

known varieties of skeletal minerals and most of the different kinds of mineral skeletons appeared within a few tens of millions of years at the beginning of the Phanerozoic. Innovations such as molluscan nacre, echinoderm stereom, and the characteristic prismatic calcite of the shells of articulate brachiopods were being manufactured by at least the Middle Cambrian. Hardly any new types of skeletal materials were evolved after the Cambrian and the only kinds of mineral skeletons that appeared during the invasion of the land were the carbonate eggshells of snails and vertebrates. Thus, although new kinds of organisms began to build mineral skeletons in post-Cambrian time (corals, bryozoans, calcareous and siliceous plankton, etc.), they used pathways pioneered previously by cyanobacteria,

eukaryotic algae, animal-like protists, and a large number of metazoan phyla.

References

- Bengtson, S. 1985. Taxonomy of disarticulated fossils. *Journal of Paleontology* **59**, 1350–1358.
- Jones, D.S. 1983. Sclerochronology: reading the record of the molluscan shell. *American Scientist* **71**, 384–391.
- Lowenstam, H.A. 1981. Minerals formed by organisms. *Science* **211**, 1126–1131.
- Mann, S. 1988. Molecular recognition in biomineralization. *Nature* **332**, 119–124.
- Seilacher, A. 1979. Constructional morphology of sand dollars. *Paleobiology* **5**, 191–221.
- Vermeij, G.J. 1970. Adaptive versatility and skeleton construction. *American Naturalist* **104**, 253–260.

4.3 Biomechanics

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Introduction

Biomechanics is the application of mechanical principles to the study of organisms. In palaeontology, only recently have sufficient biomechanical studies accumulated to constitute a bibliography of the subject. These studies span almost the entire range of taxa; their objectives are usually functional morphological and commonly, but not necessarily, quantitative. Conversely, quantitative studies using mathematical or physical principles (e.g. growth form in Bryozoa or vision in trilobites) are not necessarily biomechanics. The major contribution which biomechanics makes to palaeontology is in testing hypotheses of functional morphology that are based on deduction from morphology or external factors, such as sediment, associated biota, or distribution. Biomechanics can be a powerful tool in hypothesis testing, but quantitative results, even on living organisms, must be interpreted with caution because of the inherent complexity of the natural world.

Undoubtedly the most important textbook on biomechanics is that by Alexander (1983) and his chapter headings are used here as a basis for

grouping examples of the uses of biomechanics in palaeontology.

Strength

An important branch of biomechanics investigates the structural design of organisms, and in particular the properties of the materials of which plants and animals are made (Wainwright *et al.* 1976). The common questions asked are about the strength of biological materials under stress, i.e. subject to a force, usually gravity, or a current flow in a static situation or during movement. There is considerable overlap here with *constructional morphology* (Section 4.1). Biological structural materials are usually complex, since they have to operate in a variety of mechanical environments and also perform other feats, like growing. They are mainly composites, good examples being wood, arthropod cuticle, and echinoderm stereom and stroma. Such materials are very resistant to fracture and other forms of failure because they combine both rigid and elastic materials, and laminates are used extensively for their crack-stopping properties. It is, of course, almost impossible to study the biomechanics of fossils

with soft skeletons. On the other hand, it may be as easy to investigate the mechanical properties of rigid, calcareous fossil skeletons as those of their living relatives.

As well as the building materials themselves, the architecture of plant and animal structures is extremely important for maximizing strength over energy expenditure. In general, tubes are as efficient as, but less costly than, solid beams, which is one reason why bones, arthropod limbs, bicycle frames, and many plant stems are hollow cylinders. There are optimum materials and designs, for example for cylinders required to support heavy, static loads, those which act as levers, and those which suffer heavy impacts. The principles of beam theory are relatively straightforward and have been used in a number of palaeontological analyses with enlightening (but perhaps not surprising) results.

As this point it is necessary to mention scaling (see McMahon & Bonner 1983). In many palaeobiomechanical studies either the aim of the work or a consequence of it involves consideration of a range of sizes of organisms. Dinosaurs are a good example. Large terrestrial animals must have disproportionately thicker limbs than their smaller relatives, or minimize the stresses involved in walking. The reason for this is that cross-sectional area of the limbs is proportional to [body weight]^{0.67} whilst the stresses due to gravity are proportional to [body weight]^{0.33}. *Apatosaurus* was probably quite capable of walking without the aid of water buoyancy, provided it did not indulge in acrobatics. Similarly, Dalingwater (see Briggs *et al.* in Rayner & Wootton 1991) investigated whether eurypterid arthropods (especially the large Carboniferous forms) could have walked on land, using living *Limulus* for comparison. *Limulus* can walk on land, even though it is an aquatic animal, but if the cuticle of the giant Carboniferous eurypterid *Hibbertopterus* had the same Young's modulus (a measure of elasticity) as that of *Limulus*, it is unlikely that the latter animal could have done so. A particular problem for arthropods on land is moulting; Dalingwater found that even a small *Limulus* is unable to support itself out of water in its soft, newly-formed cuticle. His calculations used simple expressions for buckling under static axial load, on the basis that if failure resulted under these conditions, then walking, with its associated greater, non-axial stresses, would be impossible.

Arthropod podomeres are hollow cylinders, the axial lumen housing the muscles which operate them, so the thickness (t) of cuticle cannot equal the

radius (r) of the cross-section ($r:t \neq 1$). This is another constraint on the size of terrestrial arthropods. In flying animals (Section 1.9) and swaying plant stems, the problem is less the result of weight and more that of failure by bending. Flight imposes a number of constraints, particularly on large animals like giant pterosaurs (*Quetzalcoatlus* from the Upper Cretaceous of Texas had a wingspan of 12 m, and was thus the largest flying creature ever). $r:t$ ratios below about eight give considerable strength against impact but are heavy. Where $r:t$ exceeds eight there is considerable weight saving, but brittle fracture is a problem, and buckling becomes a problem when $r:t$ exceeds 15. So how do large pterosaurs combine lightness with strength in their wing bones? (1) Their bones are laminated to lessen cracking under impact or load; (2) larger pterosaurs have higher $r:t$ ratios for lightness (the bone thickness is the same as in small ones but the lumen is wider); and (3) to prevent buckling, a number of devices (Fig. 1) are employed which effectively lower the $r:t$ ratio and produce strong 'T' sections without adding a significant weight of bone. Geological evidence shows that, not surprisingly, giant pterosaurs, like large birds, lived in open treeless surroundings where impact damage was minimized.

At the other extreme, low $r:t$ ratios are useful in situations where impacts are common. Kitchener (in Rayner & Wootton 1991) used beam theory to show that the $r:t$ ratio of the cross-section of the proximal part of Irish Elk antlers was far smaller than would be expected if the antlers were used for

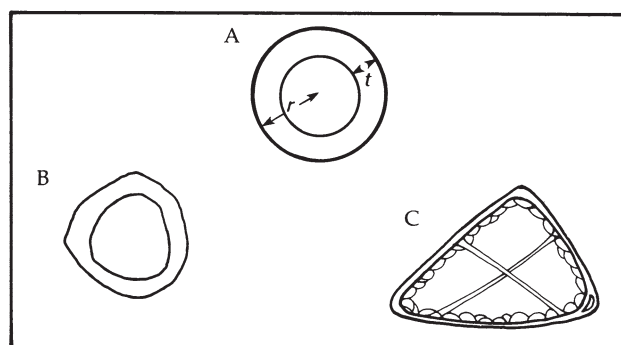


Fig. 1 A, Cross-section of a tube showing radius (r) and thickness (t); $r:t = 2.4$. B, Thick-walled section near base of Irish Elk antler; $r:t = 3$. C, Section of first phalanx of pterosaur, showing devices for combining strength and lightness: thin walls, triangular section with thickened corners (commonly hollow), struts, and spongy bone layer; $r:t = 11$. All are diagrammatic and not to scale.

display alone, and since antlers are shed annually they are a significant expense. Antlers of other Old World deer are used for fighting among males — vital for the breeding success of the species. The high $r:t$ ratio, together with the preferred orientation of osteons in the maximum impact direction of the proximal antler bone, is good evidence that fighting was the real function of Irish Elk antlers.

Force and energy

The force (in newtons) which Irish Elk antlers needed to withstand was that of an equal but opposing weight of stag colliding at the same rate of deceleration ($500 \text{ kg} \times 30 \text{ m/s}^2 = 15000 \text{ N}$ per antler). In this situation the force is maximum in the direction of motion of the deer. In a lever system, such as when muscles move a bone or an arthropod podomere, the resultant force is in a different direction to that of the muscle contraction. Alexander (1983, p. 5) gave an example of how some knowledge of the action of levers helps to explain the evolution of the mammalian jaw articulation from that of a primitive reptile. Claws (chelae) of crustaceans and chelicerates work in a manner similar to that of mammalian jaws. In a lever system, the ratio *resultant force:applied force* ($F_2:F_1$) is known as the mechanical advantage (MA), and $L_1:L_2$ is the velocity ratio (VR) (Fig. 2). A high MA or VR (i.e. close to 1) provides strong but slow movements; in contrast, a low MA or VR leads to weak but fast movements with the same power input. These simple relationships are useful for understanding the function of chelae or jaws in fossils, such as eurypterids (Selden 1984).

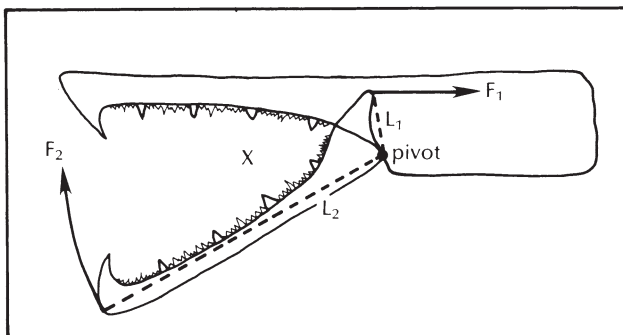


Fig. 2 Mechanics of cheliceral claw of a pterygotid eurypterid; VR ($L_1:L_2$) = 0.2 for tip of movable finger, therefore MA ($F_1:F_2$) is also low, and adapted for fast capture of prey. Prey inserted into claw at X could be sliced with high MA.

Similar principles apply to walking: long legs are good for fast running, short legs for strong pushing. The analysis of walking is complex (e.g. for arthropods see Briggs *et al.* in Rayner & Wootton 1991). For example, a surprising but useful source of information on the biomechanics of walking in fossils is their tracks. Stride length, and hence leg length, can be measured from footfalls. Alexander (1983, p. 35) used the concept of kinematic similarity, which allows extrapolation from the scale of a small animal to that of a dinosaur provided that their Froude numbers are the same. Froude number, like Reynolds number (see later), is a dimensionless quantity, u^2/gl , where u , g and l are a velocity, acceleration due to gravity, and a length respectively. Alexander calculated the speeds of some dinosaurs from Texas and found that the biped walked at *c.* 2.2 m/s while the quadruped strolled at *c.* 1 m/s; both are reasonable human walking speeds.

Pressure, density, and surface tension

Hydrostatic skeletons in plants and animals come under this heading, but the fossil record can tell us little about them. Surface tension may seem to be a phenomenon which cannot be studied easily in fossils, yet it is important wherever biological tissue encounters an air–water interface (e.g. in lungs). Alexander (1983, p. 176) discussed the importance of surface tension in the operation of plastrons in aquatic insects and mites; the surfaces of eurypterid respiratory organs resemble those of plastrons in morphology, but not in size, and therefore could not have worked in the same way.

Buoyancy is another hydrostatic phenomenon, and has been of interest to cephalopod palaeobiologists in particular. Fish and endocochleate (internal-shelled) cephalopods have nearly coincident centres of buoyancy and mass, which allows for accurate swimming and controlled manoeuvrability. This was probably true of the belemnites and some straight-shelled ectocochleates as well. The coiled ectocochleate nautiloids and ammonoids, on the other hand, had their centre of buoyancy above their centre of mass. This is inherently more stable when static, but jet thrust sets up a couple which rotates the animal, and a restoring moment is provided by the body mass when the thrust force subsides. A further disadvantage in the cephalopod model of a buoyant camerate shell, counterbalanced by solid or liquid ballast, is that it is costly in energy, both to secrete and to move, in contrast to the fish solution.

Motion in fluids

As soon as cephalopods start to move, they experience a variety of phenomena associated with motion in fluids. The dimensionless number describing kinematic similarity in fluid motion, equivalent to the Froude number where gravity is important, is the Reynolds number (Re). Two forces which act on objects moving through a fluid, and which are dependent on Re , are lift (L) and drag (D). These concepts are explained in Section 4.4. In biology, motion of a body through a fluid can initially be classified into *swimming* (in water) and *flying* (in air). Flight is discussed in Section 1.9; only swimming is reviewed here.

Jet propulsion is used extensively by cephalopods; water is drawn into the mantle cavity and then expelled rapidly through the funnel to push the body forward. Broadly speaking, the larger the mantle cavity, the greater the thrust which can be achieved and sustained; this is limited in ectocochleates by the size and buoyancy requirements of the shell. Endocochleates have no such restraint on the size of the mantle cavity. Progression consists of cycles of alternating propulsive jet thrusts (power stroke) and inhalation (recovery stroke). Such burst swimming may not be as inefficient as it appears, since it is common in fish, and bounding flight is efficient in small birds. Chamberlain (e.g. in Rayner & Wootton 1991) has analysed various aspects of swimming in ectocochleates; in particular, he showed how drag varies with changes in expansion rate, whorl shape, and position of whorls relative to the coiling axis. In general, involute oxycone shells have a lower drag coefficient (and hence were more efficient) than depressed cadicones. In some cases the amount of soft part protrusion has an effect on the drag, and fine ribbing can also reduce the drag coefficient significantly. Using experimental measurements of drag on fossil ammonite shells, calculations of body volumes, and comparison with the rotational moments experienced by living *Nautilus*, Chamberlain estimated the swimming speeds of these extinct animals. They were undoubtedly poor swimmers in comparison with modern fish.

Vertebrates and arthropods swim by one of two methods: axial or paraxial. The former method involves undulations of the body; it is predominant in fish, in which group direct comparison between living and fossil forms can be made. Paraxial locomotion is of more interest to palaeontologists because it was used by such extinct forms as eurypterids and plesiosaurs, and involves move-

ments of paired limbs to drive the body through the water. There are essentially two types of paraxial locomotion: drag-based rowing; and lift-based 'flying', so-called because the mechanical principles involved are the same as those in aerial flight (Section 1.9). In rowing, the paddles, with high drag, are moved backwards to propel the streamlined body forwards; during the recovery stroke, the paddles are feathered to reduce their drag. In subaqueous flight the flipper is moved up and down at right angles to the direction of body movement; the limb's hydrofoil cross-section produces a force, *lift*, which is directed forwards by rotating the flipper. Lift can be generated on both the up and down strokes, so that forward progression is continuous.

At Reynolds numbers below about 10^2 , viscous forces are important, so drag-based rowing mechanisms are used by small and/or slow swimmers. Above about $Re = 5 \times 10^3$, inertia dominates, so it is more efficient to fly, if possible. Eurypterids straddle this Re transition; small species undoubtedly rowed (Fig. 3B), but it seems most likely that the large (up to 2 m) pterygotids flew underwater. The biomechanics of eurypterid swimming was discussed by Selden (1984) and Briggs *et al.* (in Rayner & Wootton 1991). Using a simple rowing model, the maximum sustainable speed was calculated at 38 cm/s for a 16.5 cm long *Baltoeurypterus*, which conforms with extrapolations from the swimming speeds of water beetles. Estimates of Re at this velocity give approximately 2×10^4 , which is just into the range in which flying should be more efficient, so it is possible that swimming was normally slower than this, or that constructional morphology was a constraint. Morphology suggests that the paddles of *Baltoeurypterus* moved in phase, as in water boatmen (e.g. *Corixa*), a further example of burst swimming. Tilting of the oar blades would have produced lift for up, down, and sideways manoeuvrability.

Examples of living subaqueous fliers are penguins, and the Humpback Whale (*Megaptera*). Over the years, plesiosaurs have been visualized as either rowers or fliers, but recently, closer comparison has been made with the swimming of sea-lions. These animals generate thrust partly as lift when the flipper is moved downwards from a horizontally outstretched position at the start of the propulsive stroke, and partly as drag when it is then swept backwards to lie alongside the body at the end of the stroke. Recovery is passive and feathered, but some upward lift can be produced if required.

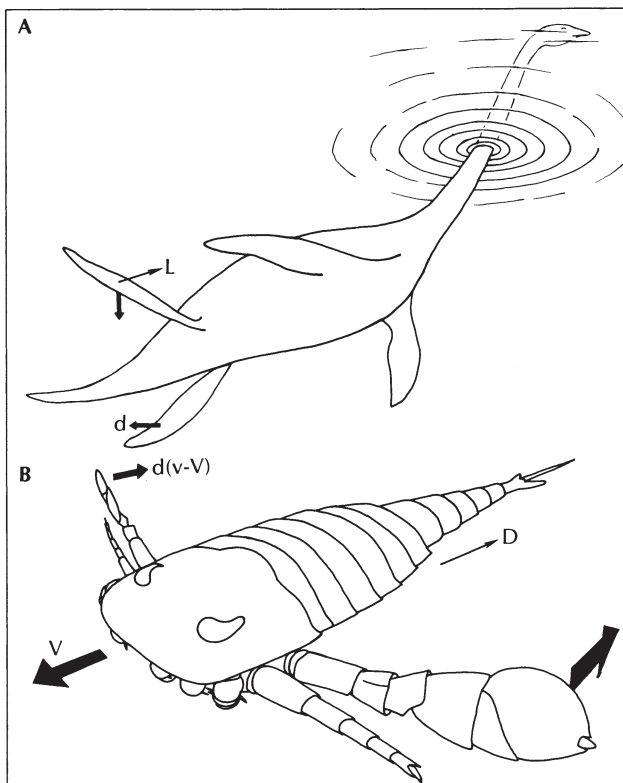


Fig. 3 A, Swimming mode of plesiosaur; right pelvic flipper on downward part of propulsive stroke, hydrofoil section gives lift (*L*) in forward direction; left pelvic flipper on backward thrust (drag) part of propulsive stroke; pectoral flippers on passive recovery stroke. B, The eurypterid *Baltoeurypterus* rowing, shown with oar blades half-way through propulsive stroke; *D*, *d*, and *V*, *v* are drag and velocity of body and limbs respectively.

In sea-lions, the pelvic limbs are used solely for manoeuvring, but in plesiosaurs with similar sized pectoral and pelvic limbs, propulsion was probably achieved by both pairs of limbs, working out of phase to produce continuous motion (Fig. 3A) (Frey and Riess in Rayner & Wootton 1991).

Conclusions

Biomechanics is a powerful tool in palaeontology, if used with care. The paucity of palaeobiomechanical studies to date may simply reflect a lack of appreciation of its possible applications, but as the studies reviewed here indicate, it has considerable potential for refining our interpretations of the palaeobiology of extinct animals.

References

- Alexander, R.McN. 1983. *Animal mechanics*, 2nd edn. Blackwell Scientific Publications, Oxford.
- McMahon, T.A. & Bonner, J.T. 1983. *On size and life*. Scientific American, New York.
- Rayner, J.M.V. & Wootton, R.J. (eds) 1991. *Biomechanics in evolution*. Society for Experimental Biology, Seminar Series. Cambridge University Press, Cambridge.
- Selden, P.A. 1984. Autecology of Silurian eurypterids. In: M.G. Bassett & J.D. Lawson (eds) *Autecology of Silurian organisms. Special Papers in Palaeontology* No. 32, pp. 39–54.
- Wainwright, S.A., Biggs, W.D., Currey, J.D. & Gosline, J.M. 1976. *Mechanical design in organisms*. Edward Arnold, London.

4.4 Hydrodynamics

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Introduction

The field of fluid mechanics is classically divided into two subdisciplines: *hydrostatics* and *hydrodynamics*. Hydrostatics is concerned with the pressures and pressure variation within a fluid at rest, and the pressures exerted on immersed solid bodies. Hydrodynamics encompasses a much broader diversity of phenomena — the forces and flow patterns that result from relative motion between a fluid and

either a solid object or another fluid. Although hydrostatics is central to some aspects of geophysics (e.g. the concept of isostasy), its application to palaeontological problems has been largely limited to studies on shelled cephalopods, where it has illuminated the mechanisms of septal chamber emptying and (with empirical data and theory derived from solid mechanics) helped in estimating maximum depths for living or fossil forms.