Reprinted from *Biomechanics and evolution*
edited by J. M. V. Rayner and R. J. Wootton

Printed in Great Britain

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Biomechanics of locomotion in fossil arthropods

Introduction

Only a limited number of studies of fossil arthropods have employed a biomechanical approach. When direct comparison with living relatives is possible, as for example in many Crustacea, theoretical or experimental biomechanical studies are not usually necessary to interpret functional morphology. The approaches have therefore been most widely applied to extinct arthropod groups or to taxa whose morphologies differ significantly from that of their living relatives. In such cases biomechanical studies may allow the mode of life of the arthropod to be elucidated more precisely than is possible from comparisons with living relatives or analogues, from deductions based on morphology, or from the evidence of external factors (such as the associated sediments and organisms, or distribution as an indication of benthic or nektonic habit). However, strictly biomechanical and other approaches should be complementary, the one providing a method of testing the other. Some biomechanical studies are of value to our general understanding of arthropod evolution.

The arthropods owe their outstanding evolutionary success in large part to their firm, jointed exoskeleton. Arthropod cuticle is a complex tissue with a variety of functions, but its use in conjunction with internal muscles in a simple, elegant and highly modifiable lever system is the most obvious characteristic of the arthropod grade of organization. A biomechanical approach to the study of arthropods implies consideration of the structures and movements of the exoskeletal system in a quantitative or semi-quantitative way.

Detailed biomechanical studies of the cuticle and limbs of fossil arthropods are relatively few, although there is a comparatively extensive literature on Recent arthropod material (see, for example, Herreid & Fourtner 1981). The approaches involved cover a wide area, impinging, for example, on the physics of lever systems, fluid mechanics, and material sciences. In this chapter we present a review of biomechanical studies on fossil arthropods and the methodologies involved, with a view to identifying directions for future investigation in this nascent research area.

Because of limitations of space, and because the biomechanical factors influencing the different major arthropod groups are similar, our treatment is functionally rather than taxonomically based. We consider the biomechanics of fossil arthropods under two major headings walking and swimming.

Walking

Walking has been extensively treated in living arthropods (see, for example, Manton (1977 and references therein) on uniramians and Hessler (1981, 1982) on eumalacostracan crustaceans), based essentially on observation and on the morphology of muscles and articulations. Manton also used trackways in her studies of uniramian gaits. The articulations of arthropod limbs are well preserved in fossils only occasionally, and direct evidence of the configuration of muscles, such as the tendons preserved in the eurypterid *Baltoeurypterus* (figure 1, Selden 1981), is rarely available. Restoration of the musculature must usually rely on the configuration of podomeres and the articulations between them. In some cases trace fossils can be used to deduce likely gait patterns.

Manton (1977 and references therein) demonstrated the two simple movements employed by arthropods in walking. These are promotor–remotor movements at the coxa–body junction (or coxa–trochanter in Chelicerata) and levator–depressor movements which are effected by the articulations between the more distal podomeres. Most arthropod limbs conform to a plane (the 'limb-plane') in which the levator–depressor movements take place. This plane may be orientated in different attitudes to the body during the promotor–remotor movement at the coxa–body junction. Movement which is not confined to the limb plane usually occurs in appendages which are used for functions other than walking (e.g. grooming, feeding, burrowing). Walking as a result of movement in a limb plane is more effective than that achieved by bending the limb plane (whether the limb functions as an extensible strut, or as a lever (Hessler (1982, p. 291) gives a brief discussion)).

Manton (1977 and references therein) has elucidated the controls on the gaits of living myriapods. The stepping movements of long series of limbs have to be regulated in metachronal waves to avoid interference between successive appendages. The phase difference between appendages and the

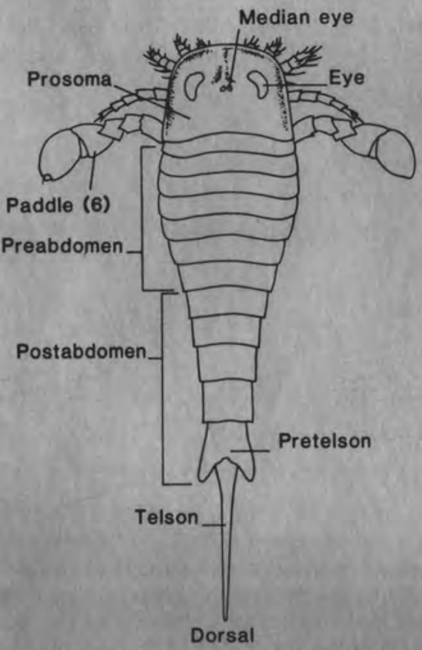

Figure 1. The Silurian eurypterid *Baltoeurypterus tetragonophthalmus*, seen in dorsal view.

consequent length of the metachronal wave can be varied to some extent in response to functional requirements. The ratio of recovery forward stroke to propulsive backstroke will also influence the force exerted by the arthropod on the substrate; a millipede will use a much lower geared gait (large proportion of limbs in contact with the ground at any time) when it is pushing through vegetation than when it is running on open ground.

The gaits employed by fossil arthropods have been studied in two ways the first is based on functional analysis including aspects of biomechanics, the second on trace fossils.

Functional analysis

Analysis of gaits relies on evidence for the nature of the limbs. Such an approach can therefore be applied only to arthropod groups with well sclerotized and therefore readily preserved appendages such as eurypterids and arthropleurid myriapods. Rarely, exceptional circumstances lead to the preservation of the lightly sclerotized limbs of other arthropods such as trilobites.

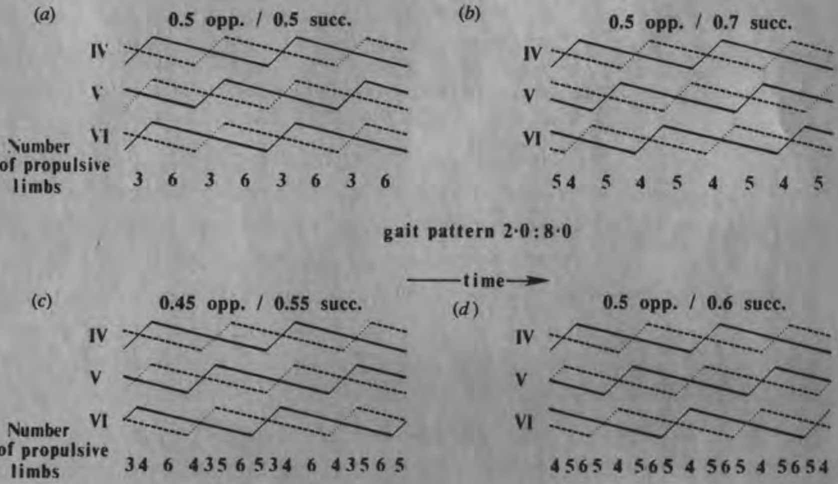

Figure 2. (*a–d*) Diagrams of four possible gaits in *Baltoeurypterus* in the style of Manton (e.g. fig. 7.3 of Manton 1977). Right limbs are denoted by solid lines: thin in the forward (recovery) stroke and thick in the backward (propulsive) stroke. Left limbs are denoted by broken lines: dotted in the forward stroke and dashed in the backstroke. Two cycles are shown in the diagram for limbs 4, 5 and 6. (After fig. 15 of Selden 1981, phase difference notation modified to conform to Manton's (1977) conventions.)

The most detailed analysis of eurypterid gaits based on functional analysis is that of Selden (1981) on *Baltoeurypterus* (figure 1) from the Silurian of Estonia and Gotland. The evidence both from morphology (length of limbs, position of centre of gravity) and from trace fossils indicates that eurypterids employed hexapodous gaits. Assuming hexapody, the range of possible gaits can be discussed on the basis of considerations of stability Walking is more efficient with the limbs on opposite sides of the body out of phase. The gait patterns are likely to have been low geared: this would have ensured a relatively long overlap in the time during which successive limbs are in contact with the substrate, thus conferring greater stability Speed could have been increased by reducing the pace duration as in arachnids, rather than by altering the gait pattern as in uniramians.

It is likely that eurypterids would usually have walked with a ratio of forward to backstroke of about 2.0:8.0 (that is 80% of the limbs would have been in contact with the substrate at any one time). Assuming this pattern, Selden generated a series of gait diagrams (figure 2) in the style of Manton (1977 and references therein) varying the phase differences between opposite and between successive limbs. The number of limbs in contact with the substrate at different points in the diagram gives an indication of the stability of the gait. Selden (1981) showed how a three-dimensional graph (figure 3) could be plotted to show the number of limbs in contact with the substrate over the possible range of phase differences in both opposite and successive limbs and of ratios of forward to backstroke duration. The diagram clearly shows that phase differences around 0.5 opposite and 0.5 successive produce the most stable gaits. High or low phase differences result in gaits which include intervals when no limbs are in contact with the substrate or when all three limbs in contact are on the same side of the eurypterid!

In analysing walking in *Baltoeurypterus*, Selden (1981) had the advantage of well preserved isolated cuticle, which permitted accurate restoration of the articulations between the podomeres. His analysis suggested minor flaws (Selden 1981, p. 29) in the gaits previously deduced from morphology for *Parastylonurus* (Waterston 1979) and for *Mixopterus* (Hanken & Størmer 1975) based on a fossil trackway. Both these studies, however, also indicated a hexapodous gait with the limbs on opposite sides of the body out of phase.

Olenoides, from the Middle Cambrian Burgess Shale of British Columbia, is perhaps the most completely known of fewer than ten trilobites so far discovered with well preserved appendages. Trilobites, unlike myriapods, were incapable of lateral flexure. Whittington (1975) argued that walking in *Olenoides* involved all the biramous appendages apart from the last two in the pygidium. The gait which he deduced was based largely on a comparison with the gaits of living myriapods (and the work of Manton (1977 and references therein)). The opposing limbs of each pair probably moved in phase. The nature of the limb articulations in *Olenoides* is unknown; Whittington argued that the coxa–body articulation may have been followed by two pivot joints and then hinge joints. This deduction is based largely on the requirement for a hanging stance to promote stability Considerations of leg length and the likelihood of slow movements close to the substrate led Whittington to postulate a relative duration of forward and backward strokes of 3 to 5 (a gait pattern of 3.75 6.25). An angle of swing of 16° was selected (4° in front of a transverse plane, 12° behind) and a phase difference of 0.125. By using this postulated gait, Whittington was able to generate a theoretical trail, but a closely similar trackway has yet to be discovered in the fossil record.

Trace fossils

Seilacher (1955) made an early contribution to the study of fossil arthropod trackways in his interpretations of trilobite trails from the Cambrian of the Salt Range in Pakistan. Osgood (1970) attempted to assign

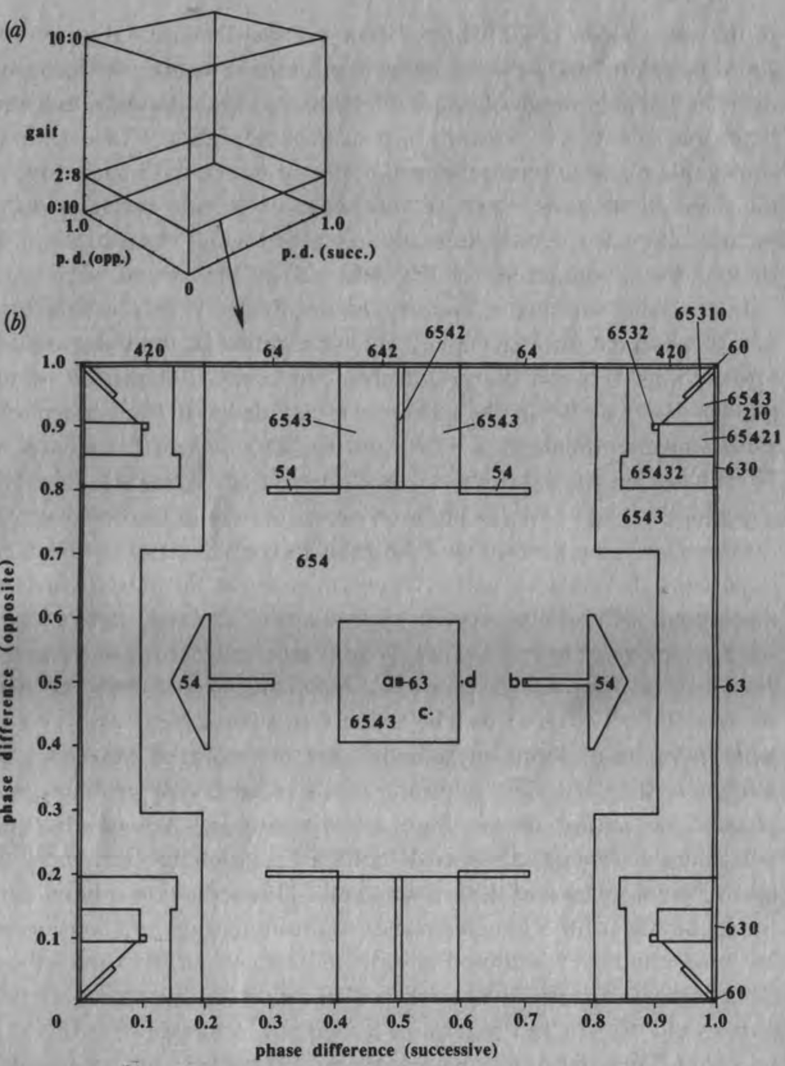

Figure 3. Gaits in *Baltoeurypterus*. (*a*) Three-dimensional graph of phase difference between opposite limbs (*x* axis), phase difference between successive limbs (*y* axis), and gait pattern (*z* axis). The position of the two dimensional slice at gait 2.0·8.0 shown in (*b*) is indicated. (*b*) Matrix of the number of propulsive limbs during hexapodous walking in the gait pattern 2.0.8.0 related to the phase differences between opposite and between successive limbs. The numbers (654, 63, etc.) refer to the number of propulsive limbs at all points in the cycle of the gait, for example, in figure 2*a* the number of propulsive limbs covering all points in the cycle is referred to as 63. The positions a, b, c, and d refer to the gaits in figure 2. Minimum stability is afforded by three limbs, no gait with a number less than this is possible. Equally, gaits (such as 6543 on the left and right sides of the

trail makers to arthropod trace fossils from the Ordovician of Ohio based essentially on number of imprints in a set, size, and associated (and therefore 'available') body fossils. Briggs & Rushton (1980) identified the influence of bottom currents on the formation of a trilobite trail from the Upper Cambrian of north Wales. A major shortcoming of all such studies is the absence of independent evidence on the nature of the limbs. Indeed, owing to the different conditions required for their preservation, body fossils of organisms are rarely found in association with the traces which they produce. Thus the two most useful lines of evidence for the gaits of fossil arthropods, preserved appendages and trackways, can rarely be used in association.

On rare occasions it is possible to identify the arthropod responsible for a particular trail. This necessitates first a knowledge of the limbs, and second a characteristic morphology which results in a trail with diagnostic attributes. Such a combination is usually confined to arthropods with well sclerotized appendages. The trackway of the Silurian eurypterid *Mixopterus* (Hanken & Størmer 1975) has been briefly mentioned above. The most detailed analyses of walking based on trace fossils are those of the giant Carboniferous myriapod *Arthropleura* (figure 4).

Arthropleura is one of the largest arthropods known, reaching lengths of up to 1.8 m. Trackways are known from the Upper Carboniferous of Arran (Scotland), Montceau-les-Mines (France) and New Brunswick (Canada). The best preserved of these is the example from Arran (Briggs, Rolfe & Brannan 1979, Briggs 1986*b*). The Arran trackway allowed the identification of repeated imprints of the shorter limbs which plotted inside the rest and were not obscured by subsequent footfalls. This indicated a stride length of 22 cm. Identifying the stride length made the following possible

(1) Estimation of the number of limbs used in walking. All of the limbs must plot within the stride. Briggs *et al.* (1979) identified 23 imprints within the stride in the Arran trace. Where appendages are evident near the posterior of some of the small arthropleurids from Montceau-les-Mines, two pairs appear to correspond to each tergite (Almond 1986) as opposed to the one previously reconstructed

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matrix) in which three limbs of one side only are in contact with the ground at one point in the cycle are ruled out. Note that the matrix is symmetrical, but that the shapes of the enclosed areas would be different at different gait patterns (z values). The matrix for 8.0:2.0 gait pattern would look the same, but have different numbers in the enclosed areas. (After fig. 14 of Selden 1981, phase difference notation modified to conform to Manton's (1977) conventions.)

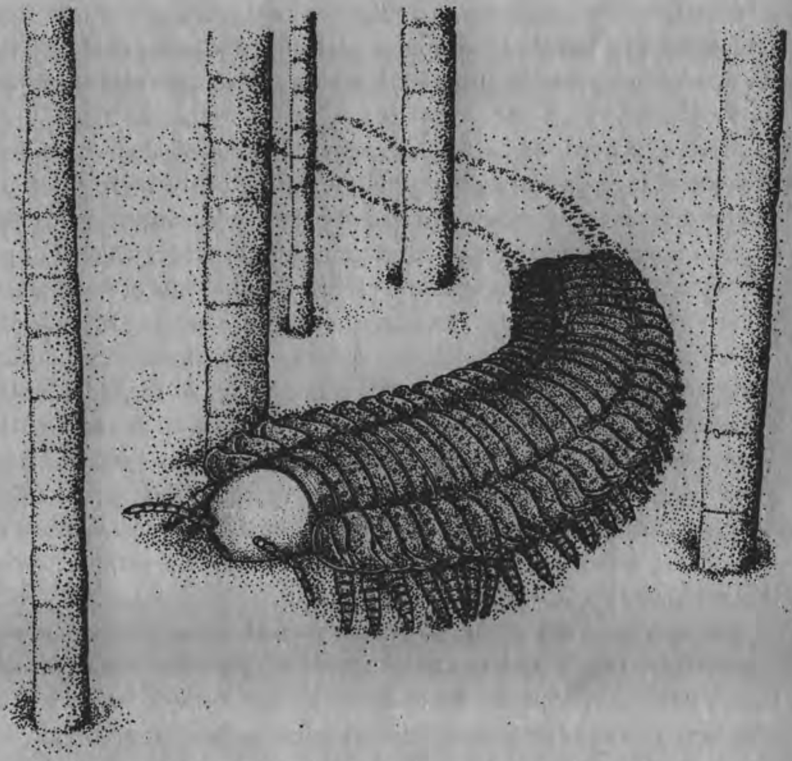


Figure 4. The giant late Carboniferous myriapod *Arthropleura armata* making the New Brunswick trackway as it walked through a stand of calamites. The detailed morphology of the head is unknown (and reconstructed differently by Hahn *et al.* (1986)). This reconstruction shows one pair of walking limbs per tergite (see discussion in text). (After fig.5 of Briggs *et al.* 1984.)

(Rolfe 1969). In addition, W. D. I. Rolfe (personal communication) has drawn our attention to evidence of an excess of paired limbs over tergites in the largest known body fossil of *Arthropleura* illustrated by Hahn, Hahn & Brauckmann (1986). Their figure (Pl. 2 of Hahn *et al.* 1986) of a portion of the ventral surface shows eight limbs corresponding in position to not more than five, possibly only four, of the dorsal tergites (see their Pl. 1). None the less, Hahn *et al.* (see their fig. 2) restored *Arthropleura* with only one pair of limbs per tergite. If the number of paired walking limbs in *Arthropleura* did exceed that of tergites, the interpretation of 23 pairs of walking limbs in the Arran trace will require revision (diplotergites would imply an individual with perhaps as few as 12 tergites, but a width between the limb extremities of about 36 cm!). It is possible that Briggs *et al.* (1979) underestimated the number of limbs plotting within the stride, and that some of the depressions represent multiple footfalls (Briggs 1986*b*).

(2) *Demonstration that opposing limbs moved in phase.*

(3) *Analysis of the gait.* Assuming a maximum angle of swing and length of limb (based on body fossils) it was possible to calculate that the backstroke is unlikely to have exceeded 10 cm. Given a stride length of 22 cm this indicates a gait of 12 10 (that is 5.5.4.5). Such a gait is much faster (higher geared) than is suggested by the usual habit of the arthropod, pushing through coal-swamp vegetation. It is likely, however, that *Arthropleura* employed a different range of gaits when walking on more open ground.

(4) *Plotting of a theoretical trail.* This trail compared closely with the trace-fossil and confirmed the major conclusions of the analysis.

The New Brunswick trail (Briggs, Plint & Pickerill 1984) confirmed that the trunk of *Arthropleura* was laterally flexible and showed that the anterior appendages were used to probe laterally as the arthropod changed direction (figure 4). Thus, where the trail maker can be identified, trackways can yield important insights into the functional morphology and biomechanics of the arthropod.

Walking on land· limitations on body size

Dalingwater (1985) attempted to assess whether large Carboniferous eurypterids could have walked on land. He used extant *Limulus* as a model, as it is primarily an aquatic animal but capable of excursions onto land. Although many of the mechanical properties of *Limulus* cuticle are known, calculation of the maximum stresses imposed on limb podomeres while the animal is walking would require a knowledge of limb postures and the effects of muscular action. Experiments with some type of force platform would probably produce more accurate results, but that approach is clearly not applicable to fossil arthropods! Calculation of the stresses on the limbs of extinct eurypterids in an indirect biomechanical approach requires many assumptions and approximations (about the mechanical properties of the cuticle, its original thickness, limb postures, gaits etc.) but an alternative approach, still with *Limulus* as a model, involves a consideration of scaling exponents. This provides more useful, and considerably more general, conclusions.

Measurements were made from a size series (32–147 mm carapace width) of *Limulus* to document the changes in relative dimensions (length, diameter and cuticle thickness) of a particular limb podomere with increasing mass. The exponent for increase in cuticle thickness against carapace width was 1.15. This lies within the range reported by Prange (1977) for wolf-spiders (1.0) and cockroach (1.38), but is well below that expected from theoretical considerations if the increase in cuticle mass is achieved solely by an increase in cuticle thickness (Dalingwater 1985, Anderson, Rahn & Prange 1979). Thus one of the factors traditionally considered to limit the size of land arthropods – that in order to maintain mechanical similarity with increasing size, cuticles would become too thick to leave sufficient space for muscles within the limbs – may not be such a crucial factor after all. Clearly larger arthropods offset potentially unacceptable stresses on limbs in other ways, for example by changes in shape or in skeletal materials, or by a reduction in locomotory performance.

The soft cuticle of a newly moulted arthropod of even moderate size would be unlikely to support its body mass on land, let alone resist the stresses imposed in crawling out of the exuvium. (Dalingwater (1985) calculated that the newly formed cuticle of tibia 1, walking leg 3, of a *Limulus* with 75 mm carapace width could support the static axial load resulting from the weight of the animal, but that with increased size even the static axial load would become near-critical. He concluded that it is unlikely that even a relatively small *Limulus* could moult on land.) Thus truly terrestrial arthropods could not even approach the cow-sized mass conjured up by Neville (1975) to illustrate the constraints on moulting in larger arthropods. *Arthropleura* (figure 4) had to return to water in order to moult. Célérier (1986) showed that exuvia production represents 5.2–16.2% of growth production for the whole period of post-embryonic development in six spider species. It reaches 50% of growth production in large adult females of the theraphosid spider *Scodra griseipes*, which, unusually for spiders, moults throughout life (few spider species moult after reaching adulthood). Thus the energy costs of exuviation may have limited the size of arthropods. To this must be added Dalingwater's (1985) suggested size constraints on aquatic arthropods, some of which are also related to moulting. These include (1) the time taken to produce the cuticle, since the surface area of the epidermal cells produces a volume of material which becomes disproportionately greater with increasing size; (2) the cells must also produce increasing volumes of moulting fluid, and (3) the effects of impact and of wear and tear on the cuticle become more critical with increasing size and concomitantly longer periods between moults. It must be conceded, however, that none of these factors, all of which are related to the properties of the exoskeleton, may be critical in limiting size. Others, such as respiration, might be more important. Size may well be limited by a cumulative combination of the disadvantages accruing from various factors.

It seems unlikely on theoretical grounds that a spider could have achieved a body length of about 35 cm (Hünicken 1980), or that eurypterids with body lengths around 2 m could have thrived (Plotnick & Baumiller 1988), albeit in water where there were fewer limitations on large size than on land. That such sizes were achieved, in spite of the number of possible constraints, indicates that there were considerable ecological and evolutionary advantages in being large during certain periods of geological time. The advantages may have differed at different times· Rolfe (1980) has suggested that large size in some Devonian eurypterid stocks may have served to reduce desiccation in periods of drought, or to facilitate regular forays onto land. Large size was presumably an adaptive response to optimal environmental conditions which were stable for significant intervals of time, as giant arthropods would have been particularly susceptible to resource fluctuations (Briggs 1985).

Biomechanical considerations thus indicate that larger eurypterids are likely to have been at best amphibious rather than fully terrestrial. In addition Selden (1985) has argued that the true gills of eurypterids are not known, and that the so-called gill tract preserved in some eurypterids may be an accessory respiratory organ for air-breathing. The area of the gill tract relative to body mass is an order of magnitude lower than that of the gills in living Crustacea. If the eurypterid gill tract is an air-breathing organ it is closer in morphology to the pseudo-tracheae which occur in the limited number of terrestrial isopods and crabs rather than the book-lungs of scorpions, the development of which led to a much more extensive terrestrial radiation.

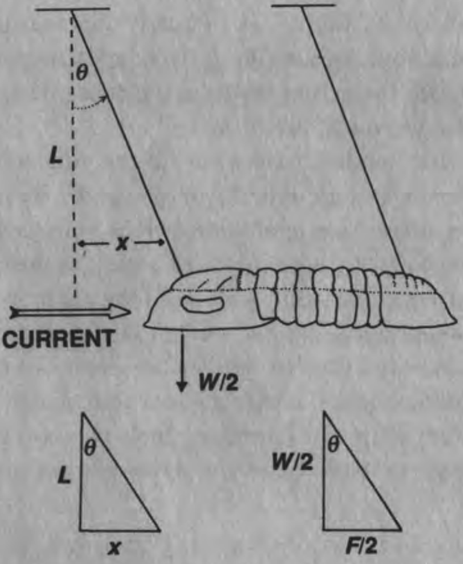
There is also limited (and equivocal) evidence from palaeoecology and trace fossils that eurypterids were not fully terrestrial. A population of eurypterid trackways from the late Silurian of the Murchison district of Western Australia which were apparently made sub-aerially indicate that the animals used a 'lurching' hexapodous gait with the opposing appendages in phase. Although there is no median groove produced by dragging the abdomen, readjustment of the gait at intervals indicates that the arthropods were not well adapted for walking on land (personal communication by K. J. McNamara, who is studying these trace fossils). A large, probably terrestrial, eurypterid trackway 79 cm wide from the Mississippian of Pennsylvania (Briggs & Rolfe 1983) suggests that this giant eurypterid was not primarily adapted for locomotion on land. The trace fossil preserves a median groove, and the right and left tracks are in phase. This indicates that the arthropod was unable to keep the trunk clear of the substrate, and adopted a powerful low-geared gait keeping most of the appendages in contact with the ground at any time. This allowed it to walk slowly out of water, dragging the abdomen along. Thus large eurypterids with thick cuticles may have invaded coal-swamp forests during the early Carboniferous, when such a relatively new habitat would have provided little opposition or competition. Small eurypterids occur inside hollow Carboniferous (Westphalian) tree-stumps at Joggins, Nova Scotia (Rolfe 1980), which they may have inhabited to avoid desiccation. Trackways of some of the later Carboniferous forms would be more significant in the search for evidence of terrestrial eurypterids.

Swimming

The assumption that an extinct arthropod could swim may be tested by biomechanical analysis but this invariably involves comparison with swimming models derived from studies on living animals. If virtually the whole animal is preserved, as in many eurypterids, then the entire natatory system can be investigated; if, as in most trilobites, the appendages are not preserved then only certain aspects of the model can be tested. Three approaches are reviewed here: (1) measurements of body drag on arthropods without preserved appendages, (2) studies of fossil arthropods with tail flukes, and (3) investigations of the swimming system as a whole in well preserved arthropods, illustrated by the eurypterids.

Body drag

Fortey (1985) used pelagic trilobites to illustrate the methods used in deducing the modes of life of extinct arthropods. He recognized three important criteria· (1) analogy with living forms, (2) mechanical design, and (3) geological evidence. Only the second of these involves biomechanics, but the other two can sometimes provide an independent test of an hypothesis. Fortey (1985, p. 223) identified two categories of pelagic trilobite· poorly streamlined, generally spinose forms, and well streamlined forms. Body drag was measured by using resin casts suspended in a water current and the flow around the body was studied with potassium permanganate. Drag was calculated on the basis of the deflexion of a thread supporting the trilobite in the current (figure 5). The absolute values of drag are largely irrelevant to this study, but the relative values supported the hypothesis of active



$$\tan\theta = \frac{x}{L} = \frac{F}{W} \qquad F = \frac{Wx}{L}$$

Figure 5. Experimental measurement of total drag F on a trilobite model suspended in a current. W is the immersed weight of the model, x the deflexion of the thread measured through a travelling microscope at given length L. (After fig. 8 of Fortey 1985.)

swimming in the well streamlined group. Additionally, one of the 'control' genera, *Ogygiocarella*, bucked and planed even in a gentle current, but proved to be very resistant to lifting even by strong currents when settled on the bottom of the flume, thus supporting a benthic mode of life.

Fisher (1975) investigated swimming in Recent *Limulus* and the related Jurassic *Mesolimulus*, a more flattened form. These arthropods swim inverted, presenting the carapace to the water in the form of the hull of a boat. Fisher, like Fortey (1985) after him, made models of the animals and studied the flow patterns (by using oxygen bubbles) in a tank, at various angles of attack. By observing at which angle of attack and flow speed the wake vortex offered least resistance to propulsion, Fisher deduced the optimum values for normal swimming. Observations of live *Limulus* swimming at the same speed (10–15 cm/s) and angle of attack (20–30°) provided an independent test of the experimental results. The flatter carapace of *Mesolimulus* would have enabled it to swim at 15–20 cm/s with an angle of attack of 0–10°. The stroking rate of the propulsive appendages (f_s) should equal the vortex shedding rate (f_v), and calculations and observations on *Limulus* showed both rates to be about 2 Hz. Equally the measured f_v of *Mesolimulus* of 1.7 Hz should approximate the f_s of its appendages in life. Thus it is possible to investigate the action of the appendages of an extinct arthropod on the basis of fossils which lack them!

Fisher (1977) also used resin models to investigate the function of the prosomal spines in the Carboniferous limuline *Euproops danae*. He prepared models of enrolled *Euproops* at two sizes and with various lengths of spine. During passive settling through a water column, those closest in morphology to the real animal at both juvenile and adult sizes equilibrated most rapidly and descended with the least amount of lateral oscillation. Vertebrate visual and lateral line systems are tuned to detect the lateral movements of potential prey rather than passively falling objects. Fisher therefore concluded that the *Euproops* prosomal spines were adapted to produce stable passive settling in the enrolled animal as a device to avoid detection by vertebrate predators.

Tail flukes

Undulations of the body (axial swimming) are rare in arthropods, which more commonly use paired appendages (paraxial locomotion) in swimming. The reverse is true in vertebrates (Herreid 1981, Riess & Frey, this volume). Decapod crustaceans such as lobsters and crayfish use a tail fan (telson and uropods) in rapid backward escape-responses, but their abdominal morphology does not allow undulatory swimming. Some of the eurypterids, the pterygotids, had broad, dorso-ventrally flattened telsons which might have been used in undulatory swimming, in a tail-flip escape-response, or to aid stability These eurypterids had flipper-like sixth prosomal appendages which clearly functioned in swimming. Some pterygotid telsons had a dorsal, vertical, median keel in addition to the lateral flukes (figure 6), in these species the telson probably functioned in steering and stabilizing (Størmer 1936, Briggs 1981) and is unlikely to have been used in axial propulsion (Plotnick & Baumiller 1988). A triradiate tail also occurs in the non-swimming eurypterid *Parastylonurus ornatus* and was used to provide stability and lift for the opisthosoma during walking (Waterston 1979). A unique triradiate tail occurs in the large Middle Cambrian nektonic arthropod *Odaraia* (Briggs 1981). The vertical fluke and very high aspect ratio indicate that the tail was used in stabilizing (particularly critical with an essentially tubular carapace) and steering. Further investigations of fluked tails in eurypterids should consider three paradigms (1) a steering/stability organ, (2) an undulatory swimming device, and (3) a tail-flip escape mechanism. Analyses to date suggest that the first was the normal function.

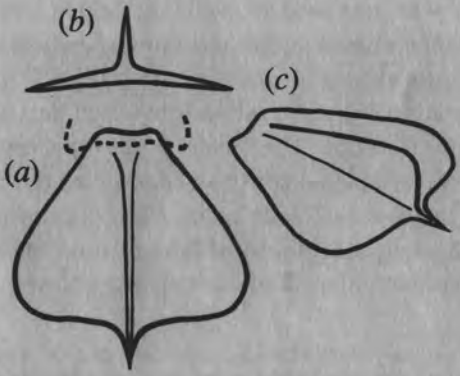


Figure 6. Telson of the pterygotid eurypterid *Jaekelopterus rhenaniae*. (*a*) Dorsal view, with dashed outline of pretelson. (*b*) Cross-section. (*c*) Oblique view. (After fig. 6 of Størmer 1936.)

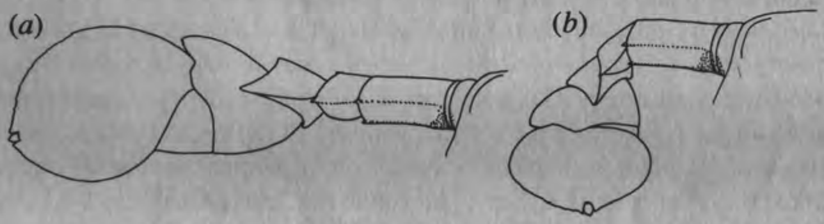


Figure 7 Left swimming appendage (6) of *Baltoeurypterus tetragonophthalmus* viewed from above and behind. (*a*) Outstretched halfway through the propulsive stroke. (*b*) Collapsed halfway through the recovery stroke. (After fig. 7 of Selden 1981.)

Studies of swimming considering the arthropod as a whole

eurypterids

The eurypterids included the largest known arthropods, ranging up to 2 m in length, thus at least the larger ones must have swum at Reynolds numbers (*Re*) which are more suited to a lift-based rather than a drag-based swimming system (fig. 2 of Nachtigall 1978). Eurypterids are often sufficiently well preserved to allow their swimming appendages (modified sixth prosomal limbs) to be reconstructed in detail, and none more so than the Silurian eurypterid *Baltoeurypterus* (figures 1, 7). This eurypterid reached lengths of 45 cm and thus had a lower *Re*, in the range in which either lift – or drag-based swimming was appropriate (Selden 1984).

A comparison of the morphology of the swimming appendage in *Baltoeurypterus* (figure 7) with drag-based (paddle) and lift-based (flipper) mechanisms in living animals indicates that the *Baltoeurypterus* limb functioned as a paddle (but was also used in walking; Selden 1981). The evidence for this includes (1) the proximal joint morphology, which allowed anterior–posterior but not dorso-ventral movement, and (2) the long proximal podomeres and broad 'oarblade' termination, which had neither a flipper-like shape nor a hydrofoil section. The 'blade' is not broadest distally as in an ideal oar, owing to constructional constraints and the need to use it in walking. Complex joints enabled the blade to be folded in the recovery stroke to reduce drag, the drag on the cylindrical femur cannot be reduced in this stroke in any model. Tilting of the paddle would have allowed steering up, down and sideways.

The morphology of the *Baltoeurypterus* paddle and that of portunid crabs is remarkably convergent. Plotnick (1985) studied swimming in these crabs by using high-speed filming and measurements of lift and drag in a flow tank. He also made a model of a *Baltoeurypterus*—like eurypterid to determine body drag and mass. Plotnick's model of eurypterid swimming differed from that of Selden (1981) only in the introduction of a small amount of lift in the recovery stroke to counteract the presumed negative buoyancy (see Briggs (1986*a*) for discussion). This combination of drag in the propulsive phase and lift in the recovery phase is also a feature of Godfrey's (1984) model of plesiosaur locomotion, which is based on a comparison with otariid pinnipeds (see also Riess & Frey, this volume). Clearly drag- and lift-based modes of swimming need not be mutually exclusive. The largely drag-based mechanism deduced for *Baltoeurypterus*, which swam with a relatively high *Re*, remains anomalous. Investigations of swimming in the much larger pterygotid eurypterids will prove interesting in this context. The functional and constructional requirements for using the paddle in walking may have constrained any potential for evolving lift-based underwater flying.

Selden (1984) investigated the possible swimming speed of *Baltoeurypterus*. His estimates of *Re* (1.65×10^4) and body drag (3.0×10^{-3}N) compare well with those obtained experimentally by Plotnick (1985) with a wax model of a eurypterid at *Re* between 1.0×10^4 and 4.1×10^4, which gave 2.5×10^{-3}N. Selden's (1984) analysis was based on a simple rowing model (Alexander 1968), and compared the possible mean power-output of the coxal muscles with the mean power requirements of the oarblade system to obtain an estimate of maximum sustainable speed. A mean body velocity of about 38 cm/s and a mean paddle velocity of 109 cm/s were obtained. The efficiency was 0.29. For an animal about 16.5 cm long, a maximum speed of 2.5 times its body length per second does not seem to be unreasonable, and also conforms to that predicted by Hughes (in Selden 1984) based on an extrapolation of Nachtigall's (1977) studies of speeds in water beetles.

While such an estimate of swimming speed is intrinsically interesting, it also provides some corroboration of Selden's (1981) original model of drag-based rowing in *Baltoeurypterus*. However, a number of simplifications have been introduced into the calculation. A steady-state rowing mechanism (Alexander 1968) is assumed, although the animal proceeds in a sequence of faster propulsive phases and slower recovery phases under the effect of momentum. Total musculature was used in the calculation, although that for propulsion is more massive (as evidenced by the strong antero-inferior coxa–trochanter articulation; Selden 1981) than that for recovery. In addition, neither the power output of the muscles nor how it changed through the stroke cycle is known. Some power must have been used to provide lift, as the animal was certainly slightly denser than water. However, specific gravity and the lift requirement were probably minimized in an actively swimming eurypterid such as *Baltoeurypterus*, as in actively swimming Crustacea (Spaargaren 1980).

Conclusions

Even the small number of investigations which have so far used a biomechanical approach in research on fossil arthropods illustrate the important insights which such studies can yield. The paucity of applications to date may stem partly from a lack of appreciation of the potential of biomechanics, but may also reflect a suspicion of results far more precise than is apparently warranted by the nature of the data. However, as this review shows, the absolute values obtained in a biomechanical calculation are usually irrelevant to the broader questions addressed. Was *Arthropleura* relatively agile when moving across open ground compared to its presumed low-geared gait for pushing through coal-swamp vegetation? Could very large arthropods walk on land? Were certain widely distributed trilobites streamlined? How did eurypterids swim? Although we ultimately retreat from the exactitude of results obtained and draw conclusions on safer ground, the biomechanical approach is in no sense devalued. It introduces a precision into comparisons that is unobtainable with more qualitative methods of interpreting functional morphology. However, all biomechanical analyses, whether on living or fossil organisms, involve assumptions and simplifications. We have therefore emphasized the necessity of using a range of independent approaches to test conclusions (the shotgun approach of Brower & Veinus 1974). Thus not only should mathematical models or inferences drawn from analogy be tested by experiments, where appropriate, but geological evidence (trace fossils, distribution patterns etc.) should also be considered. Biomechanics has considerable potential for refining our interpretations of the palaeobiology of arthropods.

Acknowledgements

We are grateful to the Royal Society of Edinburgh and the Palaeontological Association for permission to reproduce figures.

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