

years, would be consistent with the palaeomagnetically determined rotations of post-middle-Miocene rocks in the region (R. Walcott, Victoria University).

A superficial examination of the thermal conditions beneath the North Island of New Zealand suggests that it is a classic paired metamorphic belt, but in a tectonic setting not usually attributed to these belts: high temperature—low pressure (high T —low P) metamorphism is occurring beneath the central volcanic region, which is extending and subsiding, while low T —high P metamorphism is occurring in the Hikurangi Margin to the east, which is uplifting and extending. Thus, a future episode of compression is required before erosion can expose the high T —low P metamorphism, whereas the exhumation of low T —high P rocks, which is usually thought to require the cessation of subduction, requires no more than the

continuation of the present underplating and extension of the Hikurangi Margin.

A similar process is believed to have operated in the preservation of high-pressure rocks in the Franciscan Formation, Betic Cordillera and Western Alps (J. Platt, Oxford University); large normal faults parallel to the mountain range are also observed in the High Himalaya (J.-P. Burg, Melbourne University). But nobody was prepared to propose such an extensional mechanism for the preservation of a 50-square kilometre area of coesite-bearing rocks that appear to have been metamorphosed at about 30 kilobars in the early stages of the Alpine orogeny (C. Chopin, Ecole Normale Supérieure, Paris). □

Philip England is in the Department of Geological Sciences at Harvard University, Hoffmann Laboratory, 20 Oxford Street, Cambridge, Massachusetts 02138, USA.

Palaeontology

How did eurypterids swim?

from D.E.G. Briggs

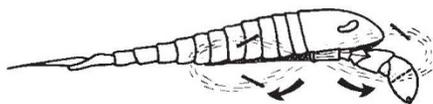
EURYPTERIDS, a group of extinct Palaeozoic arthropods, existed for more than 200 million years from the early Ordovician to the Permian, and were the largest arthropods ever to have evolved—at least half of the eurypterid families included species containing individuals of more than 80 cm long. They became extinct in the most severe mass extinction in the late Permian. A recent report suggests that these large swimming arthropods may have been capable of hovering (Plotnick, *R. Trans. R. Soc. Edinb.* **76**, 325; 1985).

Eurypterids had a long streamlined body divided into an anterior prosoma (cephalothorax) and posterior opisthosoma (abdomen). Trace fossil evidence and functional analysis show that eurypterids used the posterior three pairs of prosomal appendages to walk in a hexapodous gait. The last of these, the sixth prosomal appendage, was modified to some extent in all eurypterids, the distal podomeres being commonly flattened and expanded to form a paddle.

Early interpretations of swimming in eurypterids were based largely on comparisons with the horse-shoe crab (*Limulus*), a member of the only major living group of aquatic chelicerates, and envisaged eurypterids as swimming ventral side upmost using mainly the opisthosomal limbs (equivalent to the gills of *Limulus*). More detailed studies of the few well-preserved examples (Waterston, C.D. *Fossils and Strata* **4**, 241; 1975) showed that eurypterid gills were more similar to the lung sacs of scorpions, consisting of an area or tract on the ventral body wall, rather than appendages modified as book-gills. These

tracts were protected by stiff cuticle and could not have been used for propulsion.

Recent research demonstrates that the paddle provided the primary means of swimming. Paul Selden redescribed the Silurian eurypterid *Baltoeurypterus tetragonophthalmus* (*Trans. R. Soc. Edinb.* **72**, 9; 1981) based on the spectacular fossil specimens from the Silurian of Gotland



Hovering in *Baltoeurypterus*. The paddle is moved in a shallow horizontal figure-of-eight, the angle of attack (dashed on the paddle, solid elsewhere) altering to maintain lift. Other prosomal limbs are omitted. This specimen is about 20 cm long.

and Estonia, in the Baltic. The eurypterid cuticle can be isolated from limestone by dissolution in acid and provides information comparable to the exoskeleton of a living arthropod. Most importantly, the mechanics of the joints between the limb podomeres can be reconstructed.

Appendicular swimming may be either predominantly drag-based (the appendages rowing, as oars) or lift-based (the appendages 'flying', as hydrofoils). Selden's analysis of the mechanics of the paddle in *Baltoeurypterus* indicates that the large flat seventh and eighth podomeres could have been alternately expanded to create maximum drag in a power stroke, and then rotated about the paddle and folded to present much less resistance in a recovery stroke. He suggested that the paddles functioned as oars, moving in phase to reduce the likelihood of yawing;

pitching and rolling would have been prevented by the flattened body, tergal projections and outstretched limbs.

But *Baltoeurypterus* was about 20 cm long, a size that exceeds the limit at which drag-based swimming becomes inefficient (at Reynolds numbers of about 10^2). The limited degree of lift produced by rowing would also be an important consideration if eurypterids were negatively buoyant, as seems probable. Using Selden's detailed analysis of the morphology of *Baltoeurypterus*, Plotnick's new work extends the model of swimming in eurypterids to incorporate a greater element of lift. Plotnick's conclusions are based largely on a study of swimming in portunid crabs, which have a paddle (the fifth pereopod) strikingly similar to that in eurypterids. Portunids are very manoeuvrable, using a lift-based swimming mechanism that even enables them to hover.

Eurypterids were unable to swim by 'subaqueous flying' (in the manner of penguins) because the nature of the joints prevented up-and-down movement of the paddle at right angles to the direction of progress. But they could move the paddle in a flattened figure-of-eight which, while concentrating the thrust in the backstroke as in rowing, produced lift and a modest degree of thrust in the forestroke. The paddle tapered to a point distally, like a hydrofoil. (It should be noted, however, that the morphology of the paddle is likely to be a compromise between the different requirements of swimming and walking.) Lift-based swimming is more efficient for a large animal than rowing, as a propulsive thrust is produced on both the forestroke and the backstroke and a constant lift is created to counteract the negative buoyancy of the animal. In the eurypterids, the dorsal position of the articulation between podomeres 4 and 5 exaggerated the downward component of the paddle's movement, thus favouring lift.

Not all eurypterids conformed to the morphology of *Baltoeurypterus*. The remarkable late Silurian pterygotids, for example, were more elongate with very slender limbs (including the paddles) and may have been more than 2 metres long. This large size indicates that a lift-based mode of swimming was likely (Selden, P.A. *Spec. Pap. Palaeont.* **32**, 39; 1984).

Only a few eurypterids have been subjected to the kind of detailed analyses pioneered by Selden and Plotnick. Although material of the quality of *B. tetragonophthalmus* from the Baltic is rare, research on the biomechanics and hydrodynamics of other well-preserved eurypterids will yield further insights into the functional strategies adopted by these remarkable arthropods. □

D.E.G. Briggs is in the Department of Geology, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK.