The function of forks: *Isotelus*-type hypostomes and trilobite feeding

THOMAS A. HEGNA

Despite previous investigations, the function of the forked morphology of asaphid trilobite hypostomes is enigmatic. The focus of this study is the large and robust forked hypostome of the largest known genus of trilobite, *Isotelus*, and the independently-derived forked hypostome of *Hypodicranotus*, the longest hypostome relative to body size of any trilobite. Although the trilobite hypostome is analogous to the labrum in other arthropods, forked hypostomes lack an obvious modern functional counterpart. The *Isotelus* hypostome is distinguished from other trilobite hypostomes by closely-spaced terrace ridges on a greatly thickened inner surface of the forked posterior margin, with the scarp of the terrace facing antero-ventrally. This is compatible with a grinding function, suggesting possible limb differentiation to complement this structure. The inner face of the tine (one of the two, prominent, sub-parallel posterior projections) is also unique in that it has a microstructure which is evident in section, running perpendicular to the surface. Macropredatory and filter-feeder roles are ruled out, and previous characterizations of the hypostome as knife-like or serrated are rejected. Its function is incompatible with that of other non-asaphid trilobites with forked hypostomes, like the remopleuridid *Hypodicranotus*, which lack similar terrace ridges and thickened inner-edge cuticle. □ Arthropoda, Asaphida, ecology, functional morphology, Trilobita.

Forked hypostomes represent a derived morphology in several disparate groups of trilobites, like asaphids (Figs 1–2) and remopleuridids (Fig. 4). The posterior margin has two prominent, backward-facing projections. Forked hypostomes are always rigidly attached to the cephalic doublure, limiting their mobility but increasing their strength. Trilobites with a forked hypostome range from the Cambrian to the Upper Palaeozoic. This hypostomal feature is much more common in its weaker incarnations (i.e. subtly forked), where it is represented by a notched posterior margin (Fortey & Owens 1999).

Background

The trilobite hypostome is a small, sclerotized plate under the head, positionally (if not functionally) analogous to the crustacean labrum. Whether the hypostome and head appendages interacted during feeding is unknown, as is the exact position of the mouth relative to the hypostome. Because of these uncertainties, research on the feeding habits of trilobites has focused on hypostome attachment style (Fortey 1990; Ivantsov 1990; Fortey & Owens 1999), limb morphology (Raymond 1920; Babcock 2003), preserved gut traces (Snajdr 1987; Chatterton et al. 1994; Vannier & Chen 2002; Bergström et al. 2007; Lin 2007), trace fossils (Campbell 1975; Jensen 1990; Brandt et al. 1995; Rydell et al. 2001; English & Babcock 2007) and unique exoskeletal morphology (Bergström 1972; Campbell 1975; Sloan 1992).

The general mode of feeding in trilobites appears to have involved a ventral food-groove between the limb gnathobases – passing food forward along the axis to a posteriorly-directed mouth. Some trilobites may have generated a feeding current similar to that of some modern anostracan crustaceans (Cannon 1928, 1935a) to propel food particles towards the mouth. Trilobites have been attributed to all the major guilds of vagile, benthic marine invertebrates (i.e. predator, scavenger, detritivore and filter-feeder). Spiny gnathobases, as in *Olenoides serratus* and *Naraoia compacta*, have been cited as evidence of predatory/scavenging habits, while sediment-filled guts have been interpreted as indicative of deposit feeding (Bergström et al. 2007; but see Vannier & Chen 2002; for an alternative taphonomic interpretation of sediment-filled guts). Filter-feeding has also been suggested as a life mode for some trilobites on the basis of an inferred filter-chamber (Fortey & Owens 1999) or a planktonic lifestyle (Schoenemann et al. 2008). For a review of trilobite feeding, see Fortey & Owens (1999) and Hughes (2001).
Methods

Specimens are housed at the Yale Peabody Museum (YPM) and Harvard Museum of Comparative Zoology (MCZ). Photographs were taken with a microscope-mounted digital camera or with a macro lens. SEM photography was conducted at Yale (all SEM specimens save Fig. 2J, K are gold coated). A single posterior fork from the YPM collections was transversely sectioned with one-half becoming the petrographic thin section in Figure 2A, B and the other half etched in dilute HCl and illustrated in Figures 1G and 2C–I. Petrographic thin sections were viewed under both polarized and cross-polarized light. Usage of the term ‘cuticle’ instead of ‘exoskeleton’ follows Dalingwater & Mutvei (1990).

Hypostome morphology

Isotelus

Hypostome suturally joined to anteromedial portion of the cephalic doublure; surface covered in terrace ridges with varying degrees of regular spacing. Length of hypostome roughly half of cranidium, bearing two prominent, sub-parallel posterior projections (tines), triangular in section with widest angle facing dorsally (Fig. 1). Smooth ventrally with slight raised lip near posterior tip (ventrally). Surface of hypostome with irregularly spaced, wavy terrace ridges sub-parallel to long axis of fork. Inward face of tine covered with dense, parallel terrace ridges, asymmetrical in section, roughly parallel to dorsal edge of fork-tip, ridges strongest ventrally becoming effaced dorsally; steepest edge of terrace facing towards crotch of fork; ridges in plan view with gentle curve opening antero-ventrally (Fig. 2A). Terraces on inner surface generally more asymmetrical in section than terraces elsewhere on hypostome. Terrace density decreases through ontogeny (Fig. 3), but difficult to assess at what rate further terraces are added, if at all, because of the paucity of pristine specimens. Terraces on the inner surface of the tine occasionally interfinger. Cuticle with inner terrace ridges as much as seven times thicker than cuticle elsewhere on hypostome; petrographic thin-sections (Fig. 2A, B) reveal a perpendicular microstructure manifest under cross-polarized light which matches the regularity of the terrace ridges (section perpendicular to long axis). Etched cuticle under SEM shows same perpendicular structures corresponding to terrace ridges (Fig. 2C; section perpendicular to long axis), with no similar structures visible on other
sectioned areas of hypostome. Perpendicular features are not manifest on the innermost layer of cuticle – it most likely represents the endocuticle. Microstructure (Fig. 2E, F) appears to represent the central laminate zone of Dalingwater & Mutvei (1990).

**Hypodicranotus**

Differs from *Isotelus* with a hypostome equipped with two long, posteriorly-directed projections nearly equal to thoracic length, sub-parallel terrace ridges run length of tines ventrally with the steep side facing away from midline, deep terrace ridge at inner edge of tine creating a marginal border-like structure on the ventral surface; medial body of hypostome slightly raised and faintly bilobed ventrally. Posterior tips of tines pointed and flattened dorso-ventrally, weak keel runs length of tines medially on dorsal surface with no other ornamentation (Fig. 4). When viewed laterally, tines curve slightly dorsally. Cuticle on fork not thickened (Fig. 4G, H), roughly uniform thickness around the circumference of each tine.

---

*Fig. 2. Images (A–I) are from YPM 37253. A, B, petrographic thin section of an *Isotelus* sp. hypostomal fork tine perpendicular to the long axis, in the medio-ventral corner of the fork tine. Images show plain and polarized light. Section made from specimen in Fig. 1G. Images are approximately 4-mm across. C, etched section of thickened inner surface of hypostomal fork tine, scale is 1 mm (see Fig. 1G). Note terrace ridges on left side. D, close up of etched terraces perpendicular to the cuticle’s edge in C, scale is 200 µm. E, magnified image of etched terrace ridge cuticle, scale is 50 µm. F, magnified image of etched cuticle on the thickened inner surface of hypostomal fork tine cut perpendicular to the tine’s longest axis, scale is 20 µm. G, SEM images of transition from thick to thin cuticle, scale is 500 µm. H, image of etched cuticle from thin wall of hypostome, scale is 100 µm. I, SEM image of transition from thick to thin cuticle, scale is 500 µm. J, SEM image of right fork tine, inner surface terrace ridges, anterior to right, scale is 1 mm. K, magnified view of terraces in J, scale is 200 µm. Images (L–O) are from YPM 510851. L, close up of terrace ridges on the inner surface of the immature *Isotelus* sp. hypostome. Anterior is up. Image is approximately 28-µm across. M, magnified surface of left fork tine of immature hypostome (N). Image is approximately 490-µm across. N, dorsal view of immature *Isotelus* sp. hypostome from the Walcott Rust Quarry, NY, scale bar 500 µm. O, close up of terrace ridges on the inner surface of the immature *Isotelus* sp. hypostome (N). Anterior is to the upper right corner. Image is approximately 54-µm across.*
The parallel nature of the ridges on the inner surface of the repose, coupled with the facing direction of the ridge terraces that oppose posterior movement in the food groove, also support a grinding function. The orientation of the microstructure perpendicular to the surface may have strengthened it to lateral forces. Several aquatic crustaceans have mandibles with superficially similar surfaces that they use for grinding food (Ocioszyńska-Bankierowa 1933, 1936; Mahoon 1960; Tyson & Sullivan 1981; Mura 1995, 1996). The size of the terraces on a grinding surface bear a relationship with the size of the objects to be ground – the objects must be larger than the height of the terrace, otherwise they will clog the surface (this is the same relationship discussed by Savazzi et al. 1982, between sediment size and the terrace ridge/sediment ratchet function). This also makes filter-feeding unlikely – food filtered out of the water column or suspended sediment will generally be soft and not require grinding. Furthermore, soft food pushed against a rigid grinding surface will clog the surface by filling in the troughs. The density of the terraces decreases with body size, suggesting that food size increased with body size.

Grinding surfaces require a force to act against them, presumably supplied by the limbs. This could have occurred in several ways: an enlarged, specialized coxa or an anterior limb with a modified orientation. The few examples of asaphid trilobites known with limbs are too poorly preserved to reveal cephalic limb differentiation (Woodward 1870; Walcott 1884; English & Babcock 2007); the presence of a forked hypostome with a grinding surface, however, suggests that these limbs may have been specialized in order to operate against the grinding surface. If such a limb was attached near the base of the fork, motion in a posterior arc (pivoting at the coxal joint posteriorly from a sub-vertical orientation to horizontal) would directly oppose the terrace ridges. If this hypothesis is true, it would be the first example of trilobite cephalic limb differentiation to be discovered. Furthermore, it would be the only known example of limb motion directly opposing the exoskeleton (rather than another limb) in an arthropod.

Asaphid trilobites may have sought out small, lightly cuticularized animals (live or dead) from the sediment-water interface. The large, broad exoskeleton of the trilobite blocked escape upward as the many legs

**Functional interpretation**

This distinctive *Isotelus*-type hypostome is present in many of the Asaphidae (Fortey & Chatterton 1988; Ivantsov 1990, 2002; Krueger 2003), although dying out with them at the end of the Ordovician. The size and shape of the hypostome would have made it difficult to position and handle large items of food – particularly struggling prey items, or scavenging on large carcasses. The buttressing of the hypostome to the anterior margin in asaphids implies a need for strength (Fortey 1990), as do the preferentially thickened inner surfaces of the tines. The long series of homonymous limbs in trilobites suggests a coxal food processing mechanism shared by disparate groups of modern arthropods (limulids, branchiopods, etc.) and many early fossil arthropods. The two modern analogues notably do not rely on their vision for locating their food – suggesting by analogy that food detection in asaphids must have been mainly chemosensory or tactile.

The closely-spaced terrace ridges on the inner surface of the repose, coupled with the facing direction of the ridge terraces that oppose posterior movement in the food groove, also support a grinding function. The orientation of the microstructure perpendicular to the surface may have strengthened it to lateral forces. Several aquatic crustaceans have mandibles with superficially similar surfaces that they use for grinding food (Ocioszyńska-Bankierowa 1933, 1936; Mahoon 1960; Tyson & Sullivan 1981; Mura 1995, 1996). The size of the terraces on a grinding surface bear a relationship with the size of the objects to be ground – the objects must be larger than the height of the terrace, otherwise they will clog the surface (this is the same relationship discussed by Savazzi et al. 1982, between sediment size and the terrace ridge/sediment ratchet function). This also makes filter-feeding unlikely – food filtered out of the water column or suspended sediment will generally be soft and not require grinding. Furthermore, soft food pushed against a rigid grinding surface will clog the surface by filling in the troughs. The density of the terraces decreases with body size, suggesting that food size increased with body size.

Grinding surfaces require a force to act against them, presumably supplied by the limbs. This could have occurred in several ways: an enlarged, specialized coxa or an anterior limb with a modified orientation. The few examples of asaphid trilobites known with limbs are too poorly preserved to reveal cephalic limb differentiation (Woodward 1870; Walcott 1884; English & Babcock 2007); the presence of a forked hypostome with a grinding surface, however, suggests that these limbs may have been specialized in order to operate against the grinding surface. If such a limb was attached near the base of the fork, motion in a posterior arc (pivoting at the coxal joint posteriorly from a sub-vertical orientation to horizontal) would directly oppose the terrace ridges. If this hypothesis is true, it would be the first example of trilobite cephalic limb differentiation to be discovered. Furthermore, it would be the only known example of limb motion directly opposing the exoskeleton (rather than another limb) in an arthropod.

Asaphid trilobites may have sought out small, lightly cuticularized animals (live or dead) from the sediment-water interface. The large, broad exoskeleton of the trilobite blocked escape upward as the many legs

![Graph of terrace ridges density on the hypostomal inner surface](image)
searched for food via tactile or chemical sensation. Once located, the food was propelled anteriorly by the coxae, and the cuticle was broken against the hypostome before consumption. Such a scenario is more likely than macropredatory (i.e. feeding on large prey items like other trilobites) or filter-feeding ecologies. If this hypothesis is true, one would expect to find wear patterns on the inner surface of the hypostome. However, the identification of wear-patterns on fossil hypostomes is complicated – to do so, one needs to rule out the effects of mechanical preparation and molt stage. Unambiguous wear patterns were not observed on the specimens examined during this study.

_Hypodicranotus_ does not possess any of the specialized hypostome features observed in _Isotelus_. Its long hypostome would have made feeding on large food items difficult, as in _Isotelus_, but it does not show any adaptations for grinding. Shorter forked morphologies may have played a role in food/prey positioning, restraint (Fortey & Owens 1999) or bracing (perhaps analogous to the chilaria of living xiphosurans, see Manton 1964), but the elongated tines of _Hypodicranotus_ appear too long for such a function. Food processing seems to have been accomplished solely by the limbs without hypostomal involvement. The tines of the fork would have approximately lain beneath the coxae. If the viscera and limbs took up enough space such that the coxae directly abutted the dorsal surface of the tines, then the elongated hypostomal forks may have actually functioned as a boundary between the coxae and the distal portions of the limbs. This would have prevented the distal portions of the limbs from easily passing food to the food groove and may have restricted the distal portions of the limbs to a locomotory role (as reaching ventrally around the tines would have been difficult). This would seemingly preclude any sort of filter-feeding. If, however, the viscera and limbs did not fill all of the space between the hypostome and the thorax, the distal portions of the limbs could have been directly involved in feeding (by reaching above the hypostomal tines).

The hypostome in _Hypodicranotus_ may not have played any role in feeding – instead it may have served to protect the animals’ ventral side while still allowing access to the ventral food groove. But, this protection would have come at the cost of the ability to enroll (Whittington 1952), something that asaphid trilobites, despite their forked hypostomes, could do. Sacrificing

---

**Fig. 4.** _Hypodicranotus striatulus_, scale bar in lower left (1 cm) applies to all images save (G–H). A, D–E, lectotype MCZ 1616, dorsal (A), left oblique (D), and anterior views (E). B, left oblique view of paratype MCZ 1618 showing _in situ_ hypostome. C, F, dorsal and posterior views of hypostome MCZ 1617. G–H, anterior and posterior ground sections of a _Hypodicranotus striatulus_ hypostome YPM 510850, scale bar is 5 mm.
the ability to enroll suggests that the long fork was very important. Further evaluation of its autecology must await the discovery of specimens with preserved appendages.

Discussion

The function of the *Isotelus*-type forked morphology has been considered by several workers (Ivantsov 1990; Sloan 1992; Brandt et al. 1995; Fortey & Owens 1999; Babcock 2003). Brandt et al. (1995) documented putative *Isotelus* trace fossils juxtaposed with worm burrows and interpreted the association as evidence of predation. Yet, this example lacks any evidence of a struggle – either the trilobite changing its body position to facilitate the kill or the worm attempting to escape (Neto de Carvalho 2006). Furthermore, the timing of the traces may be very different (see Rydell et al. 2001) with the worm deforming the trilobite trace long after it had been made.

Sloan (1992) suggested that the edges of the hypostomal forks acted as cutting edges. Babcock (2003) and English & Babcock (2007) expanded this *Isotelus*-qua-predator idea further, working from observations made on a specimen of *Isotelus maximus* originally described by Mickleborough (1883; see also Walcott 1884). Babcock (2003) described ‘...the bases of rather robust spines...’ (p. 77) which he speculated were used in capturing and manipulating prey. He also noted that the inner blade of the hypostome is ‘sharp’ and the edge is ‘serrated’ (p. 80), which together with a gut tract devoid of mud or shell debris, he interpreted as evidence of non-duprophagous predatory habits. However, when considered as a three-dimensional object, the hypostome would be a poor facsimile for a serrated knife (Fig. 1). The presence of robust limb spines in also in doubt. Mickleborough’s (1883) specimen is preserved like the trilobites from the Walcott-Rust Quarry (Brett et al. 1999) as a calcite spar filled cast of the animal. The bases of broken spines should, therefore, appear as circles of spar on the limbs set apart from the brown matrix – no such structures are present, implying that the features described by Babcock and English as spine bases are bits of matrix on the limbs.

Fortey (1990) had previously characterized the inner hypostomal surface as ‘rasp-like,’ and suggested that it may have functioned in concert with the limbs to aid in the shredding of food. He supported this observation with the fact that the hypostome is strongly braced to the anterior margin of the cranidium (implying a passive rather than active function for the hypostome). Fortey & Owens (1999) hypothesized that longer tines may have helped prevent prey escape. Ivantsov (1990) noted the rasp-like surface and thicker inner hypostomal wall – hypothesizing that the *Isotelus*-type hypostome functioned as an immobile grater for larger food particles.

An alternative role for terrace ridges is as a burrowing sculpture. The function of terrace ridges (as sediment ratches) has been explored by several authors in several situations (Schmalfuss 1978a,b, 1981; Savazzi 1981, 1982, 1991; Savazzi et al. 1982). In burrowing, the terraces seem to function as a ‘sediment ratchet,’ providing purchase in the sediment to aid movement in the direction of burrowing. The terrace ridges on the inner surface of the hypostome are difficult to picture playing any role in burrowing. Terrace ratcheting is advantageous when the motion is perpendicular to the terrace.

A number of workers have conducted detailed functional studies on a variety of arthropods that feed with a ventral ‘food groove’ (Cannon & Manton 1927; Cannon 1927, 1928, 1932, 1935a,b; Cannon & Leak 1932; Fryer 1962, 1966, 1988; Manton 1964; Attramadal 1981; Waloszek et al. 2007). These arthropods (e.g. *Chirocephalus*, *Limulus*, *Triops*, etc.) likely provide the closest analogues for how trilobites may have fed. However, considering the known limb morphology of trilobites, they differ in several important ways. First, modern arthropods have a highly differentiated set of head appendages (Manton 1977; Schram 1986), something that trilobites lack. Furthermore, not all arthropods with apparent ventral ‘food grooves’ fed by moving food anteriorly within the food groove (Cannon 1927; Attramadal 1981) – the mere presence of a ‘food groove’ does not necessarily indicate the mode of feeding. The feeding mode of certain filter-feeding crustaceans, like the branchiopod anostracan, *Chirocephalus diaphanus* (see Cannon 1935a), may be applicable to certain trilobites (inferred ‘pelagic’ or nektic trilobites, see Fortey 1985), but are inapplicable to the known range of trilobite limb morphology.

Two groups of modern arthropods may serve as living models for aspects of trilobite feeding: horseshoe crabs (i.e. *Limulus*) and branchiopods. Horseshoe crabs (*Limulidae: Chelicera*), like trilobites, have a posteriorly-directed mouth and spiny gnathobases on their walking limbs which are used to shred food. However, horseshoe crabs only have five walking limbs, half the number possessed by most trilobites (between ~10 and 25 for most species). Food is located and manipulated into position by the chelicera and then the animal sits atop its food and either shreds and chews it with the gnathobases or subjects it to the ‘nut-cracking apparatus’ (chilaria) at the sixth coxae (Manton 1964). The gnathobases of the five walking limbs make for an effective ‘conveyor belt’ that shreds food on its way to the mouth.
Branchiopod crustaceans, in contrast, have a much longer series of homonomous thoracic limbs creating a ventral ‘food groove’. The branchiopod notostracan *Triops* envelops its prey or food with its anterior limbs, tearing at the prey with its thoracic limb spines (Fryer 1988) – similar to feeding in *Limulus*. Suitably sized particles are then moved dorsally into the food groove and conveyed towards the mouth. The operation of the thoracic limbs in notostracans resembles the operation of the walking limbs of xiphosurans; but notostracans are distinguished by the presence of crushing mandibles and two pairs of maxillae. The mandibles and maxillae are incorporated into an external throat-like chamber called the atrium oris. The atrium oris is immediately posterior to the rear-facing mouth, where the mandibles process food. It essentially envelopes the mandibles between the body wall (dorsally), labrum (ventrally) and paragnaths (two triangular fleshy sternal outgrowths positioned opposite the posterior edge of the labrum). The maxillae serve to force food into the atrium oris.

The closest analog in modern arthropods to the hypostome is the labrum. However, following Walossek & Müller (1990); see also Walossek 1993), it is regarded as a positional analogy only. Walossek & Müller (1990) define the crustacean labrum as ‘...a complex organ with sensorial and glandular functions...’ (p. 416). It forms the ‘floor’ of the atrium oris. In contrast, the trilobite hypostome is a skeletal element of the ‘forehead’ (Müller & Walossek 1987) as the mouth is thought to have been positioned immediately posterior to the hypostome rather than underneath.

As an exoskeletal element, it is hard to imagine the hypostome possessing the range of sensory/glandular functions of the crustacean labrum (although these functions could have been performed by tissue immediately adjacent to the hypostome). However, the morphology of certain trilobite hypostomes suggests that they may have possessed an atrium oris. Well-preserved, silicified trilobite hypostomes of certain odontopleurids (Chatterton & Ludvigsen 1976; Chatterton & Perry 1983; Chatterton et al. 1997), lichids (Chatterton & Ludvigsen 1976; Chatterton et al. 1979), calymenids (Chatterton et al. 1990), cheirurids (Chatterton & Ludvigsen 1976) and encrinurids (Edgecombe et al. 1998), for example all have a significant dorsal doublure on the posterior margin of the hypostome. This may indicate that soft tissue attached to the hypostome significantly in front of the hypostomes’ posterior margin. Some lichids had small recesses in the dorsal doublure of their hypostome, suggesting an as-yet unknown function (Chatterton & Ludvigsen 1976; fig. 19.19). Likewise, the hypostome of some odontopleurids (Chatterton & Perry 1983; fig. 23.12) phacopids (Bruton & Haas 1997, 2003), and dalmanitids (Budil et al. 2008) had a tuberculate/denticulate region medially on the posterior margin of their hypostome – possibly used in food manipulation (i.e. shredding or grinding). Budil et al. (2008) broadly compared the denticulate posterior margin in dalmanitids to the forked margin in asaphids, and suggested a possible common function (i.e. food manipulation) supported by their proximity to the food groove.

Doublures present elsewhere on trilobites suggest: (1) that they were exposed like the dorsal exoskeleton as is suggested by the presence of terrace ridges; and (2) that they sheltered soft-tissue attachment sites. Therefore, by analogy, the hypostome overhung the mouth with the dorsal doublure exposed. The function of this sclerotized lower lip would have been different than that of the flexible, fleshy labrum in living crustaceans, but both would create sheltered spaces in which to process food. Additionally, it is possible that the mouth was situated much farther anteriorly underneath the hypostome, and that the hypostome was only covered dorsally by tissue creating a ‘labrum-like’ structure with a hard ventral surface and a soft dorsal surface – a ‘floor’ to the atrium oris. Functionally, this would be like a modern crustacean labrum with a sclerotized outer surface. However, known mouths in both *Agnostus pisiformis* (Walossek 1993) and the stem crustacean *Oelandocaris oelandica* (Stein et al. 2005) emerge at the posterior margin of the hypostome/labrum.

The position of the mouth notwithstanding, the hypostome of *Isotelus* bears an uncanny resemblance to a grinding surface. This level of hypostome differentiation is otherwise unknown in trilobites, and would hint at a hitherto undocumented level of cephalic limb specialization. However, this line of reasoning cannot be extended to all forked hypostomes; nothing about the long-forked hypostome of *Hypodictyonatus* suggests that it possessed differentiated cephalic limbs. A detailed examination of other distinctive hypostomes may yield further insights into trilobite ecology.


References


Cannon, H.G. 1935b: Function of the labral glands in Chiroteu-

Cannon, H.G. 1927: On the feeding mechanism of the Branchio-


Cannon, H.G. 1935b: Function of the labral glands in Chiroteu-


Ivantsov, A.Y. 1990: Relationship between hypostome morphology and method of feeding of Asaphus trilobites. Trudy Instituta geologii i Geofiziki 764, 128–130. [In Russian].

Ivantsov, A.Y. 2002: Ordovician trilobites of the Subfamily Asaphi-
ne of the Ladoga Glint. Palaeontological Journal, 37(Suppl. 3), S229–S337.


Lin, J.-P. 2007: Preservation of the gastrointestinal system in Oleno-
ides (Trilobita) from the Kaili Biota (Cambrian) of Guizhou, China. Memoirs of the Association of Australasian Palaeontologists 33, 179–189.


