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3 1 *Caryosyntrips*: a radiodontan from the Cambrian of Spain, USA and Canada
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25 11 **ABSTRACT**
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29 13 *Caryosyntrips* appendages have previously been reported from the Burgess Shale (Cambrian,
30 14 Stage 5), British Columbia, Canada. New specimens of the genus are here reported from the
31 15 Wheeler Formation (Cambrian, Drumian) and Langston Formation, Spence Shale Member
32 16 (Cambrian, Stage 5), Utah, USA. The original Burgess Shale specimens are re-examined
33 17 alongside the new specimens. *Caryosyntrips* is shown to have paired ventral spines on each
34 18 podomere. Three species of *Caryosyntrips* are recognised: *C. serratus* Daley and Budd, *C.*
35 19 *camurus* nov. sp. and *C. durus* nov. sp., differentiated by the overall shape of their
36 20 appendages and arrangement of dorsal and ventral spines. These differences have potential
37 21 implications for the feeding methods employed by different species of *Caryosyntrips*. A
38 22 specimen collected from the upper Valdemiedes Formation of Spain (Cambrian, Stage 4),
39 23 previously described as the lobopodian *Mureropodia apae* Gámez Vintaned et al., is
40 24 reinterpreted as a *Caryosyntrips* appendage. This identification is supported by the overall
41 25 shape of the fossil, and the presence, orientation, and height:width ratio, of ventral spines.
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1 However the dorsal surface of the appendage is not well preserved, and the appendage and its
2 ventral spines are larger than other known *Caryosyntrips*. Therefore it is left in open
3 nomenclature as *C. cf. camurus*. These new finds increase the temporal range of
4 *Caryosyntrips* (Cambrian Series 2, Stage 4 to Series 3, Drumian) and the geographic range to
5 a new continent, Gondwana.

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7 **Key words:** *Caryosyntrips*, Radiodonta, Cambrian, Burgess Shale, Murero, Great Basin.

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9 THE study of radiodontans, soft-bodied nektonic apex predators known mostly from the
10 Cambrian, is crucial for understanding the evolution of arthropods. Recent studies have shed
11 light on the origin of the biramous limb (Van Roy et al. 2015), compound eyes (Paterson et
12 al. 2011) and the evolution of head structures (Cong et al. 2014). The evolution of
13 radiodontans and their phylogenetic relationships has been the focus of much recent work
14 increasing our knowledge of the diversity, feeding modes and ecology of these animals (e.g.
15 Daley et al. 2009; Daley & Budd 2010; Daley & Bergström 2012; Daley et al. 2013*a, b*;
16 Daley and Edgecombe 2014; Vinther et al. 2014; Van Roy et al. 2015).

17 The morphology of radiodontans consists of a body region of repeated segments with
18 lateral flaps, a head region consisting of radially arranged mouthparts (oral cone), two large
19 stalked eyes, and a pair of frontal appendages (Whittington & Briggs 1985). The paired
20 appendages are robust, and often preserved isolated or as exuviae, and rarely attached to the
21 rest of the body. Indeed many radiodontan taxa are known from frontal appendages only, for
22 example *Anomalocaris pennsylvanica* (Briggs 1979; Lieberman 2003), *Caryosyntrips*
23 *serratus* (Daley & Budd 2010), and *Tamisiocaris borealis* (Daley & Peel 2010; Vinther et al.
24 2014). Isolated *Caryosyntrips* appendages have been known for over a decade (Caron 2005)

1 and were first described by Daley & Budd (2010) alongside other new appendages from the
2 Burgess Shale.

3 In this paper we present new specimens of *Caryosyntrips* from the Spence Shale
4 (Cambrian Series 3, Stage 5) and Wheeler Formation (Cambrian Series 3, Drumian) of the
5 Great Basin, USA. We also reinterpret the putative lobopodian *Mureropodia apae* Gámez
6 Vintaned et al., 2011, from the upper Valdemiedes Formation (Cambrian Series 2, Stage 4) of
7 Spain as a *Caryosyntrips* appendage, and, in light of these new findings, identify new features
8 from the original *Caryosyntrips* material from the Burgess Shale (Cambrian Series 3, Stage
9 5), Canada. Information about the anatomical characters of *Caryosyntrips* allows for
10 separation of *Caryosyntrips* into three distinct species (Fig. 1), and comparison of their
11 functional morphology.

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13 **MATERIALS AND METHODS**

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15 The Langston Formation (Spence Shale Member) and Wheeler Formation specimens are held
16 at the University of Kansas Natural History Museum, Lawrence, Kansas, USA (KUMIP).
17 The Gunther Family collected KUMIP 314070 and 314071 from the Drum Mountains, Utah,
18 and KUMIP 314275 Miners Hollow, Wellsville Mountains, Utah. An additional Wheeler
19 Formation specimen, KUMIP 415223, was donated by Daniel Windhofer for this study. All
20 Burgess Shale specimens are held at the Royal Ontario Museum, Toronto, Ontario, Canada
21 (ROM). The single specimen from the Valdemiedes Formation (MPZ 2009/1241) is held at
22 the Museo de Ciencias Naturales de la Universidad de Zaragoza, Spain (MPZ).

23 Photographs were taken using a Canon EOS 500D camera with Canon EF-S 60 mm
24 macro lens, controlled with EOS Utility 2 remote shooting software. Measurements were
25 taken of all known *Caryosyntrips* specimens from photographs using ImageJ 2 software. The

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1 angles between the two edges of the appendage and from the podomere edge to the proximal
2 edge of each ventral spine were measured for each appendage and each ventral spine. The
3 mean angle from the podomere edge to ventral spine was calculated for each specimen and
4 this was plotted against the angle between the two edges of the appendage (see Fig. 2).
5 Photoshop was used to remove white paper arrows from photographs of MPZ 2009/1241.
6 The plot of length of appendage vs. length of longest spine was constructed using R Studio.
7 Lengths of incomplete appendages were reconstructed by calculating the mean length per
8 podomere, and extrapolating to 14 podomeres (see Supplementary Data).

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10 **INSTITUTIONAL ABBREVIATIONS**

11 KUMIP, University of Kansas Natural History Museum, Lawrence, Kansas, USA; MPZ,
12 Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, Spain; ROM, Royal
13 Ontario Museum, Toronto, Canada.

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15 **SYSTEMATIC PALAEOLOGY**

16 This published work and the nomenclatural acts it contains, have been registered in
17 ZooBank: <http://zoobank.org/References/XXXXXXXXXX>

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19 (stem group) EUARTHROPODA Lankester, 1904

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Order RADIODONTA Collins, 1996

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Genus CARYOSYNTRIPS Daley & Budd, 2010

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Type species. *Caryosyntrips serratus* Daley & Budd, 2010

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1 Diagnosis. A radiodontan with 14 podomeres per frontal appendage, which are elongated and
2 tapering in outline. A pair of ventral spines extends from the ventral surface of each
3 podomere. Appendages have a convex bell-shaped proximal margin, a terminal spine
4 protrudes from the distal end in some species. (emended from Daley & Budd 2010, p. 727).

6 Occurrence. Cambrian Valdemiedes Formation, Spain (Cambrian Series 2, Stage 4); Spence
7 Shale Member, Langston Formation, Utah, USA (Cambrian Series 3, Stage 5); Burgess
8 Shale, British Columbia, Canada (Cambrian Series 3, Stage 5); and Wheeler Formation,
9 Utah, USA (Cambrian Series 3, Drumian).

11 *Caryosyntrips serratus* Daley & Budd, 2010

12 Figs. 1A, 3

14 2005 ‘Dinocarida A’ Caron, App. 2. 3G.

15 2010 *Caryosyntrips serratus* Daley & Budd, p. 730-1, text-figs. 5A-I, 6H (non text-figs. 6A-
16 G, I)

18 Holotype. ROM 57161

20 Paratypes. ROM 59497, ROM 59498, ROM 59499, ROM 59502

22 Additional material. KUMIP 415223

24 Diagnosis. *Caryosyntrips* with one pair of distally pointing ventral spines on each podomere.
25 Ventral spines are less broad than for other *Caryosyntrips* species. A single row of small

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1 curved dorsal spines, spaced 1 mm apart, point distally. Distal most podomere ends in
2 recurved terminal spine.
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4 Description. The length of complete appendages (l in Fig. 2A) varies from 64.86 mm to
5 108.37 mm (mean = 83.57 mm, sd = 16.18 mm, n = 5). The angle between the dorsal and
6 ventral surface (θ in Fig. 2) varies from 11° to 18° (mean = 14.3°, sd = 3.4°, n = 6).
7 Podomere boundaries can usually be clearly seen on the inner edge of the specimens,
8 separated by arthrodistal membrane. Appendages have a row of small dorsal spines
9 (approximately 1 mm tall) spaced 1 mm apart, visible either as simple triangles (ROM
10 59499) (Fig 3B), curved spines pointing distally (ROM 57161) (Fig 3A) or as small circles
11 interpreted as attachment points (ROM 59497, ROM 59502, ROM 59458 and KUMIP
12 415223) (white arrows in Fig. 3C-F). One pair of ventral spines is present on each podomere,
13 although in most cases only one of the pair can be seen. ROM 59497 (Fig. 3F; Daley & Budd
14 2010, text-fig. 5C) displays three spines that appear to be on the dorsal surface of the
15 appendage at the distal end. These are interpreted as being one of a pair ventral spines which
16 during compression of the fossil have been preserved apparently on the dorsal surface. They
17 are shorter and face at a different angle to the ventral spines preserved on the ventral surface,
18 supporting this interpretation. The number of ventral spine pairs preserved per specimen for
19 this species varies from nine in the holotype (ROM 57161) to two in KUMIP 415223 and
20 ROM 59499 (Daley & Budd 2010, text-fig. 5G). Two specimens (ROM 57161 and 59502)
21 display recurved terminal spines, slightly longer than the ventral spines, however for many
22 specimens the distal end is incomplete (e.g. ROM 59498, KUMIP 415223).
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24 Occurrence. Burgess Shale, British Columbia, Canada (Cambrian Series 3, Stage 5) and
25 Wheeler Formation, Utah, USA (Cambrian Series 3, Drumian).

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Caryosyntrips camurus nov. sp.

Figs. 1B, 4

LSID. urn:lsid:zoobank.org:act:XXXXXXXXXX

2010 *Caryosyntrips serratus* Daley & Budd, p. 731, text-figs. 6A-G, I

Derivation of name. From Latin *camurus* (=hooked, bent) referring to the shape of the distal end.

Holotype. ROM 59503 (Daley & Budd, 2010, text-fig. 6I)

Paratype. ROM 59501

Other material. ROM 59500, 59598, 59599, KUMIP 314275

Diagnosis. *Caryosyntrips* with one pair of ventral spines on each podomere, and no dorsal spines. Distal most three podomeres are less tall than the others. Distal most podomere ends in a recurved terminal spine.

Description. This species has 14 podomeres (shown by the only complete appendages for this species, the paired appendages of ROM 59501, Fig. 4A). The measured lengths of the two complete appendages (l in Fig. 2A) are 71.74 mm and 70.69 mm. The angle between the

1 outer and inner edge of the appendages (θ in Fig. 2) varies from 13° to 17° (mean = 14.3° , sd
2 = 1.6° , n = 6).

3 Podomere boundaries are usually most visible on the dorsal surface and at the
4 proximal end of the appendage. ROM 59501, ROM 59503, ROM 59599 and KUMIP 314275
5 show clear boundaries on the dorsal surface, but not on the ventral surface (white arrows in
6 Fig. 4A-C, E). There are no dorsal spines of any size preserved, or circular spine attachment
7 points, on any of the specimens of this species.

8 Ventral spines are simple triangular shapes. One pair of ventral spines is present on
9 each podomere, although usually only one of the pair is visible. Three specimens (ROM
10 59500, ROM 59501, and ROM 59503) show clear evidence for paired ventral spines. ROM
11 59500 has two sets of paired spines visible (black arrows in Fig. 4D). ROM 59501 has two
12 paired spines at the proximal end of the podomere on the left side (black arrow in Fig. 4A),
13 and ROM 59503 has two spines on one podomere at the proximal end of the appendage
14 (black arrow in Fig. 4B). ROM 59599, and KUMIP 314275 (black arrows in Fig. 4C, E)
15 display ventral spines at the distal end on both sides of the appendage. This is interpreted as
16 being a pair of ventral spines, one of which, during compression of the fossil, has been
17 preserved on the dorsal surface. They are shorter and face at a different angle to the spines on
18 the inner edge, supporting this interpretation. The terminal spine, visible on ROM 59501, is
19 recurved (grey arrow in Fig. 4A).

20 The distal three podomeres of *C. camurus* are thinner than would be expected for an
21 appendage with a simple triangular shape when flattened, and is sometimes preserved
22 distorted. This is most visible in ROM 59500 (Fig. 4D), and less pronounced in KUMIP
23 314275 and ROM 59503 (Fig. 4B, C) where the distal end curves slightly ventrally.

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1 Remarks. *C. camurus* can be differentiated from the other two species as it lacks dorsal
2 spines completely. It has paired ventral spines, and podomere boundaries tend to be clearest
3 on the outer edge. The distalmost three podomeres are less tall than for the other species, and
4 is sometimes preserved distorted, giving it a hooked appearance.

5 Daley & Budd (2010) mention that *Caryosyntrips* appendages should not be confused
6 with distal ends of anterior appendages of *Sidneyia* (Bruton 1981; Stein 2013; Zacaï et al.
7 2016) based on segmentation, angle of inner spines and presence of dorsal spines. Although
8 this species of *Caryosyntrips* does not have dorsal spines, it is still possible to distinguish
9 them from *Sidneyia* on account of the segmentation of appendages and angle of ventral
10 spines.

12 Occurrence. Spence Shale Member, Langston Formation, Utah, USA (Cambrian Series 3,
13 Stage 5); Burgess Shale, British Columbia, Canada (Cambrian Series 3, Stage 5).

15 *Caryosyntrips durus* nov. sp.

16 Figs. 1C, 5

18 LSID. urn:lsid:zoobank.org:act:XXXXXXXXXX

20 Derivation of name. From Latin *durus* (=hard, inflexible).

22 Holotype. KUMIP 314071

24 Paratype. KUMIP 314070

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1 Diagnosis. *Caryosyntrips* with dorsal and ventral surfaces straight, a rounded distal end and
2 no terminal spine. Paired ventral spines on each podomere are simple triangles that end in a
3 sharp point. A single row of small (1 mm tall), curved, distally pointing, dorsal spines spaced
4 1 mm apart runs along the length of the appendage. A single large dorsal spine, the same size
5 and shape as the ventral spines, is present on each of the distal most seven podomeres.

7 Description. The two specimens are partial *Caryosyntrips* appendages, with 9 podomeres
8 preserved for each (lengths: KUMIP 314070 = 41.09 mm, KUMIP 314071 = 29.05 mm).
9 Podomere boundaries are preserved as faint, simple curved lines. The proximal shape of the
10 appendages cannot be ascertained, as it is missing in both. The angle between the ventral and
11 dorsal surfaces (θ in Fig. 2) is 17° for KUMIP 314070 and 15° for KUMIP 314071. The inner
12 edge has a stepped appearance and the outer edge is straight. A row of small spines (1 mm
13 tall, spaced 1 mm apart) run along the dorsal surface, preserved as simple triangles in KUMIP
14 314070 (Fig. 5A) and curved pointing distally in KUMIP 314071 (Fig. 5B).

15 Large spines (h in Fig. 2B: 1.1—3.0mm, w in Fig. 2B: 1.2—2.0 mm) are present on
16 both the dorsal and ventral surfaces of the appendage. The large dorsal spines are spaced
17 evenly (3 mm apart in KUMIP 314070), with one spine on each podomere. The angle
18 between the dorsal surface of the appendage and the large dorsal spine (β in Fig. 2B) varies
19 from $115\text{-}160^\circ$. There is a gap of 8 mm between the proximal-most dorsal spine in KUMIP
20 314070 (Fig. 5A) to the sediment covered margin, indicating that large dorsal spines are
21 present only on the distal most seven podomeres. Large ventral spines are paired, just as in
22 other species of *Caryosyntrips*. This is most visible on the 6th—8th most distal podomeres of
23 KUMIP 314070 (black arrows in Fig. 5A). The angle from the ventral surface of the
24 appendage to the proximal edge of the ventral spines (α in Fig. 2B) varies from $128\text{-}152^\circ$.

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1 There are no ventral spines on the distalmost podomere, and no terminal spine. The
2 appendage tapers to a rounded point, with the inner edge extending slightly beyond the outer
3 edge. The distal region of KUMIP 314070 is not preserved, and so no comparison can be
4 made between the two.

6 Remarks. Although only known from two partial appendages, *C. durus* is significantly
7 different from the other species to warrant a formal description. It can be differentiated as it
8 has paired large ventral spines on each podomere, and a single dorsal spine on the distal most
9 seven podomeres, in addition to a row of small dorsal spines. *C. camurus* and *C. c.f. C.*
10 *camurus* have no dorsal spines, and *C. serratus* has only a row of small dorsal spines.

12 Occurrence. Wheeler Formation, Utah, USA (Cambrian Series 3, Drumian).

14 *Caryosyntrips* cf. *camurus*

15 Fig. 6

16 2011 *Mureropodia apae* Gámez Vintaned et al. figs. 12.3, 12.4, 12.5 and 12.9

18 Material: MPZ 2009/1241

20 Description: MPZ 2009/1241 is a partial appendage of six podomeres, which measures 82.82
21 mm in length (giving an extrapolated length for 14 podomeres of 193 mm). The appendage
22 ('body' of Gámez Vintaned et al. 2011 fig. 12.4) tapers in outline towards the distal end,
23 which is distorted ('proboscis' of Gámez Vintaned et al. 2011, fig. 12.4). The angle between
24 the dorsal and ventral surfaces (θ in Fig. 2) is 14° . The number of podomeres is indicated by
25 the number of ventral spines ('left lobopods' of Gámez Vintaned et al. 2011 fig. 12.4) and

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1 faint boundaries on the dorsal surface, which are visible under low angle light. The ventral
2 spines measure 5.1—6.9 mm in length (h in Fig. 2B). Evidence for paired ventral spines is
3 visible on the third most distal podomere (black arrows in Fig. 6A, B). There is no evidence
4 for dorsal spines, however the dorsal surface is not well preserved.

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6 Remarks. MPZ 2009/1241 was originally described as a lobopodian, *Mureropodia apae*, and
7 to date is the only member of the genus. *Mureropodia* is significantly different to the most
8 similar lobopodian morphologically, *Paucipodia* Hou et al. (2004), as it has a different
9 overall shape, lacks annulation, has a distinct putative ‘proboscis’ and its putative ‘legs’ have
10 a length/trunk width ratio far lower than legs in *Paucipodia*. The overall shape of the
11 specimen is very similar to other *Caryosyntrips* appendages, and the 14° angle between the
12 dorsal and ventral surfaces (θ in Fig. 2) is similar to other *Caryosyntrips* appendages (11-
13 18°). Radiodontan appendages do not have annulation, and faint podomere boundaries are
14 visible under low angle light. The ‘proboscis’ is here interpreted as a distorted distal end of
15 the appendage, similar to some *C. camurus* specimens (e.g. Fig. 4D) and the ‘legs’ are
16 reinterpreted as paired ventral spines, whose height:width ratio (h and w in Fig. 2B) fits
17 within the measurements of other *Caryosyntrips* ventral spines. These features support the
18 reinterpretation of MPZ 2009/1241 as a partial isolated *Caryosyntrips* appendage, most
19 similar to *C. camurus*. However both the ventral spines and appendage are longer than for
20 other *C. camurus* specimens (Fig. 7), the dorsal surface of the appendage is not well
21 preserved and this specimen would greatly increase the known geographic and stratigraphic
22 range for the species. For these reasons we leave the identification in open nomenclature as
23 *C. cf. camurus*.

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25 Occurrence. Valdemiedes Formation, Spain (Cambrian Series 2, Stage 4).

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3 1 However within *C. serratus* not all specimens clearly show podomere boundaries (Fig. 3B,
4 E) suggesting that the differences in preservation of podomere boundaries is also affected by
5 taphonomy. The distal end of *C. camurus* and *C. cf. camurus* is often preserved distorted (e.g.
6 Figs. 4D; 6). This is interpreted as a taphonomic artefact, however it may be more common in
7 *C. camurus* and *C. cf. camurus* because the distalmost three podomeres are less tall compared
8 to *C. durus* and *C. serratus*, and so more susceptible to taphonomic stretching and
9 deformation. Ventral spine length (h in Fig. 2B) also varies within all species of
10 *Caryosyntrips* (Fig. 7). It does not correlate clearly with appendage length, although the
11 limited number of appendages longer than 100 mm means that this is difficult to test. The
12 variation of longest ventral spine lengths for appendages of similar lengths suggests that the
13 range of ventral spine lengths is not solely due to the size of the animal. Ventral spines are
14 not always preserved on every podomere of appendages, particularly *C. serratus* (see Fig. 3).
15 *C. serratus* may be more affected than the other species as ventral spines tend to be
16 proximally pointing, and so require a smaller rotation of the appendage to be concealed after
17 compression.

18 19 *Geographic and temporal range*

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22 *Caryosyntrips*, previously only known from the Burgess Shale (Cambrian Series 3,
23 Stage 5), is here reported from the older Valdemiedes Formation (Cambrian Series 2, Stage
24 4) and Spence Shale Member, Langston Formation (Cambrian Series 3, Stage 5), as well as
25 the younger Wheeler Formation (Cambrian Series 3, Drumian). *Caryosyntrips cf. camurus*
from the Valdemiedes Formation is the oldest *Caryosyntrips* known, the first radiodontan
reported from this Lagerstätten, and the first *Caryosyntrips* from outside Laurentia. All three
species of *Caryosyntrips* are now known from Utah Lagerstätten (Spence Shale and Wheeler

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1 Formation), increasing the faunal overlap in radiodontans between the Burgess Shale and
2 Utah. *Anomalocaris* (Briggs et al. 2008; Lerosey-Aubril et al. 2014), *Hurdia victoria*, *Peytoia*
3 *nathorsti* (Conway Morris & Robison 1982; Pates et al. *in press*), and *Stanleycaris* (Pates et
4 al. *submitted*) are all known from both the Burgess Shale and Utah Lagerstätten.

5 *Caryosyntrips* cf. *camurus* is added to the other Gondwanan Radiodonta:
6 *Anomalocaris* cf. *canadensis* and *A. briggsi* from the Emu Bay Shale (Cambrian Series 2,
7 Stage 4), Australia (Nedin 1999; Daley et al. 2013*b*; Paterson et al. 2016); and *Hurdia* from
8 the Jince Formation (Cambrian Series 3, Drumian), Czech Republic (Chlupáč & Kordule
9 2002; Daley et al. 2013*a*). The discovery of *Caryosyntrips* in the Cambrian Series 2, Stage 4
10 of Gondwana shows that its global distribution is much wider than initially thought.
11 *Caryosyntrips* is only known from the high latitude Valdemiedes Formation, not the
12 equatorial Emu Bay Shale. This suggests that *Caryosyntrips* originated at a high latitude in
13 Gondwana during the Cambrian Series 2, and expanded its range to more equatorial
14 Laurentia, where it is known from the Cambrian Series 3. Appendages of *Caryosyntrips* are
15 found in much lower abundance in the Burgess Shale (12) than *Anomalocaris* (385), *Peytoia*
16 (229) and *Hurdia* (290) (Daley & Budd 2010; Daley et al. 2013*a*). This suggests that
17 *Caryosyntrips* may have been a part of Laurentian communities older than the Series 3, Stage
18 5 Spence, such as the Series 2, Stage 4, Eager, Kinzers, Latham and Pioche Formations
19 (Briggs 1979; Briggs & Mount 1982; Lieberman 2003), but it has not yet been discovered
20 either because of low numbers in the original population, or because it may have a lower
21 fossil preservation potential than other radiodontan appendages.

22
23 *Ecological interpretation*
24

1 The large appendages of radiodontans were located at the front of the head adjacent to the
2 mouthparts, as indicated by taxa known from full body specimens such as *Anomalocaris*,
3 *Peytoia*, and *Hurdia* (Whittington & Briggs 1985; Collins 1996; Daley et al. 2009; Daley &
4 Edgecombe 2014), and were involved in feeding. In other radiodontan taxa, the functional
5 morphology of frontal appendages has been used to distinguish between the dextrous
6 grasping motion of the actively durophagous *Anomalocaris* (Briggs 1979; Collins 1996;
7 Nedin 1999) and the less specialised prey trapping or sediment sifting motion of taxa with
8 longer ventral spines, such as *Hurdia* and *Peytoia* (Daley & Budd 2010). Filter feeding has
9 been suggested for the giant Ordovician radiodontan *Aegirocassis* because of the presence of
10 dense setae on its frontal appendage (Van Roy et al. 2015). *Caryosyntrips* was previously
11 interpreted as an actively durophagous predator similar to *Anomalocaris*, based on the
12 elongated nature of the frontal appendage and its relatively short ventral spines, however the
13 movement differs between the two taxa. *Caryosyntrips* is thought to have moved its stiffer
14 frontal appendage by pivoting at the bell-shaped basal attachment joint (see Fig. 3A, C-F) to
15 create a scissor-like grasping or slicing motion between the opposing appendage pair (Daley
16 & Budd 2010). *Anomalocaris* displays greater flexibility along the appendage as indicated by
17 its more prominent arthrodistal membranes and preservation exhibiting 180° of motion, but
18 appears to have had an immobile basal attachment joint (Whittington & Briggs 1985; Daley
19 & Edgecombe 2014). Both *Caryosyntrips* and *Anomalocaris* may have relied on suction
20 created by the mouthparts to bring prey items towards the mouth, after crushing and slicing
21 by the appendages. While the mouthparts of *Caryosyntrips* are unknown, the flexible oral
22 cone of *Anomalocaris* has been suggested to provide suction rather than a chewing or
23 crushing motion (Hagadorn et al. 2010; Daley & Bergström 2012). The newly discovered
24 material of *Caryosyntrips* allows for further elaboration of the ecological interpretation of
25 this taxon, supporting a durophagous predatory nature and suggesting that morphological

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1 differences between taxa indicate different feeding behaviours and access to different prey
2 items.

3 While all *Caryosyntrips* taxa are considered to be durophagous predators, the
4 differences in frontal appendage morphology between the species (Fig. 1; Table 1) indicate
5 that the behaviour and prey choice may have differed. The ventral spines in *C. serratus* are
6 the most slender, and generally point distally. Ventral spines in *C. camurus* and *C. durus* tend
7 to point more proximally, and *C. durus* has the most robust ventral spines. This suggests that
8 *C. durus* sought out the most robust prey items. Although the preservation of arthrodial
9 membrane is likely to have been affected by taphonomy, the current evidence suggests that
10 flexibility along the appendage may have varied between taxa. *C. durus* had the most rigid
11 frontal appendage, as indicated by its overall shape and membranes preserved as simple lines,
12 whereas *C. serratus* and *C. camurus* have visible arthrodial membrane between all
13 podomeres along the length of the appendage and so appear more flexible. The thin
14 distalmost three podomeres in *C. camurus* may also have provided additional flexibility. The
15 unique presence of large dorsal spines in *C. durus* (in addition to the smaller dorsal spines
16 present in *C. serratus* and *C. durus*) may have provided additional strength and protection to
17 the frontal appendages of this taxon as its sought out more robust prey items than the other
18 two *Caryosyntrips* species, which would have been more able to manipulate prey items, and
19 so would have sought out less robust, but more difficult to catch, prey.

20 The study of *Caryosyntrips* has implications for understanding Cambrian ecosystems
21 and ecology. Its putative durophagous predatory lifestyle makes it a potential culprit for
22 Cambrian trilobite repaired injuries that have previously been attributed to *Anomalocaris*
23 (e.g. Rudkin 1979; Babcock 1993). While these damages were thought to have been inflicted
24 by *Anomalocaris* using the dextrous nature of the claw to create fracture lines by repeated
25 bending and twisting (Nedin 1999), the robust ventral spines and strong crushing motion

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1 implied for *Caryosyntrips* could provide another way to break mineralized trilobite
2 exoskeletons and cause these injuries. The variation seen between the morphology of the
3 three *Caryosyntrips* species and their corresponding ecological interpretations suggests that
4 this taxon may have been an important factor driving community composition in the
5 Cambrian.

6
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16 positive, thorough and helpful reviews, which greatly improved the manuscript.

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1 **Figure captions**

2 **FIG 1.** Idealised sketch of each *Caryosyntrips* species. A. *C. serratus* Daley and Budd, 2010,
3 small spines along outer edge preserved as either circular attachment points or as spines; B.
4 *C. camurus* nov. sp., proximal boundary inferred as it is not preserved in any specimen; C. *C.*
5 *durus* nov. sp., proximal five podomeres inferred as these are not preserved in either
6 specimen.

7
8 **FIG 2.** Explanation of measurements. A. length (l) and angle between edges (theta); B. angle
9 between large spine and inner edge (alpha), angle between large spine and outer edge (beta),
10 length of large spine (h) and width of large spine (w); C. how angle between edges (theta) is
11 measured for specimens with a bent end.

12
13 **FIG 3.** *Caryosyntrips serratus* specimens. A. ROM 57161 (holotype); B. ROM 59499; C.
14 ROM 59502; D. ROM 59498; E. KUMIP 415223; F. ROM 59497. White arrows indicate
15 circular small spine attachment points. All scale bars 10 mm.

16
17 **FIG 4.** *Caryosyntrips camurus* specimens. A. ROM 59501; B. ROM 59503 (holotype); C.
18 KUMIP 314275; D. ROM 59500; E. ROM 59599. White arrows indicate podomere
19 boundaries, black arrows indicate paired spines mentioned in text, grey arrow indicates
20 terminal spine. All scale bars 10 mm.

21
22 **FIG 5.** *Caryosyntrips durus* specimens. A. KUMIP 314070 (paratype), black arrows indicate
23 paired spine on lower level of rock; B. KUMIP 314071 (holotype). All scale bars 10 mm.

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1 **FIG 6.** *Caryosyntrips* cf. *camurus*, MPZ 2009/1241. A. dry; B. underwater. Scale bars 10
2 mm.

4 **FIG 7.** Plot of length of appendages against length of longest spine. Circles = *Caryosyntrips*
5 *serratus*, diamonds = *C. camurus*, triangles = *C. cf. camurus*, squares = *C. durus*. Complete
6 appendage length measurements in black, extrapolated lengths from incomplete appendages
7 in grey. Raw data in Supplementary Files.

9 **Table captions**

11 **TABLE 1.** Comparison of *Caryosyntrips* species. Measurements for individual specimens in
12 Supplementary Data.

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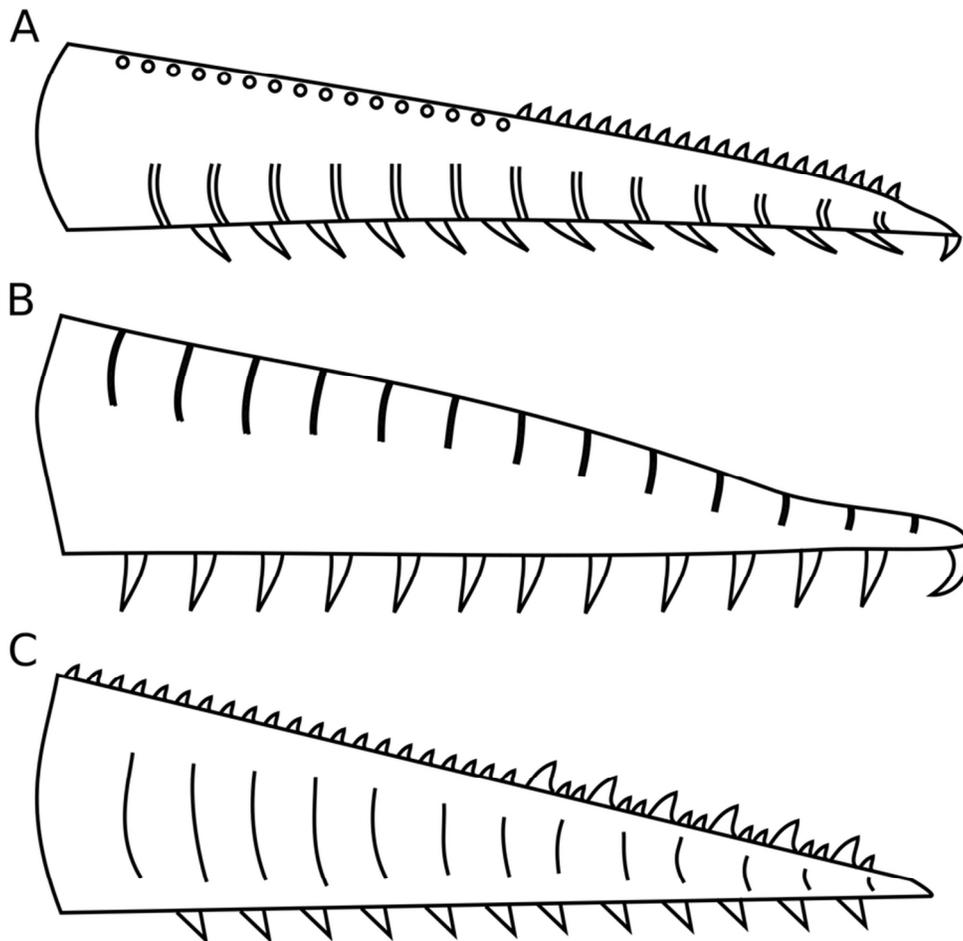


FIG 1. Idealised sketch of each Caryosyntrips species. A. *C. serratus* Daley and Budd, 2010, small spines along outer edge preserved as either circular attachment points or as spines; B. *C. camurus* nov. sp., proximal boundary inferred as it is not preserved in any specimen; C. *C. durus* nov. sp., proximal five podomeres inferred as these are not preserved in either specimen.!! †

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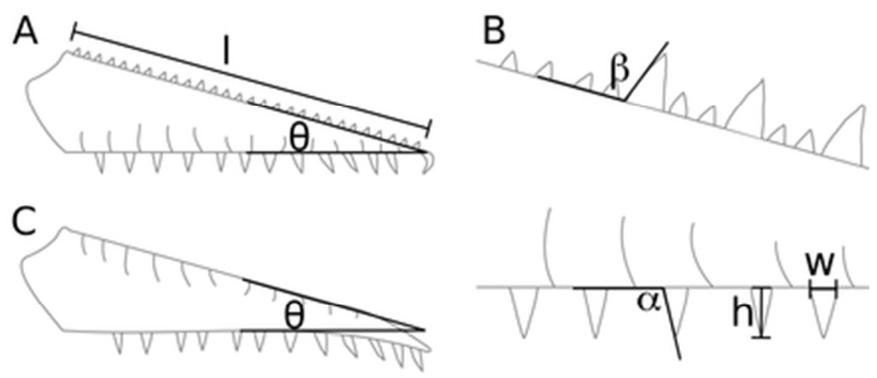


FIG 2. Explanation of measurements. A. length (l) and angle between edges (θ); B. angle between large spine and inner edge (α), angle between large spine and outer edge (β), length of large spine (h) and width of large spine (w); C. how angle between edges (θ) is measured for specimens with a bent end.

36x16mm (300 x 300 DPI)

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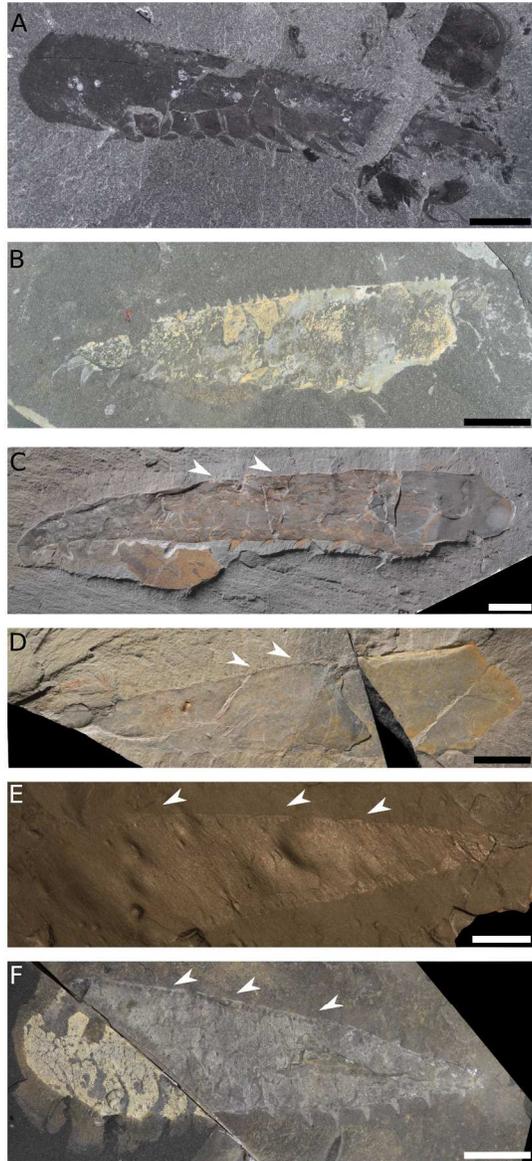


FIG 3. *Caryosyntrips serratus* specimens. A. ROM 57161 (holotype); B. ROM 59499; C. ROM 59502; D. ROM 59498; E. KUMIP 415223; F. ROM 59497. White arrows indicate circular small spine attachment points. All scale bars 10 mm.

172x369mm (300 x 300 DPI)

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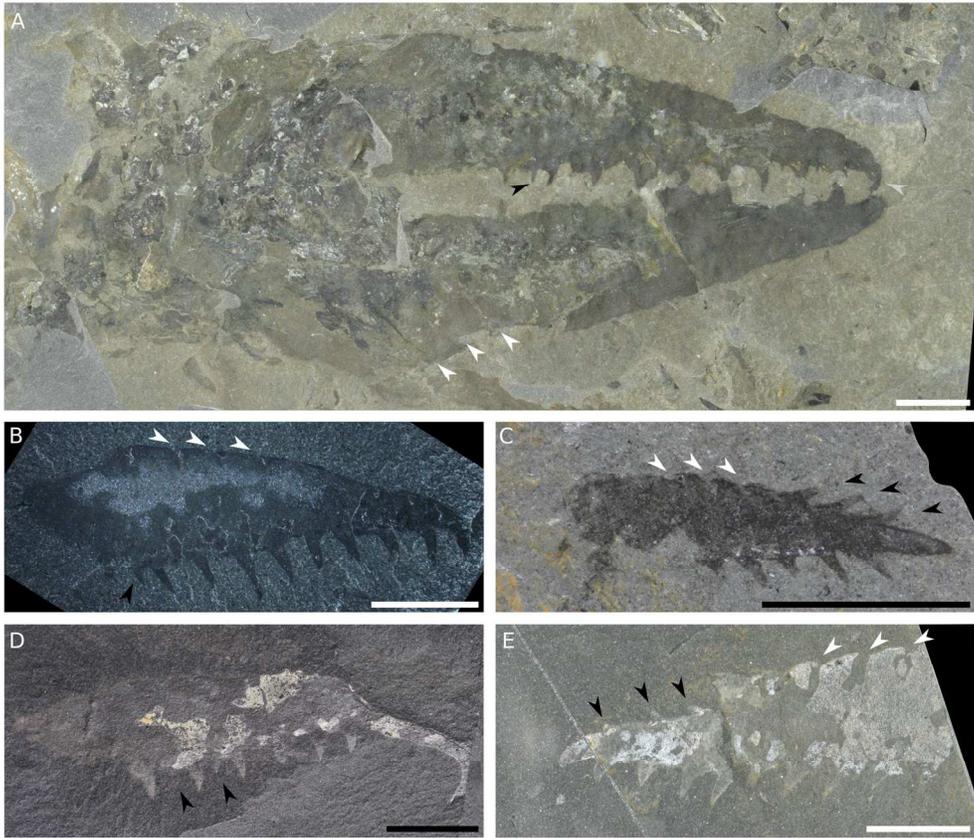


FIG 4. *Caryosyntrips camurus* specimens. A. ROM 59501; B. ROM 59503 (holotype); C. KUMIP 314275; D. ROM 59500; E. ROM 59599. White arrows indicate podomere boundaries, black arrows indicate paired spines mentioned in text, grey arrow indicates terminal spine. All scale bars 10 mm.

143x124mm (300 x 300 DPI)

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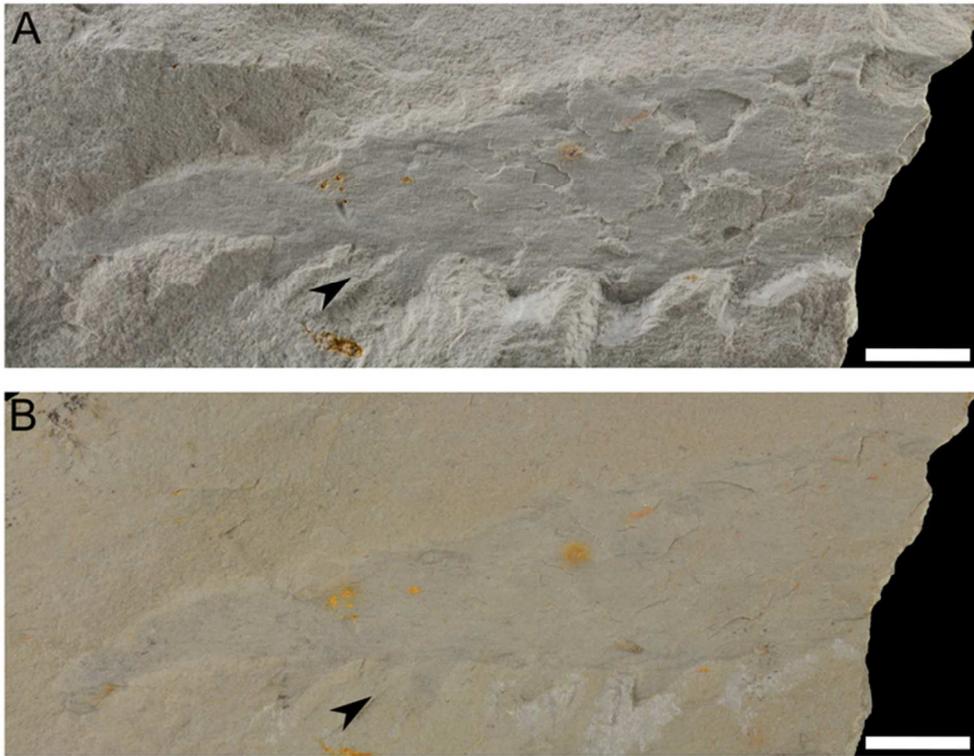


FIG 6. *Caryosyntrips* cf. *camurus*, MPZ 2009/1241. A. dry; B. underwater. Scale bars 10 mm.!! †

62x48mm (300 x 300 DPI)

Table 1: Comparison of <i>Caryosyntrips</i> species				
	<i>Caryosyntrips serratus</i>	<i>Caryosyntrips camurus</i>	<i>Caryosyntrips durus</i>	<i>Caryosyntrips</i> cf. <i>camurus</i>
Number of specimens	6 isolated appendages	5 isolated appendages, 1 pair of appendages	2 isolated appendages	1 isolated appendage
Row of dorsal spines	Yes	No	Yes	No
Other dorsal spines	No	No	Yes: same size as ventral spines. One on podomeres 8-14.	No
Ventral spines	One pair per podomere	One pair per podomere	One pair per podomere	One pair per podomere
α range	11-18°	13-17°	15-17°	14°
l range	65-108 mm	28-72 mm	45-64 mm	193 mm
Stratigraphic occurrence	Burgess Shale; Wheeler Formation	Spence Shale; Burgess Shale	Wheeler Formation	Valdemiedes Formation
Age range	Stage 5 - Drumian	Stage 5	Drumian	Stage 4
Continent	Laurentia	Laurentia	Laurentia	Gondwana
References	This study; Daley & Budd 2010	This study; Daley & Budd 2010	This study	This study; Gámez Vintaned et al. 2011
Measurements for individual specimens in Supplementary Data.				

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		l	h of longest spine	h of shortest spine	theta	n. pods	
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2	<i>Caryosyntrips serratus</i>						
3	ROM 57161	76.55	5.71	2.74	11	14	
4	ROM 59499	61.64	2.84	5.78	16	12	
5	ROM 59502	108.37	7.90	2.85	11	14	
6	ROM 59498	80.05	2.38	1.71	12	14	
7	KUMIP 415223	88.02	2.21		18	14	
8	ROM 59497	64.86	3.04	2.20	18	14	
9	<i>Caryosyntrips camurus</i>						
10	ROM 59501 (A)	71.74	3.44	2.22	15	14	
11	ROM 59501 (B)	70.69	2.83	2.53	17	14	
12	ROM 59503	40.84	4.67	3.05	13	10	
13	KUMIP 314275	17.99	2.12	1.88	15	9	
14	ROM 59500	27.35	3.09	2.33	13	6	
15	ROM 59599	37.26	3.25	2.27	13	9	
16	<i>Caryosyntrips durus</i>						
17	KUMIP 314070	41.09	2.38	1.50	17	9	
18	KUMIP 324071	29.05	2.46	1.86	15	9	
19	<i>Caryosyntrips cf. camurus</i>						
20	MPZ 2009/1241	82.82	6.90	4.29	14	6	
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2	extrapolated length
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5	108.37
6	80.05
7	88.02
8	64.86
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12	71.74
13	70.69
14	57.18
15	27.98
16	63.82
17	57.96
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22	63.92
23	45.19
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26	193.25
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