The Kinzers Formation (Pennsylvania, USA): the most diverse assemblage of Cambrian Stage 4 radiodonts

Journal:	Geological Magazine
Manuscript ID	GEO-18-1993.R1
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
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Keywords:	Cambrian, Kinzers Formation, Anomalocaris, Amplectobelua, Laminacaris, Tamisiocaris, Radiodonta

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22	9	Category: Original article
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24	10	Short title: Kinzers Formation Radiodonta
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28	12	Keywords: Cambrian, Kinzers Formation, Anomalocaris, Amplectobelua, Laminacaris,
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17 Abstract

19	Radiodonta, apex Cambrian predators such as Anomalocaris, have been known from the
20	Kinzers Formation (Cambrian Series 2, Stage 4 - Pennsylvania, USA) for nearly 100 years.
21	Work over the last 10 years mainly on radiodont material from the Chengjiang (Cambrian
22	Series 2, Stage 3 – Yunnan, China) and Burgess Shale (Cambrian Series 3, Stage 5 – British
23	Columbia, Canada), has greatly improved our knowledge of the diversity and disparity of
24	radiodonts and their frontal appendages, including the description of new species, genera
25	and families. Previous work identified two species of radiodonts from the Kinzers
26	Formation: Anomalocaris pennsylvanica Resser 1929 and Anomalocaris? cf. pennsylvanica
27	based on isolated frontal appendage material (Briggs 1979). A restudy of Kinzers Formation
28	material shows that only some of the specimens can be confirmed as Anomalocaris
29	pennsylvanica, and a number of specimens previously attributed to Anomalocaris in fact
30	belong to other more recently discovered radiodont genera Amplectobelua and
31	Tamisiocaris. This reinterpretation makes the Kinzers Formation the most diverse Cambrian
32	Stage 4 Burgess Shale Type Lagerstätten in terms of number of radiodont species. This
33	assemblage includes the youngest known Tamisiocaris and the first from outside Greenland,
34	the only Amplectobelua from Stage 4 and the oldest from Laurentia, two specimens
35	tentatively assigned to the recently described Chengjiang genus Laminacaris, and the
36	endemic Anomalocaris pennsylvanica. The identification of these new radiodont taxa
37	increases the total known diversity of the Kinzers Formation to more than 10 species, and so
38	it should now be considered a Tier 2 Lagerstätten.
39	

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1. Introduction

43	Soft-bodied fossil biota (Konservat-Lagerstätten) such as the famous Chengjiang (Cambrian
44	Series 2, Stage 3) and Burgess Shale (Cambrian Series 3, Stage 5), offer an unrivalled
45	opportunity to study assemblages of animals at snapshots in time. Konservat-Lagerstätten
46	are not distributed evenly through time, but instead are most common in the Cambrian
47	Series 2 and Series 3 (Allison and Briggs 1993; Gaines 2014). The Kinzers Formation
48	(Pennsylvania, USA), has been recognized as a Konservat-Lagerstätten for nearly 100 years,
49	since the discovery of antennae in Olenellus getzi (Dunbar 1925) and the subsequent
50	description of soft-bodied animals (e.g. Resser 1929; Resser and Howell 1938). The
51	exceptionally preserved fauna is confined to the Dyeran (Cambrian Series 2, Stage 4) Fine
52	Pelitic Facies of the Emigsville Member (Skinner 2005). Preservation at different localities
53	varies in iron content, which sometimes overlays and obscures parts of the fossils, owing to
54	differences in the concentration of algae and cyanobacteria of the original sediment
55	(Skinner 2005). The currently known soft-bodied fauna of the Kinzers Formation includes
56	the worms Selkirkia (Conway Morris 1977), Kinzeria crinita and Atalotaenia adela (Garcia-
57	Bellido and Conway Morris 1999), the sponge Hazelia walcotti (Rigby 1987), arthropods such
58	as Serracaris lineata (Briggs 1978), Isoxys (Campbell and Kauffman 1969), Sidneyia
59	(Campbell and Kauffman 1969), Protocaris (Campbell and Kauffman 1969), and Tuzoia
60	(Resser 1929; Campbell and Kauffman 1969; Vannier et al. 2007), and stem-group
61	euarthropod radiodonts (Resser 1929; Briggs 1979), which are the focus of this study.
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64	Since the original description of radiodont material from the Kinzers Formation, including
65	Anomalocaris pennsylvanica (Resser 1929), and subsequent redescription of material
66	following the recognition that Anomalocaris was the appendage of a euarthropod and not
67	the body of a shrimp (Briggs 1979), the number of known species, genera and families of
68	Radiodonta described from other localities has increased substantially. Complete
69	Anomalocaris body fossils were discovered and described (Whittington & Briggs 1985),
70	Radiodonta were shown to be stem-group euarthropods (Daley et al. 2009) and what began
71	three species described from isolated appendages (Anomalocaris canadensis, A.
72	pennsylvanica and 'appendage F' – Briggs 1979) has exploded into a diverse group of apex-
73	predators, many known from complete specimens (Whittington & Briggs 1985; Chen et al.
74	1994; Hou et al. 1995; Collins 1996; Daley et al. 2009), with diverse feeding strategies
75	representing over 10 genera (Daley et al. 2009; Daley & Budd 2010; Cong et al. 2014, 2016,
76	2017, 2018; Vinther et al. 2014; Pates et al. 2017; 2018a; Pates & Daley 2017). Radiodonta
77	fossils have been identified worldwide, from the Great Basin, USA (e.g. Briggs and Mount
78	1982; Lieberman 2003; Briggs et al. 2008; Lerosey-Aubril et al. 2014; Pates et al. 2018b);
79	Iberian Chains, Spain (Pates & Daley 2017); Holy Cross Mountains, Poland (Daley & Legg
80	2015); Bohemia, Czech Republic (Chlupáč & Kordule 2002; Daley et al. 2013a); Hunsruck,
81	Germany (Kühl et al. 2009); as well as more famous sites such as the Burgess Shale, Canada
82	(e.g. Whittington & Briggs 1985; Collins 1996; Daley and Budd 2010), Chengjiang and Haiku
83	biotas, China (e.g. Chen et al. 1994; Hou et al. 1995; Cong et al. 2014, 2016, 2017, 2018; Guo
84	et al. in press) and Emu Bay Shale, Australia (Nedin 1995; Daley et al. 2013b).
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86 In this study, the known Radiodonta material from the Kinzers Formation is reassessed in
87 light of the substantial increase in knowledge of these iconic Cambrian animals. Significantly

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88	for this study, two genera, <i>Tamisiocaris</i> Daley & Peel 2010 and <i>Amplectobelua</i> Hou et al.
89	1995, with frontal appendages superficially similar to Anomalocaris, were described since
90	the last review of the Kinzers Radiodonta by Briggs (1979). Our restudy of the material
91	ascribed to Anomalocaris pennsylvanica and Anomalocaris? cf. pennsylvanica shows that it
92	in fact belongs to at least four different taxa, and confirms that A. pennsylvanica is a distinct
93	species from A. canadensis.

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95 2. Identifying Radiodonta using frontal appendages

96

97	Although rare complete body fossils are known, Radiodonta are most commonly found as
98	isolated elements of the body plan: frontal appendages, mouthparts, carapace elements, or
99	flaps. Of these, isolated frontal appendages are the most common radiodont body element
100	found outside of Tier 1 BSTs, deposits with greater than 100 taxa known, preserved in high
101	fidelity and high abundance (Gaines 2014), and a number of species are known only from
102	frontal appendages, especially from Tier 2 (from 10 to 100 taxa, intermediate fidelity and
103	abundance) and Tier 3 (less than 10 taxa, low fidelity and abundance) BST deposits. Frontal
104	appendages are taxonomically informative, and even partial specimens often provide
105	enough evidence to recognise families, genera or species of radiodonts.

106

107 Radiodont frontal appendages consist of a series of podomeres bearing a diverse 108 morphology of spines and/or endites along their length. Radiodont frontal appendages can 109 be separated into the 'shaft' (sensu Hou et al. 1995, sometimes referred to as the 110 'peduncle') and the 'distal articulated region' (sensu Cong et al. 2018). The shaft normally

111 has more weakly defined boundaries between podomeres and is less sclerotized than the

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112	rest of the appendage, and accordingly it is not always preserved or is only incompletely
113	preserved. It joins the appendage to the body and is joined to the distal articulated region at
114	an angle between 100-180° on the dorsal surface (Fig. 1a, $artheta$). The shaft often bears an
115	endite at the distalmost point of the ventral surface (Fig. 1a, shaft endite), and rarely other
116	ventral endites are present on the shaft (e.g. Ramskoeldia platycantha, Cong et al. 2018).
117	The boundary between the shaft and the distal articulated region can be further identified
118	by the presence, in most taxa, of an enlarged or morphologically differentiated ventral
119	endite on the most proximal podomere of the distal articulated region (e.g. Amplectobelua,
120	Lyrarapax) (Fig. 1a, hypertrophied endite). The distal articulated region can itself often be
121	separated into two parts. The proximal part bears ventral endites of the same morphology,
122	differentiating it from the distal part, which often bears either no ventral endites, or
123	reduced and simplified endites, together with dorsal spines (Fig. 1a, dorsal spines, reduced
124	endites).
125	
126	The morphology and pattern of ventral endites in particular have been used to identify
127	isolated appendages (Table 1). In Hurdiidae, blade-like ventral endites are the same width
128	(frontal view) as the podomere, and only one ventral endite projects from each podomere
129	(Fig. 1c). Hurdiids always have five of these large identical blade-like ventral endites in the
130	distal articulated region (Fig. 1a, from 1-5). For all other families, the ventral endites are
131	paired on each podomere, and are less than half the width (frontal view) of the podomere

- to which they attach (Fig. 1b). Families can be differentiated using the relative lengths of
- 133 ventral endites, the presence of enlarged ventral endites on the post-shaft podomere,
- 134 and/or the morphology of dorsal spines in the distal articulated region. Anomalocarididae (a
- 135 clade that includes all species of Anomalocaris except for Anomalocaris briggsi) and
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3	136	Amplectobeluidae both have enlarged spine-like ventral endites in the distal articulated
5 6	137	region, which alternate in length long/short on odd/even podomeres, with a general
7 8	138	reduction in the length of ventral endites over the length of the appendage.
9 10	139	Amplectobleuidae differ from Anomalocarididae as the ventral endite on the fifth podomere
12 13	140	in the distal articulated region is longer than that on the third, and the distal region often
14 15	141	bears thickened dorsal spines, in contrast to Anomalocarididae where they are thinner.
16 17	142	Tamisiocarididae ('Cetiocaridae' of Vinther et al. 2014), a clade comprising Tamisiocaris
18 19 20	143	borealis and Anomalocaris briggsi (Vinther et al. 2014; Cong et al. 2014; Van Roy et al. 2015)
20 21 22	144	have a pair of elongated and slender ventral endites that have a length at least 1.5x the
23 24	145	height (sag) of the podomere to which are attached. The appendage is simple, with the
25 26	146	same morphology of ventral endite along the distal articulated region. There is no
27 28 29	147	differentiated post-shaft podomere in Tamisiocaris appendages, although Anomalocaris
30 31	148	briggsi does have an enlarged post-shaft ventral endite and an additional endite of similar
32 33	149	morphology on the distalmost position of the shaft. There is no alternation of long/short
34 35 26	150	ventral endites in these taxa, with the overall length of ventral endites decreasing along the
37 38	151	length of the appendage. Caryosyntrips, Laminacaris, and Lyrarapax have an uncertain
39 40	152	placement at family level, but can be distinguished based on features of the frontal
41 42	153	appendages. Caryosyntrips appendages taper distally with an approximately triangular
43 44 45	154	outline. Similar to tamisiocaridids, the appendages are simple, with no alternation of
46 47	155	long/short ventral endites, and no enlarged endite distal to the shaft. Laminacaris, a
48 49	156	recently described monospecific genus from the Chengjiang biota, bears a ventral endite on
50 51	157	the most proximal podomere in the distal articulated region similar in morphology to Hurdia
52 53 54	158	ventral endites, but the remainder of the distal articulated region is similar to
55 56 57	159	Anomalocarididae and Amplectobeluidae. Lyrarapax appendages superficially resemble

2 3	160	those of Amplectobeluids, as appendages have an enlarged ventral endite on the post-shaft
4 5 6	161	podomere, and simple ventral endites alternating long/short or present/absent in the distal
7 8	162	articulated region. Appendages differ in podomere shape (near square in Lyrarapax and
9 10	163	rectangular in Amplectobelua) but the major differences are in the oral cone morphology
11 12 13	164	(tetraradial arrangement of large plates with smaller plates between in Lyrarapax, an
14 15	165	association of tuberculate and smooth plates in Amplectobluidae) and gnathobase-like
16 17	166	structures present in Amplectobeluidae but not <i>Lyrarapax</i> (Cong et al. 2018; Liu et al. 2018).
18 19 20	167	
20 21 22	168	3. Materials and Methods
23 24	169	
25 26	170	Eight specimens of Radiodonta from the Kinzers Formation are known. Material is held at
27 28 29	171	the National Museum of Natural History, Washington D.C., USA (USNM), North Museum,
30 31	172	Franklin and Marshall College, Lancaster, Pennsylvania, USA (PA), and Yale Peabody Musem,
32 33	173	New Haven, Connecticut, USA (YPM).
34 35 26	174	
37 38	175	For historical reasons, the part and counterpart of most of the specimens are held at two
39 40	176	institutions, the USNM and PA. Some material was not available for study by Briggs (1979),
41 42	177	namely the part of the Holotype of Anomalocaris pennsylvanica, and USNM 90827 (Resser
43 44 45	178	and Howell 1938, pl. 13, fig. 5). As another specimen was also labelled USNM 90827 that
46 47	179	was available for study by Briggs (1979), there is confusion in the literature about the
48 49	180	specimens labelled with this number. The USNM 90827 specimen figured in Resser and
50 51 52	181	Howell (1938, pl. 13, fig. 5) is different to that figured by Briggs (1979, pl. 81, fig. 11, text-fig.
53 54	182	34), and Briggs (1979) noted that the specimen figured by Resser and Howell (1938) was
55 56	183	different to those in the collection. Both specimens labelled USNM 90827 were available for
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2 3 4	184	this study, but are not part and counterpart. The specimen figured first, by Resser and
5 6	185	Howell (1938) retained the number USNM 90827, and the specimen figured second, by
7 8	186	Briggs (1979) has been given the altered number USNM 90827A. Both specimens are
9 10 11	187	radiodonts, described herein.
12 13	188	
14 15	189	Specimens were photographed wet and dry under polarized and non-polarized light using a
16 17 18	190	Canon EOS 500D digital SLR Camera with a Canon EF-S 60 mm Macro Lens, controlled for
19 20	191	remote shooting using EOS Utility 2. Digital measurements were made using Image J
21 22	192	(Schneider et al. 2012). Modern longitude and latitude coordinates were reconstructed to
23 24 25	193	510Ma using GPlates (Scotese 2016). Coordinates were obtained from the literature. Where
26 27	194	it was not possible to obtain the exact coordinates of the fossil locality, the nearest town
28 29	195	was used in its place.
30 31 22	196	
32 33 34	197	4. Systematic Palaeontology
35 36	198	
37 38	199	Total-group EUARTHROPODA Lankester 1904
39 40 41	200	Order RADIODONTA Collins 1996
41 42 43	201	
44 45	202	?Laminacaris sp.
46 47	203	Figure 2
48 49 50	204	v. 1979 Anomalocaris? cf. pennsylvanica; Briggs, pl. 81, figs 9-11, text-figs 33, 34
50 51 52 53 54 55 55 56 57 58 59	205	
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20)6	Material: Two partial isolated frontal appendages collected from the Kinzers Formation,
20)7	Pennsylvania, USA, are known from part and counterpart: USNM 213993, PA 394
20)8	(counterpart), locality 22L; USNM 90827A, PA 393 (counterpart), locality 12x.
20)9	
21	0	Description. USNM 213993/PA 394 (Fig. 2a,b) is a partial appendage, with one shaft
21	1	podomere (Fig. 2b, pd1) and six podomeres in the distal articulated region preserved (Fig.
21	2	2b, pd2-7). A pair of thickened recurved ventral endites with distally pointing auxiliary
21	3	spines is present on the shaft podomere, at the distalmost ventral point (Fig. 2b, pd1).
21	4	Ventral endites attach to the midpoint of the other podomeres. The ventral endite on the
21	5	podomere immediately distal to the shaft is curved distally, and approximately the same
21	.6	length and the height (sag) of the podomere, and bears a distally pointing auxiliary spine 2/3
21	7	of the way down the spine (Fig. 2b, en2). The other ventral endites in the distal articulated
21	8	region are paired and approximately the height (sag) of the podomere to which they are
21	9	attached. Distally pointing auxiliary spines are present along the length, and rarely a
22	20	proximally pointing spine is visible (Fig. 2b, en6). Auxiliary spines point slightly ventrally.
22	21	Podomeres are tall (sag) rectangles, approximately twice as tall as wide, decreasing in size
22	22	distally. No dorsal spines are visible.
22	23	
22	24	USNM 90827A (Fig. 2c,d) preserves 6 rectangular podomeres approximately twice as high
22	25	(sag) as wide (trans) with ventral endites attached, and traces of two ventral endites that
22	26	have been prepared out the matrix (Fig. 2d, en9? & en10?). Just as for USNM213993/PA394,
22	27	USNM 90827A ventral endites are straight and approximately the same height as the
22	28	podomere (e.g. Fig. 2d, en5), and an enlarged endite is present with a single auxiliary spine
22	29	2/3 of the way along its length at the proximal end, inferred to be pd2 (Fig. 2d, en2). One

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endite (Fig. 2d, en5) is longer than the others. Auxiliary spines project both distally and
proximally, with a slight ventral tilt.

233 Remarks: This taxon is similar to Lamincaris chimera from the Chengjiang biota (Guo et al. in 234 press). This animal, known only from frontal appendages, has straight ventral endites in the 235 distal articulated region with distally pointing auxiliary spines, and enlarged ventral endites 236 on the distalmost point of the shaft and proximal-most post-shaft podomere. The distally 237 pointing auxiliary spines along the length of the endite in Laminacaris chimera from 238 Chengjiang is similar to the arrangement of auxiliary spines in the Kinzers material. The 239 ventral endites are shorter than the height of the podomere to which they attach in both 240 the Chengjiang and Kinzers material, but the alternating long and short endites of 241 Laminacaris chimera is not present in the incompletely preserved Kinzers specimens which 242 are approximately the same length. The enlarged ventral endite in the Kinzers material does 243 not have the distinctive blade-like morphology with a strong similarity to Hurdia ventral 244 endites that is seen in Laminacaris chimera, however it is enlarged relative to the other 245 endites and recurved. This enlarge endite in the Kinzers material bears more similarity to 246 the post-shaft ventral endite of Lyrarapax trilobus or Amplectobelua stephenensis, although 247 it is not as thickened as these two taxa. The endite on the shaft is similar in Laminacaris and 248 this Kinzers taxon, as it bears a single distally facing auxiliary spine approximately two thirds 249 of the distance from the base to the tip. The Kinzers Laminacaris sp. material could also be 250 compared to Anomalocaris briggsi from the Emu Bay Shale, particularly the shape of the 251 podomeres and the possible lack of alternating long/short ventral spines. However, the 252 auxiliary spines point both distally and proximally in A. briggsi, in contrast to the distally 253 pointing spines of the Kinzers specimens, the ventral endites are shorter relative to

2 3 4	254	podomere height in the Kinzers material than in A. briggsi, and the enlarged ventral endites
5	255	on the shaft and proximal podomere in the distal articulated region are of a different
7 8	256	morphology.
9 10 11	257	
12 13	258	
14 15	259	Family ANOMALOCARIDIDAE Raymond 1935
16 17	260	Genus ANOMALOCARIS Whiteaves 1892
18 19 20	261	
21 22	262	Type species. Anomalocaris canadensis Whiteaves 1892 from the Stephen Formation
23 24	263	(Cambrian Series 3, Stage 5) of British Columbia, Canada.
25 26 27	264	
27 28 29	265	Anomalocaris pennsylvanica Resser 1929
30 31	266	Figure 3
32 33	267	
34 35 36	268	v. 1929 Anomalocaris pennsylvanica; Resser, pl. 5, fig. 5, pl. 79, fig. 5
37 38	269	v. 1938 Anomalocaris pennsylvanica; Resser and Howell, pl. 10, fig. 4
39 40	270	v. 1979 Anomalocaris pennsylvanica; Briggs, pl. 79, fig. 5, text-fig. 18, pp. 641
41 42 42	271	
43 44 45	272	Holotype. Isolated appendage, Kinzers Formation, Pennsylvania, USA, USNM 80487 (part
46 47	273	and counterpart), locality 12x.
48 49	274	Paratype. Isolated appendage, Kinzers Formation, Pennsylvania, USA, YPM 10425 (part
50 51 52	275	only), locality 12x.
53 54	276	Other material. Partial isolated appendage, Kinzers Formation, Pennsylvania, USA, USNM
55 56 57 58 59	277	255611, locality 22L.

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2	270	
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4 5 6	279	Diagnosis. Anomalocaris appendage composed of 14 podomeres; one podomere in the
7 8	280	shaft wider than tall; 13 podomeres in the distal articulated region taller than wide; all
9 10 11	281	podomeres in the shaft and the distal articulated region bear a pair of ventral endites
12 13	282	projecting from the midpoint of the ventral surface; ventral endites are present on pd1-13,
14 15	283	lack auxiliary spines, and alternate long/short on even/odd numbered podomeres; ventral
10 17 18	284	endites on proximal podomeres at least as long as the height of the podomere they attach
19 20	285	to, and decrease in length relative to podomere height distally; ventral endite of the shaft is
21 22	286	not distinct from the ventral endites of the distal articulated region; thin straight dorsal
23 24 25	287	spines project forward from distal dorsal margin of pd9-14; single robust terminal spine.
26 27	288	
28 29	289	Description: Anomalocaris pennsylvanica is known from three specimens: the holotype (part
30 31 22	290	and counterpart) measuring 23 mm (Fig. 3a,b); a partial small appendage (USNM 255611)
32 33 34	291	(Fig. 3e,f); and a large complete appendage (YPM 10425) measuring 75 mm (Fig. 3c,d).
35 36	292	Complete specimens have 14 podomeres, one in the shaft and 13 in the post-shaft region.
37 38	293	The presence of a podomere boundary between pd13 and pd14 is confirmed in the
39 40 41	294	holotype by counting the dorsal spines in the distal region, where the podomere boundaries
42 43	295	are not well preserved (see Fig. 3b: ds13, ds14). The holotype also potentially shows a
44 45	296	second shaft podomere, an approximately square feature preserved as a faint outline,
46 47 48	297	however it joins at an oblique angle to the ventral surface, not the dorsal surface like shaft
49 50	298	podomeres in other species (Fig. 3b: ?S). YPM 10425 shows that the shaft bears a large
51 52	299	ventral endite at the distal margin (Fig. 3d: en1). YPM 10425 also appears to have a longer
53 54	300	ventral endite on pd6 than pd4 (compare Fig. 3d en4 and en6), however the overprint of
55 56 57	301	iron minerals in the rock means that this cannot be confirmed. This is similar to what is seen

in Amplectobleuidae, however the number of podomeres (14) is consistent with

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Anomalocaris.

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305	Although the material is limited, the three specimens of different size suggest that the
306	podomeres grew taller relative to the width of podomeres and length of ventral endites
307	through ontogeny, and so larger appendages have smaller ventral endites relative to
308	podomere height. The smallest of the specimens (USNM 255611) has the longest endite to
309	podomere height ratio, at 2:1 at the proximal end. The largest specimen (YPM 10425) has
310	the lowest ratio, at close to 1:1 with the ratio in the holotype approximately 1.5:1. Similarly
311	the podomere height:width ratio is higher (2.5:1) in YPM 10425 than the holotype (1.5:1).
312	Podomere boundaries are not preserved in USNM 255611.
313	
314	Remarks: Much of the material previously assigned to Anomalocaris pennsylvanica is here
315	reassigned to other radiodont genera (see below). PA 389, PA 395A, and YPM 63295 are
316	removed from Radiodonta altogether because these likely represent partial bodies and
317	appendages of non-radiodont euarthropods.
318	
319	The counterpart to the holotype was not available for study by Briggs (1979) however the
320	interpretation of this specimen, and the description of this species has not changed
321	significantly. Briggs (1979) also noted that larger Anomalocaris pennsylvanica appendages
322	had shorter ventral endites relative to podomere height than smaller appendages of this
323	species. Although the material with the shortest ventral endites is here reassigned to other
324	genera, this observation still holds.
325	

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2 3	326	Anomalocaris pennsylvanica Resser 1929 was the second radiodont species to be described,
4		
5 6	327	and is only known from isolated frontal appendages. It can be distinguished from
7 8	328	Anomalocaris canadensis, the type species, based on the morphology of its ventral endites.
9 10 11	329	In A. pennsylvanica these are simple, whereas for A. canadensis each ventral endite bears
12 13	330	two auxiliary spines, creating a trident shape (Briggs 1979). It has been suggested that the
14 15	331	lack of auxiliary spines on ventral endites could be taphonomic, in which case A.
16 17	332	pennsylvanica could be synonymized with A. canadensis, however it was retained as a valid
18 19 20	333	taxon based on the limited material available (Briggs 1979; Lieberman 2003; Daley and Peel
20 21 22	334	2010). Anomalocaris pennsylvanica is here confirmed as a valid taxon. The ventral endites
23 24	335	have smooth margins and show no evidence of taphonomically removed auxiliary spines.
25 26	336	Furthermore, the three known specimens of A. pennsylvanica show other differences that
27 28 29	337	distinguish it from other Anomalocaris species. It can be differentiated from the most
30 31	338	similar species, A. canadensis, not only by the lack of auxiliary spines on the ventral endites,
32 33	339	but also by the ventral endites being longer relative to podomere height towards the
34 35 26	340	proximal end of the appendage, and by the distal end of the appendage not having
30 37 38	341	differentiated shorter and simplified ventral endites, as is seen in A. canadensis. A.
39 40	342	canadensis also has a reduced ventral endite on the distalmost ventral point of the shaft,
41 42	343	whereas A. pennsylvanica has a long ventral endite similar to those of the distal articulated
43 44 45	344	region.
46 47	345	
48 49	346	Anomalocairs pennsylvanica is endemic to the Kinzers Formation, as other specimens
50 51	347	attributed to this species from the Pioche Formation (Lieberman 2003) bear auxiliary spines
52 53 54	348	and will be described as a new species of Anomalocaris in an upcoming review of Southern
55 56	349	Great Basin material.
57 58		

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3	350	
4 5 6	351	Family TAMISIOCARIDIDAE nov.
7 8	352	
9 10	353	Type genus. Tamisiocaris Daley & Peel 2010
11 12	354	
13 14 15	355	Diagnosis. Radiodont with a frontal appendage bearing slender blade-like ventral endites
16 17	356	longer than the podomere to which they are attached; ventral endites do not alternate
18 19	357	long/short.
20 21	358	
22 23 24	359	Remarks. The family 'Cetiocaridae' was named by Vinther et al. 2014, however this name is
25 26	360	invalid by ICZN conventions (see Van Roy et al. 2015). The family comprises Tamisiocaris and
27 28	361	Anomalocaris briggsi, which were recovered together by a phylogeny of radiodonts (Vinther
29 30 31	362	et al. 2014, fig. 3), and subsequently by Cong et al. (2014) and Van Roy et al. (2015).
32 33	363	
34		
35 36	364	Genus TAMISIOCARIS Daley & Peel 2010
37 38	365	
39 40	366	Type species. Tamisiocaris borealis Daley & Peel 2010.
41 42 43	367	
44 45	368	Diagnosis. Radiodont with paired frontal appendages adjacent to an oval shaped central
46 47	369	carapace element; appendage has at least one podomere in the shaft, with 17 podomeres in
48 49	370	the distal articulated region separated by a triangular mebrane; shaft podomere is wider
50 51 52	371	(trans) than tall (sag) and bears a straight proximally pointing endite at the distal ventral
53 54	372	margin approximately the same length as the height (sag) of the podomere; podomeres in
55 56 57 58	373	the distal articulated region reduce in height towards the distal end and bear paired slender

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2 3 4	374	ventral endites at least twice the length (sag) of the height (sag) of the podomere; length of
5	375	ventral endites decreases distally forming a straight line between the distal ends of the
7 8	376	ventral endites (emended from Daley and Peel, 2010).
9 10 11	377	
12 13	378	Remarks. Fine auxiliary spines were not preserved in the holotype of Tamisiocaris, and so
14 15	379	not included in the original Diagnosis. They were subsequently recognized in new material
16 17	380	described by Vinther et al. (2014), although the diagnosis of genus and species was not
18 19 20	381	updated in that study. As the specimen from the Kinzers Formation assigned to this genus
21 22	382	does not have apparent auxiliary spines (see below) the presence of fine auxiliary spines is
23 24	383	not included in the diagnosis of this genus.
25 26 27	384	
28 29	385	Tamisiocaris borealis Daley & Peel, 2010
30 31	386	
32 33	387	2010 Tamisiocaris borealis; Daley & Peel, fig. 1
35 36	388	2014 Tamisiocaris borealis; Vinther et al., figs 1, 2, extended data figs 1-4, 6, 7
37 38	389	
39 40	390	Holotype. Isolated frontal appendage, Peary Land, central North Greenland, base of the
41 42 43	391	Buen Formation, MGUH 29154, by original designation.
44 45	392	Paratypes: Isolated frontal appendages, from same locality as holotype. MGUH 30500
46 47	393	(displays articulating triangular membranes); MGUH 30501 (displays fine auxiliary spines),
48 49 50	394	designated herein.
50 51 52	395	Other material: Three other isolated frontal appendages of this species are known, also
53 54	396	from same locality as holotype. MGUH 30502 – 4.
55 56 57 58 59 60	397	

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2 3	398	Diagnosis. Tamisiocaris with an appendage that bears fine auxiliary spines along the length
4 5 6	399	of both proximal and distal surfaces of the ventral endites; auxiliary spines are straight, do
7 8	400	not change length along the appendage and are separated vertically by less than the width
9 10	401	(trans) of the ventral endite (emended from Daley & Peel, 2010).
11 12	402	
13 14	102	Remarks, Tamisjocaris horaglis was originally described as a radiodent frontal appendage by
15 16	405	Kennurks. Turnisiocuris boreuris was originariy described as a radiodorit frontar appendage by
17 18	404	Daley and Peel (2010). A subsequent study by Vinther et al. (2014) with new material
19 20	405	provided new information about the appendage, including the presence of triangular
21 22	406	articulating membrane between the podomeres and fine auxiliary spines along the length of
23 24	407	the ventral endites. This confirmed the hypothesis that the taxon belongs to Radiodonta,
25 26	408	and suggested a sifting/filtering feeding ecology, however Vinther et al. (2014) did not
27 28 20	409	update the Diagnosis of the genus or species, nor designate new paratypes with these new
30 31	410	features. This has been done here to allow comparison with the Kinzers Formation material.
32 33	411	
34		
35 36	412	Tamisiocaris att. borealis
37 38	413	Figure 4
39 40	414	v. 1938 Anomalocaris pennsylvanica; Resser and Howell, pl. 13, fig. 5
41 42	415	v. 1979 Anomalocaris pennsylvanica; Briggs pp. 641
43 44	44.6	
45	416	
46 47	417	Material: Partial isolated frontal appendage, Kinzers Formation, Pennsylvania, USA, USNM
48		
49 50	418	90827, PA 388 (counterpart).
51 52	419	
53 54	420	Description. USNM 90827/PA 388 (Fig. 4) shows a partial appendage of 9 podomeres (Fig.
55 56 57	421	4b, ?pd10-?pd18), each bearing a long and slender ventral endite (Fig. 4b, en). The
58 59		

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2 3 4	422	podomeres are approximately square where boundaries can be discerned (e.g. Fig. 4b,
5 6	423	?pd14) with the ventral endites twice the height (sag) of the podomeres. The podomeres
7 8	424	reduce in height towards the distal end, where the shape becomes an elongate rectangle
9 10 11	425	(e.g. Fig. 4b, ?pd18). No auxiliary spines are visible on the ventral endites, and no dorsal
12 13	426	spines are visible on the appendage.
14 15	427	
16 17 18	428	Remarks: This specimen is no longer considered Anomalocaris pennsylvanica as the
19 20	429	podomeres are square to elongate rectangular in shape (as opposed to tall rectangles), and
21 22	430	the ventral endites, although they lack auxiliary spines, do not alternate long/short on
23 24 25	431	even/odd numbered podomeres and instead reduce in length along the appendage.
26 27	432	
28 29	433	This specimen is instead considered to belong to the genus <i>Tamisiocaris</i> as it has long,
30 31 32	434	paired, ventral endites which do not alternate long/short, similar to <i>T. borealis</i> from Sirius
33 34	435	Passet. The approximate square-shape of the podomeres is consistent with the distal end of
35 36	436	known Tamisiocaris specimens from Sirius Passet. Just as in Tamisiocaris borealis, this
37 38	437	specimen lacks any dorsal spines, which would instead indicate affinities with Anomalocaris
39 40 41	438	briggsi. There is no evidence that this specimen bears auxiliary spines, which are visible in
42 43	439	some specimens of <i>T. borealis</i> (although not the type specimen), and it is only known as a
44 45	440	partial appendage so the number of podomeres cannot be ascertained. Because of this the
46 47 48	441	specimen is left in open nomenclature as <i>T.</i> aff. <i>borealis</i> .
49 50	442	
51 52	443	This is the youngest Tamisiocaris known (Cambrian Stage 4) and the first from outside the
53 54	444	Sirius Passet Lagerstätte (Cambrian Stage 3, Greenland). Tamisiocaris is still only known
55 56 57	445	from Laurentia.
58 59		

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3	446	
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5	447	Family AMPLECTOBELUIDAE Vinther et al. 2014
6	,	
7	110	Convert AMPLECTORELLIA How at al. 100E
8	448	Genus AMPLECTOBELUA Hou et al. 1995
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10	449	
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12	450	Amplectobelua aff. symbrachiata
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14	451	Figure 5
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16	452	
17	452	
18	450	1020 Annu line in Decemental Inc. It is C
19	453	1938 Anomalocaris pennsylvanica; Resser and Howell, pl. 13, fig. 6
20		
21	454	1953 Anomalocaris pennsylvanica; Roger, pl. 2 fig. 4
22		
23	455	1979 Anomalocaris pennsylvanica; Briggs, pl. 79 figs 4, 6, text-figs 17, 19
25		
26	456	
27		
28	457	Material Isolated frontal annendages Kinzers Formation Pennsylvania LISA VPM 1/1388
29	437	waterial. Isolated Holital appendages, Kineers Formation, Fernisylvania, OSA, FFW 14500
30	450	(next) and DA 207 (accurtement) (acclify 12), DA200 (next and accurtement) (acclify 22)
31	458	(part) and PA 387 (counterpart) locality 12x; PA390 (part and counterpart) locality 22L.
32		
33	459	
34		
35	460	Description: Two Amplectobelua appendages can be recognized from the Kinzers Formation.
36		
37	461	YPM 14388 (Fig. 5a, b), with counterpart PA387, is a complete isolated appendage with 12
38		
39	462	nodomeres. The nodomeres are tall and rectangular but become more square towards the
40	402	podomeres. The podomeres are tail and rectangular bat become more square towards the
41	462	distal and (compare add to add) in Fig. (b). A long and start and its with the base of three
42	405	distal end (compare public pullo in Fig. 5b). A long and stout endite with the base of three
45		
44	464	spines preserved is present on the most proximal podomere (Fig 5b, pd1, en1). The central
46		
47	465	spine base is the thickest, with the proximal-most spine preserved in its entirety. Short and
48		
49	466	paired spinose endites are present on the remaining podomeres, although most are
50		
51	467	incomplete, and the endite on pd6 shows that they were simple spines shorter than the
52		
53	160	nodomere to which they attached (Fig. 5h. enf.). The broken have on pdF is wider than the
54	400	podomere to which they attached (Fig. 50, end). The broken base on pub is whiler than the
55	466	has been affected to a basis of the state of
56	469	proken base of pd3, implying that the ventral endite on this pd5 was more robust than that
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1		
2 3 4	470	of pd3 (en3, en5, Fig. 5b). The distalmost two podomeres (pd11-12) bear robust paired
5 6	471	dorsal spines which are recurved following the outline of the appendage and combine with
7 8	472	a reduced terminal spine to make a claw-like termination (Fig. 5b, ds & ts). PA 390 (Fig. 5c,
9 10 11	473	d) is a partial appendage with the 10 most distal podomeres visible. Podomeres are tall and
12 13	474	rectangular, but become more square at the distal end (compare Fig. 5d, pd4 to pd9 and
14 15	475	pd12). All the ventral endites are short (e.g. Fig. 5b, en6-8) and robust recurved dorsal
16 17	476	spines are visible at the distal end (Fig. 5d, ds) alongside a reduced terminal spine (Fig. 5d,
18 19 20	477	ts). In both YPM 14388 and PA 390 some smaller and straight dorsal spines are visible
21 22	478	proximal to the robust dorsal spines (e.g. Fig. 5b, ds10).
23 24	479	
25 26 27 28 29	480	Remarks: These specimens are no longer considered Anomalocaris pennsylvanica as the
	481	dorsal spines at the distal end are paired and much more robust, the ventral endites along
30 31	482	the appendage are short, and the number of podomeres (where they can be counted) is 12
32 33 34	483	instead of 14. This interpretation differs slightly from the previous descriptions, where both
35 36	484	these appendages were interpreted to have 14 podomeres (Briggs 1979, plate 79 figs 4, 6;
37 38	485	text-figs 17, 19). The podomere labelled as j6 of PA 390 (Briggs 1979, plate 79 fig 4, text fig
39 40 41	486	17) is here interpreted as the eighth podomere, j1 and j2 of YPM 14388 (Briggs 1979, plate
42 43	487	79 fig 6, text fig 19) are interpreted as being an enlarged 1 st podomere (Fig. 5b, pd1) as no
44 45	488	podomere boundary is visible here (none was drawn in Briggs 1979, text fig 19). The
46 47	489	structure labelled as j14 is here interpreted as one of a pair of robust dorsal spines (Fig. 5b,
40 49 50	490	ds12).
51 52	491	
53 54	492	A number of lines of evidence support the reinterpretation of these two appendages as
55 56 57 58	493	Amplectobelua, including the presence of paired but short ventral endites along the

1		
2 3 4	494	majority of the appendage, the rectangular podomeres, and paired robust dorsal spines at
5 6	495	the distal end. In addition YPM 14388 has an enlarged ventral endite on pd1 (pd1 is not
7 8	496	preserved in PA 390), and the base of the endite on pd5 appears more robust than that of
9 10 11	497	pd3. These specimens are most similar to Amplectobelua symbrachiata, as they both bear
12 13	498	short ventral endites along the appendage alternating long/short and the morphology of the
14 15	499	enlarged ventral endite is constructed of three spines with the thickest in the centre, unlike
16 17	500	in Amplectobelua stephenensis where there is only one very enlarged and thickened spine
18 19 20	501	on the most proximal podomere. Amplectobelua symbrachiata also bears smaller dorsal
21 22	502	spines proximally to the enlarged recurved dorsal spines, as is also seen in both the
23 24	503	specimens from the Kinzers Formation. The material from the Kinzers however does not
25 26 27	504	have exactly the same morphology as Amplectobelua symbrachiata, because it has a
28 29	505	reduced terminal spine, not present in the Chengjiang species, and evidence for paired
30 31	506	dorsal spines not reported from the Chinese animal, but a feature known from
32 33	507	Amplectobelua stephenensis. The podomeres become more square shaped towards the
34 35 36	508	distal end in the Kinzers species, a feature not seen in either Amplectobelua symbrachiata or
37 38	509	Amplectobelua stephenensis.
39 40	510	
41 42 43	511	The preservation does not allow all the anatomical features to be recognized. For example
44 45	512	the morphology of the enlarged ventral endite is not completely known, specifically the
46 47	513	length of the central thickened spine. In addition there is no evidence of the shaft, which is
48 49	514	expected to be of three podomeres in Amplectobleua. For these reasons this species is left
50 51 52	515	in open nomenclature.
53 54	516	
55 56		
50 57		

3 4	517	These are the first Amplectobelua from the Cambrian Stage 4, the first from the USA, and
5 6	518	the oldest in Laurentia. Amplectobelua was previously known from the Stage 3 of China and
7 8	519	Stage 5 of Canada. They bear more similarity to the Chinese species, Amplectobelua
9 10 11	520	symbrachiata than the Canadian Amplectobelua stephenensis perhaps indicating an invasion
12 13	521	by the Chinese species at the end of Stage 3 followed by a subsequent radiation in
14 15	522	Laurentia.
16 17	523	
18 19 20	524	5. Discussion
21 22	525	
23 24	526	5.a. Diverse feeding strategies of Kinzers Formation Radiodonta
25 26 27	527	
28 29	528	The Kinzers Formation contains one species of Anomalocaris, Amplectobelua, Tamisiocaris,
30 31	529	and tentatively Laminacaris (Fig. 6; Table 2). The presence of a number of different
32 33 24	530	radiodonts from the same site is not unusual for Cambrian Lagerstätten, and supports
35 36	531	previous suggestions that these stem-group euarthropods employed a number of different
37 38	532	feeding strategies (Daley & Budd 2010; Vinther et al. 2014; Van Roy et al. 2015).
39 40	533	Anomalocaris pennsylvanica would have used its flexible appendages to actively grab likely
41 42 43	534	soft-bodied prey and slice it with the simple elongate ventral endites. Amplectobelua aff.
44 45	535	symbrachiata would have used its more robust proximal ventral endite and thickened distal
46 47	536	dorsal spines to more tightly hold and slice or potentially crush prey. The presence of
48 49 50	537	reduced ventral endites between the proximal and distal end would have allowed the
51 52	538	appendage to coil more tightly, allowing the distal and proximal robust spines to come
53 54	539	together more easily in a slicing or crushing motion. Tamisiocaris aff. borealis may not have
55 56 57 58	540	been a filter feeder targeting plankton like the Sirius Passet species if the lack of fine

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541	auxiliary spines is not an artefact of preservation, and so instead may have sifted or raked
542	through the sediment. It is also possible that it filtered larger particles than the Greenland
543	species, and so did not require auxiliary spines. ?Laminacaris sp. likely used its straight
544	ventral endites with auxiliary spines to function as a net-like apparatus, potentially similar to
545	some hurdiids, and as suggested for Anomalocaris briggsi from the Emu Bay Shale (Daley et
546	al. 2013b). Its longer ventral spines, and lack of clear alternating long/short ventral endites
547	make a raptorial feeding strategy similar to that inferred for Laminacaris chimera, less likely.
548	
549	5. b. Importance of the Kinzers Formation
550	
551	Radiodonta are known from other Cambrian Series 2, Stage 4, Konservat-Lagerstätten,
552	however the Kinzers Formation (30°S palaoelatitude, Laurentia) is uniquely important for
553	understanding the palaeogeographic and palaeolatitudinal distribution of these animals (Fig.
554	7) because of the high diversity of taxa found there. Radiodonta are known from four other
555	broadly coeval formations in North America from Laurentia (all equatorial): Latham Shale
556	(Briggs and Mount 1982), Comet Shale Member, Pioche Formation (Lieberman 2003), Eagar
557	Formation, Cranbrook Shale (Briggs 1979), and Pyramid Shale Member, Carrara Formation
558	(unpublished material). Radiodonta have also been reported from two formations of this
559	age on the South China paleocontinent (ca. $30^\circ N$ palaeolatitude): the Balang Formation (Liu
560	2013), and Wulongqing Formation (Wang et al. 2013); and from two Gondwanan sites: the
561	Emu Bay Shale in Australia (ca. 15° N palaeolatitude) (Nedin 1995; Daley et al. 2013b) and
562	Valdemiedes Formation in Spain (ca. 60°S palaeolatitude) (Pates & Daley 2017) (Table 3; Fig.
563	7).
564	

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3 4	565	The recognition of four different radiodont taxa, from at least three different families,
5 6	566	means that the Kinzers Formation has the most diverse Radiodonta fauna of all the Stage 4
7 8	567	Konservat-Lagerstätten, despite relatively few specimens being known - especially
9 10 11	568	compared to the Emu Bay Shale and Wulongqing Formation (Table 3). The fauna contains
12 13	569	links with both the older Sirius Passet (Tamisiocaris) and Chengjiang (Amplectobelua,
14 15	570	Anomalocaris and Laminacaris) faunas, as well as the younger Burgess Shale (Amplectobelua
16 17	571	and Anomalocaris). It has a named endemic species with Anomalocaris pennsylvanica, with
19 20	572	at least two (and potentially all four) of its radiodont species not yet known from other
21 22	573	localities. Its unique position at a non-equatorial latitude in Laurentia, as well as the lack of
23 24	574	any Tier 1 Burgess Shale Type deposits (<i>sensu</i> Gaines 2014) in the Cambrian Series 2 Stage 4
25 26 27	575	highlights the importance of the Kinzers Formation. The previous categorization of the
28 29	576	Kinzers Formation as a Tier 3 Lagerstätten was because of limited rock exposure, not
30 31	577	fossilization conditions (Gaines 2014). The recovery of a highly diverse radiodont fauna from
32 33 34	578	a relatively low number of specimens suggests that further exploration of the Kinzers
35 36	579	Formation could yield new taxa rapidly. Caryosyntrips and Hurdia could also be present in
37 38	580	the Kinzers Formation, as the former is present at the higher latitude coeval Valdemiedes
39 40 41	581	Formation (Spain) and equatorial Laurentia in Stage 5 (Pates & Daley 2017), and the latter
41 42 43	582	present at the coeval equatorial Laurentian Pioche Formation (unpublished material) and
44 45	583	higher latitude Stage 5 Bohemia (Chlupáč & Kordule 2002; Daley et al. 2013a). Their absence
46 47	584	might also be due to similar inferred feeding niches are already occupied in the Kinzers
48 49 50	585	Formation by Amplectobelua, Tamsiocaris, and ?Laminacaris, a result of unfavourable
51 52	586	environmental conditions, or reflect the dominance of Amplectobeluidae, Anomalocarididae
53 54	587	and Tamisiocarididae in older, Series 2, deposits and later dominance of Hurdiidae in Series
55 56 57	588	3.

589	
590	6. Conclusions
591	
592	The vast progress in our understanding of the diversity of Radiodonta since the previous
593	study of Kinzers Formation radiodonts allowed the identification of Tamisiocaris and
594	Amplectobelua in the USA for the first time. These reinterpretations mean that the Kinzers
595	Formation can now be considered a Tier 2 BST with more than 10 soft-bodied taxa (sensu
596	Gaines 2014), and has the highest known diversity of Radiodonta of any Cambrian Series 2
597	Stage 4 Konservat-Lagerstätten. The radiodonts found in the Kinzers Formation are
598	potentially all endemic species, and include the youngest Tamisiocaris known, and the
599	oldest Amplectobelua in Laurentia. This highlights the importance of the Kinzers Formation
600	in understanding the diversity and evolution of Cambrian Radiodonta, and supports further
601	exploration of this Lagerstätten.
602	
603	Acknowledgements
604	We would like to thank the editor, Paul Upchurch, and two anonymous referees for their
605	comments on the manuscript. SP is funded by an Oxford-St Catherine's Brade-Natural
606	Motion Scholarship. A Palaeontological Association Sylvester-Bradley Award (PA-SB201503)
607	allowed travel to Franklin Marshall College, USNM and YPM. For facilitating access to
608	specimens, we thank Susan Butts and Jessica Utrup at YPM, Mark Florence at USNM, and
609	Roger DK Thomas at Franklin Marshall. This manuscript benefitted from discussions with P.
610	Cong, G. Edgecombe, R. R. Gaines, B. S. Lieberman, and R. D. K. Thomas.
611	
612	Declaration of Interest

2 3	613	None.
4 5 6	614	
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787	Figure Captions
788	
789	Figure 1. Schematic radiodont frontal appendage showing terminology used. Podomeres in
790	dark grey, ventral endites in light grey. (a) sagittal view. Abbreviations: $artheta$, angle between
791	shaft and distal articulated region on dorsal surface; 1, post-shaft podomere; 3 and 5, third
792	and fifth podomere in the distal articulated region. For anomalocaridids, the ventral endites
793	on 3 are longer than those on 5, for amplectobeluids the ventral endites on 5 are longer
794	than those on 3. In hurdiids all podomeres from 1 to 5 will have enlarged endites of the
795	same morphology and equal length. (b) frontal view of non-hurdiid podomere, showing
796	relative width and separate attachment of two ventral endites to one podomere. (c) frontal
797	view of hurdiid podomere showing relative width and attachment of one ventral endite to
798	one podomere.
799	
800	Figure 2. ?Laminacaris sp. from the Kinzers Formation. (a,b) USNM 213693; (c,d) USNM
801	90827A. Scale bars 10 mm. Abbreviations: enX, ventral endite X; pdX, podomere X.
802	

2 3 4	803	Figure 3. Anomalocaris pennsylvanica from the Kinzers Formation. (a,b) Holotype USNM
5 6	804	80487; (c,d) YPM 10425; (e,f) USNM 255611. Scale bars 10 mm. Abbreviations: dsX, dorsal
7 8	805	spine X; enX, ventral endite X; pdX, podomere X; ?S, putative shaft podomere; ts, terminal
9 10 11	806	spine.
12 13	807	
14 15	808	Figure 4. Tamisiocaris aff. borealis from the Kinzers Formation. (a,b) PA 388. Scale bars 10
16 17 18	809	mm. Abbreviations: en, ventral endite; ?pdX, podomere X, inferred from complete <i>T</i> .
19 20	810	borealis appendages.
21 22	811	
23 24 25	812	Figure 5. Amplectobelua aff. symbrachiata from the Kinzers Formation. (a,b) YPM 14388;
26 27	813	(c,d) PA 390. Scale bars 10 mm. Abbreviations: ds, dorsal spines; enX, ventral endite X ; pdX,
28 29	814	podomere X.
30 31 32	815	
33 34	816	Figure 6. Reconstructions of Radiodonta from the Kinzers Formation, and other frontal
35 36	817	appendages with similar morphology. (a) Anomalocaris pennsylvanica; (b) Anomalocaris
37 38 39	818	canadensis; (c) Tamisiocaris aff. borealis; (d) Tamisiocaris borealis; (e) Anomalocaris briggsi;
40 41	819	(f) Amplectobelua aff. symbrachiata; (g) Amplectobelua symbrachiata; (h) Amplectobelua
42 43	820	stephenensis; (i) ?Laminacaris sp; (j) Laminacaris chimera. Dotted lines show parts of
44 45 46	821	appendage that are not preserved. Line drawings (b), (g), and (h) adapted from Daley &
40 47 48	822	Budd (2010, text-fig. 1A, F, G), (d) adapted from Vinther et al. (2014, extended data fig. 6a),
49 50	823	(e) adapted from Daley et al. (2013b, fig. 2), and (j) redrawn from Guo et al. (<i>in press</i> , fig.
51 52	824	3A).
55 54 55	825	
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826	Figure 7. Palaeogeographic reconstruction to 510 Ma from GPlates (Scotese 2016). White
827	star shows Kinzers Formation; black stars show other Stage 4 sites where radiodont fossils
828	have been found. Abbreviations: B, Balang Formation; Ca, Carrara Formation; Cr, Cranbrook
829	Formation; E, Emu Bay Shale; K, Kinzers Formation; L, Latham Shale; P, Pioche Formation; V,
830	Valdemiedes Formation; W, Wulongqing Formation.
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Table 1: Frontal appendage characters used to distinguish radiodont families

	Podomeres and numbers of ventral endites						Morphology of large ventral endite(s)			
	# pd. in shaft	# pd. in distal articulated region	Triangular membrane between pd.	# rows en.	# of longest en.	en. in d.a.r. alternate long/short	as. paired	as. increase in size from base to tip	# Large as.	Small as. between large as.
Amplectobeluidae	3	12/13	Yes	2	1	Yes	Yes	No	0/2	No
Anomalocarididae	1-3	13	Yes	2	1	Yes	Yes	No	0/2	No
Hurdiidae	1/2	8-10	No	1	5	No	No	Yes	0-5	<i>Hurdia</i> only
Laminacaris	2	13	Yes	1?	1	Yes	No	Yes	5	Yes
Tamisiocarididae	?1	13/17	Yes	2	0/1*	No	Yes*	?Yes*	?*	No*

*A. briggsi bears an enlarged post-shaft endite, and Tamisiocaris does not. Hence all characters referring to the morphology of the large ventral endite for
 this family refer to A. briggsi only. Abbreviations: as, auxiliary spine; d.a.r., distal articulated region; en, ventral endite; pd, podomere

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 Table 2: Current and previous interpretations of Kinzers radiodont appendages.

Catalogue #	Fig.	Site	Previous interpretation	Current interpretation	References
USNM 213693,	1a h	221	Anomalocaric2 of pennsylvanica	21 amingcaris sp	Briggs 1070 pl 81 figs 0 10 toxt-fig 22
PA 394 (cpt)	14,0	221	Anomalocuns: cl. pennsylvanica	Lumnucuns sp.	Diggs 1979 pl. of ligs. 9,10, text-lig. 55.
USNM 90827A,	1 a d	221			
PA 393 (cpt)	10,0	221	Anomalocarise ci. pennsylvanica	<i>rumnacaris</i> sp.	Briggs 1979 pl. 81 lig. 11, text-lig. 34.
			Anomalosaris poppsylvanica		Resser 1929, pl. 5, fig. 5; pl. 79, fig. 5; Res
	2a,b	12x	Anomalocaris pennsylvanica	Anomalocaris pennsylvanica (holotype)	and Howell 1938, pl. 10, fig. 4; Briggs 197
(part and cpt)			(nolotype)		79 fig. 5, text-fig. 18.
YPM 10425	2c,d	12x	Anomalocaris pennsylvanica	Anomalocaris pennsylvanica	Briggs 1979
USNM 255611	2e,f	22L	Anomalocaris pennsylvanica	Anomalocaris pennsylvanica	Briggs 1979
USNM 90827,				Or a	Resser and Howell 1938, pl. 13, fig. 5; Br
PA 388 (cpt)	3	22L	Anomalocaris pennsylvanica	Tamisiocaris aff. borealis	1979*
					Resser and Howell 1938, pl. 13, fig. 6; Ro
YPM 14388,	4a,b	12x	Anomalocaris pennsylvanica	Amplectobelua aff. symbrachiata	1953, pl. 2 fig. 4; Briggs 1979 pl. 79 fig. 6,
PA 387 (cpt)					fig. 19.
PA 390 (part and cpt)	4c,d	22L	Anomalocaris pennsylvanica	Amplectobelua aff. symbrachiata	Briggs 1979, pl. 79 fig. 4, text fig 17
PA 389	-	22L	Anomalocaris pennsylvanica	Euarthropoda indet.	Briggs 1979
PA 395a	-	22L	?Anomalocaris pennsylvanica	Indet.	Briggs 1979
YPM 63295	-	12x	Anomalocaris pennsylvanica	Euarthropoda indet.	Lieberman 2003
Site numbers: 12x, one a	nd three q	uarter mi	les north of Rohrerstown, Pennsylvan	ia; 22L, half a mile south of East Petersburg	, Pennsylvania (Briggs 1979). References r
to previous interpretation	n. *Briggs	(1979) on	ly had PA 388 available, and was not a	able to study USNM 90827.	

 Table 3: Cambrian Series 2, Stage 4 Radiodonta bearing Konservat-Lagerstätten.
 Formation Palaeocontinent Palaeolatitude # Specimens # Radiodont taxa References **Kinzers Formation** Laurentia 30°S Resser 1929; Briggs 1979; this study 8 4 Unpublished material **Carrara Formation** 0° (equator) (4) (1) Laurentia Cranbrook Shale Laurentia 0° (equator) 2 1 Briggs 1979

Latham Shale 3 (+1) Briggs and Mount 1982 Laurentia 0° (equator) 1 **Pioche Formation** 0° (equator) 24 (+1) 1 (+1) Lieberman 2003; unpublished material Laurentia Nedin 1995; Daley et al. 2013b Emu Bay Shale Gondwana 15°N 69 2 Valdemiedes Formation Gondwana 60°S Pates & Daley 2017 1 1 **Balang Formation** South China 30°N 2 Liu 2013 2 Wulongging Formation South China 30°N 48 2 Wang et al. 2013

Number of known specimens and known taxa, with palaeocontinent and palaeolatitude reconstructed using GPlates (Fig. 7; Scotese 2016). Numbers

of unpublished specimens studied by authors in brackets.

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Figure 1. Schematic radiodont frontal appendage showing terminology used. Podomeres in dark grey, ventral endites in light grey. (a) sagittal view. Abbreviations: 9, angle between shaft and distal articulated region on dorsal surface; 1, post-shaft podomere; 3 and 5, third and fifth podomere in the distal articulated region. For anomalocaridids, the ventral endites on 3 are longer than those on 5, for amplectobeluids the ventral endites on 5 are longer than those on 3. In hurdiids all podomeres from 1 to 5 will have enlarged endites of the same morphology and equal length. (b) frontal view of non-hurdiid podomere, showing relative width and separate attachment of two ventral endites to one podomere. (c) frontal view of hurdiid podomere.

54x17mm (300 x 300 DPI)

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Figure 2. ?Laminacaris sp. from the Kinzers Formation. (a,b) USNM 213693; (c,d) USNM 90827A. Scale bars 10 mm. Abbreviations: enX, ventral endite X; pdX, podomere X. \parallel + \parallel +

202x510mm (300 x 300 DPI)



Figure 3. Anomalocaris pennsylvanica from the Kinzers Formation. (a,b) Holotype USNM 80487; (c,d) YPM 10425; (e,f) USNM 255611. Scale bars 10 mm. Abbreviations: dsX, dorsal spine X; enX, ventral endite X; pdX, podomere X; ?S, putative shaft podomere; ts, terminal spine.

152x138mm (300 x 300 DPI)





107x145mm (300 x 300 DPI)







117x82mm (300 x 300 DPI)





Figure 6. Reconstructions of Radiodonta from the Kinzers Formation, and other frontal appendages with similar morphology. (a) Anomalocaris pennsylvanica; (b) Anomalocaris canadensis; (c) Tamisiocaris aff. borealis; (d) Tamisiocaris borealis; (e) Anomalocaris briggsi; (f) Amplectobelua aff. symbrachiata; (g)
Amplectobelua symbrachiata; (h) Amplectobelua stephenensis; (i) ?Laminacaris sp; (j) Laminacaris chimera. Dotted lines show parts of appendage that are not preserved. Line drawings (b), (g), and (h) adapted from Daley & Budd (2010, text-fig. 1A, F, G), (d) adapted from Vinther et al. (2014, extended data fig. 6a), (e) adapted from Daley et al. (2013b, fig. 2), and (j) redrawn from Guo et al. (in press, fig. 3A).

234x326mm (300 x 300 DPI)

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Figure 7. Palaeogeographic reconstruction to 510 Ma from GPlates (Scotese 2016). White star shows Kinzers Formation; black stars show other Stage 4 sites where radiodont fossils have been found. Abbreviations: B, Balang Formation; Ca, Carrara Formation; Cr, Cranbrook Formation; E, Emu Bay Shale; K, Kinzers Formation; L, Latham Shale; P, Pioche Formation; V, Valdemiedes Formation; W, Wulongqing Formation.

