Anomalocaris

Anomalocaris (from Ancient Greek ανώμαλος, meaning "unlike", and καρίς, meaning "shrimp", with the intended meaning "unlike other shrimps") is an extinct genus of radiodont, an order of early-diverging stem-group marine arthropods.

It is best known from the type species *A. canadensis,* found in the Stephen Formation (particularly the Burgess Shale) of British Columbia, Canada. The other named species *A. daleyae* is known from the somewhat older Emu Bay Shale of Australia.[2] Other unnamed *Anomalocaris* species are known from China and the United States.[3]

Like other radiodonts, *Anomalocaris* had swimming flaps running along its body, large compound eyes, and a single pair of segmented, frontal appendages, which in *Anomalocaris* were used to grasp prey. Estimated to reach 34.2–37.8 cm (13.5–14.9 in) long excluding the frontal appendages and tail fan,[4] *Anomalocaris* is one of the largest animals of the Cambrian, and thought to be one of the earliest examples of an apex predator,[5][6] though others have been found in older Cambrian lagerstätten deposits.

Since the original description in late 19th century,[7] the frontal appendages were the only known fossilized parts and misidentified as the body parts of other animals.[8] Its radiodont affinity was revealed in 1980s, specifically in a 1985 journal article by Harry B. Whittington and Derek Briggs.[9] The trunk and mouth were reconstructed after another radiodont genus until the corrections done in 1996[8] and 2012.[10] It is the type genus of Anomalocarididae, a family which previously included all radiodonts but recently only *Anomalocaris* and a few closely-related taxa.[3]

Discovery and identification

From the start, *Anomalocaris* fossil was misidentified, followed by a series of misidentifications and taxonomic revisions.[9][8] As Stephen Jay Gould, who popularised the Cambrian explosion in his 1989 book *Wonderful Life*, appropriately described:

> [The story of *Anomalocaris* is] a tale of humor, error, struggle, frustration, and more error, culminating in an extraordinary resolution that brought together bits and pieces of three "phyla" in a single reconstructed creature, the largest and fiercest of Cambrian organisms.[11]

Anomalocaris

Temporal range: Early Cambrian to Middle Cambrian (Stage 3 to Guzhangian),

ROMIP 51212, a largely complete specimen of *Anomalocaris canadensis*

Life restoration of *Anomalocaris canadensis*

Scientific classification

Domain:	Eukaryota
Kingdom:	Animalia
Phylum:	Arthropoda
Order:	†Radiodonta
Family:	†Anomalocarididae
Genus:	†*Anomalocaris* Whiteaves, 1892

Species

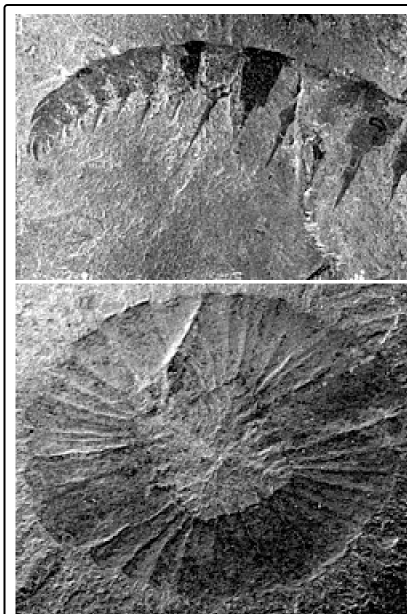
- ***A. canadensis*** Whiteaves, 1892
  - =***A. whiteavesi*** Walcott, 1908

- =***A. gigantea*** Walcott, 1912
- =***A. cranbrookensis*** Resser, 1929
- *A. daleyae* Paterson, García-Bellidob & Edgecombe, 2023[2]

(8 more unnamed species[3])

Anomalocaris fossils were first collected in 1886[8] by Richard G. McConnell of the Geological Survey of Canada (GSC). Having been informed of rich fossils at the Stephen Formation in British Columbia, McConnell climbed Mount Stephen on 13 September 1886.[12][13] He found abundant trilobites, along with two unknown specimens.[7] In August 1891, Henri-Marc Ami, Assistant Palaeontologist at GSC, collected many trilobites and brachiopod fossils,[14] along with 48 more of the unknown specimens.[15] The fifty specimens were examined and described in 1892 by GSC paleontologist Joseph Frederick Whiteaves.[16][17] Whiteaves interpreted them as the abdomens of phyllocarid crustaceans, and gave the full scientific name *Anomalocaris canadensis*. He describes the crustacean characters:

> Body or abdominal segments, which, in all the specimens collected, are abnormally flattened laterally, a little higher or deeper than long, broader above than below, the pair of ventral appendages proceeding from each, nearly equal in height or depth to the segment itself... The generic name *Anomalocaris* (from *ανώμαλος*, unlike,—*καρίς*, a shrimp, *i.e.*, unlike other shrimps) [the species name referring to Canada] is suggested by the unusual shape of the uropods or ventral appendages of the body segments and the relative position of the caudal spine.[7]



Frontal appendage of *Anomalocaris canadensis* (top) and mouthpiece of *Peytoia nathorsti* (bottom) from British Columbia. The latter was originally assigned to the former species.

In 1928, Danish paleontologist Kai Henriksen proposed that *Tuzoia*, a Burgess Shale arthropod which was known only from the carapace, represented the missing front half of *Anomalocaris*.[8] The artists Elie Cheverlange and Charles R. Knight followed this interpretation in their depictions of *Anomalocaris*.[8]

Not known to scientists at the time, the body parts of relatives of *Anomalocaris* had already been described but not recognized as such. The first fossilized mouth of such a kind of animal was discovered by Charles Doolittle Walcott, who mistook it for a jellyfish and placed it in the genus *Peytoia*. Walcott also discovered a frontal appendage but failed to realize the similarities to Whiteaves' discovery and instead identified it as feeding appendage or tail of the coexisted *Sidneyia*.[18] In the same publication in which he named *Peytoia*, Walcott named *Laggania*, a taxon that he interpreted as a holothurian.

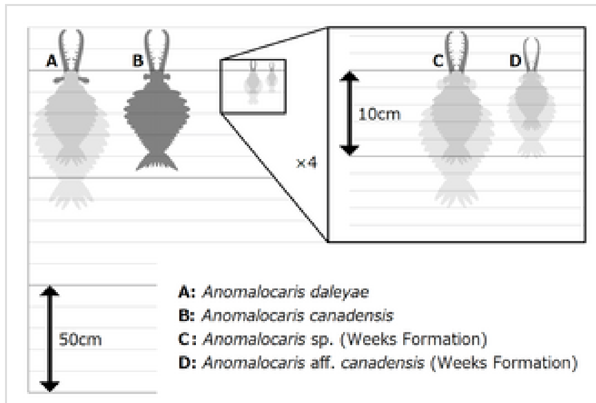
In 1966, the Geological Survey of Canada began a comprehensive revision of the Burgess Shale fossil record, led by Cambridge University paleontologist Harry B. Whittington.[8] In the process of this revision, Whittington and his students Simon Conway Morris and Derek Briggs would discover the true nature of *Anomalocaris* and its relatives, but not without contributing to the history of misinterpretations first.[18] In 1978, Conway Morris recognized that the mouthparts of *Laggania* were identical to *Peytoia*, but concluded that *Laggania* was a composite fossil made up of *Peytoia* and the sponge *Corralio undulata*.[19] In 1979, Briggs recognized that the fossils of *Anomalocaris* were appendages, not abdomens, and proposed that they were the walking legs of a giant arthropod, and that the feeding appendage Walcott had assigned to *Sidneyia* was the feeding appendage of similar animal, referred to as "appendage F".[16] Later, while clearing what he thought was an unrelated specimen, Harry B. Whittington removed a layer of covering stone to discover the unequivocally connected frontal appendage identical to *Anomalocaris* and mouthpart similar to *Peytoia*.[18][20] Whittington linked the two species, but it took several more years for researchers to realize that the continuously juxtaposed *Peytoia*, *Laggania* and frontal appendages (*Anomalocaris* and "appendage F") actually represented a single group of enormous creatures.[9] The two genera have now been placed into the order Radiodonta[8] and are commonly known as radiodonts or anomalocaridids. Since *Peytoia* was named first, it is the accepted correct name for the entire animal. However, the original frontal appendage was from a larger species distinct from *Peytoia* and "*Laggania*" and therefore retains the name *Anomalocaris*.[10]

In 2011, compound eyes of *Anomalocaris* were recovered from a paleontological dig at Emu Bay Shale on Kangaroo Island, Australia, proving that *Anomalocaris* was indeed an arthropod as had been suspected. The find also indicated that advanced arthropod eyes had evolved very early, before the evolution of jointed legs or hardened exoskeletons.[21] This specimen was later identified as that of a new species of *Anomalocaris*, *A. daleyae*.[2]

Numerous species have been previously referred to *Anomalocaris*, but subsequent analyses have doubted this generic assignment,[22][23][24] and reclassified them within different genera. In 2021, "*A.*" *saron*[25] and "*A.*" *magnabasis*[26] were reassigned to the new genus *Houcaris* in the family Tamisiocarididae,[27] but subsequent analysis suggests that *H. saron* is a member of the family Amplectobeluidae instead and that *H*? *magnabasis* (recovered as a sister taxon of Amplectobeluidae) does not form a monophyletic clade with other species of *Houcaris*.[28] In the same year, "*A.*" *pennsylvanica* was reassigned to the genus *Lenisicaris*.[3] In 2022, specimen ELRC 20001 that was treated as an unnamed species of *Anomalocaris* or whole-body specimen of *A. saron* got a new genus, *Innovatiocaris*.[29] In 2023, *"A". kunmingensis* was reassigned to the new genus *Guanshancaris* in the family Amplectobeluidae.[30] Multiple phylogenetic analyses also suggested that *"A". briggsi* (tamisiocaridid) was not a species of *Anomalocaris* either,[4][31][32][33] and it was reassigned to the genus *Echidnacaris* in the family Tamisiocarididae in 2023.[2]

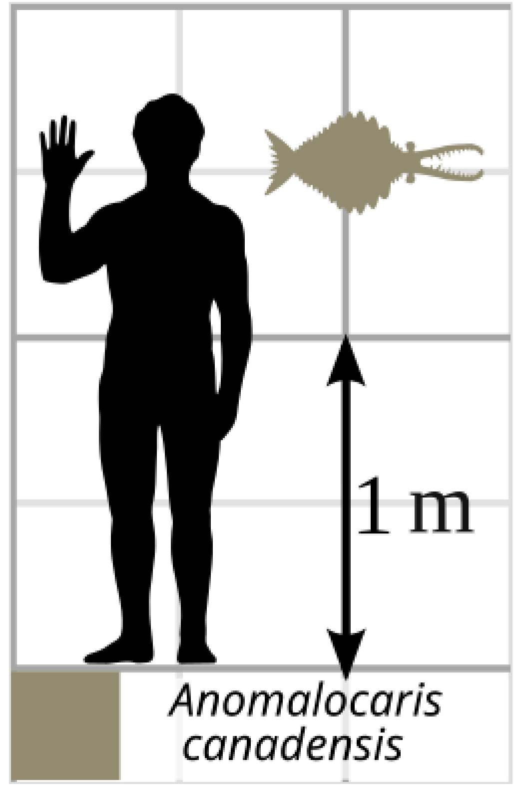
Description

For the time in which it lived, *Anomalocaris* was gigantic. A complete specimen of *A. canadensis*, ROMIP 51211, is measured up to 20.5 cm (8.1 in) long[8][34] (17.4 cm (6.9 in) long when excluding the frontal appendages and tail fan[4]). The largest frontal appendage is measured up to 18 cm (7.1 in) long when extended,[35] and this specimen of *A. canadensis* would have reached up to 34.2–37.8 cm (1.12–1.24 ft) in body length excluding the frontal appendages and tail fan.[4]Dryad data 04 [29] Previous body length estimation up to 1 m (3.3 ft)[16] is unlikely based on the ratio of body parts[35] (body length measured only about 2 times the length of frontal appendage in *A. canadensis*[4]) and the size of largest frontal appendage.[35] *A. daleyae* (formerly *A.* cf. *canadensis* or *A.* aff. *canadensis*) from the Emu Bay Shale of Australia is larger than *A. canadensis*, with the largest known appendage measuring up to 18.3 cm (7.2 in) long, which would have belonged to an individual between 34.8–51.2 cm (1.14–1.68 ft) long.[2][4]

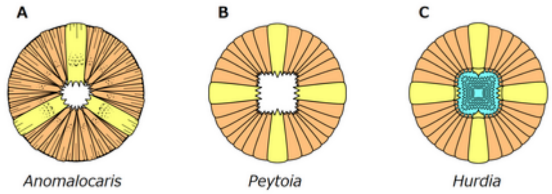


Size estimation of *Anomalocaris*

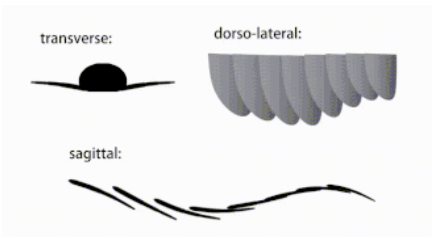
Anomalocaris propelled itself through the water by undulating the flexible flaps on the sides of its body.[36] Each flap sloped below the one more posterior to it,[37] and this overlapping allowed the lobes on each side of the body to act as a single "fin", maximizing the swimming efficiency.[36] The construction of a remote-controlled model showed this mode of swimming to be intrinsically stable,[38] implying that *Anomalocaris* would not have needed a complex brain to manage balance while swimming. The body was widest between the third and fifth lobe and narrowed towards the tail, with additional three pairs of small flaps on the constricted neck region.[8][35] It is difficult to distinguish lobes near the tail, making an accurate count difficult.[37] For the main trunk flaps, the type species *A. canadensis* had 13 pairs.[35]



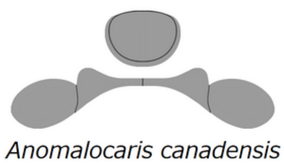
Size of a large *Anomalocaris canadensis* compared to a human



Oral cones of *Anomalocaris* (A), *Peytoia* (B) and *Hurdia* (C), the former showing unique triradial, tuberculated and wrinkled structures



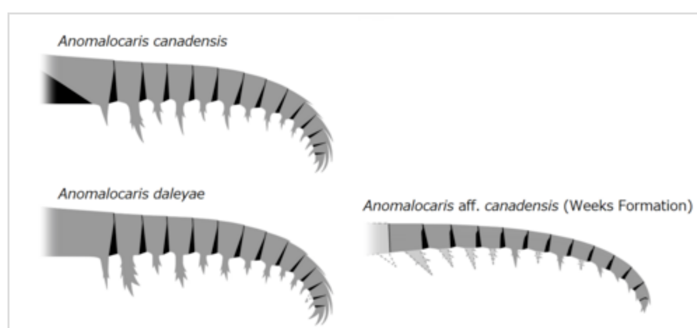
The mobility of radiodont trunk appendages (like *Anomalocaris*)



The head sclerite structure of *Anomalocaris*

Anomalocaris had an unusual disk-like mouth known as an oral cone. The oral cone was composed of several plates organized triradially. Three of the plates were quite large. Three to four medium sized plates could be found between each of the large plates, and several small plates between them. Most of the plates wrinkled and have scale-like tubercles near the mouth opening.[10][39] Such an oral cone is very different from those of a typical hurdiid radiodont like *Peytoia* and *Hurdia*, which is smooth and tetraradial.[10][32] As a shared character across radiodonts, *Anomalocaris* also had three sclerites on the top and side of its head.[32] The top one, known as a head shield, dorsal carapace or H-element, was shaped like a laterally-elongated[40] oval, with a distinct rim on the outer edge.[35] The remaining two lateral sclerites, known as P-elements, were also ovoid, but connected by a bar-like outgrowth.[32] The P-elements were previously misinterpreted as two huge compound eyes.[35][32]

Two large frontal appendage were positioned in front of the mouth, at the front of the head.[8] Each frontal appendage of *Anomalocaris* usually had 14 podomeres (segmental units, at least 1 for shaft and 13 for distal articulated region), with each appendage being laterally-flattened (taller than wide).[35] Most podomeres were tipped with a pair of endites (ventral spines).[35] The endites themselves were both equipped with multiple auxiliary spines, which branches off from the anterior and posterior margin of the endites.[25][39][41][35][1]



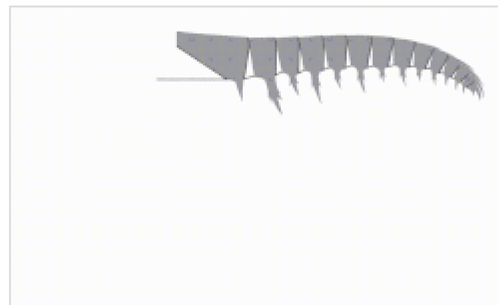
Frontal appendages of *Anomalocaris*, with examples from multiple species

The tail was a large tail fan, composed of three[8][35] pairs of large, lateral fin-shaped lobes and one terminal lobe-like tailpiece.[35] Previous studies suggest the tail fan was used to propel it through Cambrian waters,[20][36] while further hydrodynamic study rather suggest it was more adapted to provide steering function.[34] The gills of the animal, in the form of long, thin, hair-like structures known as lanceolate blades, were arranged in rows forming setal blades. The setal blades were attached by their margin to the top side of the animal, two setal blades per body segment. A divide ran down the middle, separating the gills.[35]

Based on fossilized eyes from the Emu Bay Shale, which belong to the species *Anomalocaris daleyae,*[2] the stalked eyes of *Anomalocaris* were 30 times more powerful than those of trilobites, long thought to have had the most advanced eyes of any contemporary species. With one specimen having over 24,000 lenses in one eye, the resolution of the 3-centimetre-wide (1.2 in) eyes would have been rivalled only by that of the modern dragonfly, which has 28,000 lenses in each eye.[21] Additionally, estimation of ecdysozoan opsins suggest that *Anomalocaris* may have had dichromatic color vision.[42]

Paleobiology

Diet


Grasping movement of the frontal appendage of *A. canadensis*

The interpretation of *Anomalocaris* as an active predator is widely accepted throughout the history of research,[9][8][10] as its raptorial frontal appendages and mid-gut glands strongly suggest a predatory lifestyle.[43][44][5] In the case of *A. canadensis*, its outstanding size amongst Burgess Shale fauna also make it one of the first apex predators known to exist.[5]

However, the long-standing idea that *Anomalocaris* fed on hard-bodied animals, especially its ability to penetrate mineralized exoskeleton of trilobites, has been questioned, with many recent studies considering it more likely that *Anomalocaris* exclusively hunted soft-bodied prey.[45][10][5][6] Some Cambrian trilobites have been found with round or W-shaped "bite" marks, which were identified as being the same shape as the mouthparts of *Peytoia* (previously misidentified as those of *Anomalocaris*[46][10]). Stronger evidence that *Anomalocaris* ate trilobites comes from coprolite, which contain trilobite parts and are so large that the radiodonts are the only known organism from that period large enough to have produced them.[46] However, since *Anomalocaris* lacks any mineralized tissue, it seemed unlikely that it would be able to penetrate the hard, calcified exoskeleton of trilobites.[46] Rather, the coprolites may have been produced by different organisms, such as the trilobites of the genus *Redlichia*.[39] Another suggested possibility was that *Anomalocaris* fed by grabbing one end of their prey in its oral cone while using its frontal appendages to quickly rock the other end of the animal back and forth. This produced stresses that exploited the weaknesses of arthropod cuticles, causing the prey's exoskeleton to rupture and allowing the predator to access its innards.[46] This behaviour was originally thought to have provided an evolutionary pressure for trilobites to roll up, to avoid being flexed until they snapped.[46]

The lack of wear on radiodont mouthparts suggests they did not come into regular contact with mineralized trilobite shells, and were possibly better suited to feeding on smaller, soft-bodied organisms by suction, since they would have experienced structural failure if they were used against the armour of trilobites.[45][39] *A. canadensis* was suggested to have been capable of feeding on organisms with hard exoskeletons due to the short, robust spines on its frontal appendages.[39][26] However, this conclusion is solely based on the comparison with the fragile frontal appendages of suspension feeding radiodonts (e.g. *Echidnacaris* and *Houcaris* spp.).[27] The typical lack of damage to the endites on the frontal appendages of *A. canadensis* (with damage only present on a single specimen) suggests that they were not used to grasp hard-shelled prey.[6] As opposed to *Peytoia* whose oral cone is more rectangular with short protruding spines, the oral cone of *A. canadensis* has a smaller and more irregular opening, not permitting strong biting motions, and indicating a suction-feeding behavior to suck in softer organisms.[10] Three-dimensional modelling of various radiodont frontal appendages also suggest that *A. canadensis* is more capable to prey on smaller (2–5 cm in diameter), active, soft-bodied animals (e.g. vetulicolian; free-swimming arthropods like isoxyids and hymenocarines; *Nectocaris*).[5][6]

Ecological reconstruction of *Anomalocaris* hunting *Isoxys*, after posture estimated in Bicknell *et al.* (2023)

Bicknell *et al.* (2023) examined the frontal appendages of *Anomalocaris*, suggesting it was an active nektonic apex predator. Postured with the frontal appendages outstretched, *Anomalocaris* would have been able to swim with maximized speed, similar to modern predatory water bugs. Its eyes would be suitable to hunt prey in well-lit waters. *Anomalocaris* would have hunted various free-swimming animals since there are a large diversity of nektonic and pelagic soft-bodied animals. It probably would have not hunted benthic animals like trilobites, considering the possibility of damaging the frontal appendages on the substrate while trying to grab prey from seafloor at speed. Instead, other animals such as other radiodonts (e.g. *Hurdia*, *Cambroraster*, *Titanokorys*, *Stanleycaris*) and artiopods (e.g. *Sidneyia*) would have been benthic predators in the Burgess Shale.[5][6]

Paleoecology

Specimens of *Anomalocaris* have been found worldwide spanning from Cambrian Stage 3 to the Guzhangian. Aside from the Burgess Shale and Emu Bay Shale, fossils have been found in the Chengjiang Biota, Hongjingshao Formation, Balang Formation and the Kaili Formation of China, as well as the Eagar Formation and Weeks Formation in the United States.[3]

Anomalocaris canadensis lived in the Burgess Shale in relatively great numbers.[1] In the Burgess Shale, *Anomalocaris* is more common in the older sections, notably the Mount Stephen trilobite beds. However, in the younger sections, such as the Phyllopod bed, *Anomalocaris* could reach much greater sizes—roughly twice the size of its older, trilobite bed relatives. These rare giant specimens have previously been referred to a separate species, *Anomalocaris gigantea*; however, the validity of this species has been called into question,[16] and is currently synonymized to *A. canadensis*.[35]

Other unnamed species of *Anomalocaris* live in vastly different environments.[3] For example, *Anomalocaris* cf. *canadensis* (JS-1880) lived in the Maotianshan Shales,[3] a shallow tropical sea or river delta[47] in what is now modern China. *Anomalocaris daleyae* (Emu Bay Shale) lived in a comparable environment; the shallow, tropical waters of Cambrian Australia.[3] The Maotianshan Shale and the Emu Bay Shale are very close in proximity, being separated by a small landmass, far from the Burgess Shale.[3] These two locations also included *"Anomalocaris" kunmingensis* and *"Anomalocaris" briggsi* respectively, species that previously attributed[48][49][39][50] but taxonomically unlikely to be a member of *Anomalocaris* nor even Anomalocarididae.[3][51]

See also

- 8564 Anomalocaris, an asteroid named after this animal.
- Radiodonta, extinct arthropod order composed of *Anomalocaris* and its relatives.

Paleontology portal

- *Houcaris*, *Lenisicaris*, *Innovatiocaris*, *Guanshancaris*, *Echidnacaris*, radiodont genera containing species originally named as *Anomalocaris*.
- *Aegirocassis*, a giant filter-feeding radiodont from Ordovician Morocco.
- Cambrian explosion, the large bio-diversification event that occurred during the Cambrian.
- *Opabinia*, a genus of bizarre stem-group arthropod distantly related to the radiodonts.
- *Wiwaxia*, a genus of possible mollusk that had copious numbers of carbonaceous scales, and lived alongside *Anomalocaris*.
- Paleobiota of the Burgess Shale

Footnotes

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External links

- "*Anomalocaris canadensis*" (https://web.archive.org/web/20201112025257/http://burgess-shale.rom.on.ca/en/fossil-gallery/view-species.php?id=1). *Burgess Shale Fossil Gallery*. Virtual Museum of Canada. 2011. Archived from the original (http://burgess-shale.rom.on.ca/en/fossil-gallery/view-species.php?id=1) on 2020-11-12. Retrieved 2023-01-21.
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