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# Trilobite spines and beetle horns: sexual selection in the Palaeozoic?

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**Raphiophorid trilobites commonly bore median cephalic protuberances such as spines or bulbs, showing a remarkable variety of form. It is unlikely that their primary function was for protection or in hydrodynamics. A case is made that they were secondary sexual features, by comparison with similar morphological structures developed on rhinoceros beetles and other arthropods. This interpretation is supported by four lines of evidence: their ontogeny, their diversity, the existence of plausible examples of sexual dimorphs in some cases and the fact that they show positive allometry.**

**Keywords:** trilobite; Raphioridae; sexual selection; secondary sexual characteristics

## 1. INTRODUCTION

Trilobites were among the dominant invertebrates in Palaeozoic seas (251–543 Myr ago) and exhibited an extraordinary array of exoskeletal morphology. However, the recognition of different sexes among trilobites has remained elusive. Claims of sexual dimorphs based on exoskeletal criteria, such as differences in size between pairs of co-occurring ‘species’, have been made for a number of examples (e.g. Hu 1971); however, these have not stood up to critical examination (Hughes & Fortey 1995). A few trilobites show possible examples of brood pouches (Fortey & Hughes 1998), but even in this case the evidence is not unequivocal. There remain a number of species that carry distinctive dorsal protrusions, such as bulbs or spines, which are suggestive of secondary sexual characteristics. Here, we examine the evidence for such possible secondary sexual exoskeletal structures in one particular Ordovician trilobite family, Raphiophoridae.

## 2. RAPHIOPHORIDAE AS A TEST CASE FOR SECONDARY SEXUAL CHARACTERISTICS

The family Raphiophoridae were a diverse clade of predominantly Ordovician trilobites, which were common in outer shelf palaeoenvironments worldwide. Raphiophorids are small, blind trilobites, and all of them have slender genal spines that are usually much longer than the rest of the body, excluding any frontal spine. They are considered to have had benthic or nektobenthic habits, which are matched by their inferred weak thoracic musculature in relation to their peripherally extended exoskeletal structures. Within the family there is a variety of median glabellar structures, mostly variations on spines (figure 1), although the existence of several genera (*Mendolaspis*, *Ampyxina*), in which the median spine is reduced or absent, demonstrates that it was not a *sine qua non* for successful life as a raphiophorid.

(i) Anterior spine in *Ampyx* is long and slender, tapering slowly, with a round cross-section. The silicified species from the Middle Ordovician of North America, including *Ampyx virginiensis* (figure 1*a*,*b*), have distally upturned spines, but *Ampyx spongiosus* (figure 1*c*) has a spine that is declined gently distally. Here, we figure an undescribed species of *Ampyx* in which the spine rises vertically from the mid-part of the glabella and curves backwards distally (figure 1*d*).
(ii) Anterior spine in *Lonchodomas* has a prismatic cross-section, and the glabella often protrudes towards it, making a lance-like structure.
(iii) Anterior spine of *Bulbaspis* (Chugaeva 1958), from the Ordovician of Kazakhstan and China is also directed upwards, but distally it is inflated into a balloon-like structure (figure 1*e*).
(iv) Anterior spine of *Ampyxoides* is short and straight.

As to function, several possibilities might be suggested for use of the anterior spine, which can be largely discounted by a consideration of the functional morphology of the animal as a whole, or by comparison with related species. The production of such a striking structure is likely to have entailed a considerable metabolic cost, and it surely played an important role in the life of the trilobite.

### (a) *Hydrodynamic streamlining*

Glabellar extensions that reduce surface turbulence are known from a number of actively swimming trilobites (Fortey 1985), but in these cases, the rest of the exoskeletal morphology is completely different. *Symphysops*, for example, has very large eyes, a compact thorax and pygidium with evidence of strong musculature—all features associated with pelagic habits. Raphiophorids are, by contrast, blind, flattened and weakly muscled, and their occurrence seems to be closely related to substrate type. Furthermore, although some of the structures may seem hydrodynamically efficient, it is evident that the balloon structures of *Bulbaspis*, or the vertical spines of some *Ampyx* species, are anything but. This does not rule out other hydrodynamic effects of spines, such as increasing drag to allow greater velocity gradients during filter feeding, but these effects are most pronounced in small planktonic animals (less than 0.5 mm in length; Emlet & Strathman 1985) and would be unlikely to be important in these trilobites, which were usually between 10 and 30 mm in length.

### (b) *Protection*

It is possible the anterior spines of *Ampyx*, in conjunction with the genal spines, may have served to present a comparatively large, spiny target for any potential

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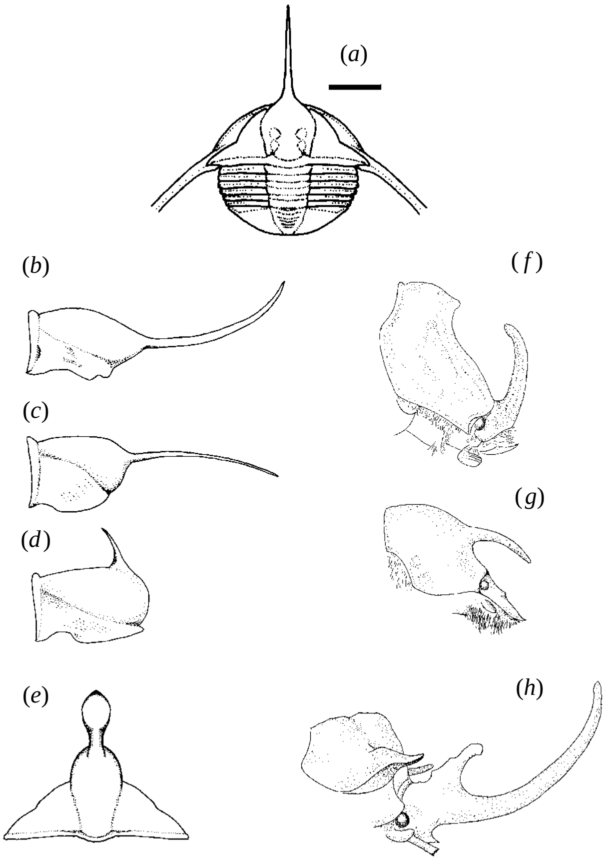

Figure 1. Diversity of anterior structures in the Raphiophoridae compared with similar structures in the Coleoptera. (*a*) Reconstruction of *A. virginiensis*, dorsal view, after Whittington & Campbell (1967). Scale bar represents 5 mm. Note that the long genal spines are not shown completely. (*b*) Cranidium of *A. virginiensis*, right lateral view. (*c*) Cranidium of *A. spongiosus*, right lateral view. (*d*) Cranidium of undescribed species of *Ampyx* (see text), right lateral view. (*e*) Cranidium of *Bulbaspis mirabilis*, dorsal view. (*f*) *Oryctes rhinoceros*, (*g*) *Oxysternon spiniferum* and (*h*) *Megasoma elephas*, all from the Coleoptera. (*b*)–(*e*) all approximately ×3, (*f*) ×1, (*g*) ×3, (*h*) ×1/2.

predator, in a similar fashion to the inducible spines of modern *Daphnia* that limit the ability of gape-limited predators (Dodson 1989). However, such adaptations in modern animals are mostly found on free-swimming animals, and anti-predator defences on benthic arthropods, such as odonate nymphs (Arnqvist & Johansson 1998) and also many trilobites (Fortey & Owens 1999), often consist of more robust spines carried on the back. The diversity of the spines of the Raphiophoridae also argues against a defensive role: it is not easy to imagine a defensive role for the full variety of spines found in the family. Thus, in the case of raphiophorids it does not seem likely that the prime function of the spines was for protection, although it is not possible to rule it out completely. The fact that there are several ‘spineless’ genera in the same family indicates that such putative protection was not invariably required.

### (c) *Sensory apparatus*

The known examples of raphiophorid frontal spines show no evidence of distal perforation or other openings for subcuticular organs, or sensory cells. Small spines on the dorsal cephalic surface of many trilobites frequently do have such terminal perforations, which are often interpreted as marking the site of sensory setae. As far as one can tell, the raphiophorid spine is an extension of normal cuticle, and carries no such structures. This does not rule out any use of the spine as a sensory apparatus, of course, and even without sensory setae on the spine, sensory information could be transmitted to receptors at the base of the spine, but it does make a primary sensory function unlikely.

### (d) *Camouflage*

It has been suggested (G. Kloc, personal communication) that strongly spinose trilobites such as odontopleurids may have encouraged dorsal epibionts that served as camouflage. There is no evidence of attachment scars for epibionts on any raphiophorid known to us.

These functional explanations are all unsatisfactory. The remaining explanation is that the anterior structures are secondarily sexual in character.

## 3. WERE THE ANTERIOR SPINES OF *AMPYX* ANALOGOUS TO BEETLE HORNS?

Secondary sexual characters are widespread throughout the animal kingdom (Andersson 1994) and structures arising from the head of the animal are very common. Among the arthropods the greatest diversity of these is found in the Coleoptera, and in particular, in the many species of Scarabaeidae and Dynastinae that bear horns (Andersson 1994; Emlen 2000). These horns exhibit a wide range of forms. One of the most common is a single median horn, protruding forwards and upwards from the head of the beetle and curving slightly backwards—the iconic examples of which are found in the dynastid genus *Oryctes*, the rhinoceros beetles (figure 1*f*), but other beetles carry a huge diversity of horns (figure 1*g*,*h*) that may grow from the thorax (figure 1*g*) or from other parts of the body as well as from the head. Functionally, a number of studies have demonstrated that these horns are used as weapons in intraspecific contests between males competing for access to mates (Palmer 1978; Eberhard 1978; Rasmussen 1993; Emlen 2000). The anterior spines of the Raphiophoridae are structurally similar to some beetle horns, and it is tempting to interpret them as being analogous structures: sexually selected weapons that played a role as weaponry in intrasexual contests and were used, like beetle horns, to overturn, push or lift rivals. A number of other lines of evidence support sexual selection as an explanation for the evolution of these spines: their ontogeny, their diversity, their allometry in the holaspid and the presence of possible examples of sexual dimorphism in some cases.

## 4. ONTOGENY

Whittington (1959) described the ontogeny of *A. virginiensis*. While the anterior spine was present on the juvenile stages of the trilobite, it was much reduced, being only a short stub in the protaspid and relatively much shorter in the meraspid than in the holaspid. This observation implies that the spine was either non-functional in the juveniles or that the importance of spine length in determining juvenile fitness was much less than its importance in the adult trilobite.

## 5. DIVERSITY

Both the horns of beetles and the anterior spines of raphiophorids are highly variable between species, with quite radical differences in structure between members of the same genus. This diversity argues against a common functional explanation that is not associated with sexual selection; the adaptive peak associated with many other possible functions (such as hydrodynamic advantage) would be narrow and we would expect less diversity of form. In the case of beetles, the variability of structure is probably a consequence of antagonistic intrasexual coevolution leading to different evolutionary trajectories in different species, and it may be that a similar process operated in these trilobites.

## 6. SCALING RELATIONSHIPS

The scaling relationships (static allometry) of sexually selected characters have been widely studied (Gould 1973; Petrie 1988; Simmons & Tomkins 1996) and the most common finding is that such characters are positively allometric; in other words, bigger animals tend to have relatively larger traits when these are sexually selected. This is not a universal pattern (Emlen & Nijhout 2000), but it is by far the most common type of allometry observed for sexually selected characters. Figure 2 shows the scaling relationship of spine length versus cranidium width for a sample of 12 *A. virginiensis*. Despite the small sample size, we find statistically significant positive allometry for spine length.

## 7. SEXUAL DIMORPHISM

Many animals that carry secondary sexual characters are also sexually dimorphic. If the spines of raphiophorids are secondarily sexual in nature we should be able to identify at least some examples of sexual dimorphism—fossils of trilobites that always co-occur in the same deposits, but having no, or a reduced spine—and there are some possible examples of this. In the case of *A. virginiensis*, for example, a spineless raphiophorid trilobite *Ampyxina* occurs in the same deposits. However, there are also examples where spine–bearing raphiophorids do not co-occur with a similar but spineless species; an example would be the early Ordovician formations described by Fortey & Owens (1987) from South Wales. Sexual dimorphism for the presence or absence of sexually selected characters is not universally observed in modern arthropods; however, there are many examples of beetle species with horned females as well as males (e.g. *Onthophagus vacca*), not to mention the entire family Diopsidae (Diptera), in which both males and females carry elongated eyestalks, even though they have no known function in females (Al-Khairulla *et al.* 2003).

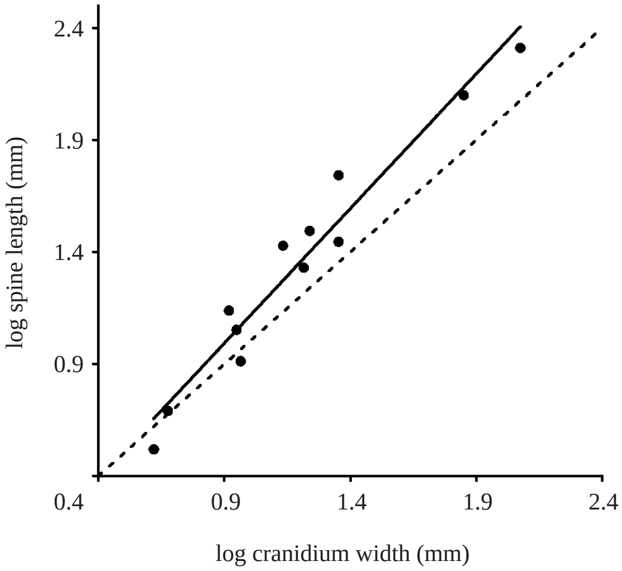

Figure 2. The positively allometric relationship between spine length and cranidium width for 12 specimens of *A. virginiensis*. The specimens used were from a bulk collection of silicified fossils dissolved out of limestone and held in the Natural History Museum, London. Only fossils from the same deposit were used. The fitted line is from a standard least-squares linear regression, and has a slope that is greater than 1 (slope = 1.20, $t_{10} = 2.34$, $p < 0.05$). Using a reduced major axis regression (Harvey & Pagel 1991) to take account of error in the $X$ coordinate gives a similar result (RMA slope = 1.24, 95% confidence intervals 1.041–1.430). The dashed line shows a slope of 1.

To summarize, a number of independent arguments favour the interpretation of the anterior spines of raphiophorid trilobites as secondary sexual structures. The evidence for positive allometry combined with morphological comparison makes the case a reasonable one, with further support from the diversity of these structures and the existence of at least some possible examples of sexual dimorphism. Taken individually, none of these would make a convincing case, but when these various lines of evidence are considered together, we find a strong case for these structures being sexually selected weapons, albeit not yet proven. By analogy to the horns of beetles, a function for the spines as weaponry used during intrasexual contests seems the most likely, but alternatives such as ornaments used during mate choice are also possible. There remain reasonable alternative explanations that we cannot discount entirely, such as protection, and of course it is possible that these spines had more than one function during the lives of these animals.

## 8. OTHER POSSIBLE EXAMPLES IN THE TRILOBITES OF SECONDARY SEXUAL CHARACTERS

Raphiophorids provide the best test case for the hypothesis that some cephalic structures had a secondary sexual function, but there are other trilobites with curious spines and processes that might suggest a similar purpose, for example, *Teratorhynchus*, an Ordovician remopleuridid with a vertical spine arising from the forward part of the glabella. The Cambrian *Diceratocephalus* has a long pair of anteriorly directed spines originating on the cephalic border, while the eodiscoid *Dicerodiscus* has a pair of very long spines directed largely laterally. The most striking such example is the Devonian asteropygine *Walliserops trifurcatus* (see Morzadec 2001), which carries an extraordinary trident on the cephalon. At least two more species of *Walliserops* with smaller tridents are known in the field, but are not yet formally named (B. D. E. Chatterton, personal communication). It will be interesting to discover whether these species consistently co-occur with others in a way consistent with them being sexual dimorphs.

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