



Head segmentation of trilobites

TAE-YOON S. PARK AND JI-HOON KIHM

LETHAIA



Park, T.-Y.S. & Kihm, J.-H. 2017: Head segmentation of trilobites. *Lethaia*, Vol. 50, pp. 1–6.

Although trilobites have provided research subjects for more than two centuries, their head segmentation has remained unresolved. Four glabella furrows (SO and S1–S3) marking the segmental boundaries are generally present in the cephalic axis, but there are trilobites with one more pair of furrows, the so-called S4, in the cephalic axis, causing confusion in understanding trilobite head segmentation. Recent advances in developmental biology and palaeontology have shed light on the arthropod head problem, and thus, trilobite head segmentation can be reviewed in the light of this knowledge. Based on the information from the anatomy of exceptionally preserved trilobites and arthropods closely related to trilobites, it is inferred that trilobite head contains five segments: the anteriormost ocular segment potentially associated with the hypostome, the antennal segment and the following three segments with walking legs. When present, the S4 furrows are situated where the eye ridges meet the cephalic axis of trilobites, indicating that the furrows are incised ‘within’ the anteriormost segment in trilobites with an anteriorly enlarged frontal lobe. Trilobites of the Order Redlichiida, the most primitive stock, show variable conditions in the frontal glabella conditions, while in other more derived groups, the condition is rather constant. The frontal glabella condition, therefore, could provide a clue to elucidate the unresolved Cambrian trilobite phylogeny and the Cambrian roots of the post-Cambrian trilobites.

Trilobites are known as the most diverse and best represented group among the extinct Palaeozoic arthropods, due mainly to the biomineralized dorsal exoskeleton. Almost 20,000 species are known, spanning the early Cambrian to the Permian. The systematic position of trilobites within the arthropod phylogeny has varied from placements as stem euarthropods, stem chelicerates or stem mandibulates (Scholtz & Edgecombe 2005; Budd & Telford 2009; Legg & Vannier 2013). The trilobite dorsal exoskeleton is characterized by a wide cephalon comprising a glabella (including the occipital ring), genal fields, genal spines, borders, eye lobes and eye ridges. Despite the long history of trilobite research over two centuries, the number of segments in the trilobite cephalon has long been a matter of debate (e.g. Størmer 1942; Hupé 1951; Palmer 1957; Bergstöm 1973; Whittington 1997). Scholtz & Edgecombe (2005, 2006) presented a five-segment model for the trilobite head, which fits well with the five axial lobes of trilobite cephalon, defined by four pairs of glabella furrows (SO–S3). However, there are many trilobites with seemingly one more pair of glabella furrows (S4), which causes confusion in understanding the head segmentation of trilobites.

Arthropod head segmentation has been a subject of debate for more than a century. The loss or severe modification of appendages and reorganization of segments have hampered the correct recognition of composition of the arthropod head (Rempel 1975; Scholtz 1997; Richter *et al.* 2013). Debates on the presence of the anteriormost segmental entity of extant arthropods and the head segmentations of many Cambrian arthropods with the so-called great appendages have persisted (Budd 2002; Scholtz & Edgecombe 2006; Edgecombe & Legg 2014). However, recent discoveries of the nervous system in the stem-group and crown-group arthropods have begun to cast a light on the nature of the great appendage problems and the anteriormost segmental entity (Ma *et al.* 2012; Tanaka *et al.* 2013; Cong *et al.* 2014). Therefore, with the current advance of knowledge on the arthropod head

segmentation, it is now possible to reappraise the trilobite head segmentation in detail.

This study not only re-evaluates the segment composition in the axis of the trilobite cephalon, but also provides a model of the segmental nature of the frontal part of the trilobite axis. Because the frontal part of the trilobite axis is one of the most conserved structures in terms of trilobite ontogeny and phylogeny, differences in the shape of the anteriormost part may provide characters which could provide a clue to elucidate the poorly resolved Cambrian trilobite phylogeny. Further data and illustrations (Figs S1–S4) are provided in the Supporting Information.

Previous research on trilobite head segmentation

Head segment composition of trilobites is known to have been fixed early in ontogeny, as in other arthropods (Hughes 2003). Most debate has originated from the segmental entities in the frontal part of cephalon. Størmer (1942, fig. 14) and Bergstöm (1973, fig. 5) suggested a model in which the posterior part of the frontal glabella lobe represents the antennal segment; Størmer (1942) allocated the rest of the anterior part the ‘pre-antennal segment’, while Bergstöm (1973) assumed the presence of the acron in front of the pre-antennal segment. Hupé (1951) inferred the presence of two segments before the pre-antennal segment, concluding that there are at least eight segments in trilobite cephalon. Palmer (1957) supported Hupé’s (1951) interpretation that the olenellid cephalon is composed of eight segments. Interestingly, most of these early models were suggested on the basis of the cephalon of an olenellid trilobite with an extraordinarily large frontal glabella lobe, assuming that such forms

represented the most primitive condition of trilobites. However, with the current knowledge, the most primitive group of trilobites is the fallotapidiids (Palmer & Repina 1993; Jell 2003), which did not possess a large frontal lobe, and thus, the large frontal lobes of some olenellids were derived features. In contrast, Scholtz & Edgecombe (2005) suggested a five-segment model for the trilobite cephalon, based on trilobites with appendages preserved and their phylogenetic context; the conservative number of glabellar furrows (SO–S3) across the Trilobita was regarded as consistent with the fixed number of cephalic appendages.

Labrum and trilobite hypostome

The labrum is a lobe-like structure lying in front of arthropod mouth. Embryological research on panarthropods has revealed that the early anlage of the labrum is bilobed, which is consistent with an appendage-derived nature of the structure (Thomas & Telford 1999; Eriksson *et al.* 2003; Browne *et al.* 2005). The bilobed anlage fuses during the development to form the mature morphology of the labrum (Kimm & Prpic 2006). The recognition of the pre-protocerebral frontal appendage in an anomalocaridid, which is a stem-group euarthropod, was interpreted in the context of homology between the pre-protocerebral appendage and labrum (Cong *et al.* 2014), which is in line with the paleontological (Budd 2002; Budd & Telford 2009) and developmental (Thomas & Telford 1999; Eriksson *et al.* 2003; Browne *et al.* 2005) perspectives.

The hypostome is a sclerotized ventral plate in front of the mouth, usually present in primitive arthropods including trilobites. The trilobite hypostome is unique in that it is a calcified exoskeletal plate. It was situated below the anterior portion of the glabella, showing various morphologies (Fortey 1990; Fortey & Owens 1999) not seen in any other arthropod group. These structures were used to aid not only feeding, but also enrolment and swimming (Fortey & Owens 1999; Lerosey-Aubril & Feist 2006; Hegna 2010; Shiino *et al.* 2012). The calcified nature of the trilobite hypostome likely enabled the versatile evolution of this structure into something more than just a feeding structure.

There have been various interpretations on the origin of the hypostome, from a composite of several segments to a structure that arose by the posterior deflection of the mouth (Dewel *et al.* 1999), or the sternite of the antennular segment (Waloszek *et al.* 2007). However, given the overall morphology and the position in front of the mouth, hypostomes are often regarded as homologous to the labrum (Bitsch & Bitsch 2010). The trilobite hypostomes have often been compared to and considered homologous to the labrum of crustaceans (Eldredge 1971; Fortey 1990; Eriksson & Terfelt 2012), or the exoskeletal cover of the labrum (Bergstöm 1973). In particular, anatomical features of the digestive structures, glands and connective strands harboured in a juvenile trilobite hypostome from Swedish 'Orsten' fauna suggest that the trilobite hypostome is functionally analogous to the labrum of euarthropods (Eriksson & Terfelt 2012).

Segmentation in the cephalic axis

One pair of antennae and three pairs of post-antennular walking legs have been observed in exceptionally preserved trilobite specimens (Cisne 1975; Whittington 1997; Bruton & Haas 2003), as in many 'artiopodans' (Whittington 1985; Stein *et al.* 2013). The four post-ocular segments can also be inferred from the presence of four pairs of midgut diverticula (Stein *et al.* 2013), and trilobites are also known to have four pairs of gut diverticula (Lerosey-Aubril *et al.* 2011), corresponding to the four appendage-bearing segments of the cephalon. Therefore, it can be inferred that the trilobite cephalon consists of five segments, as suggested by Scholtz & Edgecombe (2005): the ocular segment with hypostome, the antennal segment and the following three segments with walking legs (Figs 1, S1). The positions of the gut diverticula and walking legs might be under the segmental boundary of

tergites rather than being directly under the tergites, due to segmental mismatch between tergites and sternites (Edgecombe & Ramsköld 1999; Ortega-Hernández & Brena 2012). This mismatch might be the reason for the claims that some trilobites had four pairs of walking legs under the cephalon. It should be noted that this study focuses on the segment composition only in the axial part of the trilobite cephalon, because how each segment contributes to the other parts of the cephalon (such as the genal field) is more speculative.

First and anteriormost segment

The first segment of the arthropod head includes the first neuromere of the brain, the protocerebrum, which is connected to the optic nerves. In many trilobites, the optic organs (visual surface and palpebral lobe) are connected to the frontal part of the glabella by eye ridges. This is the basis for our recognizing the frontal part of the glabella as the first and anteriormost segment in the trilobite head. This segment is termed the frontal glabellar lobe (LA or L4). The boundary between the first and second segments is marked by the S3 glabellar furrows. If the arthropod labrum is derived from the appendages of the anteriormost segment, the trilobite hypostome could be also regarded as placed in the first head segment. Other structures in front of the glabella, such as pre-glabellar field and anterior cranial border, do not form an independent segmental entity; they are apparently simple outgrowths of the first segmental tergite.

Second segment

The second head segment of the arthropod head contains the second neuromere of the brain, the deutocerebrum. In the trilobite axis, the second segment is represented by the L3 glabellar lobe. The appendages of the second head segment are chelicerate in the Chelicerata (see Brenneis *et al.* 2008 and references therein). In the Mandibulata including crustaceans, hexapods and myriapods, the appendage of the second segment forms an olfactory sensory structure, the antennae. In some trilobite literature, the uniramous antennae were presumed to have been attached to the segment before the L3 glabellar lobe (e.g. Størmer 1942; Hupé 1951; Bergstöm 1973). The fossula, a small depression at or near the anterolateral edge of the glabella, was often considered as a structure for antennal attachment; this depression has been even called an antennary pit or antennular pit. However, it is now known that the trilobite antenna is attached behind the anterior wing of the hypostome, being accommodated by a groove at the lateral side of the hypostome (Whittington 1997; Scholtz & Edgecombe 2005), which means the antenna can be interpreted as derived from the second segment. The soft part-preserved specimen of *Triarthrus* clearly shows that the antennae are attached to the segment behind the first segment (Figs 1, S1).

Third segment

The third neuromere of the brain, the tritocerebrum, represents the position of the third head segment of arthropods. This segment is represented by the L2 glabellar lobe in the trilobite axis. The appendages of third head segment are second antennae in crustaceans, and pedipalps in chelicerates, while this segment is intercalary in myriapods and insects. In trilobites, the appendages of this segment were the first pair of biramous walking legs.

Fourth segment

The fourth head segment corresponds to the L1 glabellar lobe in the trilobite axis. The appendages of fourth head segment were modified into strong mandibles in mandibulates, but they form simple walking legs in chelicerates. In trilobites, they were the second pair of walking legs. In some well-preserved pyritized specimens of

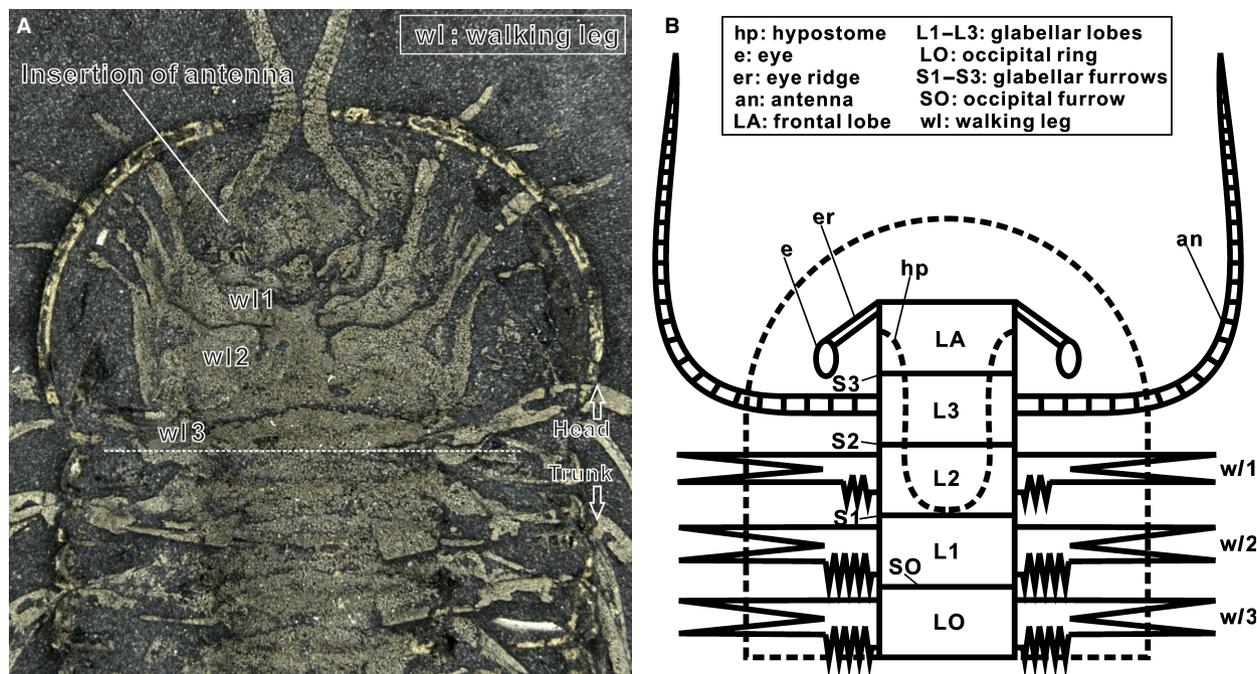


Fig. 1. A, ventral view of a pyritized *Triarthrus eatoni* with antennae and walking legs preserved; KOPRIF40001, $\times 7.4$, collected from the Martin Quarry (see Farrell *et al.* 2009 for locality details), housed in Korea Polar Research Institute. B, diagram summarizing the segmental composition of the trilobite cephalic axis.

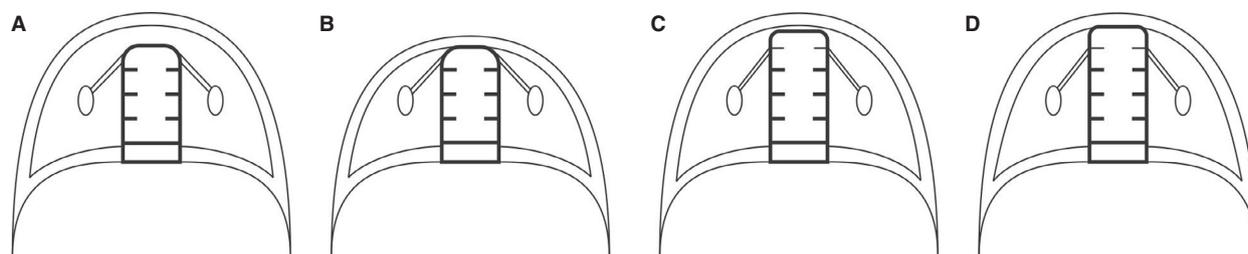


Fig. 2. Four different conditions for the trilobite cephalic front. A, pre-glabella field present without enlarged frontal glabella. B, pre-glabella field absent without enlarged glabella front. C, pre-glabella field present with enlarged glabella front. D, pre-glabella field absent with enlarged glabella front.

Triarthrus, the gnathobasic coxa of this pair of legs are larger than those of other walking legs (Fig. S1A). The posterior boundary of this segment is marked by the occipital furrow (SO).

Fifth segment

The fifth head segment forms the occipital ring in the trilobite axis. The most posterior diverticular pair in *Arthroaspis bergstroemi*, an arthropodan closely related to trilobites, is in the occipital ring, indicating that the occipital segment is the dorsal expression of the last cephalic segment (Stein *et al.* 2013). The appendages of the fifth head segment are the first maxillae in mandibulates and walking legs in chelicerates. In trilobites, the third pair of walking legs is connected to the fifth head segment.

Nature of S4 glabellar furrows and the frontal cephalic condition

Trilobites usually have four pairs of furrows in the cephalic axis (SO–S3), which correspond to the segmental boundaries of five

cephalic segments. But the ‘fifth pair’, the so-called S4, is known in many trilobites (Sundberg 1995). Despite the morphological similarity, the serial homology of S4 to the other pairs of furrows has been considered uncertain (Hughes 2003). The so-called S4 furrows are almost invariably situated near the point where the eye ridges meet glabella, but in some trilobites including the most primitive stock, the eye ridges end at the anterolateral corner of glabella. This indicates that the presence of the portion in front of S4 was a result of anterior enlargement of the frontal glabella. The shape of the cephalic frontal part shows great variation because this was the site of ingestion and processing of food for trilobites, which had various modes of feeding (Fortey & Owens 1999). The anterior enlargement of the frontal part of the glabella, therefore, may be related to changes in feeding strategy during evolution. The S4 furrows are shown in some, if not all, trilobites with an anteriorly enlarged frontal glabella. Because the S4 appears ‘within’ the frontal glabella, it has nothing to do with a segmental boundary. Interestingly, the presence of the anteriorly enlarged frontal lobe seems defined early in ontogeny. Protaspides of species with the anteriorly enlarged frontal lobe had the eye ridge meeting slightly posterior to the anterolateral corner of the glabella (Fig. S2A, B), whereas, in those without the structure, the eye ridge of protaspides meets at

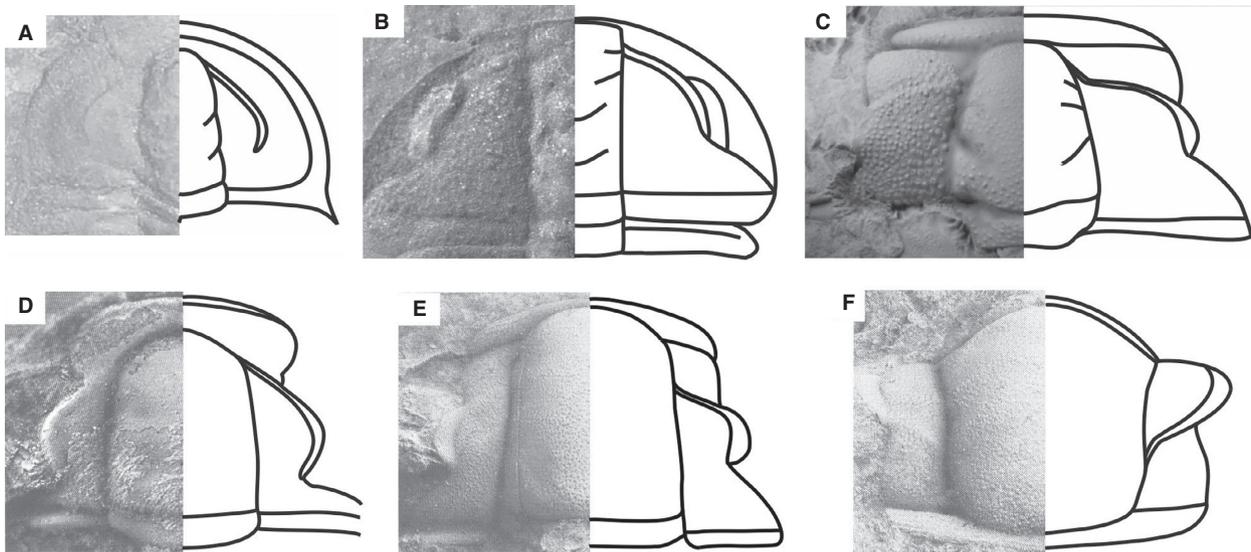


Fig. 3. Frontal cephalic conditions of several trilobites. A, *Buennellus higginsi* (Order Redlichiiida) from the Cambrian Series 2 of North Greenland, housed in Natural History Museum of Denmark, SP-2011-0018.A. B, *Arthricocephalus chauveaui* (Order Corynexochiida) from the Cambrian Series 2 of South China, housed in Nanjing Institute of Geology and Palaeontology; image courtesy of Tao Dai. C, *Damesella paronai* (Order Uncertain) from the Cambrian Series 3 of North China, housed in Korea Polar Research Institute, KOPRIF 3001. D, *Peltabellia glabra* (Order Proetida) from the Lower Ordovician of Spitsbergen, housed in the Geological Museum, Oslo, PMO 223.136. E, F, *Leioestegium spongiosum* (Order Corynexochiida) from the Lower Ordovician of Spitsbergen, housed in the Geological Museum, Oslo, PMO 208.178. D–F are re-illustrated from Fortey & Bruton (2013).

the anterolateral corner of the glabella (Fig. S2C–D). With development, a pre-glabella field may appear in front of glabella in some trilobites such as ptychoparioids. Together with the presence of a pre-glabella field, there could be four different conditions in the frontal part of the cephalon: (1) a pre-glabella field without enlarged frontal glabella lobe (Fig. 2A); (2) no pre-glabella field without enlarged frontal glabella lobe (Fig. 2B); (3) a pre-glabella field with enlarged frontal glabella lobe (sometimes S4 present) (Fig. 2C); and (4) no pre-glabella field with enlarged frontal glabella lobe (sometimes S4 present) (Fig. 2D). The anteriorly rounded glabella front in some trilobites (e.g. Figs S2D, S3C) is not regarded as having the enlarged frontal glabella lobe, unless S4 furrows are present. This frontal cephalic condition was variable within the most primitive trilobite group, the Order Redlichiiida. Members of the oldest trilobite family, the Fallotaspididae, show the plesiomorphic condition: the palpebral ridges meet the anterolateral corner of the glabella with or without pre-glabella field (Figs 3A, S3A). Those of the Olenelloidea had a rather massively enlarged frontal lobe with or without a pre-glabella field (Fig. S3B). Members of the Redlichiiina, the oldest trilobites with facial sutures, show all four conditions (Figs S2B, S3C–F, S4A–C). On the contrary, the frontal cephalic condition tended to remain rather constant in less primitive trilobite groups. Members of the Order Corynexochiida almost invariably did not have a pre-glabella field, but had an enlarged glabella frontal lobe (Fig. 3B, E). Interestingly, members of the Cambrian family Damesellidae had no pre-glabella field, and their frontal glabella lobes are not enlarged (Fig. 3C). In this regard, the four different conditions may provide a useful character for elucidating Cambrian trilobite phylogeny, which has remained unresolved. For instance, the species of the genus *Protaitzehoia* Yang in Yin & Li 1978; lack a pre-glabella field and have clearly defined S4 glabella furrows. It can be inferred that this genus has been mistakenly included in the family Damesellidae and would be better assigned to the Order Corynexochiida. The Order Ptychopariida is known as the most problematic taxonomic group. It is, at least, paraphyletic and always associated with major problems of trilobite phylogeny and classification (Fortey 2001). While many of ‘ptychoparioids’ did not possess an anteriorly enlarged frontal lobe (Fig. S3G), some others apparently did.

For instance, S4 glabella furrows are clearly visible in the middle Cambrian ‘ptychoparioid’ *Ruichengocephalus* (see Yuan *et al.* 2012, pl. 4, figs 15, 16, 18). This may indicate that the ‘ptychoparioids’ with the S4 glabella furrows (or an enlarged frontal glabella lobe) were phylogenetically distant from those without an enlarged glabella front. These frontal cephalic conditions can be also applied to the post-Cambrian trilobites. Given the position where the eye ridges meet the glabella, the Ordovician leioestegiids apparently possess an enlarged frontal glabella lobe (Fig. 3E, F), while lichids and odontopelurids did not (Figs S3H, S4F). Many of the Ordovician proetids possessed a pre-glabella field, but did not have an enlarged frontal glabella lobe (Fig. 3D), and this is true for the immature specimens of proetids (Fig. S4D). Therefore, reviewing these conditions can also be helpful in elucidating the Cambrian root of the post-Cambrian trilobite clades, which is one of the most intractable problems in trilobite phylogeny.

Acknowledgements. – We are grateful to Gregory Edgecombe and Nigel Hughes for constructive comments which significantly improved the manuscript. Associate Editor Alan Owen also provided helpful suggestions. Thanks are extended to Markus Martin and Tao Dai who kindly provided trilobite images and to H. Shim for line drawings. This study was supported by KOPRI fund, PE16030.

Tae-Yoon S. Park [typark@kopri.re.kr], and Ji-Hoon Kihm [jhhkim@kopri.re.kr], Division of Polar Earth-System Sciences, Korea Polar Research Institute, Incheon 406-840, Korea

References

- Bergstöm, J. 1973: Organization, life and systematics of trilobites. *Fossils and Strata* 2, 1–69.
- Bitsch, J.B. & Bitsch, C. 2010: The tritocerebrum and the clypeolabrum in mandibulate arthropods: segmental interpretations. *Acta Zoologica-Stockholm* 91, 249–266.
- Brenneis, G., Ungerer, P. & Scholtz, G. 2008: The chelifores of sea spiders (Arthropoda, Pycnogonida) are the appendages

- of the deutocerebral segment. *Evolution & Development* 10, 717–724.
- Browne, W.E., Price, A.L., Gerberding, M. & Patel, N.H. 2005: Stages of embryonic development in the amphipod crustacean, *Parhyale hawaiiensis*. *Genesis* 42, 124–149.
- Bruton, D.L. & Haas, W. 2003: Making *Phacops* come alive. *Special Papers in Palaeontology* 70, 331–347.
- Budd, G.E. 2002: Palaeontological solution to the arthropod head problem. *Nature* 417, 271–275.
- Budd, G.E. & Telford, M. 2009: The origin and evolution of arthropods. *Nature* 457, 812–817.
- Cisne, J.L. 1975: Anatomy of *Triarthrus* and the relationships of the Trilobita. *Fossils and Strata* 4, 45–63.
- Cong, P., Ma, X., Hou, X., Edgecombe, G.D. & Strausfeld, N. 2014: Brain structure resolves the segmental affinity of anomalocaridid appendages. *Nature* 513, 538–542.
- Dewel, R.A., Budd, G.E., Castano, D.F. & Dewel, W.C. 1999: The organization of the subsophageal nervous system in Tardigrades: insights into the evolution of the arthropod hypostome and tritocerebrum. *Zoologischer Anzeiger* 238, 191–203.
- Edgecombe, G.D. & Legg, D.A. 2014: Origins and early evolution of arthropods. *Palaeontology* 57, 457–468.
- Edgecombe, G.D. & Ramsköld, L. 1999: Relationships of Cambrian Arachnata and the systematic position of Trilobita. *Journal of Paleontology* 73, 263–287.
- Eldredge, N. 1971: Patterns of cephalic musculature in the Phacopina (Trilobita) and their phylogenetic significance. *Journal of Paleontology* 45, 52–67.
- Eriksson, M.E. & Terfelt, F. 2012: Exceptionally preserved Cambrian trilobite digestive system revealed in 3D by synchrotron-radiation X-ray tomographic microscopy. *PLoS ONE* 7, e35625.
- Eriksson, B.J., Tait, N.N. & Budd, G.E. 2003: Head development in the onychophoran *Euperipatoides kanangrensis* with particular reference to the central nervous system. *Journal of Morphology* 255, 1–23.
- Farrell, Ú.C., Martin, M.J., Hagadorn, J.W., Whiteley, T. & Briggs, D.E.G. 2009: Beyond Beecher's Trilobite Bed: widespread pyritization of soft tissues in the Late Ordovician Taconic foreland basin. *Geology* 37, 907–910.
- Fortey, R.A. 1990: Ontogeny, hypostome attachment and trilobite classification. *Palaeontology* 33, 529–576.
- Fortey, R.A. 2001: Trilobite systematics: the last 75 years. *Journal of Paleontology* 75, 1141–1151.
- Fortey, R.A. & Bruton, D.L. 2013: Lower Ordovician trilobites of the Kirtonryggen Formation, Spitsbergen. *Fossils and Strata* 59, 1–116.
- Fortey, R.A. & Owens, R.M. 1999: Feeding habits in trilobites. *Palaeontology* 42, 429–465.
- Hegna, T.A. 2010: The function of forks: *Isotelus*-type hypostomes and trilobite feeding. *Lethaia* 43, 411–419.
- Hughes, N.C. 2003: Trilobite tagmosis and body patterning from morphological and developmental perspectives. *Intergrative and Comparative Biology* 43, 185–206.
- Hupé, P. 1951: Sur les affinités des trilobites. *Bulletin de la Société Géologique de France (Series 6)*. 1, 469–486.
- Jell, P.A. 2003: Phylogeny of early Cambrian trilobites. *Special Papers in Palaeontology* 70, 45–57.
- Kimm, M.A. & Prpic, N.-M. 2006: Formation of the arthropod labrum by fusion of paired and rotated lim-bud-like primordial. *Zoomorphology* 125, 147–155.
- Legg, D.A. & Vannier, J. 2013: The affinities of the cosmopolitan arthropod *Isoxys* and its implications for the origin of arthropods. *Lethaia* 46, 540–550.
- Lerosey-Aubril, R. & Feist, R. 2006: Late ontogeny and hypostomal condition of a new cyrtosymboline trilobite from the Famennian of Morocco. *Palaeontology* 49, 1053–1068.
- Lerosey-Aubril, R., Hegna, T.A. & Olive, S. 2011: Inferring internal anatomy from the trilobite exoskeleton: the relationship between frontal auxiliary impressions and the digestive system. *Lethaia* 44, 166–184.
- Ma, X., Hou, X., Edgecombe, G.D. & Strausfeld, N.J. 2012: Complex brain and optic lobes in an early Cambrian arthropod. *Nature* 490, 258–261.
- Ortega-Hernández, J. & Brena, C. 2012: Ancestral patterning of tergite formation in a centipede suggests derived mode of trunk segmentation in trilobites. *PLoS ONE* 7, e26263.
- Palmer, A.R. 1957: Ontogenetic development of two olenellid trilobites. *Journal of Paleontology* 31, 105–128.
- Palmer, A.R. & Repina, L.N. 1993: Through a glass darkly: taxonomy, phylogeny, and biostratigraphy of the Olenellina. *The University of Kansas, Paleontological Contribution (new series)* 3, 1–35.
- Rempel, J.G. 1975: The evolution of the insect head: the endless dispute. *Quaestiones Entomologicae* 11, 7–25.
- Richter, S., Stein, M., Frase, T. & Szucsich, N.U. 2013: The arthropod head. In Minelli, A., Boxshall, G. & Fusco, G. (eds): *Arthropod Biology and Evolution*, 223–240. Springer-Verlag, Berlin, Heidelberg.
- Scholtz, G. 1997: Cleavage, germ band formation and head segmentation: the ground pattern of the Euarthropoda. In Fortey, R.A. & Thomas, R.H. (eds): *Arthropod Relationships*, 317–322. Chapman and Hall, London.
- Scholtz, G. & Edgecombe, G.D. 2005: Heads, Hox and the phylogenetic position of trilobites. In Koenemann, S. & Jenner, R. (eds): *Crustacea and Arthropod Relationships*, 139–165. CRC, Boca Raton.
- Scholtz, G. & Edgecombe, G.D. 2006: The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. *Developmental Genes and Evolution* 216, 395–415.
- Shiino, Y., Kuwazuru, O., Suzuki, Y. & Ono, S. 2012: Swimming capability of the remopleurid trilobite *Hypodicranotus striatus*: hydrodynamic functions of the exoskeleton and the long, forked hypostome. *Journal of Theoretical Biology* 300, 29–38.
- Stein, M., Budd, G.E., Peel, J.S. & Harper, D.A.T. 2013: *Arthroaspis* n. gen., a common element of the Sirius Passet Lagerstätte (Cambrian, North Greenland), sheds light on trilobite ancestry. *BMC Evolutionary Biology* 13, 99.
- Störmer, L. 1942: Studies on trilobite morphology. Part II: the larval development, the segmentation and the sutures, and their bearing on trilobite classification. *Norsk Geologisk Tidsskrift* 21, 49–164.
- Sundberg, F.A. 1995: Arthropod pattern theory and Cambrian trilobites. *Bijdragen tot de Dierkunde* 64, 193–213.
- Tanaka, G., Hou, X., Ma, X., Edgecombe, G.D. & Strausfeld, N. 2013: Chelicerate neural ground pattern in a Cambrian great appendage arthropod. *Nature* 502, 364–367.
- Thomas, R.H. & Telford, M.J. 1999: Appendage development in embryos of the oribatid mite *Archezogetes longisetosus* (Acari, Oribatei, Trhypochthoniidae). *Acta Zoologica* 80, 193–200.
- Waloszek, D., Maas, A., Chen, J. & Stein, M. 2007: Evolution of cephalic feeding structures and the phylogeny of Arthropoda. *Palaeogeography, Palaeoclimatology, Palaeoecology* 254, 273–287.
- Whittington, H.B. 1985: *Tegopelte gigas*, a second soft-bodied trilobite from the Burgess Shale, Middle Cambrian, British Columbia. *Journal of Paleontology* 59, 1251–1274.
- Whittington, H.B. 1997: The trilobite body. In Kaesler, K.L. (ed). *Treatise on Invertebrate Paleontology. Part O. Arthropoda 1. Trilobita, Revised*, 87–135. The Geological Society of America and The University of Kansas, Boulder, Colorado, and Lawrence, Kansas
- Yin, G. & Li, S. 1978: Trilobita. In Working group on stratigraphy and palaeontology of Guizhou (ed). *Paleontological Atlas of Southwest China*, 440–445, Geological Publishing House, Beijing (in Chinese).
- Yuan, J., Li, Y., Mu, X., Lin, J. & Zhu, X. 2012: Trilobite fauna of the Cahnghia Formation (Cambrian Series 3) from Shandong and adjacent area, North China. *Acta Palaeontologica Sinica* 197, New Series B, Number 35, 758, + 241.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. A ventral view of a pyritized *Triarthrus eatoni* with appendages preserved.

Fig. S2. Line drawings for the frontal cephalic condition during ontogeny of two trilobites.

Fig. S3. Line drawings of the frontal cephalic conditions in various trilobite cephalae.

Fig. S4. Line drawings of the frontal cephalic conditions in some immature trilobites.