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New anomalocaridid frontal appendages from the Guanshan biota, eastern Yunnan

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Anomalocaridids were large predators of the Cambrian seas at the top of the trophic pyramid. Complete anomalocaridid specimens have been rarely discovered and the rigid isolated frontal appendages and mouthparts are more commonly preserved. Here we study new material of the frontal appendages from the Wulongqing Formation, Cambrian Stage 4, Series 2 near Kunming, eastern Yunnan. Two new forms of anomalocaridid frontal appendages are described, namely *Anomalocaris kunmingensis* sp. nov. and *Paranomalocaris multisegmentalis* gen. nov., sp. nov. The frontal appendage of *A. kunmingensis* sp. nov. probably comprises 15 podomeres of which the first one has a weakened skeletoned, the second one is armed with small spines, and the third one is armed with remarkably robust proximal ventral spines with 6 anisomerous auxiliary spines; paired auxiliary spines are associated with podomeres 4–14; podomeres 12–14 are armed with paired dorsal spines, and the last podomere bears 2 distal spines, one spine distinctly larger than the other. The frontal appendage of *P. multisegmentalis* tapered backwards, consisting of 22 visible podomeres; the most ventral spine is armed with 5 pairs of auxiliary spines, and podomeres 12–21 bear dorsal spines, the last podomere with 2 small distal spines. The new material provides additional evidence for our understanding of the diversity of anomalocaridids in the Cambrian. The morphology of these new finds may indicate the importance of different feeding strategies of anomalocaridids in the Cambrian ecosystem.

Yunnan, Cambrian, anomalocaridids, frontal appendage, Guanshan biota

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Anomalocaridids are a group of large marine predators in the trophic pyramid. The general features of anomalocaridids are a cephalic region with a pair of large stalked eyes, disc-like mouthparts consisting of a series of plates, a pair of segmented frontal appendages, two rows of lateral lobes, and a fan-like tail is present in some forms [1]. There are at least 5 definite anomalocaridid genera including *Anomalocaris*, *Amplectobelua*, *Laggania*, *Hurdia*, and *Symbrachiata* [1–6]. Some related forms such as *Parapeytoia*, *Caryosyntrips*, and *Tamisiocaris* [6–8] have been also described from the Cambrian. Recently, Ordovician giant anomalocaridid fossils were found in the Fezouata biota of Morocco and are the latest record of anomalocaridids [9]. Anomalocaridids probably had compound eyes based on new fossil evidence from the Emu Bay Shale, Australia [10]. The Devonian arthropod, *Schinderhannes bartelsi*, from the Hunsrück Slate of Germany, displays similar frontal appendages and mouthparts probably indicating a comparable life-style [11].

Anomalocaridid fossils have been described from several Chinese Cambrian exceptionally preserved faunas such as the Chengjiang, Niutitang, Guanshan, Malong, and Kaili biotas [12–16]. In addition, a new anomaloaridid frontal appendage has been recently described from the Cambrian Mantou Formation in Tangshan, Hebei Province [17]. Three major anomalocaridid species were found in the Chengjiang fauna, namely *Anomalocaris saron*, *Amplectobelua symbrachiata* and *Parapeytoia yunnanensis*. Nevertheless, the

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morphology and affinity of *P. yunnanensis* remains a controversial issue [7,12,18]. For example some authors recently suggested that the tooth-plate fossils associated with *Parapeytoia* [7] are, in fact, the pharynx of priapulids [19] but this is not supported in the present paper.

The Guanshan biota (Cambrian Stage 4, Series 2) is a typical Burgess Shale-type fossil locality with abundant exceptionally preserved soft-bodied fossils. It provides a linkage between the Chengjiang and Kaili biotas. Very diverse animal groups have been discovered to date, including sponges, chancelloriids, cnidarians, hyoliths, lobopods, priapulids, arthropods, brachiopods, and echinoderms [14].

The anomalocaridid frontal appendages from the Guanshang biota have been described as *Anomalocaris* cf. *saron* and an unidentified species of *Parapeytoia*. Recent excavation in the Gaoloufang section has yielded abundant anomalocaridid material, including more than forty frontal appendages and a few mouthparts. Detailed study indicates that the formerly identified *A.* cf. *saron* is in fact a new species of *Anomalocaris.* Another new anomalocaridid genus and species is also described in the present paper.

1 Systematic palaeontology

Phylum Uncertain
Class Dinocarida Collins, 1996
Order Radiodonta Collins, 1996
Family Anomalocaridae Raymond, 1935
Genus *Anomalocaris* Whiteaves, 1892
***Anomalocaris kunmingensis* sp. nov.**

Etymology. From Chinese Pinyin referring to the Kunming City, from where the specimens were collected.

Material. Total of 47 frontal appendages, 27 specimens with part and counterpart present, 24 specimens completely or nearly completely preserved. One specimen preserves four appendages and 3 specimens preserve two appendages. All specimens preserved in yellowish mudstone, Wulongqing Formation. All specimens housed in Nanjing Institute of Geology and Palaeontology, Nanjing.

Holotype. A complete well-preserved frontal appendage with counterpart, NIGP154565, Figure 1(a) and (b).

Occurrence and locality. Wulongqing Formation (*Palaeolenus* and *Megapalaeolenus* Zone), Cambrian (Stage 4, Series 2), Gaoloufang Village, Kunming, eastern Yunnan, China.

Diagnosis. The frontal appendage probably comprises 15 podomeres; podomere 1 weakly mineralized, curved, ventral spines absent; podomere 2 with tiny ventral spines; podomere 3 bears remarkably robust proximal ventral spines with 6 anisomerous auxiliary spines of which the second auxiliary spine is longest; 1 or 2 pairs of auxiliary spines present on ventral spines of podomeres 4–14; podomeres 12–14 armed with paired dorsal spines; the last podomere bears two curved distal spines. The ventral spines alternate in length on successive podomeres. All ventral spines are distally directed and inclined to the medial margin at an angle of 90°–60°.

Description. Medium-sized frontal appendage, the smallest 23 mm long, the largest 117 mm long (measured along a curved median line from basal to distal points). It consists of 15 tapering podomeres. Segmentation is unclear before proximal ventral spines. Length of podomeres 3–14 decreases gradually. Podomere 1 curved and relatively elongate, weakly sclerotised. Podomere 2 armed with small ventral spines. Podomere 3 bears a pair of remarkably robust proximal ventral spines with 6 anisomerous auxiliary spines. The first auxiliary spine is relatively elongate, the second one is the longest, auxiliary spines 3–6 decreasing in length gradually (Figure 1(g)). Paired ventral spines present on podomeres 4–14 with at least 1 pair of auxiliary spines. Another pair of small auxiliary spines is visible in some specimens (Figure 1(f)). The ventral spines on podomere 7 are the largest, that of podomere 14 the smallest (Figure 1(c)). All ventral spines are distally directed and inclined to the medial margin at an angle of 90°–60° (podomeres 3–14). The ventral spines alternate in length on successive podomeres and generally decrease backwards. The longer ventral spines are on the odd numbered podomeres (Figure 1(d), (g)). The 2 distal spines are ventrally curved and the dorsal one is much longer than the ventral one (Figure 1(c)). Paired dorsal spines are visible on the podomeres 12–14 (Figure 1(e)), gradually becoming longer backwards.

Discussion. *Anomalocaris kunmingensis* sp. nov. resembles *Anomalocaris saron* in having large proximal ventral spines, podomeres bearing distinct ventral spines, the curved podomere 1, podomere 2 armed with spines, and two pairs of auxiliary spines on each ventral spine [3]. The main differences between them include *A. kunmingensis* sp. nov. having 3 pairs of relatively elongate dorsal spines (podomeres 12–14) instead of 4–5 pairs (podomeres 11–15) in *A. saron*. Moreover, if the ventral spines of the new species display two pairs of auxiliary spines, then the second pair is shorter than the first. The auxiliary spines are distinct smaller than that of *A. saron* [3]. In addition, the Maotianshan Shale at the Ercaicun Village has yielded some anomalocaridid frontal appendages assigned to *A. saron* [20]. However, they are obviously different from the type species. Even though they all have a similar model of segmentation, the frontal appendages from Ercaicun differ from others in having much larger proximal ventral spines and much longer ventral spines, the ventral spines alternating in length on successive podomeres, every ventral spine bearing 5–7 pairs of small, distinct auxiliary spines [20]. Therefore, these appendages probably represent a new genus and species. Some frontal appendages from the Kaili biota have been assigned to *A. saron* with only a brief description [16]. These appendages bear 11 podomeres in the original description, but in fact they display more than 12 or 13 podomeres recognized on the plates. From their general features,

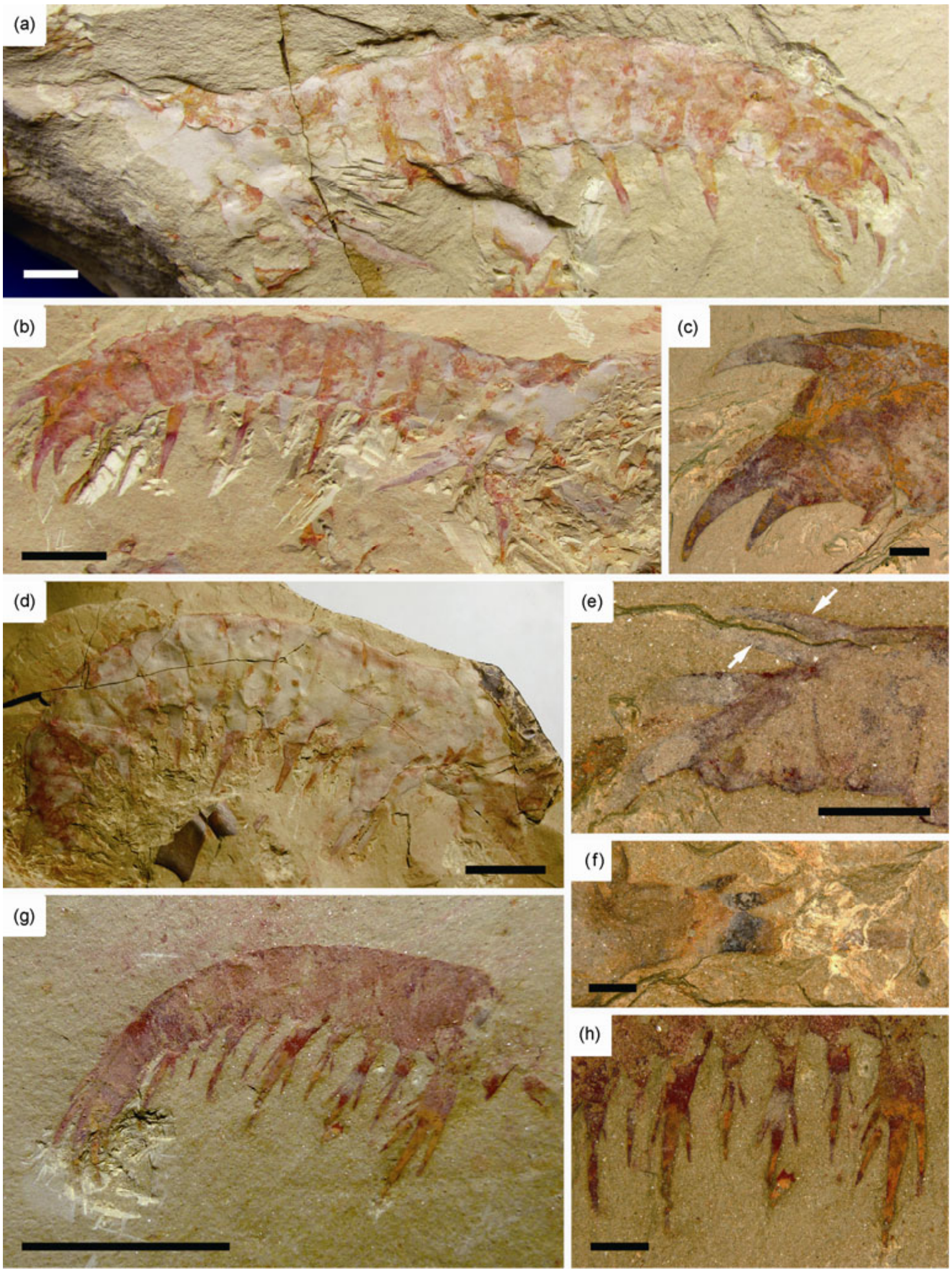

Figure 1 *Anomalocaris kunmingensis* sp. nov. from the Guanshan biota, Yunnan, China. (a) NIGP154566a, holotype, an almost complete frontal appendage, showing the general habitus; (b) NIGP154566b, the counterpart of the holotype showing the ventral spines alternating in length; (c) enlargement of (b), showing the distal spines and a small ventral spine on podomere 14; (d) NIGP154567a, an almost complete frontal appendage, showing the general habitus; (e) details of NIGP154625a, showing a pair of dorsal spines on podomere 12; (f) details of NIGP154624a showing 2 pairs of auxiliary spines on the ventral spine; (g) a small frontal appendage (NIGP154565a) showing the relatively elongate ventral spines; (h) enlargement of (g), showing the details of the proximal ventral spine and other ventral spines. Scale bars: 10 mm in (a), (b), (d) and (g); 2 mm in (c), (e), (f) and (h).

it is reasonable to assign these frontal appendages to *Anomalocaris*. They differ from *A. kunmingensis* sp. nov. and *A. saron* in having shorter and wider podomeres, and the length of the alternating ventral spines is not obvious. Two forms of anomalocaridid frontal appendages have been reported from the Pioche Formation of Nevada, United States. One species is assigned to *Anomalocaris* cf. *saron* [21]. However, it differs from *A. saron* and *A. kunmingensis* sp. nov. in having a different number of auxiliary spines. The new frontal appendage resembles that of *A. canadensis* in having 12 podomeres and paired auxiliary spines. The new species differs from the latter in its larger proximal ventral spines [22], length and number of dorsal spines, for example podomeres 12–14 have dorsal spines in *A. kunmingensis* sp. nov., instead of 11–15 as in *A. Canadensis* [2].

In addition, some small appendages (about 20 mm long) are interpreted to be the juvenile individuals of *A. kunmingensis* sp. nov. because of their close general characters. They are more elongate than the larger individuals and bear larger ventral spines on podomere 7 (Figure 1(g)). The morphology of these small appendages is similar to that of *A. saron*, but they are distinguished by the character of the dorsal and auxiliary spines.

***Paranomalocaris* gen. nov.**

Type species. *Paranomalocaris multisegmentalis* gen. nov., sp. nov.

Etymology. "para" means similar; "*Anomalocaris*" refers to type genus.

Diagnosis. Frontal appendage elongate and slender in outline, tapering backwards, with at least 22 podomeres, every podomere bearing a pair of relatively small ventral spines with 5 pairs of auxiliary spines; the ventral spines alternate in length on successive podomeres; the dorsal spines appear on podomeres 12–21 with outer margin armed with serrated spines; 2 small distal spines visible.

Discussion. Some morphological similarities of the frontal appendage of the new genus with *Anomalocaris* include the ventral spines alternating in length with paired auxiliary spines on the ventral spines, and dorsal spines appearing on the final podomeres. The major characters of the new genus differ from *Anomalocaris* in having more podomeres, the proximal ventral spines being obscure, terminal spines very small, and arming of more distal spines with a series of serrated spines. The appendage of *Tamisiocaris borealis* from Greenland bears at least 17 podomeres [8] but the simple ventral spines significantly distinguish it from the new genus.

***Paranomalocaris multisegmentalis* gen. nov., sp. nov.**

Etymology. 'Multi' referring to many, 'segmental' indicating many podomeres in this species.

Diagnosis. As for genus.

Holotype. A single, almost complete laterally compressed specimen (NIGP154564) with part and counterpart.

Description. The appendage consists of 22 podomeres with preserved length of 32 mm (measured along a curved median line from basal to distal points). Podomeres decrease in length gradually from middle section (Figure 2 (a), 3(a)). Segmentation before the proximal appendage is unclear. The preserved podomere 1 bears 2 relatively small ventral spines. Podomeres 2 and 3 armed with large ventral spines, but proximal ventral spines are poorly developed. Paired ventral spines present on podomeres 4–21. They

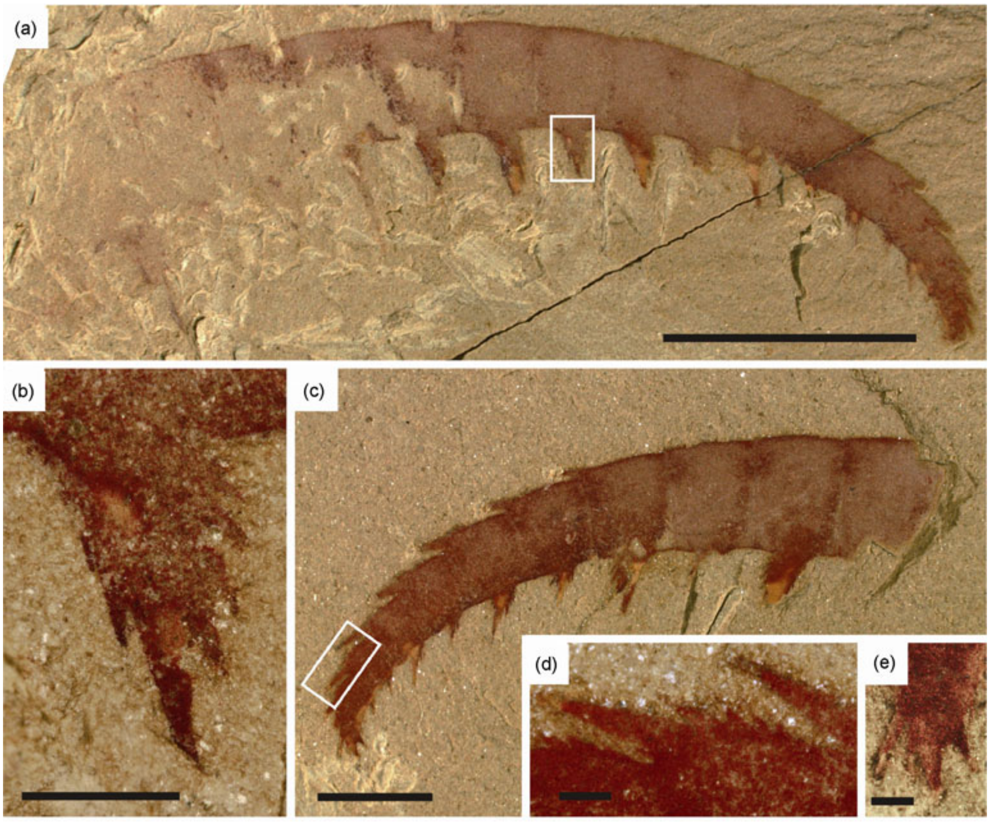

Figure 2 *Paranomalocaris multisegmentalis* gen. nov., sp. nov. from the Guanshan biota, Yunnan, China. (a) An almost complete frontal appendage (NIGP154564a) showing the general habitus; (b) enlargement of white rim of (a) showing the details of a ventral spine; (c) the counterpart (NIGP15456b) showing the dorsal and distal spines; (d) enlargement of white rim of (c) showing the details of dorsal spines; (e) details of distal spines. Scale bars: 5 mm in (a), 2 mm in (c), 500 μm in (b) and (e), 200 μm in (d).

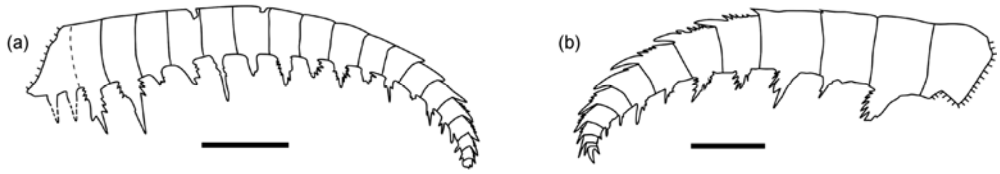

Figure 3 *Paranomalocaris multisegmentalis* gen. nov., sp. nov. from the Guanshan biota, Yunnan, China. (a) Camera lucida drawing of the frontal appendage (NIGP154564a) showing the general habitus; (b) Camera lucida drawing of the counterpart (NIGP15456b) showing the distal spines and the dorsal spines. Scale bars: 5 mm in (a), 2 mm in (b).

alternate in length on successive podomeres and clearly incline to the distal end. All ventral spines are distally directed and inclined to the medial margin at an angle of 85°–40°, and the angle decreases gradually backwards (Figure 3(a)). Some ventral spines bear 5 pairs of small auxiliary spines in the basal and middle sections. Their size increases from proximal to distal ends (Figure 2(b)). The dorsal spines are associated with podomeres 12–21 (Figures 2(c), 3(b)). Their basal section is armed with a maximum of 6 small spines. Their size increases slightly from proximal to distal ends, and the most distal spine is distinct larger than the others. The angle of the dorsal spines to the dorsal margin is circa 20° (Figure 2(d)). The distal podomere bears 2 small spines (Figure 2(e)).

Comparison. The new species resembles *A. canadensis* in comparable outline, arrangement and the size of the ventral spines, the inconspicuous proximal ventral spines, small spines on podomere 1, and small distal spines. They are essentially different in the number of podomeres, auxiliary spines (5 pairs in *P. multisegmentalis* instead of 1 pair in *A. canadensis*), and the dorsal spines (10 podomeres armed with dorsal spines in *P. multisegmentalis* (Figure 3(b)) instead of 7 podomeres in *A. Canadensis* [6,22]).

The new species also resembles *Anomalocaris* cf. *saron* from the Pioche Formation of Nevada [21] in the outline, the arrangement and the number of the ventral spines. It differs from the latter by the greater number of podomeres, shorter ventral spines, and smaller angle between the ventral spines and the ventral margin. As mentioned above, the specimens from the Ercaicun Village questionably referred to *A. saron* probably represent a new form. It resembles the new species in general outline and number of auxiliary spines, but differs in podomere number. The relatively long ventral spines on Ercaicun material [20] clearly differ from the short, cone-shaped ventral spines on the new species.

Occurrence and locality. Wulongqing Formation (*Palaeolenus* and *Megapalaeolenus* Zone), Cambrian (Stage 4, Series 2), Gaoloufang Village, Kunming, eastern Yunnan, China.

2 Feeding strategy diversity of anomalocaridids

Anomalocaridids have been described world-wide from the Cambrian including China, Australia and North America. Besides several described anomalocaridids from the Chengjiang biota, some new types have so far not been described. Through morphological analysis and description in the present study, it is concluded that some anomalocaridid frontal appendages from the Chengjiang, Guanshan and Kaili biotas of China, and the Pioche Formation of Nevada probably represent new types. This suggests a high diversity of the anomalocaridids in the Cambrian.

As the top predators in the food chain, anomalocaridids played a major role in the Cambrian marine ecosystem. The spinose frontal appendages and the rigid mouthparts revealed that these creatures were feroceous predators. The appearance of these animals represents the establishment of the complex ecosystem in the Cambrian sea [1]. Some coprolites containing trilobite fragments from the Maotianshan Shale at Shankoucun, Anning City, were probably produced by anomalocaridids [23]. Futhermore, it is considered that the healed injuries of some trilobites were caused by anomalocaridids [24,25]. Research of the functional morphology of the frontal appendages indicates different feeding strategies in the early Middle Cambrian. The sharp ventral and distal spines of these appendages may indicate that anomalocaridids are indeed fierce predators. In spite of the relatively short distal spines of *Paranomalocaris multisegmentalis* gen. nov., sp. nov., its slender appendage with more podomeres probably indicates a more flexible apparatus. The relatively small and sharp ventral spines with many auxiliary spines indicate their capability of catching small prey nimbly and efficiently. Some anomalocaridids, such as *Hudia* and *Laggania,* bear weakly developed distal spines and proximal ventral spines. However, their very elongate comb-like ventral spines with serrated spines arranged anteriorly indicate a function like a rigid net apparatus, which would be better adapted for catching swimming or benthic prey [6]. Such frontal appendage with specialized hunting function are probable a primary development in the early Cambrian as evidenced by those from the Chengjiang biota. Most anomalocaridids from the Chengjiang biota probably grasped and attacked prey by using the sharp distal and ventral spines of the frontal appendages. The so-called *A. saron* from Ercaicun bears stick-like ventral spines covered with a series of small auxiliary spines, and these auxiliary spines are more developed at the frontal edge [20]. It possibly indicates the rudiment of a rigid net appendage.

The above two kinds of anomalocaridid appendages with diverse morphology probably imply a differentiation of predation strategy, and consequently the adoption of different ecological niches. During the process of the establishment of the complex ecosystem in the Cambrian, competitor relationships become increasingly fierce between predators and prey, leading to the diversification of feeding strategy, as shown by the morphological differentiation in frontal appendages and trophic differences in anomalocaridids. Thus the ecological role played by anomalocaridids appears to have diversified during their evolution.

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1 Chen J Y, Ramsköld L, Zhou G Q. Evidence for monophyly and arthropod affinity of Cambrian giant predators. Science, 1994, 264: 1304–1308
2 Whittington H B, Briggs D E G. The large Cambrian animal, *Anomalocaris*, Burgess Shale, British Columbia. Phil Trans R Soc Lond B, 1985, 309: 569–609
3 Hou X G, Bergström J, Ahlberg P. *Anomalocaris* and other large animals in the Lower Cambrian Chengjiang fauna of southwest China. GFF, 1995, 117: 163–183
4 Collins D. The 'evolution' of *Anomalocaris* and its classification in the arthropod class Dinocarida (nov.) and order Radiodonta (nov.). J Paleontol, 1996, 70: 280–293
5 Daley A C, Budd G E, Caron J B, et al. The Burgess Shale anomalocaridid *Hurdia* and its significance for early euarthropod evolution. Science, 2009, 323: 1597–1600
6 Daley A C, Budd G E. New anomalocaridid appendages from the Burgess Shale, Canada. Palaeontol, 2010, 53: 721–738
7 Chen J Y. The Dawn of Animal World (in Chinese). Nanjing: Jiangsu Science and Technology Press, 2004. 1–366
8 Daley A C, Peel J S. A possible anomalocaridid from the Cambrian Sirius Passet Lagerstätte, North Greenland. J Paleontol, 2010, 84: 352–355
9 Van Roy P, Briggs D E G. A giant Ordovician anomalocaridid. Nature, 2011, 473: 511–513
10 Paterson J R, García-Bellido D C, Lee M S Y, et al. Acute vision in the giant Cambrian predator *Anomalocaris* and the origin of compound eyes. Nature, 2011, 480: 237–240
11 Kühl G, Briggs D E G, Rust J. A great-appendage arthropod with a radial mouth from the Lower Devonian Hunsrück Slate, Germany. Science, 2009, 323: 771–773
12 Chen J Y, Zhou G Q. Biology of the Chengjiang fauna. Bull Natl Mus Nat Sci, 1997, 1: 11–83
13 Steiner M, Zhu M Y, Zhao Y L, et al. Lower Cambrian Burgess Shale-type fossil associations of south China. Palaeogeogr Palaeoclimatol Palaeoecol, 2005, 220: 129–152
14 Luo H L, Li Y, Hu S X, et al. Early Cambrian Malong Fauna and Guanshan Biota from Eastern Yunnan, China (in Chinese). Kunming: Yunnan Science and Technology Press, 2008. 1–134
15 Hu S X, Zhu M Y, Steiner M, et al. Biodiversity and taphonomy of the Early Cambrian Guanshan biota, eastern Yunnan. Sci China Earth Sci, 2010, 53: 1765–1773
16 Zhao Y L, Zhu M Y, Babcock, et al. The Kaili Biota: Marine Organisms from 508 Million Years Ago. Guiyang: Guizhou Science and Technology Press, 2011. 162–163
17 Huang D Y, Wang Y Y, Gao J, et al. A new anomalocaridid frontal appendage from the middle Cambrian Mantou Formation of the Tangshan area, Hebei. Acta Palaeontol Sin, 2012, 51: 411–415
18 Hou X G, Aldridge R J, Bergström J, et al. The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life. Oxford: Blackwell Publishing, 2004. 1–233
19 Hou X G, Bergström J, Yang J. Distinguishing anomalocaridids from arthropods and priapulids. Geol J, 2006, 41: 259–269
20 Chen L Z, Luo H L, Hu S X, et al. Early Cambrian Chengjiang Fauna in Eastern Yunnan, China (in Chinese). Kunming: Yunnan Science and Technology Press, 2002. 1–199
21 Lieberman B S. A new soft-bodied fauna: The Pioche Formation of Nevada. J Paleontol, 2003, 77: 674–690
22 Briggs, D E G. *Anomalocaris*, the largest known Cambrian arthropod. J Palaeontol, 1979, 22: 631–664
23 Vannier J, Chen J Y. The Early Cambrian food chain: New evidence from fossil aggregates in the Maotianshan Shale biota, SW China. Palaios, 2005, 20: 3–26
24 Nedin C. *Anomalocaris* predation on non-mineralized and mineralized trilobites. Geology, 1999, 27: 987–990
25 Babcock L. Trilobites in Paleozoic predator-prey systems, and their role in reorganization of early Paleozoic ecosystems: In: Kelley P H, Kowalewski M, Hansen T A, eds. Predator-prey Interactions in the Fossil Record. New York: Kluwer Academic/Plenum Press, 2003. 55–92