

AUTECOLOGY OF SILURIAN EURYPTERIDS

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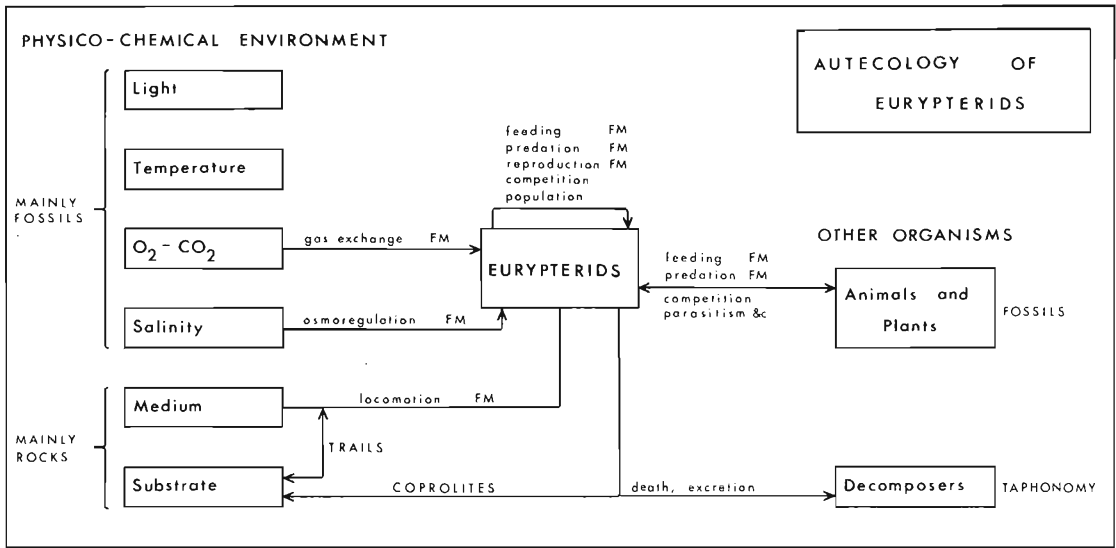
ABSTRACT. The autecology of eurypterids is reviewed, with particular reference to Silurian forms, and from a functional morphological standpoint. The three salinity-related ecological phases of Silurian eurypterids recognized by Kjellesvig-Waering (1961) appear to be valid and useful. Two of the four most probable eurypterid walking trails show in-phase gait patterns, suggesting they were made by animals partly or wholly out of their usual aqueous habitat. Pterygotoid and hughmillerioid eurypterids may have swum using the hydrofoil principle. Eurypteroids used the rowing principle; calculations based on this model reveal that *Baltoeurypterus* may have reached a maximum velocity of $2.5 \times$ its body length per second. From the generalized eurypteroid feeding type evolved two feeding strategies: enlarged spinose limbs II and III (mixopteroids) and enlarged chelicerae (pterygotoids). Pterygotoid chelicerae appear well adapted for dealing with nektonic vertebrate prey. The 'claspers' on the anterior limbs of males of some eurypterid species may have functioned as sperm transfer organs. Knowledge of the detailed morphology of Silurian eurypterids surpasses that of other contemporaneous arthropods, thus far more could be known about their mode of life.

IN the Silurian the eurypterids showed their greatest diversity and abundance, but Silurian eurypterid remains are of little use in detailed biostratigraphical studies because they occur most commonly in facies severely restricted in space and time. Where they do occur their importance in palaeoecological reconstructions should not be underestimated. Large and rare animals, they almost certainly occupied high trophic levels, probably as primary carnivores. Indeed, Romer (1933) suggested that Silurian eurypterids provoked the development of protective dermal armour in their vertebrate contemporaries.

The relatively small amount of literature on eurypterids has meant that authors of comprehensive works (e.g. Woodward 1866-1878; Clarke and Ruedemann 1912; Størmer 1934a, 1955) included excellent and wide-ranging reviews. Nearly every piece of literature on eurypterids has touched on their mode of life, and some (e.g. O'Connell 1916) have been devoted entirely to their ecology. Eurypterids interact with two environmental components: physico-chemical and biotic (including intraspecific) (text-fig. 1). Also, there are two main bodies of evidence from which inferences about eurypterid ecology can be made: external factors (rock matrix, trace fossils, associated fauna, geochemistry, etc.), and functional morphology. Certain biotic interactions of eurypterids, such as population structure and competition, more easily studied in life assemblages of sedentary organisms, are currently in need of further investigations.

This review lays particular emphasis on the evidence from functional morphology; this approach to palaeoecology was discussed by Trueman (1964). Dullemeijer (1980) compared animal ecology and morphology, concluding that whilst the explanatory methodology is the same for both disciplines, the philosophies are different. In morphology, the organism is the object of research, whereas ecology studies the relationship between organisms and environment. Thus the philosophy of ecology embraces synecology but not autecology. The latter describes the link between the two disciplines. Co-operation is necessary because the ecologist needs to know the form of the organism whilst the morphologist requires information about its ecology, but there is always the risk of circular reasoning.

Although eurypterids are rare as fossils, their appendages are nearly always preserved. In the case of *Baltoeurypterus*, the fortunate combination of excellent preservation and the meticulous work of Holm (1898) prompted Clarke and Ruedemann (1912, p. 19) to state that it was 'the most completely known of all extinct animals and our exact knowledge of it is quite comparable with that of its recent relatives'. Because we know so much about the morphology of Silurian eurypterids, answers to



TEXT-FIG. 1. Diagram showing direct interactions between eurypterids and their environment. Useful sources of palaeontological evidence shown in small capitals. *FM* = functional morphology.

questions of a far more specific and searching nature than would be asked of less well-preserved but more familiar groups are within our grasp. For example, how did the eurypterid gill function, how was fertilization accomplished, how fast could they walk or swim, and how efficient were their prey-capturing systems? Such palaeophysiological questions have been asked by vertebrate palaeontologists about Mesozoic reptiles, producing some fascinating answers. We may never know the truth but should learn a great deal in the search.

SALINITY

Did eurypterids live in fresh, brackish, or salt water? The problem is that they (and early vertebrates) are most commonly found in strata with neither good marine faunas nor easily interpretable sedimentological characteristics. Whilst details of sedimentology and associated fauna were often recorded by nineteenth-century workers, palaeoecology received little consideration except in terms of functional morphology (e.g. Laurie 1893). In contrast, in the present century, nearly every report of a new eurypterid occurrence contained some palaeoecological discussion. Brooks's (1957) annotated bibliography summarized ideas on the habitat of eurypterids contained in the most important papers to that date. Broadly speaking, there were four main opinions: (1) that all eurypterids lived in fresh water, their remains being transported into marine environments after death; (2) that fresh water was the usual habitat but that some species occasionally visited or inhabited the marine environment; (3) that eurypterids were euryhaline—tolerant of a wide range of salinities; and (4) that eurypterids were marine animals in the Ordovician, inhabited a wide range of salinities in the Silurian, and gradually became confined to brackish and fresh-water habitats in the late Palaeozoic. These categories are not mutually exclusive, however, and some authors preferred different interpretations in different instances. Størmer's (1955) views may be taken as those prevalent in that decade: 'Eurypterid remains are scarce, and particularly so in marine faunas. Most described species belong to brackish- and fresh-water faunas. In general, we may say that the eurypterids inhabited fresh and brackish waters near the coast and occasionally visited the sea. With their well-protected gills, it is possible that the eurypterids were able to spend short intervals of time on land.'

In the last twenty-five years, the most important contribution to the environment debate was that of Kjellesvig-Waering (1961), who, by combining his knowledge of the morphology of eurypterids and their sedimentological and stratigraphical occurrences, presented a picture of three more or less distinct ecological phases in the Silurian. The Carcinosomatidae-Pterygotidae phase is the most marine; it occurs in the Mocktree Shales of the Ludlow area, Lesmahagow, Czechoslovakia (Budnany and Lochkov), and the Middle Vernon Shales of New York. The Eurypteridae phase represents sheltered marine bays, lagoons, or estuaries and is typified by the Bertie Waterlime of New York and Saaremaa Fauna of Estonia. The Hughmilleriidae-Stylonuridae phase, which is associated with clastic sediments, was considered by Kjellesvig-Waering to represent brackish bays and estuaries; it is found in the Shawangunk of New York, Ringerike (Norway), the Pentland Hills and Hagshaw Hills (Scotland), and the Downton of the Welsh Borderland.

Support for Kjellesvig-Waering's (1961) general scheme was unanimous, but it has been modified by later authors. Boucot (1975, p. 209) integrated it into his Benthic Assemblage scheme. Størmer (1976) changed the names of the phases to conform to newer taxonomy. He considered phase 1 (Carcinosomatidae-Pterygotidae) to represent marine-brackish water, rather than fully marine; phase 3 (Hughmilleriidae-Drepanopteridae-Stylonuroidea) he regarded as brackish-fresh water; and phase 2 (Eurypteridae) as somehow transitional between 1 and 3, with a tendency to hypersalinity. Waterston (1979, p. 301) found that for the stylonuroid eurypterids, at least, Kjellesvig-Waering's generalizations were valid. More recently, Boucot and Janis (1983, Table 1) have utilized the ecological phases in their evidence for the environment of early Palaeozoic vertebrates.

That eurypterids alone can be used as indicators of salinity is doubtful: single occurrences of any genus might be found in any of the phases. As always, other factors, such as sediment type and associated fauna, must be taken into account: a full palaeoecological study is far preferable to speculation on ambiguous data.

Osmoregulation

The extant *Limulus polyphemus* is tolerant of a wide range of salinities, living in coastal and estuarine waters and migrating to the littoral zone in spring and summer to spawn, and sometimes getting trapped in embayments with hypo- or hypersaline conditions (Shuster 1957). *Limulus* blood is isosmotic in normal and hypersaline sea water but hyperosmotic in dilute sea water. Osmoregulation is intracellular; unlike many euryhaline Crustacea, amino-acids account for only a small proportion of nitrogen ions in the cell solution, the remaining compounds are as yet undetermined (Robertson 1970). Excretion is via four pairs of coxal glands; their ducts converge and reach the outside by an opening at the base of limb V. The digestive glands and the gut wall also have an excretory function. Unlike other aquatic arthropods the *Limulus* gill appears not to be important in osmoregulation, although work is currently under way to investigate this (see Mangum 1982 for review).

A close comparison with *Limulus* would suggest that osmoregulation and acid-base regulation occurred mainly through the coxal glands in eurypterids. A coxal gland opening occurs on coxa V of *Baltoeurypterus tetragonophthalmus* (Wills 1965; Selden 1981), *Hughmilleria socialis* and *Eurypterus remipes* (Clarke and Ruedemann 1912, p. 54). Waterston (1979, p. 309) suggested that, in comparison with certain land and fresh-water crabs which have specialized areas of gill for salt uptake, the complex eurypterid gill may also have played a major part in osmoregulation. Also, some eurypterids may have been tolerant of a wider range of salinities than *Limulus*. Crustacea are more able to tolerate hyposaline water at higher temperatures; by comparison, Waterston (1979, p. 309) suggested that the eurypterids were most able to make the transition from marine to brackish and fresh-water environments during the late Silurian and early Devonian when Laurasia entered low latitudes.

GAS EXCHANGE

Thanks to the work of Holm (1898), Wills (1965), and Waterston (1975), the detailed morphology of the eurypterid gill is now fairly well established, and seems to have been quite similar in all the animals so far studied. Woodward figured the 'branchiae' of *Erettopterus bilobus* (1868, pl. x, fig. 3a, b; 1869,

pl. xii, fig. 1a, d; pl. xiii, fig. 1h) and *Slimonia acuminata* (1871, pl. xix, figs. 3, 4). I restudied one of Woodward's specimens (1869, pl. xii, fig. 1a, d: GSM 87327, Institute of Geological Sciences, London) and the so-called branchiae are in fact the fused labrum and coxae II. Judging from Woodward's illustrations the 'branchiae' of *Slimonia* could also be anterior coxae and labrum, and the other *E. bilobus* 'branchiae' figured by him may be artefacts; they are almost certainly not gills. Laurie (1893, figs. f, 6) figured the gills of *Slimonia* in their true positions, and one of the specimens figured by him was later re-examined by Moore (1941). Detailed structure of the gills of *Baltoeurypterus* was elucidated by Wills (1965), based partly on unpublished work by Holm (1898). The gill structure of the Devonian *Tarsopterella scotica* was reconstructed by Waterston (1975).

Wills (1965) and Waterston (1975) discussed the function of the eurypterid gills as a true gill, but Størmer (1976) noted significant differences between eurypterid gills and those of other animals and found a closer comparison with the pseudotracheae of terrestrial isopod Crustacea. He concluded that 'the gill-tract might have acted both as gill and pseudotrachea' (Størmer 1976, p. 143). More recently, Rolfe (1980) compared the eurypterid gill tract to a plastron—a device for breathing air in secondary aquatic insects and mites. See Selden (in press) for further discussion.

LOCOMOTION AND MODE OF LIFE

Clarke and Ruedemann (1912, p. 76) recognized four eurypterid modes of life: (1) swimmers, with streamlined bodies, swimming legs, marginal eyes, and commonly broad telsons (e.g. *Pterygotus*, *Erettopterus*, *Hughmilleria*); (2) crawlers and burrowers, with scorpioniform bodies, swimming legs, marginal-frontal eyes, and styliform telsons (e.g. *Eusarcus*); (3) generalized forms—capable of swimming, crawling, and burrowing, with slender or broad bodies, swimming legs, dorsal eyes, and styliform telsons (e.g. *Eurypterus*, *Dolichopterus*); (4) walkers, with slender bodies, stilt-like legs, dorsal-subapical eyes, and styliform telsons (e.g. *Drepanopterus*, *Stylonurus*).

Størmer (1934a, pp. 58–66) explored the diversity of eurypterid morphology and its bearing on mode of life in some detail. He reached similar conclusions to those of Clarke and Ruedemann (1912), and also recognized a group comprising *Carcinosoma* and *Mixopterus*, with scorpioniform bodies and greatly enlarged, spinose limbs II and III.

Four basic types of eurypterid limb can be recognized: the chelicera, the spinose food-gathering limb, the spineless walking limb, and the swimming limb. The last three can all be derived from a generalized 'spiniferous leg' (Størmer 1974, p. 363) and intermediates between these types are found. The generalized leg was involved both in locomotion and food manipulation. The probable mode of life can be assessed by observing the degree of development of each limb type. For example, most stylonuroid eurypterids were considered to have been primarily walkers because their post-cheliceral limbs are of the spineless, walking type. In pterygotoids the chelicerae are greatly enlarged for prey capture, swimming paddles are developed on limb VI, whilst their walking limbs, though present, are small and slender and were probably used in a buoyant, tripping gait like that of Recent lobsters. In the mixopteroid eurypterids, two anterior pairs of limbs (II and III) are highly specialized for food capture, swimming paddles are developed on limb VI, but limbs IV and V are unspecialized and resemble the generalized leg of Størmer (1974).

Walking

Two complementary lines of evidence shed light on the manner of walking in eurypterids: functional morphology and trace fossils. Because of their morphological diversity, each kind of eurypterid probably had its own method of walking. So far, detailed functional morphological studies have been made on only two eurypterid species: *Parastylonurus ornatus* from the Silurian of the Scottish Midland Valley (Waterston 1979) and *B. tetragonophthalmus* from the Baltic Silurian (Selden 1981).

In view of the considerable increase in leg length from limb IV to limb VI, Waterston (1979, p. 313) reconstructed *Parastylonurus* with an anterior inclination of the fore part of the body of about 12°. In order to achieve an even weight distribution on all walking legs, broad epimera on the post-abdominal segments together with the broad telson were able to provide lift to the rear of the animal.

Other stylonuroids with larger epimera correlated with higher energy sedimentary environments, whilst those forms that lack epimera needed to drag their telsons to achieve stability (Waterston 1979, pp. 312–315). *P. ornatus* probably walked in a fairly precise, low gear, hexapodous gait pattern (Waterston 1979, p. 307).

Unlike stylonuroids, the prosomal appendages of *Baltoeurypterus* are differentiated into walking, swimming, and food-gathering types. Only limb V is adapted primarily for walking, so limbs IV (spinose for food-gathering) and VI (swimming paddle) must also have been used for walking. Using a graphical technique, the gait chosen for *Baltoeurypterus* (Selden 1981, fig. 13) was low gear, stable, and allowed a certain amount of irregularity in stepping without loss of balance, as befits an animal less well adapted for walking than the stylonuroids.

A low gear gait was also interpreted by Hanken and Størmer (1975) for *M. kiaeri* from the Silurian of Ringerike, Norway. Their study was exceptional because both the trail and its probable producer were known, although the functional morphology of *Mixopterus* is not known in as much detail as for *Parastylonurus* and *Baltoeurypterus*. The three eurypterid gait patterns were compared by Selden (1981). In fact, a wide range of gaits can produce similar trails, so that whilst it is possible to suggest gaits from an analysis of trace fossils, or to produce a hypothetical trail from functional morphological studies (Selden 1979; Waterston 1979), other factors, such as speed and stability, need to be considered to produce sensible reconstructions of eurypterid locomotion.

Trace fossils

A number of traces have been attributed to eurypterids, including those described by Sharpe (1932, Ordovician, New York), Størmer (1934*b*, Downton, Spitzbergen), Richter (1954, lower Devonian, Germany), Leutze (1958, upper Silurian, Ohio), Gevers *et al.* (1971, Devonian, Antarctica; see also Bradshaw 1981), Hanken and Størmer (1975, Wenlock/Ludlow, Ringerike, Norway), and Briggs and Rolfe (1983, lower Carboniferous, Pennsylvania). Additionally, an undescribed, possible eurypterid trail is known from the late Silurian of Australia (K. J. McNamara pers. comm.).

Palaeozoic trails that are generally large show a double row of three or four imprints (commonly also showing heteropody), and normally have a median groove are those which could have been produced by eurypterids (see Goldring and Seilacher 1971; Briggs *et al.* 1979). Such trails fall within the Heteropodichnia group of arthropod trails of Walter (1978), within which eurypterid trails would normally be referred to the ichnogenera *Palmichnium* or *Paleohelcura*. Briggs and Rolfe (1983) recognized three species of *Palmichnium* for three of the described eurypterid trails mentioned above: *P. palmatum* (Richter 1954), *P. stoermeri* (Hanken and Størmer 1975), and *P. kosinskiorum* (Briggs and Rolfe 1983). The trail described by Gevers *et al.* (1971) as *Arthropodichnus antarcticum* was transferred to *Beaconichnus* by Gevers (1973) and thence to *Paleohelcura* by Briggs *et al.* (1979). Sharpe's (1932) trail, *Protichnites gallowayi*, could also belong to this ichnogenus. Leutze's (1958) trail was not named, but is probably not of eurypterid creation. Similarly, most trails referred to *Merostomichnites* (e.g. Størmer 1934*b*) were not made by eurypterids but by xiphosurans or other arthropods. *Merostomichnites*, as originally described by Packard (1900), belongs to the Iso-podichnia group of Walter (1978) and is quite unlike the trails of eurypterids and other heteropodous arthropods. Lower Devonian trails from Ayrshire termed *Stiaria* by Smith (1909) may also have been made by eurypterids (Pollard and Walker *in press*; cf. Briggs *et al.* 1979, p. 288).

Hanken and Størmer (1975) considered the trail described by them to have been made by *Mixopterus* walking slowly, partly submerged, across fine silt in an intertidal or lake-shore environment. The limbs were moved out of phase, thereby producing a trail in which the rows of tracks are offset on either side of the midline.

Paleohelcura antarcticum consists of *en echelon* rows of three, commonly bifid imprints arranged slightly asymmetrically about a median groove. Whilst preferring eurypterids to trilobites as producers, Gevers *et al.* (1971) ultimately left the question open. Briggs *et al.* (1979) and Rolfe (1980) suggested that large amphibious scorpions may have been responsible for these trails, whereas Bradshaw (1981) considered them more likely to have been made subaqueously by stylonuroid eurypterids.

The trail described by Briggs and Rolfe (1983) has rows of tracks arranged symmetrically about the midline, indicating that the ?eurypterid producer walked with opposite limbs in phase. Such a gait is characteristic of animals which plough through the substrate, like limulids and diplopods, and also occurs in swimming. Briggs and Rolfe (1983) therefore suggested that the amphibious animal was dragging itself across the sand of the littoral or river flood plain, partly or completely emerged, when it made the trail. The lower Devonian trail described by Richter (1954) also shows rows of tracks in phase; Hanken and Størmer (1975, p. 269) envisaged it as having been made by an arthropod, possibly eurypterid, dragging itself 'on a wet subaerial surface'. Eurypterid gaits suggested by functional morphological studies would have been out of phase, therefore *Palmichnium kosinskiorum* and *P. palmatum* may have been made by eurypterids performing unusual gaits (Briggs and Rolfe 1983). If the eurypterids that made these trails were primarily swimmers, they may not have developed the necessary neural programmes for out-of-phase walking, and thus would continue their in-phase swimming 'gait' on land. In this connection, it is interesting to note that orthopteran insects that have developed the ability to hop (e.g. locusts) or lunge (praying mantids) with meso- and metathoracic legs moving in phase, utilize this motion when swimming; cockroaches, on the other hand, have no such capability and swim in a normal, out-of-phase walking gait (Miller 1972).

Since eurypterids are so diverse, we cannot expect a single mode of walking for the whole group, nor even one superfamily as Waterston (1979) has pointed out. Many were primarily swimming animals and poor walkers. It is therefore not so paradoxical that the four well-documented trails ascribed to eurypterids (Richter 1954; Hanken and Størmer 1975; Bradshaw 1981; Briggs and Rolfe 1983) show a trend from an out-of-phase gait in the oldest (Silurian) to in-phase in the youngest (Carboniferous) when eurypterids in general are believed to have become more terrestrialized: we are seeing four isolated events in a long history of diversity.

Swimming

The most detailed study of eurypterid swimming was that of Selden (1981) who reconstructed the possible swimming movements of *Baltoeurypteris tetragonophthalmus*. Limb VI of *Baltoeurypteris* probably worked as a paddle in rowing (cf. subaqueous flying, see Robinson 1975 or Selden 1981 for discussion). Highly specialized joints on podomere 6, analogous to those on the fifth pereopod of portunid crabs, enabled the distal paddle (flattened podomeres 7 and 8) to be rotated in order to extend it during the propulsive stroke and collapse it during recovery. In order to minimize yawing, the paired paddles were probably moved in phase, as in the large, fast water beetles and bugs. The study indicated that *Baltoeurypteris* was an accomplished swimmer and this was probably its primary mode of locomotion.

In a closer comparison with portunids, R. E. Plotnick (pers. comm. 1982) produced a model for eurypterid swimming using the paddles in a manner akin to the sculling action of these crabs. The striking convergence in paddle morphology between portunids and eurypterids may be due to the fact that this is the best way of producing a flattened, rotating paddle from an arthropod limb; however, the simple rowing model for *Baltoeurypteris* may need modification in the future, in the light of Plotnick's work.

Rowing is used as a means of propulsion only by small animals, such as arthropods, which have low body drag. Larger vertebrates which row (or paddle) include otters and ducks, which do so mainly at the surface where drag is reduced because most of the body is out of the water. It is more efficient for larger, faster animals to 'fly' under water, using flippers as hydrofoils. In this method, thrust is produced as the lift component of the force produced by the hydrofoil. Ideally, flippers should present a hydrofoil section along the whole length of the limb, they should articulate close to the body, and move up and down perpendicular to the long axis of the body during 'flying'. Which method of locomotion is more appropriate for any given animal depends not only on size, but also on other factors such as swimming speed and viscosity of the medium (air or water). At Reynolds numbers ($Re = Vl/\nu$ where V = velocity, l = length, and ν = kinematic viscosity) below about 10^2 , viscosity is the dominant factor, above about 5×10^3 inertia becomes important, at $10^2 < Re < 5 \times 10^3$ there is an influence from both components. The actual change-over from lower

Re at which rowing is more efficient to higher Re at which locomotion involving lift becomes more efficient occurs about $10^1 < \text{Re} < 10^2$ (Nachtigall 1978, fig. 2). At lower Re values, lift/drag ratios become prohibitively low, and at higher Re, the bending moments on oars become prohibitively high.

Eurypterids are known to have reached body lengths of 2 m (Clarke and Ruedemann 1912); commonly they were smaller, but still large in relation to other swimming arthropods. The kinematic viscosity of water (ν) is $0.01 \text{ cm}^2 \text{ sec}^{-1}$ and thus the Re of a small eurypterid, 10 cm long, swimming at a mere 0.1 cm sec^{-1} would be 10^2 ; at 1 cm sec^{-1} $\text{Re} = 10^3$; and at 10 cm sec^{-1} $\text{Re} = 10^4$. Therefore, even small, slow eurypterids fall within the region in which underwater flying could be more efficient than rowing. Indeed, the swimming limbs of the large pterygotoids are quite flipper-like in construction, with a long blade and only short proximal podomeres. The swimming limbs of the small hughmillerioid eurypterids are also flipper-like, but their bodies streamlined; if they swam fast, their Reynolds numbers would also fall within the region where underwater flying was more efficient. Detailed functional morphological study of the swimming limbs of these eurypterids is necessary to determine whether they acted as hydrofoils or oars. The paddles of the Eurypteroidea (including *Baltoeurypterus*) are oar-like, and could only have moved in near-horizontal planes because of the sub-vertical joint axes of their proximal podomeres; presumably they swam more slowly than the hughmillerioids.

In addition to the qualitative observations based on morphology, the possible swimming efficiency of eurypterids can be calculated from simple mathematical models. Ideally, empirical data could be obtained using actual models, but such data are not available at present. The body drag can be estimated using the equation:

$$D = \frac{1}{2} \rho V^2 A_b C_{Db} \quad (\text{Alexander 1968, p. 215})$$

where D = drag, ρ is the density of water (1 gm cm^{-3}), V is the velocity of the body, A_b is the cross-sectional area (estimated from an ellipse with width the maximum width of the body and height half the width), and C_{Db} is the drag coefficient of the body. For a *Baltoeurypterus* specimen of the size illustrated by Holm (1898, pl. 1, fig. 1), body length (excluding telson) is 16.5 cm, A_b is 12.0 cm^2 , and C_{Db} is taken as 0.5. C_{Db} for water beetles studied by Nachtigall (e.g. 1980, fig. 3d) lay around 0.4 at $10^3 < \text{Re} < 10^4$; these have smoother profiles than *Baltoeurypterus*, but 0.5 could be an overestimate. At a velocity of 10 cm sec^{-1} , this animal had a Re of 1.65×10^4 ,

$$D = \frac{1}{2} \times 1 \times 10^2 \times 12 \times 0.5 = 300 \text{ dyn.}$$

A *Baltoeurypterus* specimen this size might have had about 6.75 gm of swimming muscle (assuming each coxa VI to have had about 3.375 cm^3 of muscle). This is about 0.037 of the body weight. How fast could *Baltoeurypterus* have swum using its propulsive musculature to the fullest extent?

Mean power consumption is given by the expression

$$\bar{P} = d(v - V) + d'(v + V) + DV$$

where d and d' are the drag forces acting on a single paddle in the power and recovery strokes respectively, and v is the speed of the paddle relative to the body (assuming a relative duration of 5.0:5.0). Thus $(v + V)$ and $(v - V)$ are the velocities of the paddles relative to the water in the power and recovery strokes respectively (Alexander 1968). The mean power expression assumes a steady state in which the body moves at constant velocity V , but because of the recovery stroke, propulsive power is only produced about half the time. Therefore $D = (d - d')$. For our *Baltoeurypterus* specimen, the paddle area, A , is 4.2 cm^2 and the drag coefficients for the propulsive and recovery strokes, C_{Dp} and C_{Dr} respectively, can be read from published graphs and depend on Re. The paddle velocity v can be calculated for a given V using the expression $D = (d - d')$. The mean power consumption of *Baltoeurypterus* at maximum sustainable speed (assuming muscle power output of 0.03 W gm^{-1}) would have been:

$$6.75 \text{ gm} \times 0.03 \text{ W gm}^{-1} / 2 = 0.10125 \text{ W.}$$

At speeds of between $1 \times$ and $10 \times$ the animal's body length sec^{-1} , $10^4 < \text{Re} < 10^5$, $C_{Db} \approx 0.5$,

$C_{Dp} \approx 1$, and $0.009 < C_{Dr} < 0.04$ (see graphs in Nachtigall 1977a). To find the velocity V that may be achieved with a power input of around 0.10 W we need to find v for various values of V : using the expression $D = (d - d')$, in which $C_{Dr} = 0.02$, thus:

$$\frac{1}{2}\rho V^2 AC_{Db} = \frac{1}{2}\rho(v - V)^2 A_p C_{Dp} - \frac{1}{2}\rho(v + V)^2 A_p C_{Dr}.$$

For $V = 38 \text{ cm sec}^{-1}$, $v = 108.66 \text{ cm sec}^{-1}$, which, when substituted into the equation:

$$\bar{P} = d(v - V) + d'(v + V) + DV = 0.104 \text{ W}.$$

Therefore, a *Baltoeurypterus* specimen 16.5 cm long could be expected to achieve a speed of around two and a half body lengths per second. The efficiency is given by the expression:

$$(V/v)[(d - d')/(d + d')]$$

which gives 0.29. This compares with 0.45 for the water beetle *Acilius* (Alexander 1968, p. 228).

Great care must be taken in assessing these results because of the considerable number of assumptions made in order to gain them. However, they give an indication of the orders of magnitude of various parameters in the swimming of *Baltoeurypterus*, which fit reasonably well with results from living animals. For example, Nachtigall (1977b) showed that the absolute velocities of the water beetles he studied approximately equalled $20 \times$ their lengths sec^{-1} , but that for larger species the velocity increased more slowly. An extrapolation of Nachtigall's equation to larger (i.e. eurypterid-sized) animals by Hughes (see Appendix), taking into account changes in C_D and Re , revealed that the increase in velocity falls off as body length increases, such that at about 10 cm body length the velocity is about 18.5 cm sec^{-1} , that is only about twice the body length per second. Because of their large size, pterygotoids had high values of Re during swimming; even small projections beyond the boundary layer increase the drag coefficient (for a pterygotoid 150 cm long, at $\text{Re} = 10^5$ projections of 0.15 cm are important, at $\text{Re} = 10^6$, 0.015 cm, etc.; see Alexander 1968, p. 219; Nachtigall 1977a, fig. 6c) so that hydrofoil propulsion becomes attractive. Pterygotoids can be envisaged cruising at low speeds but with the capability of producing occasional bursts of power, producing thrust by means of the flat telson used as a tail fluke, in order to capture prey.

FOOD AND FEEDING

There is no direct evidence, in the form of gut contents, for the eurypterid diet. Alimentary canals have been described in *Carcinosoma newlini* from the Silurian Kokomo Limestone of Indiana (Ruedemann 1921a; Kjellesvig-Waering 1958), *Pterygotus (Acutiramus) macrophthalmus cummingsi* (Clarke and Ruedemann 1912), and *Eurypterus lacustris* (Heubusch 1962), both from the Silurian Bertie Waterlime of New York. A possible anal opening was described in the telson of *Buffalopecterus pustulosus* from the Bertie of New York (Kjellesvig-Waering and Heubusch 1962) but none is known from any other well-preserved form, so it is probable that the anus of most eurypterids opened through thin cuticle between the telson and the pretelsonic segment, as in *Limulus*.

A possible coprolite containing fragments of *Megalograptus ohioensis* and a trilobite cephalon, in association with *M. ohioensis* in the Ordovician of Ohio, was considered by Caster and Kjellesvig-Waering (1964) as evidence for cannibalism in this species. Unstructured masses containing disarticulated agnathan fragments are common in the Monks Water fish bed in the Hagshaw Hills Silurian inlier in Scotland, together with well-preserved fish and the eurypterid *Lanarkopterus dolichoschelus*. These were interpreted by Selden (1979) as eurypterid coprolites, possibly from the large, predatory *Lanarkopterus*. Possible coprolites composed of *Logania* denticles are known from the Lesmahagow inlier (Rolfe 1973), and may be eurypterid also.

Probably most eurypterids were carnivores. Evidence for this conclusion includes: their large size—it is advantageous to be larger than one's prey; many were active swimmers and had anterior stereoscopic vision, with overlapping visual fields of the compound eyes—e.g. *Baltoeurypterus* (Selden 1981), and, by extrapolation, pterygotoids and other forms with anteriorly directed eyes and well-developed swimming paddles. Further evidence comes from limb morphology. The archetypal

'spiniferous leg' (Størmer 1974) was used for both food gathering and locomotion, and has retained at least the former function where present anteriorly on the prosoma of many eurypterids, e.g. *Baltoeurypterus* (Selden 1981). Being generalized, this limb type may indicate an unspecialized feeder. Two main food-gathering strategies developed from this condition: first, elongation of the anterior post-chelicerallimbs (II and III) and the development of long spines, as in *Mixopterus* (Størmer 1934a) and *Lanarkopterus* (Ritchie 1968); secondly, enormous enlargement of the chelicerae in the Pterygotoidea, and to a much lesser extent in the hughmilleriids.

Evidence that smaller eurypterids were preyed upon by larger forms comes from the morphology of the dorsal ocelli. In *Baltoeurypterus*, this pair of simple eyes is situated on a small node near the centre of the carapace; the ocelli, with their overlapping visual fields, could have sensed movement in the posterodorsal direction, and thus initiated an escape reaction from an advancing predator (Selden 1981). The only larger predatory animals known from eurypterid beds are other eurypterids. Interestingly, juvenile eurypterids bear relatively larger ocelli and swimming limbs than their adult counterparts, and were thus well equipped for rapid escapes during this vulnerable period of their lives (Clarke and Ruedemann 1912).

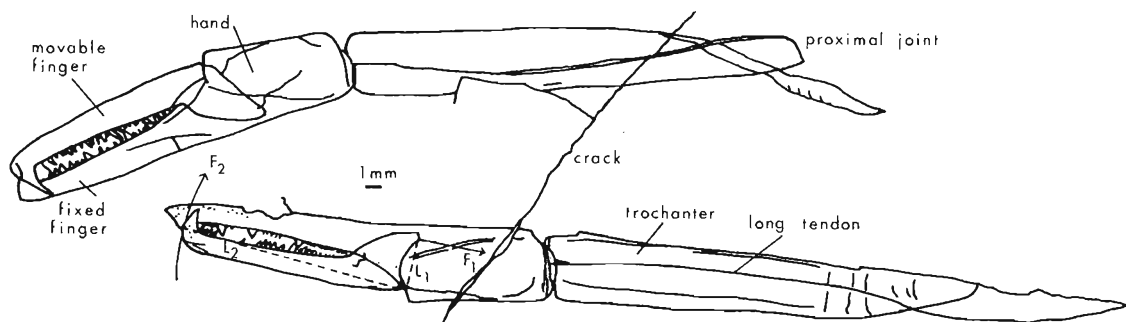
Functional morphology of pterygotoid chelicerae

Most authors have agreed with Clarke and Ruedemann (1912) that the pterygotoid chelicera is directly homologous with all other chelicerate chelicerae in bearing three podomeres: (1) trochanter; (2) hand (with fixed finger); and (3) movable finger (van der Hammen 1980). Kjellesvig-Waering (1964), on the other hand, went to great lengths to show that an additional joint was present part-way along the extremely elongated trochanter, which was necessary in order that food, caught by the chelae, could be transferred to the mouth. (Note that early authors, e.g. Huxley and Salter 1859; Page 1859; Woodward 1866–1878, restored this appendage with from four to eight podomeres, based mainly on fortuitous cracks in the specimens.) My observations on *Erettopterus bilobus* from Lesmahagow, Scotland, indicate that Kjellesvig-Waering (1964) had noticed a true morphological change, which occurs on podomere 1 consistently about $1.13 \times$ the length of podomere 2 from the podomere 1–podomere 2 joint. This adds weight to a suggestion by Størmer (pers. comm. 1976) that this change represents the true proximal end of the podomere, and material beyond this is the remains of internal structures, probably long tendons (text-fig. 2).

The possible function of a chela can readily be assessed from its mechanical advantage (MA ; Warner and Jones 1976)

$$MA = L_1/L_2$$

where L_1 is the distance from the pivot to the point of application of the force (F_1), i.e. the closer muscle attachment, and L_2 is the distance from the pivot to the point the force (F_2) is applied,



TEXT-FIG. 2. Camera lucida drawing of chelicerae of *Erettopterus bilobus*, Lesmahagow, Scotland (Royal Scottish Museum, Kinnaird 11), showing force directions F_1 and F_2 , and lengths L_1 and L_2 used in calculating maximum mechanical advantage, MA .

maximally the tip of the movable finger (text-fig. 2, note also that $F_1/L_1 = F_2/L_2$). Characteristically, chelae adapted for strong gripping (high F_2) act slowly, have a high MA , mainly tonic muscle, short fingers, and a short, thick hand to accommodate the muscle bulk. Chelae adapted for fast movements (e.g. prey capture) are weak, have a low MA , mainly phasic muscle, long fingers, and a long, thin hand to accommodate the long contraction distance of the closer muscle.

From a cursory examination of pterygotoid chelicerae, it is obvious that their maximal MA s are low. Some measurements were given by Selden (1979) and more will be published elsewhere. For *E. bilobus* the MA is around 0.2, and is similar for other pterygotoids. Thus the pterygotoid chelicera was primarily a food-capturing device. Furthermore, it is attached to the end of a very long, thin trochanter and was articulated by long muscles with long tendons. The MA of the chela-trochanter joint system must also have been very low, indicating fast movements. Pterygotoids can be envisaged cruising in the water or across the substrate with chelicerae folded, and rapidly extending the chelicerae to capture prey with an excellent aim afforded by the stereoscopic vision of their antero-marginal eyes. Comparisons can be made here with the prey-capturing mechanisms of dragonfly larvae (e.g. Carthy 1965, pp. 39–43), praying mantids (Loxton and Nicholls 1979), and mantid shrimps (Caldwell and Dingle 1975). As long as the proximal and distal trochanteral joints of the pterygotoid chelicera were capable of an angle of movement approaching 180° (as seems likely from preliminary observations on the podomere 1–podomere 2 joint), food thus caught could have been transferred to more posterior appendages or to the oral cavity directly, for mastication, without the necessity of an extra joint.

Brown *et al.* (1979) pointed out that decapod chelae do not only operate at their fingertips (maximal MA) but also bear a variety of teeth, knobs, and edges along the length of the fingers. They produced a scheme of seven mechanical analogues of the different types of chela occlusive regions in the decapods they studied, and each chela proved to be polyfunctional. Food captured by the tip of the chela could be transferred to another region (where MA would be higher) and then crushed, sheared, or torn. Similarly, pterygotoid chelicerae bear regional differences along the lengths of the fingers (see, for example, Kjellesvig-Waering 1964, text-fig. 6). The distal tips may be bifid and are incurved, either acutely or not: this is advantageous for directing prey towards the teeth on the fingers, as shown by Loxton and Nicholls (1979) for praying mantids. The teeth on the chela fingers of *Erettopterus* and *Pterygotus* are mostly short and suitable for holding prey, but the few larger ones are opposed and touch, and could therefore have effectively sliced up the prey. The most striking adaptation is seen in the 'Acutiramus' type of chela (see Waterston 1964, text-fig. 5) which bears one or more long teeth pointing obliquely distally and bearing small, saw-like teeth on the proximal side. Any prey placed in the chela proximal to this tooth could be sawn up with a high MA . Resemblance of these saw-like teeth to the fish-descaling implement on penknives suggests the possibility that these chelicerae were adapted for dealing with armoured vertebrates. A similar sawing action may have been possible in the *Erettopterus* chela, in which numerous small teeth are present proximally on the movable finger running up the distal edge of the process to which the closer muscle is attached proximally (see Waterston 1964, text-fig. 3). When closed this saw-edge lies within the base of the fixed finger, but when open would be exposed to prey inserted in the angle between the fingers.

SEX

Sexual dimorphism in eurypterids was first recognized by Woodward (1869, p. 61; 1872, p. 114). Whilst secondary sexual characteristics are known in some genera (e.g. *Baltoeurypterus*, Wills 1965), dimorphism is most readily apparent in the genital appendages of the opisthosoma. There are two types of genital appendage (Størmer 1934a): type A is generally long and narrow, type B is usually shorter and squat. Type A was considered to belong to the female by Woodward (1872, p. 115), Holm (1898), Clarke and Ruedemann (1912), Wills (1964, 1965), Kjellesvig-Waering (1979), and Selden (1981), whereas Størmer (1934a, 1936, 1955, 1973) and Størmer and Kjellesvig-Waering (1969) considered that it may have belonged to the male.

There are only two eurypterid genera in which both genital appendages A and B as well as all prosomal appendages are known; these are *Baltoeurypterus* and *Eurypterus*. In the former, specimens with type B genital appendage also have secondary sexual characteristics in the form of modified spines of limb II and a 'scimitar lobe' (Holm 1898) on limb III. However, no such modifications have been found on the latter genus, a fact that Clarke and Ruedemann (1912, p. 164) attributed to the immaturity of the specimens they studied. Unlike *Limulus*, the curious lobes on limb III of the presumed male of *Baltoeurypterus* are present, but smaller, in sub-adults (Selden 1981). Some traces of these lobes would be expected to be found amongst the many hundreds of specimens of *Eurypterus* that exist in collections if they were present in this genus. If not, it would be additional evidence in favour of the taxonomic separation of the two genera, previously a matter of some controversy (Andrews *et al.* 1974). Other eurypterids bear curious lobes on prosomal appendages, for example, *Mixopterus* (Ruedemann 1921b; Størmer 1934a), *Stylonurella* (Waterston 1979), and *Adelophthalmus* (Wills 1964), but in none of these genera are both genital appendages A and B known with certainty. A particular problem is that some type B appendages may be quite long when mature (e.g. in *Slimonia*, Waterston 1960) so both types must be found for a definite statement to be made.

These curious lobes on the prosomal appendages of one sex of certain eurypterids have generally been referred to as claspers, in the belief that they were used by the male to cling to the female during mating, as in Recent Xiphosura. Størmer and Kjellesvig-Waering (1969) suggested that if they belonged to the female, then they could have functioned in scooping out a hollow in the substrate in which to lay eggs, and Rolfe (1980) has suggested that they may have been used by the male to immobilize the female during courtship to prevent being eaten. Kjellesvig-Waering (*in* Waterston 1979, p. 290) suggested that as, in his opinion, these lobes belonged to the female, they may have been oostegites—structures forming the base of a brood chamber or marsupium. A most important observation made by Kjellesvig-Waering (*in* Waterston 1979) was that the scimitar lobe in *Baltoeurypterus* had an opening at the tip. No opening had been observed by Holm (1898) or Selden (1981), but may have been overlooked because this organ is commonly crumpled distally; any such opening could therefore conceivably be an artefact. However, if such an opening does exist, it suggests that the scimitar lobe had a secretory function; Kjellesvig-Waering (*in* Waterston 1979) suggested it may have provided nourishment for embryos developing in the marsupium.

In spiders, the male bears modified palps (limbs II) with emboli that are charged with sperm deposited on a special pad of silk, and then inserted into the spermathecae of the female's genitalia (epigyne) during mating (see, for example, Bristowe 1958). The shape of the embolus reflects that of the spermatheca, and the morphological differences in palps and epigynes between species are useful to spiders as isolating mechanisms, and to arachnologists as taxonomic characters. A similar method of insemination is utilized by the Ricinulei, but in this group it is the third leg (limb V) which is modified in the male, and sperm is transferred directly from the penis to the embolus (Cooke 1967; Legg 1977). Associated with the type A genital appendage in *Baltoeurypterus* (and other genera, Wills 1965, p. 128) is a pair of 'horns': curved internal tubes, closed distally, interpreted by Wills to have been tactile in function, but could equally be spermathecae. A curved scimitar lobe of the presumed male could have fitted snugly into one of these curved pouches, judging by their similar shapes. The scimitar lobe may thus have been a kind of embolus, which could have been charged with sperm, and later emptied into the female's spermatheca, through its distal opening.

Further investigation of eurypterid sexual organs is necessary before such speculations could be confirmed. There are considerable problems associated with eurypterids having used the method of free sperm transfer for mating: it is generally considered to be advanced, having evolved from methods using spermatophores (see Cloudsley-Thompson 1976). Nevertheless, comparison with modes of fertilization used by extant chelicerates other than the Xiphosura could be most profitable. Even if the scimitar lobe proves, on closer inspection, not to have had a distal opening in life, it could have been used to transfer a spermatophore. Such a method of fertilization is an advance on the external fertilization found in Xiphosura, and occurs in most crustacean groups.

ASSOCIATIONS

A variety of other organisms have been found associated with eurypterid specimens from the Silurian, although none has definitely been shown to have been present whilst the eurypterid was alive. Chapman (1929) described some small shells attached to a large *Pterygotus* tergite from the Silurian of Melbourne, Australia. He called them *Capulus melbournensis*, though it is doubtful whether they really belong in this genus of ectoparasitic gastropods, there being no feeding advantage in being attached half-way down the back of the eurypterid.

A large number of stalked objects were found attached to moulted skins of *Baltoeurypterus* etched from the matrix with dilute HCl by Wills (1962, 1963); he interpreted these as juvenile pedunculate cirripedes. Larvae of the cirripede, named *Cyprilepas holmi* Wills 1962, would have attached themselves to those parts of eurypterid exuviae exposed above the silt surface, as they lay on the sea bottom. *Baltoeurypterus* specimens from Saaremaa, Estonia, are also commonly found crammed with ostracodes; ostracodes are rare in the surrounding matrix, and eurypterid remains at slightly different levels on the same slab are also devoid of ostracodes (see Boucot 1981, fig. 167). It is uncertain whether the ostracodes are drifted remains trapped by the eurypterid exuviae, or whether they sought shelter or food beneath the eurypterid debris (Selden 1979).

A *Baltoeurypterus* specimen overgrown with a mass of tubules was figured by Clarke (1921, fig. 104), which he interpreted as a symbiotic or possibly parasitic association. It is more likely that these tubules represent a saprophagous organism, or were using eurypterid exuviae for anchorage. Fungal hyphae and sporangia were discovered on etched specimens of *Baltoeurypterus* in Holm's slide collection by Selden (1981); these were interpreted as Recent growths, which are commonly seen on specimens in weathered rock. Sub-spherical bodies found on *Truncatiramus serricaudatus* from Gotland, and called 'problematica' by Waterston (1964), may represent the remains of saprophagous organisms.

These relationships tell us nothing about the life of eurypterids because they all seem to be post-mortem associations; however, they would repay further study for the taphonomic information that would be revealed. The majority of published reports on eurypterid associations have concerned the well-known *Baltoeurypterus*; the acid-etching process which has revealed much of the morphology of this animal could already have produced the remains of parasites or commensals which remain unrecognized in existing slide collections. However, most eurypterid remains are exuviae; presumably arthropod ectoparasites need to transfer to the new cuticle at each moult, and would thus not be preserved on moulted cuticles.

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APPENDIX

EXTRAPOLATION OF NACHTIGALL'S MEASUREMENTS TO LARGER ANIMALS

The variation of drag coefficient with Reynolds number follows a similar shaped curve for all body shapes (see any standard work on fluid mechanics). As a rough approximation, this variation is taken to have the form $C_D = C_{D\infty} + B/\text{Re}$, where $C_{D\infty}$ is the value of the drag coefficient appropriate to high Reynolds number and B is a constant.

On average over a period of time the power delivered by the muscles must equal the drag multiplied by the velocity, and if we assume that the power available from the muscles is proportional to the animal's volume, it is easy to show that for geometrically similar creatures

$$V^3(C_{D\infty} + B/\text{Re}) \propto l,$$

where l is the characteristic length of the animal and V is its speed.

When the Reynolds number becomes large then $C_{D\infty} \gg B/\text{Re}$ and this equation reduces to

$$V \propto [l/C_{D\infty}]^{0.33} \quad (1)$$

At the other extreme of low Reynolds number $C_{D\infty} \ll B/\text{Re}$ and we get

$$V^3 B/\text{Re} \propto l.$$

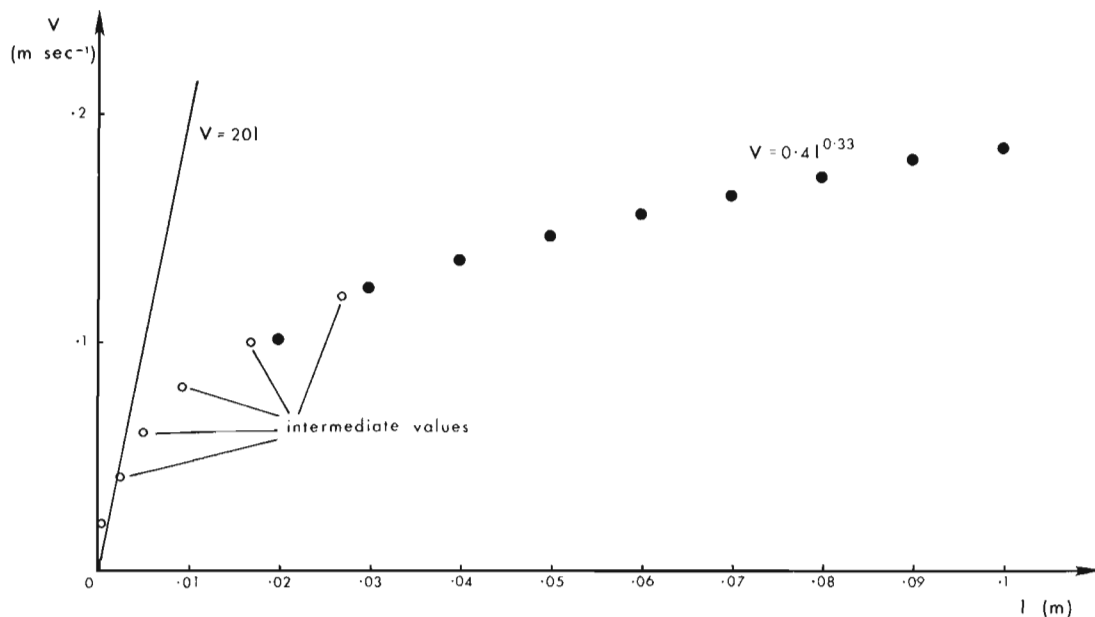
The Reynolds number $\text{Re} = Vl/\nu$ where ν is the kinematic viscosity of the fluid and substitution yields

$$V \propto l \quad (2)$$

where the constant B has been absorbed into the constant of proportionality.

Nachtigall (1977b) gave results that closely fit the line given by $V = 20l$ (using Nachtigall's units) though at larger values of l the results fall below the line.

Equation (2) is clearly of the same form and we may use Nachtigall's constant of 20 to help determine the unknowns in equations (1) and (2). The other information we require are the values of B and $C_{D\infty}$. Taking $C_{D\infty}$ as 0.35 and forcing the approximation $C_D = C_{D\infty} + B/\text{Re}$ to satisfy the conditions $C_D = 1.0$ at $\text{Re} = 90$, then $B = 58.5$.



TEXT-FIG. 3. Graph showing extrapolation of Nachtigall's results to larger animals; see text for explanation.

A small amount of algebra then gives equation (1) as

$$V = 0.4l^{0.33},$$

where l is in m and V in m sec^{-1} .

It is also possible to evaluate V as a function of l at Reynolds numbers between the extremes of equations (1) and (2), though this involves more algebra, and text-fig. 3 shows the resulting curve.

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