Eurypterid Respiration [and Discussion]

P. A. Selden and P. Whalley

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Eurypterid respiration

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The function of the eurypterid gill is discussed in comparison with possible analogues among Recent arthropod respiratory organs, and with regard to suggestions that it may have been an air-breathing organ. The pseudotrachea model is preferred, since size and morphology in particular, preclude its use as a gill. True gills may have been present, remaining undiscovered. The development of a secondary air-breathing organ, in addition to gills, appears to have been less favourable for terrestrialization than the direct conversion of book-gill to book-lung, as in the scorpion line.

The function of eurypterid gills as true gills, (aquatic respiratory organs) was accepted until Størmer (1976) pointed out their resemblance to isopod pseudotracheae (air-breathing organs) and thus suggested that some eurypterids may have been amphibious. Rolfe (1980) remarked on the similarity of the eurypterid gill to the plastron (an air-breathing organ of aquatic insects and mites) which also implies air breathing in eurypterids. In the present study, the eurypterid gill is compared with known arthropod respiratory organs, and its possible functions are discussed.

Woodward (1866–1878) figured supposed gills of *Erettopterus bilobus* and *Slimonia acuminata*; inspection of his plates and specimens revealed that these are not gills (Selden 1984). Later, Laurie (1893) and Moore (1941) figured the gills of *Slimonia*. The detailed structure of the gill of *Baltoeurypterus tetragonophthalmus* was elucidated by Wills (1965), based partly on unpublished work by Holm (see also Holm 1898). Waterston (1975) reconstructed the gills of the Devonian *Tarsopterella scotica* in great detail and partly by comparison with *Baltoeurypterus*.

The ceiling of the gill chamber (ventral body wall) bears the so-called gill tract which has been interpreted by Holm (1898), Størmer (1976), Waterston (1975) and Wills (1965) as the main respiratory surface. The gill tract is oval or triangular and has generally been reconstructed as raised into a cushion. The surface bears many spinules which provide a large surface area of cuticle, which is covered with minute polygons bearing rosettes at their corners (Wills 1965). The gill tract bears invaginations leading to poorly defined, spongy tissue; it is permeated by a dendritic system of vessels in which the branches diverge medially from a trunk that originates laterally.

There is a wide variety of arthropod respiratory organs which here are classified in five functional types (figure 1). Gills extract dissolved oxygen from water and it is transported in the body in a blood system. Blood is also used for transport from lungs and pseudotracheae, but in these organs oxygen is extracted from air. The basic tracheal system carries air direct to the tissues; the plastron is a modification of this system wherein a mat of hairs traps a bubble of air on the cuticle surface when the animal is under water. The tracheal gill is a closed system relying on oxygen diffusion across thin cuticle from water into the air of the tracheae.
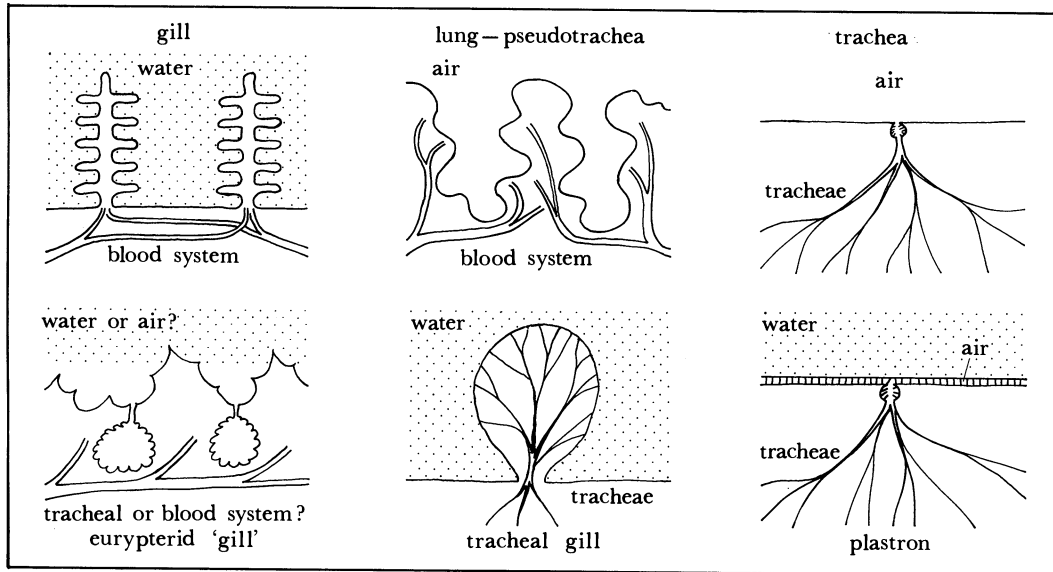
FIGURE 1. Diagram showing the basic differences between the five main types of arthropod respiratory organ, compared with the eurypterid gill tract.

AQUATIC RESPIRATION

Gills are outgrowths of the body wall mainly concerned with oxygen uptake from water (see Houlihan *et al.* (1982) and Mill (1972) for further information). Simple gills, as in the smaller Crustacea, are thin-walled epipodites of the appendages. The gills of larger Crustacea and *Limulus* are complex, consisting of many filiform or lamelliform lobes with well-developed efferent and afferent haemolymph channels. The positive correlation between body mass and gill area is well portrayed in Hughes (1982*a*, figure 15; *b*, figure 5). On this bilogarithmic plot, the slopes of the regression lines for decapod Crustacea vary between 0.5 and 1.0, though factors such as activity and mode of life (Gray 1957) affect the correlation. All measurements of gill area and body mass in larger Crustacea fall within the range for teleost fish (McMahon & Wilkens 1983, p. 295), as does an approximate value for *Limulus* (21 cm² g⁻¹) based on figures in Mangum (1982, p. 77).

Evidence weighs heavily in favour of eurypterids having been primarily aquatic animals; even stylonuroids, with no swimming appendages, are considered to have been predominantly aqueous in habit (Waterston 1979). Data comes from two sources: intrinsic (functional morphology) and extrinsic (sedimentology and associated biota), and may be positive or negative. Eurypterids are generally streamlined in shape, limb VI commonly forms a well-developed swimming paddle and a spatulate telson may be present for locomotion or stability in water. The large (up to 2 m long) pterygotids had relatively thin cuticles (Dalingwater 1975) and spindly walking legs, suggesting they would not have had sufficient strength to walk on land. A number of terrestrial adaptations of chelicerates (see Størmer 1976) are not known in eurypterids; these include trichobothria, a plantigrade 'foot' and a preoral cavity for external digestion.

The sediments and biotas of eurypterid-bearing horizons provide additional, but not conclusive, evidence of aquatism. Three eurypterid phases, ranging through hypersaline,

freshwater, brackish and marine environments, were recognized by Kjellesvig-Waering (1961) and have since been confirmed by later authors (for example, Boucot 1975; Størmer 1976; Waterston 1979). No eurypterid has yet been shown to have been wholly or primarily terrestrial. As eurypterids almost certainly evolved in the water, any air-breathing organs would have been developed secondarily. Regardless of the length of time spent on land by amphibious eurypterids, their primary organs of aquatic respiration are likely to have been retained at least in part.

Wills (1965) discussed the possible function of the *Baltoeurypterus* gill. He envisaged gas exchange taking place within the spongy masses of the gill tract and oxygenated blood being carried away by the dendritic pattern of veins towards lateral branchio-cardiac veins (the latter have not been seen but suggested by analogy with *Limulus*, after Patten & Redenbaugh (1900)). A similar dendritic pattern of vessels was described in *Slimonia* by Moore (1941) and in *Tarsopterella* by Waterston (1975). Waterston (1975) produced a model of the possible water flow through the branchial chambers of *Tarsopterella* for gill irrigation. Incidentally, parts of the eurypterid gill tract, were probably also concerned with osmoregulation (Selden 1984; Waterston 1979, p. 309).

Wills (1965) remarked upon the differences between the gills of *Baltoeurypterus* and *Limulus*. Those of the latter not only arise from the gill opercula but also consist of many lamellae which provide a large surface area for gas exchange. The spongy eurypterid gill tract is morphologically different to the complex lamellate gill of the larger invertebrates and fish.

Despite the morphological differences, does the surface area of the eurypterid gill tract bear the same relationship to body mass as in larger Crustacea and fish, which would be expected if their functions were similar? *Tarsopterella* was about 1 m long. A cylinder of this length with diameter the mean width of the animal and density that of water has a mass of about 20 kg. The gill tract of *Tarsopterella* is oval and measures about 9.0 cm by 3.5 cm. The irregular gill surface may be accounted for by trebling these measurements, so the total area of ten gills is 2835 cm^2, or 0.14 cm^2 g^{-1}. A *Baltoeurypterus* specimen the size of Holm's reconstruction (1898, plate 1, figure 1) might have weighed 182 g and have had a gill area (calculated from Holm (1898), plate 10, figure 9 and adjusted for size) of 1.97 cm^2, which gives the result of 0.38 cm^2 g^{-1}. When plotted on a bilogarithmic graph of gill area and body mass (see Hughes 1982a, figure 15) these results fall on a line with slope of about 0.8, but well below results for other animals. It is unlikely that computational errors can account for the differences because these are of an order of magnitude. For example, Gray (1957), in his study of gill areas of crabs in relation to their habitats, recorded mean values which ranged from 3.25 cm^2 g^{-1} for *Ocypode*, a supratidal species, to 13.67 cm^2 g^{-1} for *Callinectes*, a marine crab. More recent figures for Crustacea (McMahon & Wilkens 1983, p. 295) show a similar range from 4.4 cm^2 g^{-1} for *Cancer* to 10.0 cm^2 g^{-1} for *Gnathophausia*.

A number of arguments may be advanced to explain the apparent discrepancy in gill area:body mass ratio: gas exchange could also have occurred elsewhere on the body than the gills; rapid, efficient irrigation and circulatory systems would have helped; the gill could have been highly efficient. It is considered unlikely that any or all of these factors could explain such a large discrepancy as observed. Eurypterids may have been exceptionally sluggish animals, but evidence in the form of well-developed swimming and prey-capturing mechanisms argues against this (Selden 1981, 1984). A further possibility is that the eurypterid gill tract was in reality an air-breathing organ, such as a lung, pseudotrachea or plastron.

PLASTRON RESPIRATION

The tracheal systems of Uniramia consist of branching tubes (tracheae) which become increasingly finer (tracheoles) and fluid-filled as they permeate the tissues to which oxygen is served directly. The plastron of aquatic insects evolved from a device to prevent water entering the tracheal system, into an organ for breathing air under water. It consists of a mat of specialized hairs, or complex anastomosing cuticular structures, which traps a bubble of air in contact with the tracheal spiracle (Hinton 1968; Thorpe 1950). In the true plastron, gas exchange by diffusion across the air–water interface is sufficient to maintain the bubble indefinitely. The spaces across which the air–water interface is present are always small (less than 1 μm) to preserve shallow menisci and thus prevent wetting under pressure (Crisp & Thorpe 1948).

Rolfe (1980) pointed out an apparent similarity between the microstructure of the eurypterid gill tract and that of some insect plastrons. In the *Baltoeurypterus* gill tract, the reticulate cuticle with raised rosettes at the intersection of the polygons would have formed the plastron, while the dendritic structures would represent tracheae, in this model. A problem arises with the model when it is remembered that eurypterids probably evolved in water, yet the plastron is a device to enable secondarily aquatic arthropods, with tracheal systems for aerial respiration, to breathe air under water: it is unlikely that a tracheal system could develop primarily for aquatic respiration. Furthermore, insect plastrons are normally on exposed parts of the body whereas the eurypterid grill tract is concealed by gill flaps, and another difficulty with the model is that the spaces between the rosettes of the eurypterid gill tract (measured from Wills (1965), plate 3, figures 5–9; plate 6, figure 8) are about 5 μm, which may be too large to maintain menisci under pressure.

AERIAL RESPIRATION

Oxygen availability is greater in air than in water because of its higher diffusion rate in the former medium, the diffusion constant (partial pressure per unit length) at 20 °C for oxygen in air is 11.0 and in water is 0.000034 (Krogh 1941). However, while diffusion is enhanced by the respiratory membrane being wet, the membrane will leak water because the H_2O molecule is smaller than the O_2 molecule. Thus while in principle air-breathing may be more efficient than aquatic respiration, considerable energy needs to be expended to prevent water loss (e.g. by active osmoregulation, enclosure in moist chambers) and yet ensure adequate ventilation.

Crab gills tend to collapse out of water and thus work inadequately because of the reduction of surface area and ventilation. Some amphibious crabs have partly overcome these difficulties by sclerotization of the gills or retention of water in the branchial chambers, but such measures are only temporary. Terrestrial crabs have reduced gills but respiration is supplemented by lungs: highly vascularized areas of branchial chamber wall which are commonly complexly infolded or perforated (Diaz & Rodriguez 1977; Greenaway 1984). Lung-like structures within the pleopods of some terrestrial Isopoda were described by Unwin (1932) which, because of a certain resemblance to tracheae, have been termed pseudotracheae.

Størmer (1976, p. 142) pointed out a resemblance between the invaginated spongy masses of the *Baltoeurypterus* gill tract and the pseudotracheae of isopods. The plastron-like polygonal

cuticle would thus have prevented water from entering the pseudotracheae; similar structures are known to occur in isopods and in insects susceptible to drowning in which no true plastron is developed. In this model, the dendritic structures would represent blood vessels. Størmer (1976) concluded that a number of eurypterid species may have been amphibious, using the external parts of the gill tracts as true gills and the invaginations as pseudotracheae.

There appear to be no objections to the pseudotrachea–lung model on morphological grounds. The hydrofuge function of the polygonal cuticle is acceptable when the gill tract was out of water but the distances between the rosettes may have become critical when the animal was submerged and greater pressures might have forced water into the pseudotracheal invaginations. Physiological mechanisms could have prevented this, or it may not have been a problem: crab lungs are apparently unaffected.

The problem, as Størmer (1976, p. 143) recognized, is that overwhelming evidence suggests that eurypterids were aquatic for probably most, if not all, of their lives. Pseudotracheae would have been useful for air-breathing but eurypterids must also have possessed organs for aquatic respiration.

Conclusions

From this review, it is apparent that the so-called eurypterid gill tract may in fact be an accessory respiratory organ for air-breathing, and true gills of eurypterids are not known. True gills would be expected to occur within the branchial chamber (which is otherwise reconstructed as an empty space: Waterston 1975, figure 3), on the dorsal surface of the Blattfuss (operculum), where the gill tract was originally placed by Holm (1898). The homology of xiphosuran gill-flaps, eurypterid Blattfüsse and scorpion abdominal plates was convincingly argued by Størmer (1963, 1976) on comparative morphological and embryological grounds; yet while 'there seems no reason to doubt that arachnid book-lungs are the invaginated homologues of xiphosuran book-gills' (Anderson 1973, p. 439) it is hard to envisage the eurypterid gill tract as a homologue of these structures because of its quite different morphology and position, despite attempts to do so (Waterston 1975; Wills 1965).

Even in *Baltoeurypterus*, that 'most completely known of all extinct animals' (Clarke & Ruedemann 1912), the dorsal surface of the Blattfuss is not known. Holm (1898, p. 36) found no trace of it, and Wills (1965) stated: 'usually all the rest of this skin has disappeared completely...but in one or two dissections I saw fragments that I thought belonged to it, but they were so delicate that they were either lost during the etching or ceased to be visible when embedded in the Marco [plastic resin]'. It was not seen by Waterston (1975) in *Tarsopterella*, nor by Wills (1964) in his preparations of *Adelophthalmus*. A possible reason for this lack of preservation is that the majority of eurypterid fossils are moults (Selden 1981), and any thin cuticle (for example, on gills), particularly if mainly endocuticle and thus resorbed before ecdysis, is unlikely to survive fossilization and specimen preparation. An undescribed eurypterid specimen (Hunterian Museum G807), exquisitely preserved three-dimensionally in a phosphatic nodule from the Lower Carboniferous of the Montagne Noire region of France, appears to have lamellate structures within the branchial chambers in addition to gill tracts. Detailed study of this and other well-preserved eurypterid specimens will be necessary before it can be definitely stated whether or not true gills were present.

Eurypterids and scorpions co-existed during the middle to late Palaeozoic. While eurypterids had a number of pre-adaptations to land life, (for example, locomotory, feeding (Selden 1981),

224 P. A. SELDEN

possibly mating (Selden 1984)), these were more advanced in the scorpions. Early scorpions were aquatic and gill-bearing (Rolfe, this symposium; Rolfe & Beckett 1984) and following a vast radiation into amphibious and terrestrial forms during the upper Palaeozoic (Kjellesvig-Waering 1984), only those with book-lungs survive today. Eurypterids apparently did not develop book-lungs but instead used what may be termed the 'crustacean method' of air-breathing (secondary lungs–pseudotracheae), which proved successful only for terrestrial isopods and certain crabs, but not eurypterids.

Desiccation is a problem for terrestrial Crustacea, and it has been suggested (Rolfe 1980) that the large size of some eurypterids and scorpions could have been of benefit in withstanding this. However, among the many chelicerate lines which became terrestrialized (van der Hammen 1977), small size may have conferred greater advantages during the transition. Cryptic arachnids inhabited the moist environment among the first plant colonizers of the land (for example, Hirst 1923; Rolfe 1982; Shear *et al.* 1984). Small size favours rapid maturation and progenesis (*sensu* Gould 1977) and is a feature of r-selected animals (Pianka 1970). Such animals are more easily able to adapt and compete in new environments than are K-selected ones, and this may explain why many taxa arose at small body size, Cope's rule (Stanley 1973). The large, probably K-selected, eurypterids were unsuccessful in adapting to the land habitat, and thus obeyed Cope's rule by dying out at large size. On the other hand, some scorpions were apparently sufficiently pre-adapted to land life and particular physiological advantages of large size enabled their colonization of the land at reduced diversity.

References

Anderson, D. T. 1973 *Embryology and phylogeny in annelids and arthropods.* Oxford: Pergamon.

Boucot, A. J. 1975 *Evolution and extinction rate controls.* Amsterdam: Elsevier.

Clarke, J. M. & Ruedemann, R. 1972 The Eurypterida of New York. *Mem. N.Y. St. Mus. nat. Hist.* **14**, 1–439.

Crisp, D. J. & Thorpe, W. H. 1948 The water-protecting properties of insect hairs. *Discuss. Faraday Soc.* **3**, 210–220.

Dalingwater, J. E. 1975 Further observations on eurypterid cuticles. *Fossils Strata* **4**, 271–279.

Diaz, H. & Rodriguez, G. 1977 The branchial chamber in terrestrial crabs: a comparative study. *Biol. Bull. mar. biol. Lab., Woods Hole* **153**, 485–504.

Gould, S. J. 1977 *Ontogeny and phylogeny.* Cambridge, Massachusetts: Harvard.

Gray, I. E. 1957 A comparative study of the gill area of crabs. *Biol. Bull. mar. biol. Lab., Woods Hole* **112**, 34–42.

Greenaway, P. 1984 The relative importance of the gills and lungs in the gas exchanges of amphibious crabs of the genus *Holthuisana. Aust. J. Zool.* **32**, 1–6.

Hammen, L. van der 1977 A new classification of Chelicerata. *Zool. Meded., Leiden* **51**, 307–319.

Hinton, H. E. 1968 Spiracular gills. *Adv. Insect Physiol.* **5**, 65–162.

Hirst, S. 1923 On some arachnid remains from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire). *Ann. Mag. nat. Hist.* **12**, 455–474.

Holm, G. 1898 Über die Organisation des *Eurypterus fischeri* Eichw. *Mem. Acad. Sci. St. Petersb.* **8**, 1–57.

Houlihan, D. F., Rankin, J. C. & Shuttleworth, T. J. (ed.) 1982 *Gills.* Cambridge: Cambridge University Press.

Hughes, G. M. 1982 An introduction to the study of gills. In *Gills* (ed. D. F. Houlihan, J. C. Rankin & T. J. Shuttleworth), pp. 1–24. Cambridge: Cambridge University Press.

Hughes, G. M. 1983 Allometry of gill dimensions in some British and American decapod Crustacea. *J. Zool., Lond.* **200**, 83–97.

Kjellesvig-Waering, E. N. 1961 The Silurian Eurypterida of the Welsh Borderland. *J. Paleont.* **35**, 789–835.

Kjellesvig-Waering, E. N. 1984 Revision of fossil scorpions of the world. (In the press.)

Krogh, A. 1941 *Comparative physiology of respiratory mechanisms.* Philadelphia: Pennsylvania University Press.

Laurie, M. 1893 The anatomy and relations of the Eurypteridae. *Trans. R. Soc. Edinb.* **37**, 509–528.

Mangum, C. P. 1982 The functions of gills in several groups of invertebrate animals. In *Gills* (ed. D. F. Houlihan, J. C. Rankin & T. J. Shuttleworth), pp. 77–97. Cambridge: Cambridge University Press.

McMahon, B. R. & Wilkens, J. L. 1983 Ventilation, perfusion and oxygen uptake. In *The biology of Crustacea* (ed. D. E. Bliss), vol. 5. *Internal anatomy and physiological regulation* (ed. L. H. Mantel), pp. 289–372. New York and London: Academic Press.

Mill, P. J. 1972 *Respiration in the invertebrates*. London: Macmillan.

Moore, P. F. 1941 On gill-like structures in the Eurypterida. *Geol. Mag.* **78**, 62–70.

Patten, W. & Redenbaugh, W. A. 1900 Studies on *Limulus*, I and II. *J. Morph.* **16**, 1–26, 91–200.

Pianka, E. R. 1970 On r- and K-selection. *Am. Nat.* **104**, 592–597.

Rolfe, W. D. I. 1980 Early invertebrate terrestrial faunas. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 117–157. London and New York: Academic Press.

Rolfe, W. D. I. 1982 Ancient air breathers. *Field Mus. nat. Hist. Bull.* **53**, 12–16.

Rolfe, W. D. I. & Beckett, E. 1984 Other arthropods. In *Autecology of Silurian organisms* (ed. M. G. Bassett & J. D. Lawson), *Spec. pap. Palaeontol.* **32**, 295 pages.

Selden, P. A. 1981 Functional morphology of the prosoma of *Baltoeurypterus tetragonophthalmus* (Fischer) (Chelicerata: Eurypterida). *Trans. R. Soc. Edinb. Earth Sci.* **72**, 9–48.

Selden, P. A. 1984 Autecology of Silurian eurypterids. In *Autecology of Silurian organisms* (ed. M. G. Bassett & J. D. Lawson), *Spec. pap. Palaeontol.* **32**, 39–54.

Shear, W. A., Bonamo, P. M., Rolfe, W. D. I., Smith, E. L. & Norton, R. A. 1984 Oldest American fossils of land animals. *Science, Wash.* **224**, 492–494.

Stanley, S. M. 1973 An explanation for Cope's rule. *Evolution* **27**, 1–26.

Størmer, L. 1963 *Gigantoscorpio willsi*, a new scorpion from the Lower Carboniferous of Scotland and its associated preying micro-organisms. *Skr. norske Vidensk-Akad. Mat.-naturv. K1.* 1962 **8**, 1–171.

Størmer, L. 1976 Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 5: Myriapoda and additional forms, with general remarks on fauna and problems regarding invasion of land by arthropods. *Senckenberg. leth.* **57**, 87–183.

Thorpe, W. H. 1950 Plastron respiration in aquatic insects. *Biol. Rev.* **25**, 344–391.

Unwin, E. E. 1932 On the structure of respiratory organs of terrestrial Isopoda. *Pap. Proc. R. Soc. Tasmania* 1931, pp. 37–97.

Waterston, C. D. 1975 Gill structures in the Lower Devonian eurypterid *Tarsopterella scotica*. *Fossils Strata* **4**, 241–254.

Waterston, C. D. 1979 Problems of functional morphology and classification in stylonuroid eurypterids (Chelicerata, Merostomata), with observations on the Scottish Silurian Stylonuroidea. *Trans. R. Soc. Edinb.* **70**, 251–322.

Wills, L. J. 1964 The ventral anatomy of the Upper Carboniferous eurypterid *Anthraconectes* Meek and Worthen. *Palaeontology* **7**, 474–507.

Wills, L. J. 1965 A supplement to Gerhard Holm's 'Über die Organisation des *Eurypterus fischeri* Eichw.' with special reference to the organs of sight, respiration and reproduction. *Ark. Zool.* **18**, 93–145.

Woodward, H. 1866–1878 A monograph of the British Fossil Crustacea belonging to the Order Merostomata. *Palaeontogr. Soc. (Monogr.)*.

Discussion

P. WHALLEY (*Department of Entomology, British Museum (Natural History), London*). Of three slides of Rhynie Chert shown, two show *Rhyniella* and evidence that it is indeed a species of Collembola (springtails). *Rhyniella* is not considered to be the direct ancestor of the winged insects. The Collembola, which is a widespread and abundant group today, is clearly differentiated from the insects. The third slide shows *Rhyniognatha*, originally described as the jaws of an insect larva. Recent study suggests that it is not Insecta but may be Myriapoda.

The interpretation of the function of gill structures in fossils has been mentioned by previous speakers. If we only knew winged insects from their fossilized remains would we consider that their flat, veined wings could be gills? Wings in insects could have arisen for reasons other than flight and have originated from the need for gaseous and heat exchange on land. In modern insects both these functions are performed by the wings in which fluid circulates in the veins. Careful consideration should be given before structures were interpreted as aquatic or aerial in function.

P. A. SELDEN. Dr Whalley's suggestion regarding the origin of insect wings is intriguing, and reminiscent of theories involving a change in function to produce flight feathers in birds. Few

organs have but a single function; at any time there are primary and one or more secondary functions (this depends on how broadly or narrowly 'function' is defined, of course). Over time, primary and secondary functions can interchange; for example, crab chelae can have a variety of important behavioural functions in addition to their original use in capturing prey.

New discoveries from the Rhynie Chert exemplify how much new information or arthropod evolution can be brought to light by study of microfauna and cuticle fragments, as emphasized by Rolfe and Selden (this volume). The important arthropod finds of Rhynie, Gilboa and the Upper Cambrian of Sweden (Müller) were discovered by accident. Recently, A. C. Scott and K. Bartram (Chelsea College, London) have found abundant insect and scorpion remains in coals and associated shales from the Westphalian of Yorkshire, during palaeobotanical studies. The Middle–Upper Palaeozoic arthropods we seek are there: a directed programme of research in favourable facies would yield prolific important new data.