation, Utah, USA (Cambrian, Miaolingian, Drumian).

**Remarks.** The specimen from the Malong Biota extends the time range for *Caryosyntrips* and its type species *C. serratus* into Cambrian Stage 3 and the geographical range into equatorial peri-



Fig. 1. Geography, geology, and stratigraphy of the Malong Biota at Langzan, Yunnan Province, China and the Spence Shale at Miners Hollow, Utah, USA. A, Map of Yunnan showing specimen location (red star); B. Simplified stratigraphic column of the exposed upper Hongjiangshao Formation at Langzan, indicating the sample horizon (red arrow); C, Map of Utah showing specimen location (red star); D, Simplified stratigraphic column of the Spence Shale Member at Miners Hollow, indicating the sample horizon (red arrow) (modified from Kimmig and Selden, 2020).

Gondwana.

Caryosyntrips cf. C. serratus Daley and Budd (2010).

(Fig. 2A-H)

**Type specimens.** Holotype: ROM 57161 (Daley and Budd, 2010, text-fig. 5A). Paratypes: ROM 59497–59499, 59502. All appendages from the Wuliuan 'Thick' Stephen (Burgess Shale) Formation, British Columbia, Canada.

**Material.** YKLP 14589 (part), 14590 (counterpart), isolated partial appendage.

**Diagnosis.** *Caryosyntrips* with one pair of distally pointing endites on each podomere. Endites are less broad than for other

*Caryosyntrips* species. A single row of small curved dorsal spines, spaced 1 mm apart, point distally. Distalmost podomere ends in recurved terminal spine (modified from Pates and Daley, 2017).

**Occurrence.** YKLP 14589 (part), 14590 (counterpart), originates from the Hongjiangshao Formation, South China (Cambrian, Series 2, Stage 3)

**Description.** Isolated partial appendage, preserving 12 podomeres elongated and tapering distally. Number of podomeres inferred from the number of endites as podomere boundaries cannot be clearly observed. Preserved as part and counterpart. The preserved portion of the appendage measures 32.3 mm in length



**Fig. 2.** *Caryosyntrips* cf. *C. serratus* from the Malong Biota, Hongjiangshao Formation at Langzan, Yunnan Province, China. A, YKLP 14589, part; B, Interpretive drawing of A; C, YKLP 14590, counterpart; D, Interpretive drawing of C; E, Close-up of the dorsal spine attachment in the middle of the appendage; F, Close-up of the dorsal spine attachment at the proximal end of the appendage; G, Close-up of the paired endites in the middle of the appendage; H, Close-up of the distal end of the appendage. Abbreviations: ds, dorsal spine; en, paired endites. Numbers in A indicate podomeres. Scale bars: 10 mm (A, C), 1 mm (E–H).

along the dorsal margin, and 8.1 mm at its widest point. The angle between the dorsal and ventral surface is 15°. The most proximal portion of the appendage is missing, while the distal end preserves the base of a single terminal spine.

A pair of elongated triangular endites extends from the ventral surface of each podomere. In addition to the single terminal spine, the specimen preserves 11 pairs of endites. In most of the endites, only one can be seen, but in the 4th, 5th, and 9th the pair is visible (Fig. 2A and B). The endites (length 1.9–3.3 mm, Fig. 2A–B, G–H; width 1.1–2.5 mm, Fig. 2A–B, G–H) are spaced about 1.4 mm apart. Most of the endites are curved, with the point orientated towards the proximal margin.

The presence of a row of dorsal spines, spaced about 2.5 mm apart, is interpreted based on the presence of small circles (Fig. 2E and F). Similar small circles have previously been interpreted as spine attachment points (Pates and Daley, 2017). The exact number of dorsal spines is difficult to discern, based on the preservation of the specimen.

Remarks. The specimen is tentatively assigned to C. serratus,

based on its outline, the paired endites, the presence of a terminal spine, the row of small spine attachments along the dorsal margin, and the slightly curved dorsal margin.

Caryosyntrips sp.

(Fig. 3A–F)

**Material.** SMNK-PAL 73172, isolated partial appendage, no counterpart.

**Occurrence.** SMNK-PAL 73172 originates from lower carbonate cycle 3 near the middle of the Spence Shale, Wuliuan Spence Shale Member (*G. walcotti* Biozone) of the Langston Formation, Miners Hollow locality (GPS: 41.602, -112.033), Wellsville Mountains, Box Elder County, Utah.

**Description.** A partial *Caryosyntrips* appendage with ten podomeres preserved. Number of podomeres inferred from the presence of nine endites, as the boundaries separating the podomeres cannot be discerned. Specimen measures 55.9 mm along the dorsal margin, and is 15.2 mm wide at its widest point. The proximal part of the appendage is missing. The angle between the ventral and dorsal surfaces is 17°.

Large endites (length 1.9-3.3 mm, Fig. 3A-E-F; width 1.6-3.6 mm, Fig. 3A-E-F) spaced between 3.0 and 4.1 mm apart.

There are six preserved spines on the dorsal surface of the appendage, which are shorter than the endites (length 1.0-1.5 mm, Fig. 3A-C; width 0.8-1.2 mm, Fig. 3A-C). They are spaced between 3.0 and 3.6 mm apart.

**Remarks.** This specimen displays similarities with *C. camurus* and *C. durus*. A triangular outline to the appendage is shared with the latter, while a more slender distal three podomeres is shared by the former (Pates and Daley, 2017). Similar distorted distal portions of Caryosyntrips appendages have also been reported in C. camurus (Pates and Daley, 2017). The presence of large dorsal spines along most of the preserved dorsal margin distinguishes this specimen from C. camurus specimens from the Burgess Shale. Only a single specimen with small dorsal spines on the distalmost podomeres has been described in C. camurus from Canada (Pates and Daley, 2017: Fig. 4E), contrasting to the single *C. camurus* specimen from the Spence Shale where dorsal spines of a similar size to the endites are present on its distalmost three podomeres (Pates and Daley, 2017: Fig. 4C). However, spines are found along more of the dorsal margin of this new specimen than any previous C. camurus, instead drawing comparisons with C. durus where spines are found on the seven most distal podomeres (Pates and Daley, 2017). Dorsal spines in this new specimen are smaller relative to endites than in the two known C. durus from the Wheeler Formation, where they are very similar in size to the endites. Similarly, no row of small spines – or circular spine attachment points – can be observed in this new specimen, providing another difference between this specimen and *C. durus* from the Wheeler Formation.

In summary, this new specimen shares features with *C. camurus* and *C. durus* as previously diagnosed. It is possible that the presence of large dorsal spines and the absence of a row of small spines

unites the two Spence Shale *Caryosyntrips* specimens as a distinct species, however it is also possible that it indicates that characters previously used to diagnose three species of *Caryosyntrips* reflect intraspecific rather than interspecific differences (see section 4.3). For now, we leave this specimen in open nomenclature pending further fossil discoveries.

#### 4. Discussion

#### 4.1. Geographic distribution of Caryosyntrips

Konservat-Lagerstätten (Seilacher, 1970; Kimmig and Schiffbauer, 2024) provide the best information of the distribution of radiodont taxa in time and space, as they are the only deposits to preserve exceptionally preserved fossils. Caryosyntrips is distributed over large geographic and temporal range (Fig. 4, Table 1), and the most cosmopolitan species is C. serratus. The specimen described herein from the Malong Biota increases the temporal range of the species to Cambrian Stage 3 and the last reported specimens have been reported from the Drumian of Utah (Pates and Daley, 2017; Lerosey-Aubril et al., 2020; Pates et al., 2021b). Pates and Daley (2017) speculated that Caryosyntrips might have originated at high latitudes in Gondwana based on the presence of Caryosyntrips cf. C. camurus in the Valdemiedes Formation of Spain, however, the Malong Biota specimen does not support this hypothesis, as it shows that *Caryosyntrips* was already living in more equatorial latitudes in Cambrian Stage 3. However, an origin in Gondwana, as has been suggested is still plausible, unless specimens are recovered from older deposits in Laurentia. It also appears as if the genus did not survive into the Ordovician, as the last known occurrence is in the Drumian Marjum Formation of Utah, USA (Pates et al., 2021b).



Fig. 3. Caryosyntrips sp. from the Spence Shale Member, Langston Formation at Miners Hollow, Utah, USA. A, SMNK-PAL 73172, part; B, Interpretive drawing of A; C, Close-up of the dorsal spines; D, Close-up of the paired endites; E, Close-up of the proximal end of the appendage; F, Close-up of the distal end of the appendage Abbreviations: ds, dorsal spine; en, paired endites. Numbers in A indicate podomeres. Scale bars: 10 mm (A), 5 mm (C–F).



Fig. 4. Global distribution of palaeocontinents in the early Cambrian and occurrences of *Caryosyntrips* appendages. See Table 1 for details of occurrence data. Map adapted from Slater et al. (2017) and Sun et al. (2024).

#### Table 1

Occurrences, specimens, and specimens of Caryosyntrips

Cambrian Stage	Species	Member/Formation	Country	Collection Numbers	References	Number in Fig. 4
Stage 3	C. cf. C. serratus	Hongjiangshao Formation	China	YKLP 14589(p)/14590(cp)	This study	1
Stage 4	C. cf. C. camurus	Valdemiedes Formation	Spain	MPZ 2009/1241	Pates and Daley (2017)	2
Wuliuan	C. camurus	Spence Shale Member, Langston Formation	USA	KUMIP 314275	Pates and Daley (2017)	3
Wuliuan	C. sp.	Spence Shale Member, Langston Formation	USA	SMNK-PAL 73172	This study	4
Wuliuan	C. serratus	'Thick' Stephen (Burgess Shale) Formation	Canada	ROM 57161, 59497–59499, 59502, 59600	Daley and Budd (2010); Pates and Daley (2017)	5
Wuliuan	C. camurus	'Thick' Stephen (Burgess Shale) Formation	Canada	ROM 59500, 59501, 59503, 59598, 59599	Daley and Budd (2010); Pates and Daley (2017)	6
Drumian	C. durus	Wheeler Formation (Drum Mountains)	USA	KUMIP 314070, 314071	Pates and Daley (2017)	7
Drumian	C. serratus	Wheeler Formation (House Range)	USA	KUMIP 415223, UU18056.37	Pates and Daley (2017); Lerosey-Aubril et al. (2020)	8
Drumian	C. camurus	Marjum Formation	USA	BPM1100, UMNH.IP 6122	Pates et al. (2021b)	9

The *Caryosyntrips* appendage from the Spence Shale is the second occurrence of the genus in the Spence Shale Member, the new specimen comes from the same interval as the previous specimen, the carbonate cycle 3 at the Miners Hollow locality. The new specimen, with its combination of characteristics, highlights the importance of the Spence Shale. If assigned to *C. durus*, as

supported by the presence of more than three large dorsal spines, this new discovery would demonstrate the critical role of the Spence Shale in preserving taxa that are otherwise restricted to the Wuliuan Burgess Shale or the Drumian Wheeler and Marjum Formations (Kimmig et al., 2019). Alternatively, it would provide important data on the morphological variation within the genus, only possible by the higher resolution geographic and temporal sampling of targeting many Konservat-Lagerstätten.

#### 4.2. Caryosyntrips feeding ecology

The feeding appendage in radiodonts were located adjacent to the mouth and likely actively involved in the feeding process (e.g., Whittington and Briggs, 1985; Collins, 1996; Daley et al., 2009; Daley and Budd, 2010; Daley and Edgecombe, 2014; De Vivo et al., 2021; Bicknell et al., 2023). While suspension-feeding and sediment sifting have been suggested as feeding modes for hurdiid and tamisiocaridid radiodonts with appendages bearing elongated endites (Daley et al., 2013; Vinther et al., 2014; Lerosey-Aubril and Pates, 2018; Pates et al., 2018; De Vivo et al., 2021; Potin et al., 2023), other radiodonts with elongated frontal appendages and shorter endites such as *Amplectobelua, Anomalocaris* and *Caryosyntrips* have been suggested to be active hunters and grasp and potentially crush their prey (e.g., Daley and Budd, 2010; Daley and Edgecombe, 2014; Pates and Daley, 2017; Potin and Daley, 2023).

Based on the Burgess Shale specimens of C. serratus Daley and Budd (2010) suggested, that Caryosyntrips appendages likely did not have the same flexibility and range of motion as Anomalocaris appendages. This was inferred from the consistent straight dorsal and ventral margins of the known appendages, and the usually weak or missing podomere boundaries and arthrodial membranes. Indeed, in the specimen where arthrodial membrane is most visible - the holotype of C. serratus (Daley and Budd, 2010, text-fig. 5A) arthrodial membranes are only visible in the ventral half of the appendage. All specimens of Caryosyntrips that have been described since then also display consistently straight dorsal and ventral margins (Pates and Daley, 2017; Lerosey-Aubril et al., 2020; Pates et al., 2021b; this study), supporting the original hypothesis, and indicating that it is valid for all species within the genus. However, Pates and Daley (2017) suggested that there might have been differences in the prey that Caryosyntrips species targeted, indicated by differences in dorsal spine morphology and arrangement, and endite morphology. They suggested that C. durus had the most rigid frontal appendages, but also the most robust ones, and for that reason likely targeted more robust prey. This hypothesis is supported by range of motion studies of Anomalocaris canadensis feeding appendages, complemented by finite element analysis, interrogating raptorial predation in this taxon (De Vivo et al., 2021; Bicknell et al., 2023). A. canadensis appendages were flexible and able to grasp prey of varying sizes and morphologies, however, appendages were not able to exert high levels of force onto prey due to high levels of strain on their elongate endites (Bicknell et al., 2023). For these reasons Bicknell et al. (2023) suggested, that A. canadensis must have fed on soft-bodied animals, as its oral cone was also likely not strong enough to break biomineralized exoskeletons (Daley and Bergström, 2012). While an oral cone is unknown in *Caryosyntrips*, the appendages of this taxon differ from those of A. canadensis in a number of important ways. In particular, Caryosyntrips appendages would have been much less flexible on account of the lack of clear arthrodial membrane between podomeres, while the endites of this genus are much shorter, and more robust (Daley and Budd, 2010; Pates and Daley, 2017). These features hypothetically suggest, that Caryosyntrips appendages were more suitable for exerting high levels of force onto prey than anomalocaridid radiodonts, thus Caryosyntrips might have been

able to target more robust prey than radiodont species with more flexible appendages and more elongate spines. This increased robustness would come with the trade-off of reduced flexibility and thus dexterity, and indicates that *Caryosyntrips* occupied an ecological niche unique among radiodonts, and perhaps Cambrian predators more broadly.

## 4.3. Morphological variation in Caryosyntrips: inter or intra specific?

As the new Spence Shale specimen (SMNK-PAL 73172) incorporates a number of characteristics shared between C. camurus and C. durus, it is possible that the characters used to diagnose three species of Caryosyntrips are a consequence of the limited sample of 21 specimens collected thus far. Pates and Daley (2017) distinguished species primarily on the arrangement and morphology of dorsal spines: absent in C. camurus, a single row of small dorsal spines in C. serratus, and one large dorsal spine per podomere alongside a row of small dorsal spines in C. durus. The new Spence specimen shows a further combination (large dorsal spines only, with the small row of dorsal spines known in C. durus absent), while as previously noted some C. camurus display dorsal spines on the distal three podomeres (Pates and Daley, 2017). Thus, the diagnostic framework of Pates and Daley (2017) cannot be strictly applied to this new specimen. One option would be the diagnosis of a new species, which would unite the Spence specimens in possessing large dorsal spines and no small dorsal spines. However, the two specimens differ in the number of large spines, as well as finer details of spine and endite morphology. A second option is to consider variation in endite and dorsal spine morphology and arrangement as intraspecifc, rather than interspecific, variation. Variation in auxiliary spine morphology, arrangement, and size has been observed in other radiodont frontal appendages, such as hurdiids (e.g., Daley et al., 2013). When considered in the context of the shelly fossil record, where sample sizes of thousands of specimens are possible (unfeasible for non-biomineralized fossils such as Caryosyntrips), increased sampling has demonstrated that features used to diagnose species or even genera can instead represent end-members of morphological variation within a single taxonomic unit (e.g. Sheldon, 1987). Thus, additional material of Caryosyntrips are required from more localities as well as from Miners Hollow in order to determine if variation currently treated as interspecific is in fact intraspecific. As the appendages were critical for feeding and likely inform on the type of prey *Caryosyntrips* was targeting (section 4.2), variation in appendage morphology of these apex predators may also inform on differences in the broader ecology of these sites.

#### 4.4. Radiodonts of the Malong Biota and Spence Shale

In the Malong Biota, radiodont appendages are rare and other than the herein described *Caryosyntrips* appendage all other radiodonts have been considered to represent a species of *Anomalocaris* (Zhang et al., 2001; Luo et al., 2008; Zeng et al., 2014; Jiao et al., 2021; Wu et al., 2021). This apparent rarity of radiodont species in the Malong Biota might be due to the suggested shallow-water depositional environment (Luo et al., 2008; Ding et al., 2020), however, the *Caryosyntrips* appendage appears to come from the slightly deeper water deposits of the Hongjiangshao Formation, likely the inner shelf. The shallower-water deposition might also explain the lack of hurdiids in the Malong Biota, as it has been suggested that they might have a preference for deeper water environments (Wu et al., 2022, 2024). Alternatively, a collection bias towards other groups or smaller collecting efforts compared to other Cambrian deposits might explain the low abundance of radiodonts (e.g., Whitaker and Kimmig, 2020), although it is notable that radiodont appendages and carapaces are often among the first non-biomineralising taxa to be described from Cambrian deposits (e.g., Resser, 1929; Mount, 1976; Lieberman, 2003; Pates et al., 2021a).

Radiodont appendages are among the most common softbodied fossils in the Spence Shale, but most of them represent hurdiid appendages, belonging to *Hurdia* and *Buccaspinea* (Pates and Daley, 2017; Pates et al., 2018; Kimmig et al., 2019, 2023; Whitaker et al., 2022). The radiodont appendages are also limited to the Spence Shale deposits in the Wellsville Mountains (Miners Hollow, Antimony Canyon) (Pates and Daley, 2017; Pates et al., 2018; Kimmig et al., 2019, 2023; Whitaker et al., 2022) and High Creek (Kimmig and Jamison pers. obs.), which represent shelf deposits. The lower collecting effort in other areas of the Spence Shale suggests that the absence of radiodonts from shallower deposits in the Spence Shale might be an anthropogenic signal, rather than an taphonomic or biologic signal (Whitaker and Kimmig, 2020).

The low abundance of raptorial radiodonts from both the Malong Biota and the Spence Shale suggest that these predators were likely only a small part of the biodiversity in these ecosystems. However, only larger collecting efforts will lead to a more comprehensive view of the species and specimen abundances in these deposits.

#### 5. Conclusion

The herein described specimens extend the geographical and time range of *Caryosyntrips* to the Cambrian Stage 3 Malong Biota of China and increase the diversity of *Caryosyntrips* in the Spence Shale and Wuliuan Stage, which is the only Cambrian stage where all three species can be found. However, the presence of only 21 appendages in some of the most prolific radiodont assemblages in the Cambrian shows how rare *Caryosyntrips* fossils are, and the ecology and systematics of this radiodont will remain unresolved until more complete specimens are found.

#### **CRediT** authorship contribution statement

**Xianfeng Yang:** Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Julien Kimmig:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Stephen Pates:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Paul G. Jamison:** Writing – review & editing, Writing – original draft, Resources. **Shuhan Ma:** Writing – review & editing, Writing – original draft, Visualization.

#### **Declaration of competing interest**

The authors declare that they have no known competing interests or personal relationships that could have appeared to influence the work reported in this paper.

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