

Enrolment in a Middle Ordovician agnostoid trilobite

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Bruton, D.L. and Nakrem, H.A. 2005. Enrolment in a Middle Ordovician agnostoid trilobite. *Acta Palaeontologica Polonica* 50 (3): 441–448.

Study of silicified material of *Trinodus elspethi*, from the Edinburg Formation, Virginia, USA, shows there is no gliding of distal parts of segments but an articulating furrow and opposing flange with prongs, acting as apodemes for muscle attachment, allowed cephalon and thorax to move as a single unit. Articulation between thorax and pygidium was more rigid with prongs from the thorax articulating in sockets on the pygidium. Support is given to the view that agnostoids lived partially enrolled with cephalon and pygidium gaping. They are unique in lacking an articulating half-ring between cephalon and thorax and the hinge joint is modified medially to provide an opening for what is interpreted as an exhalatory organ through which water passed during feeding and swimming. Peculiarities of the thorax are connected with the presence of only two thoracic segments articulating as a unit with distal tips directed anteriorly rather than posteriorly. Otherwise articulating half rings are present in the rest of the thorax and pygidium and lack of articulating facets is not unique. It is concluded that agnostoids can be shown to be trilobites.

Key words: Trilobita, Agnostida, life habit, preservation, Edinburg Formation, Ordovician, Virginia.

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Introduction

Silicified specimens of the agnostoid trilobite *Trinodus elspethi* (Raymond, 1925), were used by Allan S. Hunt to illustrate features of a cephalic ventral plate (Hunt 1966) and the nature of size increase, variation and instar development (Hunt 1967). In the latter paper complete, enrolled specimens were figured together with isolated specimens of the thoracic segments but attention was not directed to them or their articulation. Hunt's material was from various localities in the Middle Ordovician Edinburg Limestone of Virginia (Whittington 1959: 378–383), including locality 4 from which the present senior author made collections together with Harry B. Whittington in 1969. This is labelled "Locality W12, Edinburg Formation 50 feet above the base", W12 being equivalent to locality 4, the Botetourt Member, lower part of the Edinburg Limestone in upper part of field northeast of Virginia State Highway 639, at a point 0.25 miles from its junction with U.S. Highway 11 (Harry B. Whittington, personal communication 11.10.2002). This material was etched in Oslo, mainly for teaching purposes. Using dilute hydrochloric acid, limestone blocks yielded a wealth of trilobite forms including *Trinodus elspethi*, represented by more than 50 cephalata and pygidia, two completely enrolled exoskeletons and 10 isolated first thoracic segments. No second segments were found and the illustrated specimen figured herein was found in February 2004 among specimens in the Whittington Collection housed at the Sedgwick Museum, University of Cambridge, England. All this material affords a detailed study of the enrolment mechanism which is the object of this work. The subject of enrolment in agnostoids has been discussed by Robison (1972) and more

recently has been reviewed by Whittington (1997: 56–57, fig. 48; and references) whose terminology is followed here. Additional terminology as applied to the Agnostina is from Shergold et al. (1990).

The present material was photographed by the junior author using a Jeol JSM-5200 scanning electron microscope and specimens were mounted on stubs and coated with gold palladium before being photographed.

Institutional abbreviations.—All figured and reference material used in this study is housed in the collections of the former Palaeontological Museum (abbreviated PMO with reference numbers) now incorporated in the Geological Museum, University of Oslo.

Description of material

Dorsal and ventral views of the cephalon (Fig. 1A, B) are of an holaspid and show the characteristic notch in the posterolateral border which first appears at the holaspid instar 1 stage (Hunt 1967: 208). Other holaspid features present are the anterior tapering of the glabella, the presence of a faint median preglabellar furrow and the short, adaxially directed posterolateral spines.

In ventral view the doublure is widest antero-laterally, but narrows medially and towards the notch. Behind the latter it becomes ridge-like but broadens and slopes inwards at the base of the posterolateral spine. The latter is hollow. The inner margin of the doublure forms a sub-marginal suture which, when present, separates the doublure from the horse-shoe-shaped ventral plate which is missing here but is de-

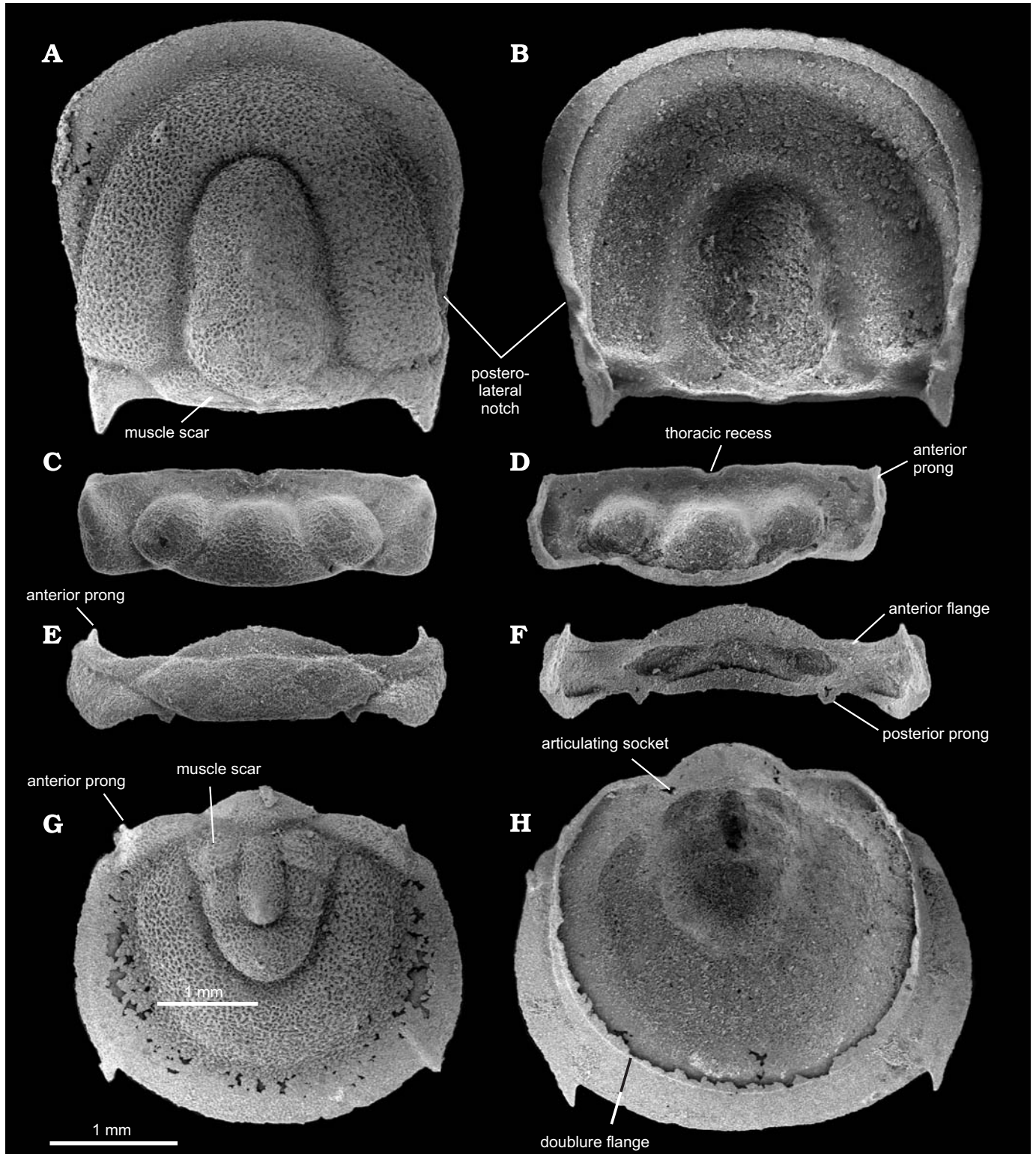


Fig. 1. *Trinodus elspethi* (Raymond, 1925), silicified specimens from Edinburg Formation, Virginia, USA. **A.** PMO 206.303/1, dorsal view of holaspisid cephalon. **B.** PMO 206.303/2, ventral view of holaspisid cephalon; the posterolateral notch accommodates the anterior border of the pygidium during enrolment. **C.** PMO 206.304/1, dorsal view of first thoracic segment. **D.** PMO 206.304/2, ventral view of first thoracic segment. **E.** PMO 206.305, dorsal view of second thoracic segment. **F.** Ventral view of second thoracic segment; note articulating half-ring. **G.** PMO 206.306/1, dorsal view of pygidium. **H.** PMO 206.306/2, ventral view of pygidium with socket for posterior prong of second thoracic segment.

scribed in detail by Hunt (1966: 1238, fig. 1). In lateral view the occipital band slopes steeply downwards (Fig. 2A₁) and

in dorsal view the posterior margin of the cephalon is straight to weakly curved, medially. In ventral view, the inner edge is

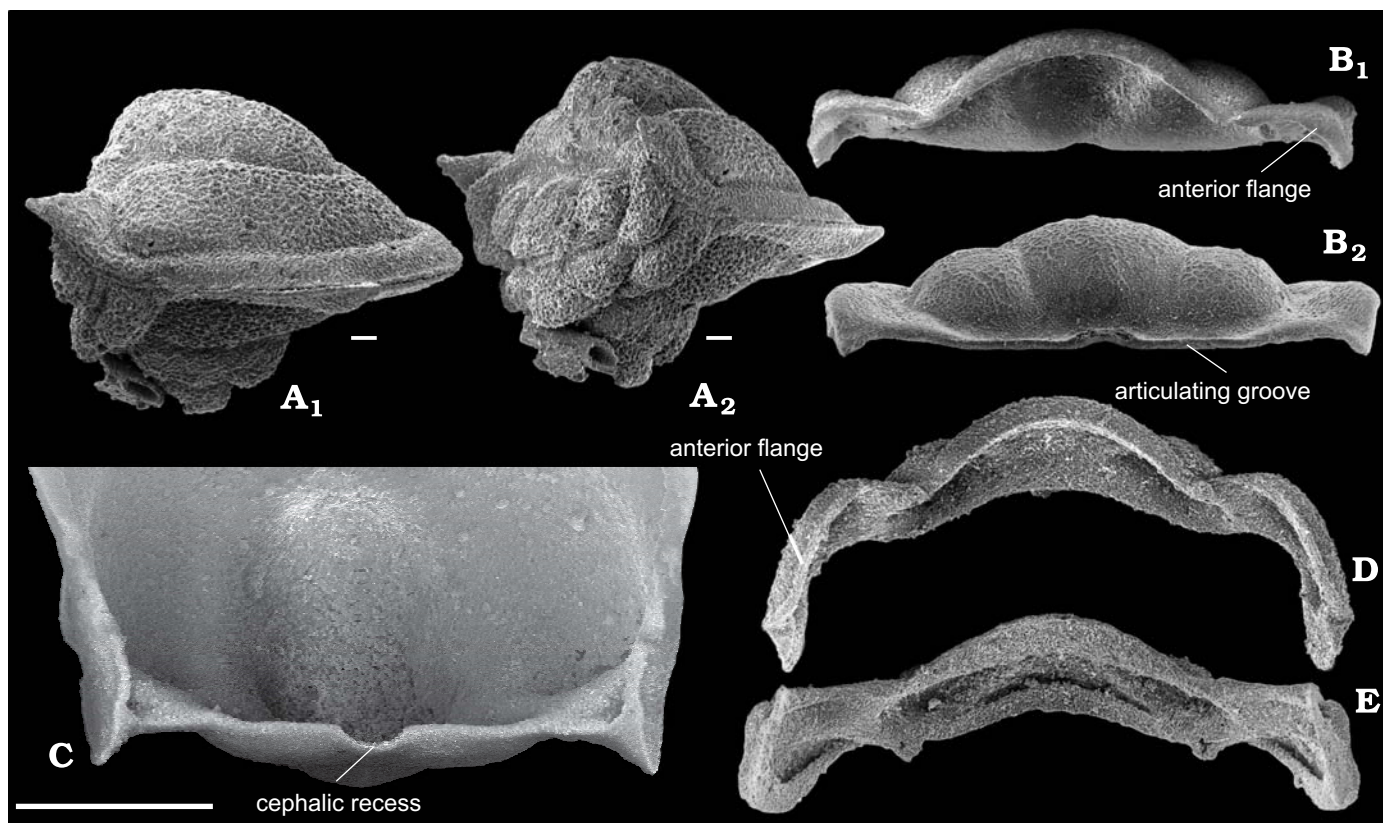


Fig. 2. *Trinodus elspethi* (Raymond, 1925), silicified specimens from Edinburg Formation, Virginia, USA. **A.** PMO 206.307. Lateral (**A₁**) and oblique lateral (**A₂**) views of completely enrolled specimen. Note attached fragment of a bryozoan on the pygidium. **B.** PMO 206.304/1. **B₁**. Posterior view of first thoracic segment showing articulating groove, which receives the articulating flange on the anterior margin of the second segment (Fig. 2D). **B₂**. Anterior view of first thoracic segment showing articulating groove along anterior margin. This groove receives the rolled posterior margin of the cephalon (Fig. 2C) in the absence of an articulating half-ring. **C.** PMO 206.303/2. Detail of rolled posterior margin of the cephalon with cephalic recess. **D.** PMO 206.305. Anterior view of second thoracic segment with articulating flange. **E.** Ventral view of second thoracic segment showing anterior margin with articulating half-ring and prongs from posterior margin. Scale bars 1 mm.

rounded (Fig. 2C) and a semicircular notch (cephalic recess) occurs medially. The rolled edge fits into a corresponding articulating groove in the anterior margin of the first thoracic segment (Figs. 2B₂, 3C) and when segment and cephalon are joined and the thorax is enrolled, the juxtaposed notches form a circular opening, the cephalothoracic aperture (Fig. 4B₂–B₄). Note here, there is no articulating half-ring on the first thoracic segment and thus no corresponding occipital ring on the cephalon.

In dorsal view the first thoracic segment is rectangular in outline, with a trapezoid-shaped median lobe and rounded lateral lobes (Fig. 1C). There is no clear differentiation into anterior and posterior bands but there is an antero-lateral change of slope where the tip of the pleura is inflated and curved steeply downwards (Fig. 3B) extending inwards on the ventral side as a narrow outwardly sloping doublure with anterior prong (Fig. 1D). The doublure continues posterior-laterally, becoming broader from the dorsal furrow towards the mid-line. During enrolment the distal end of the segment tucks inside the genal angle with a flange (Fig. 3B) and prong sliding into the cavity at the base of the posterolateral spine.

The second thoracic segment (Fig. 1E, F) differs from that of the first in possessing a broad articulating half-ring which fits under the arched rachis of the preceding first segment (Fig. 2B₁). Laterally, along the anterior margin there is an articulating flange (Fig. 2D) which fits into a corresponding groove along the posterolateral edge of the first segment (Figs. 2B₁, 3A).

The posterior band is flap-like and separated by a weak pleural furrow from a narrow anterior band (Fig. 1E). The median and lateral lobes are less inflated than on the first segment. The posterior band is inflated dorsally but a change of slope separates this from a thinner distal area which slopes steeply downwards ventrally (Figs. 1F, 2D). This area extends forward as a prong at the distal end of the articulating flange and rests in a depression at the base of the posterolateral spine while the ventral side, nestles in the concave area lateral to the spine (Figs. 1B, 2C).

From the posterior margin of the second thoracic segment, at each side of the rachis, are posteriorly-directed spines, or prongs (Fig. 1E, F). These, slot into small depressions at the distal end of the articulating furrow of the pygidium (Fig. 1H). Prongs can also project forwards from the facet of the

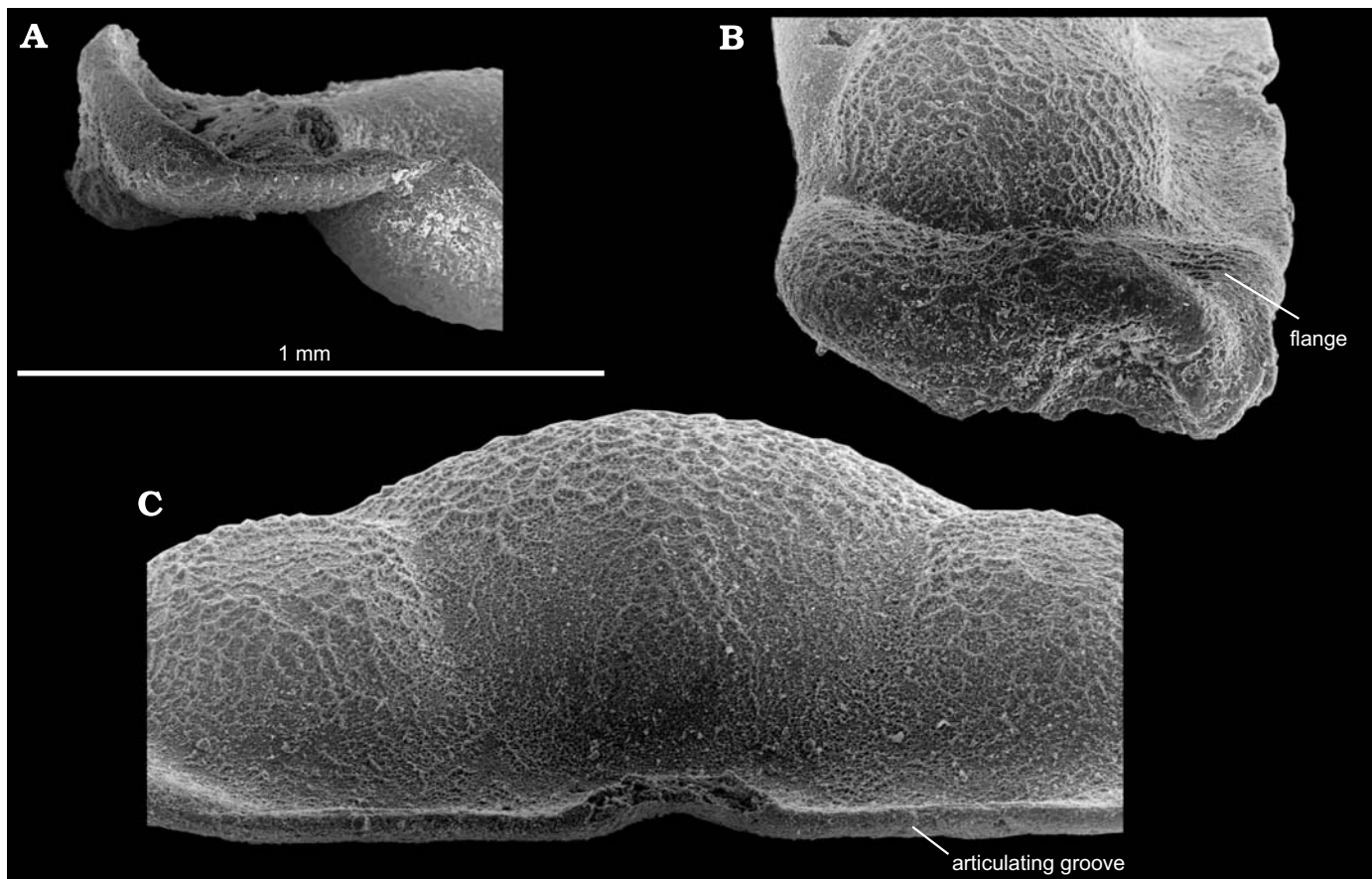


Fig. 3. *Trinodus elspethi* (Raymond, 1925), silicified specimens from Edinburg Formation, Virginia, USA, PMO 206.304/1. **A.** Detail of articulating groove on posterior margin of the first thoracic segment. **B.** Lateral view showing inflated distal end and flange. During enrolment the latter slots into the base of the posterolateral spine of the cephalon. **C.** Detail of articulating groove along anterior margin.

pygidium (Fig. 1G) but are not always present on the material examined. When fully enrolled the anterior margin of the pygidium rests in the postero-lateral notch of the cephalic doublure and both cephalic and pygidial doublures are in contact. The inner margin of the pygidial doublure is raised and forms a marked flange (Figs. 1H, 4C) which presumably fits exactly the inner margin of the cephalic doublure.

Articulation between the cephalon and the first thoracic segment

Robison (1964: 515) noted that there is no overlap between the cephalon and the first thoracic segment and that the lack of an articulating half-ring can be traced through all growth stages.

As described above, the rounded edge of the occipital band (Fig. 2C) fits that of a corresponding groove in the anterior margin of the first segment (Figs. 2B₂, 3C). This is a simple hinge joint with a ligament, of arthrodial membrane (cf. Müller and Walossek 1987: 9) and movement is a horizontal axis of rotation. Articulating processes are absent but a prong (Öpik 1979: 32) is present at the fulcrum and below the facet.

Since the latter slides inside the base of the posterolateral spine, it is likely that some form of membrane extended from the prong into the embayment at the base of the spine and held the pleural tip in position during enrolment. This interpretation suggests that the prongs were apodemes and in this case did not have a function as “stoppers” to prevent an upward rotation of the segment as supposed by Öpik (1979: 33). During enrolment, movement of the first segment relative to the cephalon was approximately 90 degrees and in this position the cephalothoracic aperture was fully exposed.

Articulation between the first and second thoracic segment

A well marked articulating groove occurs in the posterior margins of the first thoracic pleura lateral to the rachis (Figs. 2B₁, 3A) and this matches a flange (Fig. 2D) on the anterior margin of the second segment. The groove extends down the full length of the pleural tip indicating that during enrolment, segments one and two rotate as a unit and there is not the space for the amount of arthrodial membrane shown by Müller and Walossek (1987: fig. 13) nor is there an articulat-

ing facet and movement of rotation is within narrow limits (Öpik 1979: 32). Forwardly directed anterior prongs, extending from the articulating flange of the second segment (Fig. 1E) presumably acted as apodemes and sites for muscular attachment to the underside of the first segment.

Articulation between thorax and pygidium

Robison (1964: 515) and Hunt (1967: pl. 22: 10) showed that in mersapid instar 1 (= 0 degree), the pygidium lacks the rachial half-ring but this appears soon after the release of the first thoracic segment at the second instar (Hunt 1967: 207). From this stage onwards it becomes functional and articulation between the pygidium and the thorax appears to be very much the same as in other trilobites except that prominent prongs (Fig. 1E, F) extend posteriorly from the margin of the second segment of the thorax alongside the dorsal furrow. These prongs correspond to sockets in the dorsal furrow on the ventral surface of the pygidium lateral to the articulating half-ring (Fig. 1H) and are interpreted as sites for muscles extending from the prongs which therefore act as apodemes. When enrolled and seen from the dorsal side, the curved posterior lateral margin of the second thoracic segment comes to rest over the facet of the pygidium (Fig. 4B₁, B₃) which is flattened and recessed (Hunt 1967: pl. 22: 45) below forwardly projecting prongs seen only on isolated pygidia but not all (Fig. 1G). If these also functioned as apodemes then muscles could be attached to the inside of the second thoracic segment at a notch seen in the doublure. This fact strengthens our belief that movement between thorax and pygidium seems to have been quite rigid and there does not seem to have been much extension of the arthrodial membrane at the rachis.

Mechanism of enrolment

Perfect enrolment is dependent on the mechanism of interpleural articulation which, is aided by at least dorsal and ventral longitudinal muscles to allow outstretching and enrolling. Study of enrolled specimens of *Trinodus elspethi* shows that laterally there is no gliding of the distal parts of the segments over one another and an articulating facet is absent. Moreover the articulating groove and flange between the cephalon and the first thoracic segment and between the latter and the second thoracic segment, extends for the full pleural width indicating that all moved together. This suggests that this was an ideal site for an articulating membrane in the form of a ligament whilst possible unsclerotised material joined the rachial half-rings between segment one and two and between the latter and the pygidium. Obviously, some extension must have been possible here with the antagonistic action of the dorsal longitudinal muscles slung below the half

rings with slivers attached to the inside of the rings in a similar manner proposed for *Phacops* by Bruton and Haas (1997). It seems reasonable to suggest that the dorsal longitudinal muscle was attached near the cephalothorax junction and paired muscle scars (Fig. 1A) on the basal lobes of the glabella, seem a likely point of attachment. These lobes are outlined by furrows represented by ridges on the inner surface of the exoskeleton and it is the furrows that seem to remain while others become repeatedly effaced in widely differing agnostoid lineages (Robison 1972: 36). Similar muscle scars occur on the first rachial ring of the pygidium and the dorsal longitudinal muscles could be attached here. One can only speculate where the ventral longitudinal muscles were attached but we assume, as did Bruton and Haas (1997), that they were attached to folds in the ventral integument.

Öpik (1979: 32) has discussed the movements along the three joints leading to enrolment and listed the following possibilities: a simultaneous rotation of cephalon and pygidium relative to the thorax; a rotation of thorax and pygidium relative to the cephalon or the thorax and cephalon rotate relative to the pygidium. Independent movement of cephalon or pygidium relative to the thorax is also possible. Complete enrolment in agnostoids is common and Robison (1964: 515: pl. 80: 14; pl. 82: 14) illustrated a groove (fibular furrow) on the doublure of the pygidium of *Baltagnostus* and *Peronopsis*, which he believed received the inner margin of the cephalic doublure to form a “tongue in groove coupling” during enrolment (see also Bergström 1973: 30). However it is the flange inside the groove that fits into the cephalon in a manner suggested here for *Trinodus elspethi* and a similar flange is also present on *Agnostus pisiformis* illustrated by Müller and Walossek (1987: pl. 7: 8; pl. 22: 3). In this way the flange is homologous (not analagous) with certain vincular structures seen on non-agnostoid trilobites.

We believe that extension in the thorax was slight and thus rotation along the second axis was minimal, the thorax functioning as a single unit. From a functional point of view movement along the first axis allowed the cephalon to drop 90 degrees relative to the thorax thus exposing the cephalothoracic aperture which otherwise is closed when cephalon and thorax are horizontal. The cephalothoracic aperture is formed by indentations in the hinge line of the cephalon (Fig. 2C) and the anterior margin (Fig. 1D) of the first segment (cephalic recess and thoracic recess respectively) which together form a circular to oval hole (Robison 1964: pl. 81: 29; Hunt 1967: fig. 46; Müller and Walossek: 1987: pl. 2: 7, 8, pl. 30: 1, figs. 2B, 20); Whittington 1963: pl. 1: 2, 6) which could only function when the animal was enrolled (Fig. 4B₂–B₄). A flange or collar surrounds this hole (Robison 1964: pl. 80: 4, pl. 81: 7), which was filled with arthrodial membrane but open to the exterior via paired ducts (Müller and Walossek 1987: pl. 28: 7, 9). This opening is already visible before the release of the first thoracic segment and before the articulating ring of the pygidium was fully developed indicating that it was functional from a very early life stage. Fortey and Owens (1999: 458) considered the possi-

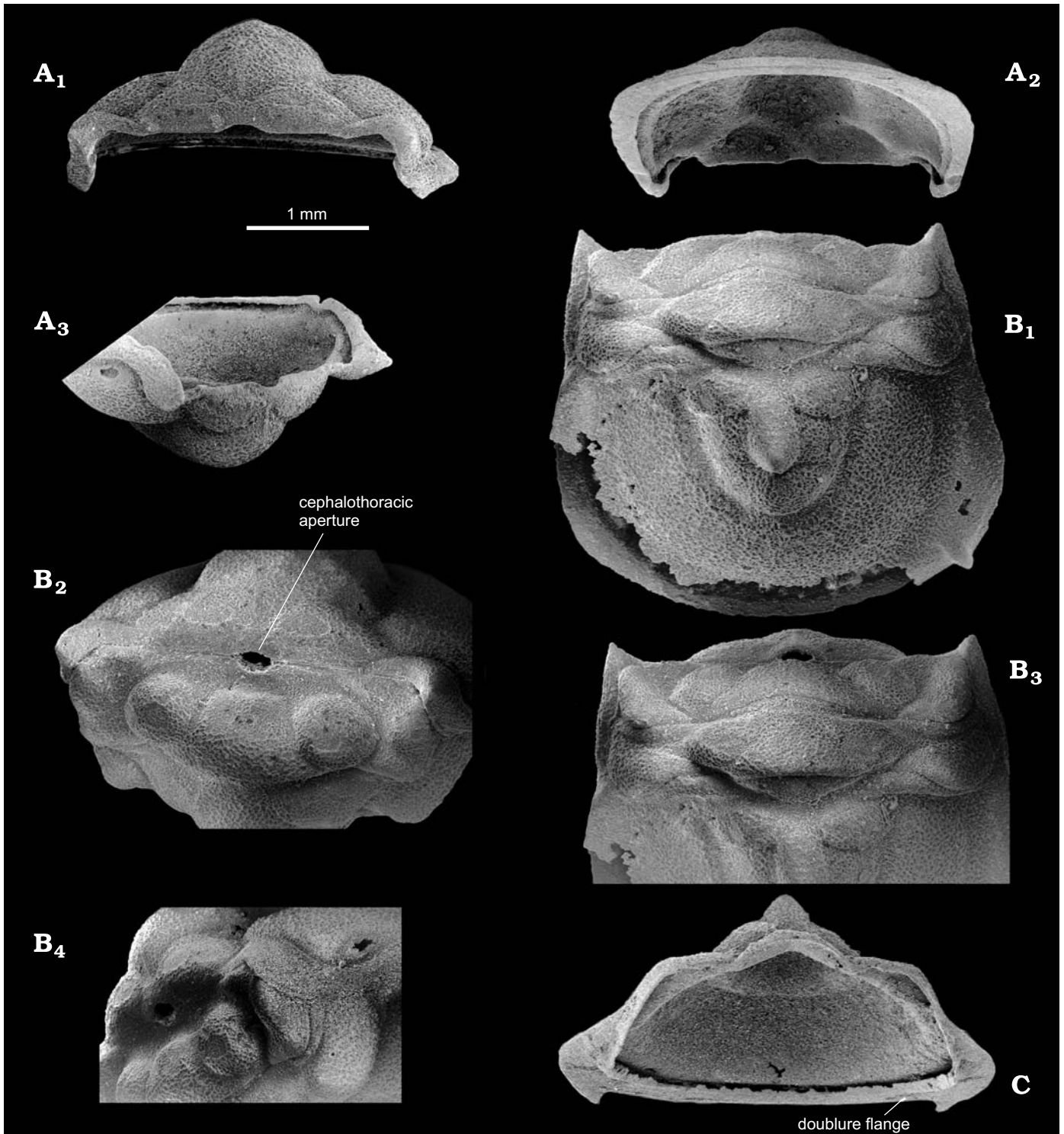


Fig. 4. *Trinodus elspethi* (Raymond, 1925), silicified specimens from Edinburg Formation, Virginia, USA. **A.** PMO 206.303. Cephalon in posterior (A₁), tilted frontal (A₂), and oblique lateral (A₃) views from ventral. Note hollow posterolateral spine. **B.** PMO 206.307. Completely enrolled specimen; B₁, ventral view, note cephalothoracic aperture is not visible and how the second thoracic segment overlaps the pygidium at the shoulder; B₂, oblique posterior view showing cephalothoracic aperture and how distal tip of first thoracic segment slots into base of posterolateral spine; B₃, specimen tilted from ventral position so that cephalothoracic aperture is visible; B₄, detail of articulation between cephalon and first thoracic segment. **C.** PMO 206.306/2. Posterior view of pygidium to show raised flange of doublure.

bility of the arthroal membrane acting as resilium which sprung open the valves on death, but this seems unlikely since its function was tied up with articulation in the absence

of an half-ring. We suggest the paired ducts were exhalatory in function and were connected with a through flow of water during the animal's feeding and swimming.

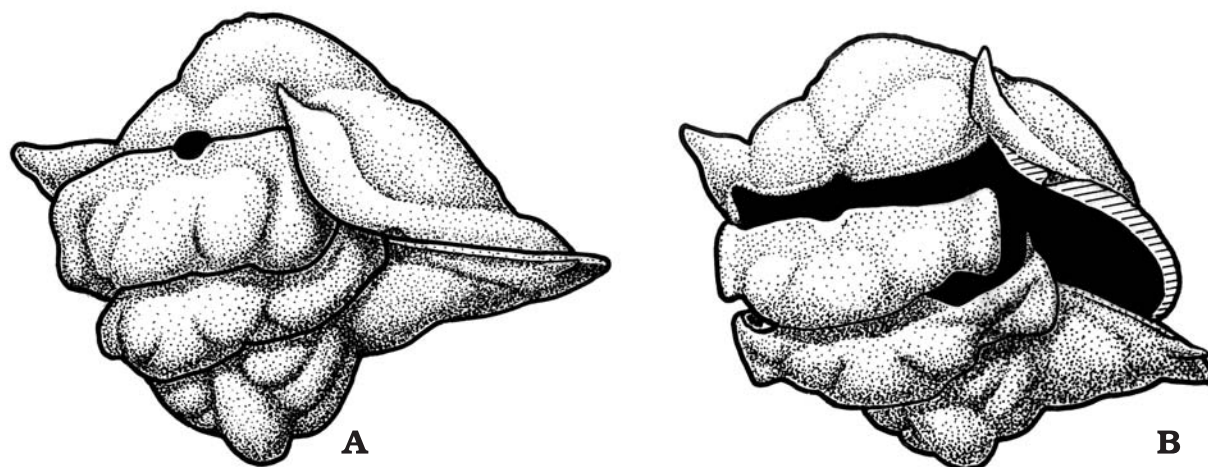


Fig. 5. Reconstruction of *Trinodus elspethi* (Raymond, 1925), Edinburg Formation, Virginia, U.S.A. A. Oblique posterior lateral view of completely enrolled individual. B. Partial pull-apart from anterior, to show articulation between cephalon and thorax. Drawn by Bogdan Bocianowski.

Movement along the third axis was more than 90 degrees to allow contact between the doublures of cephalon and pygidium and to bring the anterior margin of the pygidium to lock into the cephalic notch. Rotation and/or extension along the second axis was slight and the distal tip of the second pleural segment filled exactly any remaining space between cephalon and pygidium (Fig. 5).

Enrolment in *Trinodus elspethi* appears to have been functionally well developed with the described coaptive features of the exoskeleton allowing for complete and exact fit of juxtaposed parts. Articulating notches and grooves on the cephalic doublure to receive structures of the plural tips and pygidia, together with prongs functioning as apodemes for adductor muscles, are features preserved because the material studied is finely silicified. It is a challenge to see if such features can be identified on non-silicified, more primitive, Cambrian agnostoids for only then can one attempt a comparison of primitive and derived structures.

Life habits of agnostoids

Fortey and Owens (1999) provide an excellent summary of the various views regarding the mode of life of agnostoid trilobites which they claim is controversial and difficult to interpret. They concluded that while the evidence is still equivocal it seems likely that a range of life habits best accounts for the diverse morphologies these small arthropods display. There is no denying that the group exhibits great taxonomic variety, even within a single horizon, but common to all is a similar mode of enrolment and the presence of cephalo-thoracic aperture which can only function when the animal is enrolled and becomes closed when it is outstretched. Thus we support the view of Robison (1972) and Müller and Walossek (1987) that agnostoids spent much of their life partially enrolled and fed ostracod-like with the cephalon and pygidium gaping. Fortey and Owens (1999: 458) argue

against this form of life orientation and produce interesting field evidence including the study of agnostoid rich horizons and apparent lack of enrolled specimens which one would not expect if this was the normal life style. We too are accustomed to studying agnostid coquinas, albeit from the Late Cambrian of Scandinavia, and are aware of the paucity of enrolled specimens here. Otherwise the abundance of free cephalon and pygidia in the Scandinavian coquinas are current swept parts from sites used during periods of moulting and they occur almost to the exclusion of thoracic segments and enrolled individuals. When found, the latter are tightly closed and could represent individuals that died in this position. We have examined material from several localities where 'complete,' outstretched, agnostoids are preserved, including a small collection of *Triplagnostus* from the Middle Cambrian Burgess Shale, Canada and uncompressed specimens of *Ptychagnostus* and *Lejopyge* from the Middle Cambrian of the Oslo Region. In all these specimens, both thoracic segments are conjoined and attached to the pygidium, but are separated from the cephalon. This separation is hardly noticeable and is no more than to be expected if, after death, the thorax is outstretched. The observed separation suggests that the outstretched position is incompatible with the form of articulation between the cephalon and the thorax and that complete enrolment or partial enrolment is the natural form.

That complete enrolment was important to the agnostoid is evident from the presence of the vincular structures on both cephalon and pygidium allowing these to shut tightly supposedly in response to changes in the environment such as an abrasion event or increase in bottom currents which produced the agnostoid coquinas.

We agree with Müller and Walossek (1987) and Fortey and Owens (1999) that agnostoids must have fed on organic particles concomitant with their small size and that such food could be obtained in a benthic flocculent zone rich in detrital matter (Müller and Walossek 1987: 42). Here they could be fully enrolled while resting or in times of sediment distur-

bance but, when feeding, we suggest the anterior margin was gaping and a stream of water brought food to the mouth aided by movement of the appendages and a suction effect through the cephalothoracic aperture. Swimming within the water column could have been affected by both leg and gill activity together with forward movement caused by the exhalent water through the cephalothoracic aperture. In this way we support Robison (1972; 1975) that agnostoids also enjoyed an active planktic life within the water column and this is supported by their widespread geographical distribution.

Conclusions

Agnostoids- trilobites or not? Fortey (2001: 1143) posed this question after these small, blind arthropods with two body segments had been accepted as trilobites in the revised *Treatise on Invertebrate Paleontology* (Whittington et al. 1997). Resser (1938) questioned whether they really were trilobites and since the discovery by Müller and Waloszek (1987) of appendages in immature specimens of *Agnostus pisiformis* from the Upper Cambrian, which seem to differ from those known for trilobites, these authors and others (Ramsköld and Edgecombe 1991; Maas et al. 2003; Stein et al. 2005) have suggested that the Agnostida cannot be in-group trilobites but are derivatives of the early evolutionary lineage towards the Crustacea. We agree with Fortey (2001) that the question of the limbs, as interpreted from immature and miniscule material, is doubtful all the time we do not know what they might have been like in an adult specimen, nor do we have limbs from older Cambrian agnostoids. When we consider the exoskeleton, agnostoids are unique in that they do not possess an articulating half ring between cephalon and first segment and the hinge joint here is modified medially to provide an opening for what we here interpret as an exhalatory organ. Perhaps the absence of the half- ring is connected with this since normal articulating half-rings are functional between the first and second thoracic segments and between the latter and the pygidium. A lack of an articulating facet is not unique and any differences in articulation within the thorax are connected with the fact that only two segments are present to fill the space between cephalon and pygidium when the animal enrolls. These differences include the fact that the articulated segments move as a unit and their distal tips are directed anteriorly rather than posteriorly, which is the case in the majority of polymeroid trilobites. There is no doubt that the agnostoids are very special but, together with the eodiscoids, it is possible to combine the superfamilies Agnostina and Eodiscina in an analysis which shows them to be trilobites (Fortey and Theron 1994; Fortey 2001).

Acknowledgements

Bruton thanks Harry B. Whittington (Cambridge, England) for past guidance in the field and for recently helping to find additional material

in his collections of silicified specimens, access to which was made possible by Mike Dorling (Sedgwick Museum, University of Cambridge, England). Whittington and Winfried Haas (University of Bonn) are thanked for their advice while this work was being written and the former suggested amendments to the manuscript. We are most grateful to Richard A. Robison and Per Ahlberg for their referee comments, which very much helped to improve this presentation.

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