Musculature and systematic position of *Megalompha taenia* (Bellerophontacea; Gastropoda) from the Silurian of Gotland

JOHN S. PEEL


Circumbilical ridges interpreted as the loci of a pair of retractor muscles are described on two internal moulds of *Megalompha taenia*, a characteristic bellerophontacean from the Silurian of Gotland, Sweden. Comparison with muscle scars in other bellerophontaceans confirms an assignment to the Gastropoda.


*Bellerophon* de Montfort, 1808 and its relatives form a dominantly Palaeozoic group of bilaterally symmetrical, coiled molluscs of uncertain systematic position. Plot (1686), in what Challinor (1945) considered to be the earliest reference to bellerophontaceans, recognised that the specimen before him could not be assigned to a living animal. He denied a relationship to the similarly coiled *Nautilus*, pointing out that his specimen had a feather-like pattern on the dorsal surface not present in the living cephalopod. The accompanying illustration clearly indicates that the feather-like pattern is actually the median slit band (= selenizone) and the growth lines which gradually curve away towards the lateral areas.

A close relationship to the Cephalopoda has long been discounted and the group was generally referred to the Gastropoda by the early part of the nineteenth century. However, authors continued to disagree as to affinities within this class and close relationship of bellerophontaceans to the Heteropoda, Opisthobranchiata and Prosobranchiata have all been proposed (summary in Yochelson 1967). Gradually, the suggestion of de Koninck (1842-44) and Meek (1866) that bellerophontaceans were prosobranchs closely related to the present day key hole limpet *Fissurella* and other pleurotomariinids gathered support and has now become the most widely accepted doctrine.

Although generally followed for many years it cannot be claimed that referral of the Bellerophontacea to the Gastropoda has been unanimous. Wenz (1940) described multiple dorsal muscle scars in *Cyrtonella mitella* (Hall, 1862) and presumed that all other bellerophontaceans possessed similar muscle scars suggestive of a lack of torsion. He placed the Bellerophontacea together with the Tryblidiacea in the Subclass Amphigastropoda, effectively anticipating the Class Monoplacophora in the sense of at least some later authors (Runnegar & Pojeta 1974). However, Knight (1947) demonstrated that not all bellerophontaceans could be interpreted as untorted molluscs on the basis of the rather atypical *Cyrtonella*. In describing a pair of umbilical muscle scars in *Bellerophon* and *Sinuites* Knight drew comparisons with the musculature of extant primitive pleurotomariinid archaeogastropods and considered that torsion had taken place.

Clearly, the Amphigastropoda sensu Wenz could not be maintained and a modified Bellerophontacea (excluding *Cyrtonella*) was transferred back to the Gastropoda (Knight et al. 1960). The action was almost as dogmatic as that of Wenz (1940) for muscle scars suggestive of torsion were known in only a couple of species. However, in defense of Knight et al. (1960), it should be pointed out that these two species belonged to the nominate genera of the two main suprageneric systematic groups of the Bellerophontacea, the Bellerophontidae and the Sinuitidae.

With the benefit of hindsight it can be admitted that a number of the genera placed
within the Bellerophontacea by Knight et al (1960) could possibly have been transferred to the Monoplacophora, in proximity to Cyortonella, on the basis of gross morphology. However, it is clear that a more conservative approach is preferable in the absence of information concerning muscle scars. If justification for such a lack of reliance on external morphology alone is required, it can surely be found in the study by Rollins and Batten (1968) of the sinus bearing monoplacophoran Sinuitopsis acutilira (Hall 1861). Without knowledge of musculature it would be exceedingly difficult to justify placing this species in a separate molluscan class from Sinuites.

The special interest in the Monoplacophora which followed the discovery of Neopilina has resulted in the description of multiple paired muscle scars in a large number of cap shaped and coiled monoplacophorans (Horný 1965; Rollins 1969; Byalyi 1973). Many of these coiled taxa can be described as bellerophontiform in that they are planispirally coiled. The majority have been referred to new genera but a few of the genera placed in the Bellerophontae by Knight et al (1960) have had their musculature determined and consequently been reassigned (Rollins & Batten 1968; Horný 1965). Others have been reassigned without knowledge of the distribution of muscle scars (Starobogatov 1970).

As a result of this recent interest, it has become increasingly evident that the bellerophontiform Mollusca includes species with both monoplacophoran and gastropod affinities, although there has been a recent tendency amongst some students of molluscan phylogeny to transfer the whole group back to the untorsted Monoplacophora (Runnegar & Pojeta 1974). Perhaps this tendency reflects the relative scarcity of records of muscle scars of the gastropod type. Peel (1972) described muscle scars and related structures in Bellerophon, Salpingostoma and Tremanotus and commented that such structures were more commonly visible on specimens in collections than might be supposed from the literature.

Unfortunately, muscle scars remain unknown in the vast majority of bellerophontacean taxa and uncertainty as to systematic position consequently surrounds a number of these, particularly the sinuate as distinct from slit bearing forms. The issue is further complicated by a general lack of knowledge concerning muscle scars in Palaeozoic gastropods, the study of which has not gained any significant benefit from the recent interest in monoplacophoran muscles. It is clearly difficult to interpret muscle scars in bellerophontaceans as being of gastropod type, i.e. indicative of torsion, when muscle scars in contemporary gastropods are largely unknown. However, this should not in itself be allowed to cloud the possible magnitude of the difference between the so-called gastropod and monoplacophoran types of musculature within the bellerophontiform molluscs. The comparisons made by Knight (1947; 1952) between the musculature in recent primitive archaeogastropods and in Bellerophon and Sinuites remain valid.

Satisfactory solution of the phylogenetic and systematic problems embracing the mutual relationships of the Bellerophontacea, the cyclomyan Monoplacophora and the helically coiled Gastropoda is not possible without the accumulation of more basic data concerning the muscle scars and inferred anatomical organisation of all the respective groups. In recording muscle scars of the type interpreted by Knight (1947) as indicative of torsion in the bellerophontacean Megalomphala taenia (Lindström 1884) from the Late Silurian of Gotland, Sweden, this paper hopes to contribute towards satisfying that need.

Muscle scars in bellerophontacean gastropods

The recognition of muscle scars and subsequent interpretation of musculature in bellerophontiform molluscs is basic to the delimitation of the bellerophontacean gastropods from their homeomorphs amongst the cyclomyan Monoplacophora. The muscle scars of bellerophontacean gastropods were first illustrated, but apparently not recognised, by Koken & Perner (1925, pl. 18, fig. 16) in Sinuites ammonoides Koken, 1897 from the Ordovician of the Baltic region. More than twenty years were to pass before Knight (1947) recognised and interpreted similar structures in Bel-

Fig. 1. Right muscle scar of Bellerophon sp., drawn from an internal mould, × 5. The arrow points adaperturally. The circumbilical ridge (r) is associated with a raised platform (p) adaperturally. A median groove (g) continues adaperturally beyond the ridge and terminates at several fine crescentic striations (c) representing the anterior margin of the muscle attachment area (after Peel 1972).

lerophon and Sinuites as indicative of the musculature of a torted mollusc, namely a gastropod. Since that time, comparable structures have been but little reported although Peel (1972) described muscle scars and associated structures in two species of Bellerophon from the Carboniferous, Salpingostoma buelli (Whitfield 1878) from the Ordovician and Tremanotus alpheus Hall, 1865, from the Silurian.

As previously noted (Peel 1972), the most readily observed indication of musculature of the type described by Knight (1947) in bellerophontacean gastropods is a delicate circumbilical ridge on each umbilical wall or shoulder of internal moulds. Each ridge, and its equivalent groove on the shell interior, represents the dorsal margin of an elongate columellar retractor muscle. In cases of exceptional preservation, a series of fine crescentic striations at the adapertural margin of the ridge indicates the anterior margin of the muscle attachment area (fig. 1). An abrupt adapertural termination to the circumbilical ridge, and associated striations, may delimit the posterior margin. Details of the adumbilical margin have not been adequately elucidated due to the concealing influence of the indented suturel region. However, it would appear that this margin of the muscle attachment area is about as weakly indicated as the anterior margin. In some cases the circumbilical ridges may be partly replaced, especially anteriorly, by shallow grooves. Local swellings and angular umbilical shoulders on the internal mould are often associated with the muscle attachment areas.

The length of the circumbilical ridges and their location relative to the aperture varies from taxon to taxon, as might be expected from variations in whorl profile and the nature of coiling. However, variation within taxa is difficult to estimate since samples of more than two or three specimens with muscle scars of a particular species have not been available for examination.

The relative scarcity of such material is exemplified by the case of Megalosphala taenia from the Late Silurian of Gotland, described below. The species is well represented in collections from Östergarn in the Naturhistoriska Riksmuseet, Stockholm, but muscle scars were only found as poor circumbilical grooves on the umbilical walls of a single specimen figured by Lindström (1884, pl. 6, fig. 23). In contrast, a single specimen from the same locality in the U.S. National Museum, Washington D.C., shows excellent circumbilical ridges, as does another figured specimen of Lindström (1884, pl. 7, figs. 4, 5) recently located in the collections of the Geological Museum, Copenhagen. The latter two specimens form the basis of the present description.

Muscle scars in Megalosphala taenia

This species, from the Late Silurian Hemse Beds at Östergarn, Gotland, was well described by Lindström (1884) under the name Bellerophon taenia. Ulrich & Scofield (1897) subsequently referred Lindström's species to a new genus, Megalosphala, based on Bellerophon contortus Eichwald, from the Ordovician of the Baltic region.

The smaller of the two described specimens with muscle scars (USNM 188177, fig. 2 D–G) has two whorls with the nucleus and aperture broken away. The specimen appears worn; adherent shell is confined to a narrow patch without surface detail on the final preserved whorl. A circumbilical ridge is present on each umbilical wall of the internal mould but other fine structures are not present. The
Fig. 2. Megalomphala taenia (Lindström 1884) from the Silurian of Gotland, Sweden, × 1. A–C, H. MMH 13037, internal mould. A. Oblique umbilical view of right side showing the broad circumbilical ridge on the innermost whorl (arrow) and the third circumbilical ridge on the outer whorl. B. Same, but rotated clockwise through about 60 degrees; arrow indicates small gap between the second (below) and third (above) circumbilical ridges. C. Lateral view. H. Dorsal view. D–G. USNM 188177, internal mould. D. Oblique umbilical view of right side showing circumbilical ridge (arrow). E. Same, of left side. F. Lateral view. G. Apertural view. Specimens deposited in U.S. National Museum, Washington D.C. (USNM) and Geological Museum, Copenhagen (MMH).
ridges are acute and located close to the suture with the previous whorl. The adapertural extremity of the right ridge is covered by matrix and shell about one third of a whorl prior to the final preserved growth stage, but the ridge extends abaperturally for more than half a whorl before becoming obscure. The left ridge is seen to commence about one and a sixth whorls back from the broken apertural margin and extends over approximately one third of a whorl before being covered. Spiral traces, perhaps indicative of earlier ridges are visible on the umbilical walls of the first preserved whorl prior to the development of the prominent circumbilical ridges.

It is not possible to accurately demonstrate the equivalence of the left and right circumbilical ridges in USNM 188177 due to the partly sediment filled umbilici. However, there is some suggestion, confirmed by examination of MMH 13037, described below, that a continuous ridge of the cumulative length of the exposed parts of the left and right circumbilical ridges in USNM 188177 is not developed on each side. Rather, a pair of discrete, shorter, ridges is probably present on each umbilical wall, with each new circumbilical ridge commencing shortly after the termination of the previous ridge.

In MMH 13037, the figured specimen of Lindström (1884, pl. 7, figs. 4, 5), approximately two and a half whorls are exposed, with the aperture and nucleus again missing. The internal mould retains approximately half a whorl more of the latest growth stage than USNM 188177 and has a more pronounced elliptical whorl profile, with relatively acute umbilico-dorsal angulations. The left side is embedded in matrix. Adherent shell is confined to a small patch on the dorsum showing details of the narrow, raised selenizone, one whorl prior to the latest preserved growth stage. The right side (fig. 2C, H) is damaged such that the umbilical wall of the last quarter of the preserved final whorl is missing.

A broad circumbilical ridge bounded by a groove on its lateral margin is present on the right umbilical wall of the earliest preserved whorl, near to the suture with the missing previous whorl (fig. 2A). This structure becomes obscure one whorl prior to the latest unda-
maged stage of the right side, at which point a second ridge emerges from matrix infilling the sutural area on the inside, i.e. adumbilically of the earlier ridge (fig. 2B). About one fifth of a whorl later, this second ridge gradually disappears and, after a few millimetres, a third circumbilical ridge commences abruptly. This third ridge extends over approximately one third of a volution before gradually disappearing (fig. 2A). The final preserved fraction of the umbilical wall on the right side is smooth without any indication of musculature. Crescentic anterior margin striations are not preserved although a few minor striae are developed parallel to the main circumbilical ridge. No significance is attached to the short transverse ridge on the umbilical wall visible in fig. 2A.

The presence of a series of circumbilical ridges in MMH 13037, as distinct from a single continuous ridge, implies a degree of saltation in the migration of the muscle attachment area during growth. This naturally suggests that the length of each discrete circumbilical ridge approximates to the length of the area of attachment of the retractor muscle. Unfortunately, while the adapertural termination of the latest ridge is MMH 13037 is abrupt, the adapertural part of this and the preceding ridge is poorly defined.

The situation appears comparable to that described by Peel (1972) in a specimen of Bellerophon from the Carboniferous of Armoragh (fig. 1). In this specimen the adapertural termination is sharp and associated with fine striations clearly demarcating the margin of the muscle attachment area. Adaperturally, the circumbilical ridge loses relief and is gradually replaced by a fine groove on the surface of the internal mould. The groove terminates in a series of fine crescentic striations marking the adapertural margin of the muscle scar. In consequence, the circumbilical ridge only delimits approximately two thirds of the full length of the muscle attachment area.

Crescentic striations are not preserved in the available specimens of Megalomphala tae‌n‌ia making it impossible to estimate the full length of the muscle scar. It is by no means certain that, with increased growth, the muscle attachment areas migrated adaperturally bey-
ond the adapertural margin of the previous scars. Indeed, some degree of overlap between successive muscle scars is quite probable, with the result that structures associated with the adapertural margin of the scars are obliterated by the migrating attachment muscles and overprinted by structures of the adapertural margin. In such cases, information concerning length of the retractor muscle scars can only be gained with confidence from the ontogenetically latest pair of circumbilical ridges and even then, only if adapertural margin structures are clearly defined.

The muscle scars in *Megalomphala taenia* differ significantly from those described by Knight (1947) and Peel (1972) in *Bellerophon* and *Sinuites* in terms of position on the whorl. In the latter genera, the circumbilical ridges are located at the umbilico-lateral shoulder. In *M. taenia* the ridges occur on the umbilical walls near the sutural area. Similarly located ridges were described by Peel (1972) in *Salpingostoma buelli* and it is probable that the positional differences partly reflect variation in whorl profile. *Bellerophon* and *Sinuites* have rather globose, impressed, reniform whorl profiles with rounded umbilico-lateral areas suitable for muscle attachment. In *S. buelli* and *M. taenia* the whorl profile is transversely elliptical, only slightly impressed, and the acutely angular junctions between the dorsal and umbilical surfaces at the whorl periphery do not form suitable loci for muscle attachment.

**Systematic position**

Knight (1947; 1952) compared the paired muscles of *Bellerophon* and *Sinuites* to those in the extant primitive pleurotomariinids of the families Haliotidae and Scissurellidae. In conjunction with the general morphological similarity in terms of coiling and the possession of an anal emargination to the pleurotomarianids, he concluded that the similarity in musculature indicated that the two bellerophonacean genera were gastropods.

*Megalomphala taenia* also has paired circumbilical muscles and a deep dorsal emargination and, following the reasoning of Knight (1952), should be regarded as a gastropod. Rollins & Batten (1968) justifiably cast doubt on the significance of the anal emargination alone as an indicator of gastropod affinity in describing a sinus in the Devonian monoplacophoran *Sinuitopsis acutilira*. They concluded that the presence of a posterior train to the aperture and the formation of parietal deposits were more reliable gastropod characters. Both these features are developed in *M. taenia*, where the aperture becomes bell shaped at maturity, and further substantiate the proposed assignment to the Gastropoda.

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