Large, actively swimming filter feeders evolved several times in Earth's history, arising independently from groups as diverse as sharks, rays, teleost fishes\(^1\), and in mysticete whales\(^2\). Animals occupying this niche have not, however, been identified from the Early Palaeozoic. Anomalocarids, a group of stem arthropods that were the largest nektonic animals of the Cambrian and Ordovician, are generally thought to have been apex predators\(^3\)-\(^5\). Here we describe new material of *Tamisiocaris borealis*\(^6\), an anomalocarid from the Early Cambrian Sirius Passet Fauna of North Greenland, and show that its frontal appendage is specialized for filter feeding. The appendage bears long, slender and equally spaced ventral spines furnished with dense rows of long and fine auxiliary spines. This suggests that it was a microphagous filter feeder, using its appendages for sweep-net capture of food items down to 0.5 mm, within the size range of mesozooplankton such as copepods. *Tamisiocaris* demonstrates that large, nektonic filter feeders first evolved during the Cambrian Explosion, as part of the adaptive radiation of anomalocarids. The presence of filter-feeders in the Early Cambrian, together with evidence for a diverse pelagic community containing phytoplankton\(^7\),\(^8\) and mesozooplankton\(^7\),\(^9\),\(^10\), indicates the existence of a complex pelagic ecosystem supported by high primary productivity and nutrient flux\(^11\),\(^12\). Cambrian pelagic ecosystems appear to have been more modern than previously believed, suggesting that the Cambrian explosion drove not only the origin of modern animal phyla but also modern marine food webs.

Anomalocarids are stem arthropods well known from the Cambrian and Ordovician\(^13\)-\(^16\), and were the largest animals of their time. They are interpreted as nektonic apex predators, using their lateral flaps to swim in pursuit of prey, then seizing it with their raptorial frontal appendages\(^3\),\(^16\)-\(^18\). Recent discoveries have revealed a range of appendage morphologies\(^14\),\(^17\), suggesting diverse feeding strategies, but the anomalocarids are not known to have exploited...
plankton for food, which is a common nektonic strategy in modern oceans. In fact, the first definitive evidence for large nektonic filter-feeders is from the Mesozoic, when it evolved in the giant pachycormid fishes from the Jurassic and Cretaceous, although there is some evidence to suggest that placoderm fish may have exploited this niche in the Late Devonian. Large nektonic filter feeders are, however, unknown from the Early Palaeozoic.

*Tamisiocaris borealis*, from the Early Cambrian Sirius Passet fauna of North Greenland, has previously been described as a possible anomalocarid on the basis of a disarticulated frontal appendage. New fossils not only substantiate the anomalocarid affinities of *Tamisiocaris*, but also show that it was adapted to prey microphagously on mesozooplankton.

*Tamisiocaris borealis* is known from six isolated frontal appendages and two appendages associated with a head shield. Frontal appendages (Fig. 1) measure ≥ 120 mm in length, comparable in size to the later *Anomalocaris canadensis*. As in other anomalocarids, the appendage consists of discrete, sclerotized articles. All specimens are preserved with the ventral spines parallel to the bedding plane, and the articles show no evidence of distortion due to compaction. It is therefore assumed that the articles were transversely compressed, with an oval cross section in life. The appendage consists of at least 18 articles, versus 14 in, for example, *A. canadensis*. Articles are separated by triangular arthrodial membranes (Extended Fig. 2b,c). These extend almost to the dorsal margin of the appendage; ventrally, the membrane is 33-50% the length of the articles, suggesting a well-developed flexural ability.

The appendage curves downward distally, with the strongest curvature around the second and third article. The first article is straight, and longer than
the next three combined. It bears a single pair of ventral spines near its distal margin, which are stout and angled backwards (Fig. 1a) as in Anomalocaris briggsi. The next 17 articles each bear pairs of long and delicate ventral spines inserted at the mid-length of the article. These are evenly spaced along the appendage about 5-6 mm apart. The spines diverge ventrally such that each pair forms an inverted V-shape. Unlike A. canadensis, in which longer and shorter spines alternate and taper distally, the ventral spines are all of similar length, measuring 26-27.5 mm along the full length of the appendage (fig. 1a,b, Extended data Fig. 1-3). A similar condition is seen in A. briggsi. The ventral spines curve posteriorly, again as in A. briggsi, but unlike any other anomalocarids. Individual spines appear flattened, with a median rod and thinner lamellar margins (Extended data Fig. 1c). In addition, ventral spines are frequently kinked, and sometimes broken, suggesting that they were weakly sclerotized and flexible.

As in many other anomalocarids5,14, the anterior and posterior margins of the ventral spines bear auxiliary spines (Fig. 1c, Extended data Fig. 1c, 2d, 3), but they are unusually long in Tamisiocaris —measuring 4.2-5.0 mm in length— and extremely slender. Auxiliary spines form a comblike array, being spaced 0.3-.85 mm apart, with a median spacing of 0.49 mm. The length and spacing are such that adjacent spine combs would overlap or interdigitate.

One specimen consists of two associated appendages in subparallel orientation (Extended data Fig. 4). Proximally, they join a large, elliptical head shield. The headshield is larger than in Anomalocaris canadensis, but is not enlarged to the same degree as seen in Peytoia nathorsti and Hurdia victoria.

The affinities of Tamisiocaris were examined in a cladistics analysis to
explore its position within the anomalocarids. The analysis recovers a clade consisting of *Tamisiocaris borealis* and *Anomalocaris briggsi* (Fig. 4). This clade, the Cetiocarididae (n. nom), is diagnosed by long, slender, and recurved ventral spines, and the presence of numerous auxiliary spines. *Tamisiocaris* is more specialized, however, in having flexible ventral spines and densely packed auxiliary spines. The cetiocaridids are a sister to the Hurdiidae, a clade containing *Hurdia victoria, Peytoia nathorsti*, and related species. Outside these taxa lies a clade of presumably plesiomorphic forms including *Anomalocaris canadensis, A. saron, Amplectobelua* spp., and relatives.

The hypothesis that *Tamisiocaris borealis* engaged in filter feeding can be tested by comparisons with extant analogues (Extended data Figure 5).

Suspension feeding crustaceans, such as a cirripedes (barnacles), atyid shrimp, copepods, cladocerans, mysids and euphausiaceans (krill) share a suite of adaptations for sieving particles out of the water column which are very similar to the appendages in the cetiocarididae (Extended data figure 5). These include appendages with (i) very elongate, flexible setae and/or setules and (ii) regular spacing. These features create a net with a regular mesh size that efficiently traps all particles above a threshold set by the appendage spacing. The feeding limbs sieve particles out of the water, concentrate them by contraction, and carry them to the mouth. The filter feeding apparatuses of vertebrates have a similar morphology. Filter-feeding teleosts and some sharks use a mesh formed by long, slender, and closely spaced gill rakers. The feeding apparatus of mysticete whales consists of arrays of baleen plates that wear into elongate fringes.

The mesh size of the capture apparatus is closely related to prey size: Right whales specialise on small copepods (fringe diameter 0.2 mm) while blue
whales (fringe diameter 1 mm), feed on larger krill\textsuperscript{2}. A survey of diverse suspension feeders, from cladocerans to blue whales, shows a linear relationship between mesh size and minimum prey size (Fig. 4). While larger prey can be captured, the bulk of the prey is close to the mesh size of the filter apparatus.

Based on the morphologies seen in modern animals, a filter-feeding anomalocarid would be predicted to have evolved a setal mesh, with large appendages bearing long, flexible setae to increase capture area, with regular setal spacing. This is indeed the morphology observed in \textit{Tamisiocaris}.

Furthermore, one can use the mesh dimensions to predict the size of the prey caught by \textit{Tamisiocaris}. Spacing of the auxiliary spines in \textit{T. borealis} suggests that it could filter food items from the water column down to 0.5 mm, while linear regression from extant filter feeders (Fig. 4) predicts a slightly larger minimum particle size of 0.71 mm. Known mesozooplankton, from small carbonaceous fossil assemblages from the Cambrian Series \textsuperscript{9,10}, include isolated feeding appendages from crustaceans, including putative copepods. Based on comparisons with mandibles of modern counterparts\textsuperscript{10} the largest known specimens reached diameters of 1.5 to 2.7 mm. The filter appendage of \textit{T. borealis} predicts mesozooplankton of much smaller diameters yet to be described. Feeding was probably accomplished by alternate sweeping of the appendages, with entrapped prey being sucked up by the oral cone (Supplementary information animation 1 and 2).

In the context of the phylogenetic analysis presented here, \textit{Tamisiocaris} appears to have been part of an adaptive radiation of anomalocarids, with different clades evolving distinct frontal appendage morphologies and feeding strategies. Primitive forms such as \textit{Anomalocaris canadensis} had raptorial
appendages with stout, trident-like spines, well-suited to impaling large, free-swimming or epifaunal prey\(^3\) (Extended data Fig. 6a). *Amplectobelua* had pincer-like appendages\(^23\) (Extended data Fig. 6b) that would have been effective in seizing and tearing apart relatively large, slow-moving animals. In hurdiids, the appendages bear opposing pairs of spines, which may have functioned as jaws or in sediment sifting\(^14\) (Extended data Fig. 6c). Finally, cetiocaridid frontal appendages are specialized as sweep nets (Extended data Fig. 6d,e). This extraordinary range of appendage morphologies shows that, far from being a failed experiment, anomalocarids staged a major adaptive radiation during the Cambrian Explosion, evolving to fill a range of niches as nektonic predators, much like the later radiations of vertebrates\(^19\) and cephalopods\(^24\), by also becoming secondary filter feeders.

The existence of filter feeding in anomalocarids also has implications for the structure of Early Cambrian pelagic food webs (Extended data Fig. 7). It had been assumed that a diverse planktonic fauna and suspension feeding animals did not evolve until the Late Cambrian\(^25\) and thus the complexity of the pelagic food web evolved in a delayed, piecemeal fashion. However, the discovery of large filter feeders in the Early Cambrian suggests a well-developed pelagic biota supported by high primary productivity and abundant mesozooplankton, because large animals can only exploit small prey when they exist at high densities. Whales, whale sharks and basking sharks exploit highly productive areas such as upwelling zones and seasonal plankton blooms at high latitudes\(^26\). This general observation holds for all microphagous suspension feeders ranging from cladocerans, to anchovies, to red salmon, to blue whales: a high density of food particles is required to sustain an actively swimming filter feeder.
*Tamisiocaris* therefore indicates high productivity at the time of deposition at Sirius Passet. Other evidence suggests that high productivity may have been a global phenomenon in the Cambrian provided by vast deposits of phosphorites and increased terrestrial nutrient flux\textsuperscript{11,12,27}. Furthermore, the Cambrian also witnessed a radiation of spiny acritarchs, which presumably evolved into microscopic phytoplankton replacing the larger Neoproterozoic benthic forms\textsuperscript{7,8}. Complex minute crustacean feeding appendages also occur in lower and middle-upper Cambrian rocks\textsuperscript{9,10}, demonstrating the presence of diverse mesozooplankton preying on phytoplankton. Abundant vetulicolians in Sirius Passet\textsuperscript{28} (100s of specimens collected on recent expeditions) may also have suspension fed upon phytoplankton (Extended data fig. 6). One tier up, *Tamisiocaris* would have preyed upon the mesozooplankton as would the common bivalved nektonic arthropod *Isoxys volucris*\textsuperscript{29}. Other pelagic predators known from Lagerstätten elsewhere would likewise have fed on mesozooplankton, including ctenophores, cnidarians, chaetognaths and pelagic arthropods (Extended data Fig. 6). The Cambrian pelagic food web was therefore highly complex, containing multiple trophic levels, including pelagic predators and multiple tiers of filter-feeders. This underscores the remarkable speed with which a modern food chain was assembled during the Cambrian Explosion.

Finally, the discovery of a filter feeding anomalocarid has implications for debates concerning the predictability of evolution, or lack thereof. One view holds that evolution is ultimately unpredictable\textsuperscript{30}. The striking convergence between *Tamisiocaris* and extant filter feeders, however, suggests that while ecological niches are occupied by different groups at different times, the number of viable niches and viable strategies for exploiting them are limited.
Furthermore, the derivation of the filter-feeding *Tamisiocaris* from a large apex predator parallels the evolution of filter feeding pachycormid fish\(^1\), sharks and whales\(^2\). In each case, filter feeders evolved from nektonic macropredators. This suggests that evolution is constrained not only in terms of outcomes, but in terms of trajectories. The result is that independent evolutionary experiments by animals as different as anomalocarids, fish and whales have converged on broadly similar outcomes.

**METHODS SUMMARY**

Specimens were collected in the field and photographed in the lab, coated or uncoated submerged in water. A digital reconstruction of the *Tamisiocaris* feeding appendage were made in order to infer the range of motions. The filter mesh diameter and prey width were collated from extant filter feeders to depict the linear relationship between these (see Methods). A cladistics analysis containing XX taxa and XX characters were collated and analysed in Paup and TNT, see Supplementary information.

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Acknowledgements. Our expeditions to North Greenland were financed by Geocenter Denmark, the Agouron Institute and the Carlsberg Foundation. We are grateful for discussions with the Bristol Palaeobiology group and Misha Matz (UT Austin). M.S. is supported by the Carlsberg Foundation. We thank POLOG for logistic support. Arne T. Nielsen (Copenhagen) and M. Paul Smith (Oxford) assisted in the field in 2009. S. Powell assisted with figures.

Author contributions. J.V., M.S., and NRL designed analyzed and performed research. D.A.T.H. obtained funding for the fieldwork. J.V., M.S., N.R.L. and D.A.T.H. wrote and discussed the paper.

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Figure 1 | *Tamisiocaris borealis* Daley and Peel, 2010 frontal appendages from Sirius Passet, Lower Cambrian, North Greenland. a, Isolated and
relatively complete appendage, MGUH XXXXX. b. Isolated appendage, preserving auxiliary spines in great detail, MGUH XXXXX. c, detail of spine in b. All specimens photographed submerged in water with high angle illumination.

**Figure 2** | A digital reconstruction of *Tamisiocaris*. a. Single appendage indicating the articulating membranes (Am), articles (Art), spines (Sp) and auxiliary spines (As). b. Possible sequence of movement of the frontal appendage of *Tamisiocaris*. See also extended data movies 1 and 2.

**Figure 3** | Diagram depicting the relationship between filter mesh size and the food items consumed by suspension feeders. *Tamisiocaris* is indicated by the dotted line based on a mesh width of 0.51 mm. The diagram is collated from a range of modern filter feeders, see Methods section.

**Figure 4** | Phylogeny of anomalocarids. Cladistics analysis based on XX characters and including XX taxa analyzed in Paup and TNT. *Tamisiocaris* form a clade with *Anomalocaris briggsi*, which are here named Cetiocaridae.

**Extended data figure 1** | *Tamisiocaris borealis* MGUH XXXXX, frontal appendage. a. Part photographed in low angle lighting coated with MgO with indications of spines (s1-s15); spines, broken at the base (bs). b. Camera lucida drawing c. detail of spine preserving auxiliary spines in relief.

**Extended data figure 2** | *Tamisiocaris borealis* MGUH XXXXX, frontal
appendage. a. Part, photographed submerged in water and with high angle illumination. b. Counterpart, displaying articulating membranes across the appendage indicated by their relatively lower reflectivity. c. Detail of b, and the articulating membranes along the mid section of the appendage. d. Detail of broken spine in b, displaying auxiliary spines in.

Extended data figure 3 | Tamisiocaris borealis MGUH XXXXX frontal appendage with well preserved auxiliary spines. a. Part. b. Detail of auxiliary spines in a. c. Schematic drawing of MGUH XXXX, from a combination of part and counterpart. d. Counterpart. e. Detail of d.

Extended data figure 4 | MGUH XXXXXX frontal appendages and head shield assemblage. a. Part. b. Camera lucida drawing of the part indicating the head shield (Hs), left frontal appendage (Lfa) and right frontal appendage (Rfa).


Extended data figure 5 | Schematic drawings of different anomalocarid

Extended data figure 6 | A schematic overview of known components the Early Cambrian pelagic food web. At the base of the food chain was phytoplankton in the form of acritarchs and most likely other forms with no apparent fossil record. Diverse mesozooplankton were present as copepod and branchiopod-like crustaceans feeding on phytoplankton, along with the vetulicolians, which exhibit a morphology suggesting filter feeding similar to basal chordates. Larger pelagic predators such as chaetognaths, larger arthropods and potentially also ctenophores preyed upon the mesozooplankton. *Tamisiocaris* would similarly have fed on the mesozooplankton. The presence of a large nektonic suspension feeder suggests a high abundance of primary producers and mesozooplankton. Other anomalocarids, such as *Anomalocaris* and *Amplectobelua* were present as some of the macrophagous apex predators at this time.