PAEDOMORPHOSIS IN SCOTTISH
OLENELLID TRILOBITES
(EARLY CAMBRIAN)

by KENNETH J. MCNAMARA

ABSTRACT. *Olenellus* (*Olenelloides*) *armatus* Peach, 1894 has been restudied and interpreted as having evolved by paedomorphosis. By comparison with olenellid ontogenies, *O.* (*Olenellus*) *hamoculus*, *O.* (*Olenellus*) *intermedius*, and *O.* (*Olenellus*) *reticulatus*, also from the 'Fucoid' Beds, are likewise considered to have evolved by paedomorphosis from *O.* (*Olenellus*) *lapworthi*. Paedomorphosis may have occurred in response to adaptation to zones of higher oxygen content, in shallower water. The paedomorphic mechanism was progenesis which may have been triggered off by the higher temperatures of the shallower water environment which the olenellid larvae occupied.

DURING a restudy of the curious little olenellid trilobite *Olenellus* (*Olenelloides*) *armatus* Peach, 1894 from the 'Fucoid' Beds of north-west Scotland, it soon became apparent that this species, far from being genetically very different from the other four species of *Olenellus* which are also present in these beds (*O.* (*Olenellus*) *intermedius* Peach, 1894; *O.* (*Olenellus*) *reticulatus* Peach, 1894; *O.* (*Olenellus*) *lapworthi* Peach and Horne, 1892; and *O.* (*Olenellus*) *hamoculus* Cowie and McNamara, 1978), is closely related to them. The development of diverse olenellid species is not distinctive of the 'Fucoid' Beds but is a feature of many other olenellid-bearing Lower Cambrian rocks. This profusion of forms has caused many problems in olenellid taxonomy with new genera and species being erected and placed in synonymy with great frequency. It is hoped that this study will not only help to elucidate the evolutionary mechanisms operating within the Scottish olenellids, but also assist in explaining some of the vagaries of olenellid taxonomy in general.

In his study of *O.* (*Olenelloides*) *armatus*, Peach (1894, pl. 32, figs. 1–6) illustrated only four specimens. He used one of these, the part and counterpart of an incomplete, articulated individual, as the basis for a reconstruction which has become the standard representation of the species (Raw 1957; Moberg 1899; Poulsen *in* Moore 1959). As the specimen on which Peach based his reconstruction is very poorly preserved and is distorted, Peach's drawing is misleading in its representation of the number of thoracic segments, orientation of the spines, and other minor features. A new reconstruction based on all four known articulated specimens is presented (text-fig. 1).

O. (*Olenelloides*) *armatus* has been regarded by many previous workers (see below) as either 'larval', 'immature', 'primitive', 'degenerate', or 'aberrant'. Many even doubted its specific validity, whilst Hupé (1953a) considered it sufficiently distinct to warrant placing within a monotypic subfamily. In the present study it is hoped to clarify its taxonomic situation.

Terminology. This largely follows Harrington (*in* Moore 1959), except that 'procranidial spine' is preferred to 'perfixigenal spine' and 'intergenal spine' to 'metafixigenal spine'. The term 'intergenal ridge' is introduced to describe the pleural extension of the preoccipital segment. Palmer (1957, p. 106) is followed in using the

term 'interocular area' for the 'fixigene' of Hupé (1953a, p. 117). The genal area outside the eye lobe is termed the 'extraocular area'. The eye lobe is separated into the anterior and posterior eye ridges, between which lies the 'epipalpebral furrow'. Hypostome terminology follows Palmer (1957, p. 107).

'Paedomorphosis' was defined by de Beer (1958) as 'phylogenetic effects produced by introducing youthful characters into the line of adults', whilst 'progenesis' is a term introduced by Giard (1887) to describe precocious sexual maturation of the reproductive organs while the organism is still in the condition of a larva. De Beer (1958, p. 63) included progenesis with neoteny, as the end result, retention of larval features in the adult stage, is the same. He also included paedogenesis (von Baer 1866) with neoteny, but the mechanisms of both progenesis and paedogenesis are very different from that of neoteny resulting in variation in the maximum size of the adult. In neoteny the pre-adult rate of development of the organism (including its sexual development) is delayed or arrested, resulting in retention of larval characters in the adult. Due to a prolonged period in the pre-adult stage, the pre-adult rate of growth is prolonged, consequently the neotenous adult is larger than the non-neotenous adult. Paedogenesis is restricted to organisms which reproduce in a larval stage, but parthenogenetically, as in some Coleoptera.

Where progenesis has occurred, however, rate of development continues at normal pace until precocious sexual maturation occurs and stops, or severely restricts, the further development of many organs. The short period in the pre-adult stage only allows a small degree of fast juvenile growth, with a consequence that the adult progenetic form cannot reach as large a size as the non-progenetic form. Whereas previously neoteny has been thought to be the only mechanism producing paedomorphic evolution (de Beer 1958, p. 64), evidence is produced here to show that progenesis has been the paedomorphic mechanism in the olenellid trilobites in north-west Scotland. Gould (1977) has recently, independently, come to similar conclusions concerning the paedomorphic processes.

SYSTEMATIC PALAEONTOLOGY

Family OLENELLIDAE Vogdes, 1893
Subfamily OLENELLINAE Vogdes, 1893
[incl. OLENELLOIDINAE Hupé, 1953b]
Genus OLENELLUS Billings, 1861
Subgenus OLENELLOIDES Peach, 1894

Type species. Olenellus (Olenelloides) armatus Peach, 1894; from the 'Fucoid' Beds (Lower Cambrian), Meall a'Ghiubhais, Ross and Cromarty, Scotland.

Remarks. Although Peach (1894) erected *Olenelloides* as a subgenus, he did not present the species as '*O. (Olenelloides) armatus*', but as '*Olenelloides armatus*'. Consequently, later workers used the name in a generic sense without justification. It will be shown that although *O. (Olenelloides) armatus* is morphologically very distinct from contemporaneous olenellids from the same horizon, genetically it was probably very closely related to them. Thus *Olenelloides* is retained in its original sense as a subgenus of *Olenellus*.

Olenellus (Olenelloides) armatus Peach, 1894

Plate 71, figs. 1–9; text-fig. 1

1894 *Olenellus (Olenelloides) armatus* Peach; pp. 668–670, pl. 32, figs. 1–6.
1897 *Olenelloides armatus* Peach; Beecher, p. 191.
1899 *Olenelloides armatus* Peach; Moberg, pp. 315–316, pl. 13, fig. 6.
1910 *Olenelloides armatus* Peach; Walcott, pp. 345–350, pl. 40, figs. 2, 3.
1920 *Olenelloides armatus* Peach; Raymond, p. 129.
1925 *Olenelloides armatus* Peach; Raw, p. 287.
1937 *Olenelloides armatus* Peach; Lake, p. 248, pl. 35, figs. 7–9.
1937 *Olenelloides armatus* Peach; Raw, pp. 582–583, 590.

1938 *Olenelloides armatus* Peach; Lake, pp. 249–250, pl. 36, fig. 1.
1942 Olenelloides armatus Peach; Størmer, pp. 65, 106.
1953a Olenelloides armatus Peach; Hupé, p. 123.
1953b *Olenelloides armatus* Peach; Hupé, p. 75.
1957 Olenelloides armatus Peach; Palmer, pp. 121–122.
1957 Olenelloides armatus Peach; Raw, pp. 149, 150, 158; text-fig. 1.
1971 Olenelloides armatus Peach; Hu, pp. 63, 71, 79.
1973 Olenelloides armatus Peach; Bergström, p. 313.

Lectotype. Herein designated; an almost complete cephalon (GSE 472) from the 'Fucoid' Beds, Lower Cambrian, on the northern slopes of Meall a'Ghiubhais, Ross and Cromarty (locality 6 in text-fig. 1 of Cowie and McNamara 1978); figured by Peach (1894, pl. 32, fig. 4) and Lake (1938, pl. 36, fig. 1); figured Plate 71, fig. 1, herein.

Material, locality, and horizon. The only material available is in the Geological Survey Collection made by Mr. A. Macconochie in the latter part of the nineteenth century. Recent attempts have failed to reveal the beds which yielded *O. (Olenelloides) armatus.* The specimens are mainly housed in the Institute of Geological Sciences in Edinburgh (GSE), a small number also being housed in the Institute of Geological Sciences in London (GSM). Four articulated specimens, thirty-three largely complete and fourteen fragmentary cephala, and two hypostomes are known from the same horizon and locality as the lectotype. The specimens are preserved as ochreous internal and external moulds in a dark-grey, yellow-weathering shale.

Diagnosis. Exoskeleton long and narrow; small. Cephalon hexagonal, bearing long, equidimensional procranidial, genal and intergenal spines; genal angle in line with 2p glabellar lobe. Frontal lobe short, abutting against anterior border. Eye lobe very short and strongly curved. 2p glabellar furrow transglabellar; all glabellar furrows except 3p, directed almost transversely. Interocular area strongly lobate and similar in width to very narrow extraocular area. Hypostome denticulate; posterior lobe large, occupying one-third area occupied by anterior lobe. Thorax composed of nine segments; pleural regions very narrow (*tr.*).

Remarks. O. (Olenelloides) armatus was adequately described by Peach (1894, pp. 669–670), Walcott (1910, pp. 347–350), and Lake (1938, pp. 248–249). However, a number of further features of specific importance can be added to their descriptions. The anterior cephalic border is almost transverse, but arched slightly forward where frontal lobe abuts border (Pl. 71, fig. 1). Antero-lateral margin slightly concave and three-quarters as long as anterior margin. Postero-lateral margin strongly concave and equal in length to antero-lateral margin. Posterior margin transverse; width (*tr.*), and width of occipital ring, equal to that of anterior margin. 3p and 2p glabellar furrows

1mm
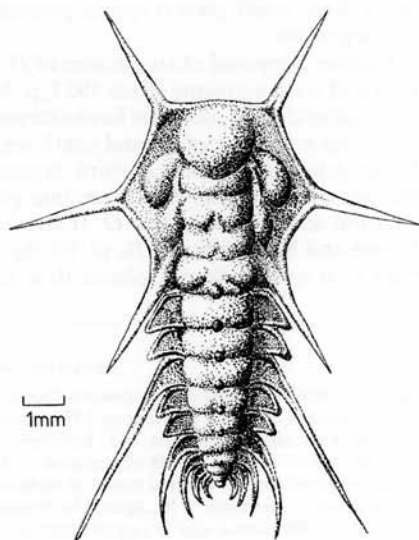
TEXT-FIG. 1. New reconstruction of *O. (Olenelloides) armatus* Peach, 1894.

transglabellar, 2p being almost transverse; 1p furrow not transglabellar. Occipital ring a little wider (*tr.*) than frontal lobe; antero-laterally bears faint lobe (Pl. 71, fig. 1). Eye lobe short, posterior tip in line with 2p lobe in mature specimens (Pl. 71, fig. 1), but 2p furrow in immature individuals (Pl. 71, fig. 7).

Hypostome (Pl. 71, fig. 6) is described for the first time; its length (*sag.*) is twice width (*tr.*) across anterior lobe. Anterior border is strongly convex; marginal flange short. Width (*tr.*) across anterior wings is twice width across anterior lobe. Anterior lobe moderately inflated and three times as long (*sag.*) as posterior lobe. Intervening middle furrow well impressed; deepening abaxially. Posterior furrow strongly impressed, whilst posterior border broad and convex, bearing ?thirteen small denticles. The two known specimens occur on a block with seven cephala of *O.* (*O.*) *armatus*, and are of corresponding size. Morphologically the hypostome is very similar to a late stage III meraspid olenellid hypostome (Palmer 1957, pl. 19, fig. 8). It differs from other hypostomes of the 'Fucoid' Beds (Cowie and McNamara 1978, pl. 69, fig. 8) in its elongate shape, large posterior lobe, and prominently denticulate posterior margin.

Differing numbers of thoracic segments have been attributed to *O.* (*Olenelloides*) *armatus*. Eight segments were observed by Peach (1894, p. 669), Lake (1938, p. 249), and Poulsen (*in* Moore 1959, p. O197). Walcott (1910, pp. 346, 349), however, could only distinguish seven, as could Hupé (1953*b*, p. 75). Peach's conclusion was based on the incomplete, distorted specimen referred to above, whilst Walcott (1910, pl. 40, fig. 3) used the external mould of another articulated individual. The posterior of this specimen has been damaged, but the internal mould has not. This shows (Pl. 71, fig. 4) three small pleural spines posterior to the elongate sixth, making a total of nine segments.

Another supposed characteristic of *O.* (*Olenelloides*) *armatus* is the 'macropleural' third and sixth segments (Raw 1957, p. 149), yet the sixth segment, although bearing a long pleural spine, does not have a larger pleura than the preceding segment; furthermore, the seventh, eighth, and ninth segments bear relatively long spines. Thus the thorax possesses a spinose third segment, first, second, fourth, and fifth pleurae without spines, whilst the succeeding pleurae are spinose. This is exactly the same situation as encountered in *O.* (*Olenellus*) *reticulatus* and *O.* (*Olenellus*) *lapworthi* (Cowie and McNamara 1978, pl. 69, fig. 2). The specimens do not show the development of a spinose fourth pleura thus Lake's (1938, p. 250) assertion that it bears

---

EXPLANATION OF PLATE 71

Figs. 1–9. *Olenellus* (*Olenelloides*) *armatus* Peach, 'Fucoid' Beds, Lower Cambrian; Meall a'Ghiubhais, Kinlochewe (Cowie and McNamara 1978, text-fig. 1, locality 6). 1, GSE 472; dorsal view of internal mould of incomplete cephalon, ×8; lectotype, figured by Peach (1894, pl. 32, fig. 4). 2, GSE 5373g; dorsal view of internal mould of cephalon, ×12; figured by Walcott (1910, pl. 40, fig. 2). 3, GSM 10660a; dorsal view of internal mould of cephalon, ×10. 4, GSE 5381a; dorsal view of internal mould of articulated specimen, ×10; figured by Walcott (1910, pl. 40, fig. 3) and Lake (1936, pl. 35, fig. 8). 5, GSE 13320b; dorsal view of cast of external mould of cephalon, ×10. 6, GSE 5373f; ventral view of internal mould of hypostome, ×20. 7, GSE 13320c; dorsal view of cast of external mould of incomplete meraspid cephalon, ×30. 8, GSE 13321; dorsal view of internal mould of incomplete cephalon, ×12. 9, GSE 5373j; dorsal view of cast of external mould of cephalon, ×10.

PLATE 71
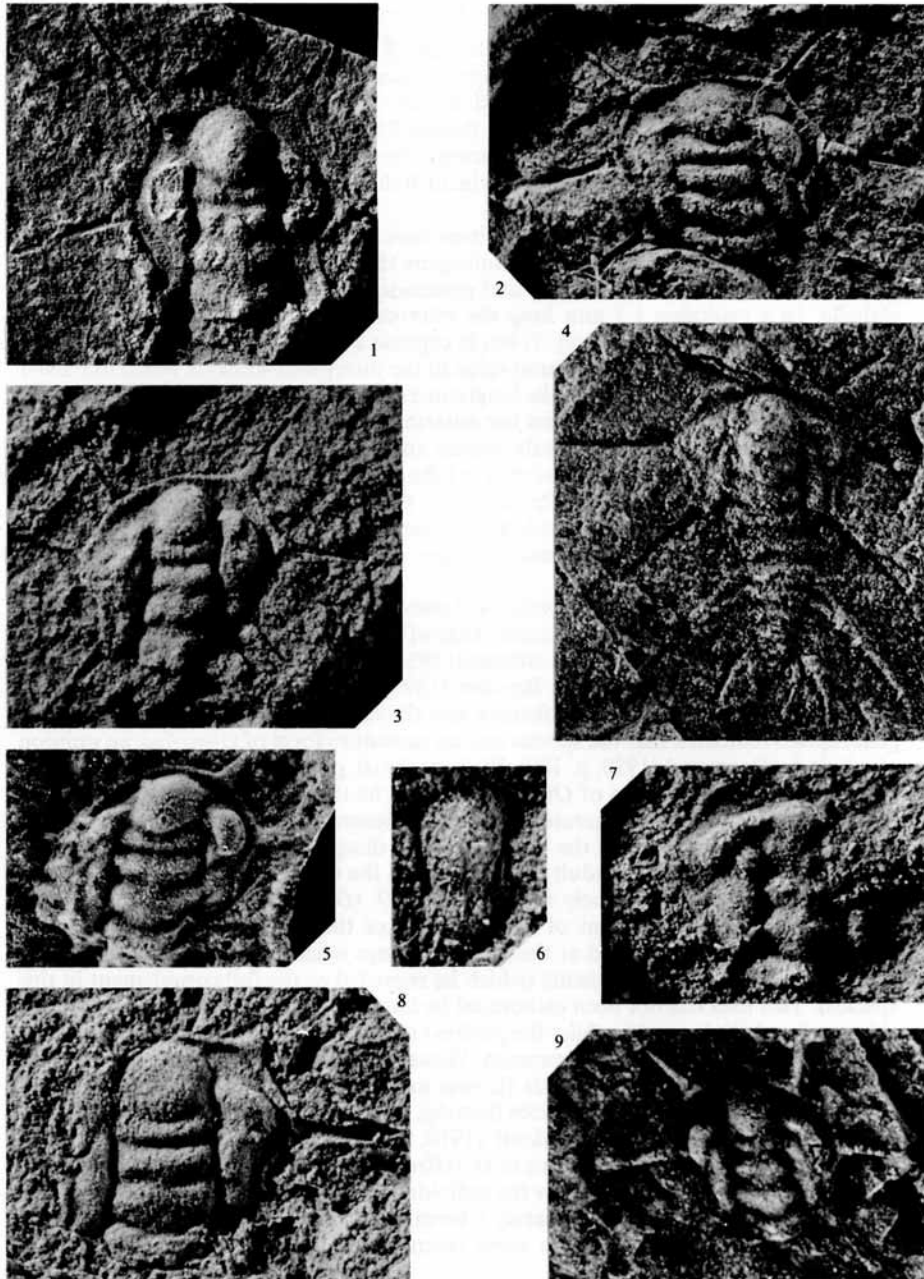
McNAMARA, *Olenellus (Olenelloides) armatus*

a spine cannot be substantiated. The thorax of *O.* (*Olenelloides*) *armatus* is very similar to that of a meraspid stage of *Elliptocephala asaphoides* Emmons as illustrated by Whittington (1957*a*, pl. 115, fig. 2 and text-fig. 2*c* herein). This meraspis possesses a cephalon only 0·5 mm in length, but the thorax, like that of *O.* (*Olenelloides*) *armatus*, has very narrow (*tr.*) pleurae, nine segments, and a prominent macropleural third segment, although pleurae posterior to the fifth do not appear to show any evidence of long pleural spines.

The smallest cephala known of *O.* (*Olenelloides*) *armatus* are a little over 1·0 mm in length; the largest 4·8 mm. During ontogeny the glabella becomes proportionally broader, slightly more so anteriorly and posteriorly producing an hour-glass shaped glabella. In a cephalon 1·3 mm long the interocular area is wider and as strongly vaulted as the eye lobe (Pl. 71, fig. 7) but in cephala 2–4 mm long the interocular area (which is connected by the intergenal ridge to the intergenal spine) is much narrower and lower (Pl. 71, fig. 2). As cephalic length increases from 1 mm to 2 mm, the frontal lobe doubles its length. This causes the anterior margin, which is almost transverse in immature forms, to become gently convex anteriorly (Pl. 71, fig. 2; text-fig. 3*a*, *b*). There is also an increase in length of the eye lobe posteriorly with growth, the posterior tip extending from opposite the 2p furrow in the immature form, to the 2p lobe in mature forms. As the eye lobe extended posteriorly so too did the genal angle, resulting in lengthening of the antero-lateral margin whilst the postero-lateral shortened (Pl. 71, figs. 1, 7).

In erecting the species, *O.* (*Olenelloides*) *armatus*, Peach (1894) was confident that this form was not an early ontogenetic stage of one of the other olenellids present at the same horizon, though he did comment (Peach 1894, p. 668) on its similarity to larval stages of other olenellids. Beecher (1897, p. 191), however, considered the elongate cephalon to be a larval feature and the disposition of the genal and inter-genal spines indicated that the species was an immature form of *Olenellus*, an opinion also held by Raymond (1920, p. 129). Walcott (1910, p. 346) likewise considered that it represented a larval form of *Olenellus*, though he thought *Olenelloides* warranted generic status, being 'a degenerate form of the Mesonacidae (Olenellidae) that came into existence shortly before the decadence and disappearance of the family'. Raw (1925, p. 287) thought it an adult and considered the taxon justifiable. Hupé (1953*a*, p. 123; 1953*b*, p. 75) tentatively suggested that *O.* (*Olenelloides*) *armatus* may have arisen by neoteny on account of the character of the thorax. He considered that neoteny would have occurred at the meraspid stage when *O.* (*Olenelloides*) *armatus* possessed seven thoracic segments (which he regarded as the full complement in this species). This idea has not been elaborated by later workers, Raw (1957, p. 158) con-sidering it to be 'aberrant', whilst Bergström (1973, p. 313) thought *O.* (*Olenelloides*) *armatus* was based on a larval specimen. However, cephala of the other four species of *Olenellus* from the Fucoid Beds (Cowie and McNamara 1978) exhibit the dis-tinguishing characters of their species (text-fig. 4), even when smaller than specimens of *O.* (*Olenelloides*) *armatus*. Walcott (1910, pl. 40, fig. 3) figured a specimen of *O.* (*Olenelloides*) *armatus* beside one of *O.* (*Olenelloides*) *reticulatus* Peach, 1894, both of which are the same size yet show the individual characters of the two species. Thus *O.* (*Olenelloides*) *armatus* is not merely a larval form, but a distinct species.

O. (*Olenelloides*) *armatus* bears some resemblance to *O.* (*Olenellus*) *intermedius*

from the same horizon (Cowie and McNamara 1978, pl. 70, figs. 10, 11). Both possess a transverse anterior margin, frontal lobe set close to the anterior border, and short, hooked eye lobe of similar length. *O. (Olenellus) intermedius*, however, has a much broader extraocular area and lower interocular area; it lacks procranidial spines and has a genal angle set further back. Hu (1971, p. 79, pl. 9, figs. 20–31) described *O. (Olenellus) canadiensis* from British Columbia, though he referred the species to *Laudonia*. However, *Laudonia* is characterized not only by the possession of an advanced genal angle, but also by short eye lobe, strongly inflated frontal lobe, and broad cephalic border (Harrington 1956, pl. 15, fig. 4), features lacking in Hu's species. As Hu points out, the 1 mm long meraspid cephalon of *O. (Olenellus) canadiensis* compares strongly with *O. (Olenelloides) armatus* in the disposition of the cephalic spines. This stage also possesses a narrow extraocular area and glabella of similar proportions to *O. (Olenelloides) armatus*, but the longer eye lobe, subsequent loss of the procranidial spine, and rounding of the anterior cephalic margin in larger individuals serve to distinguish this species from *O. (Olenelloides) armatus*.

## THE PAEDOMORPHIC ORIGIN OF THE SCOTTISH OLENELLIDS

Clark (1964) considered that paedomorphosis occurred several times during the history of the early Metazoa. This suggested to him that sexual maturation with respect to somatic development was not very precisely controlled in these animals. At this early period in their stage of development hormonal mechanisms, particularly those controlling growth and reproduction, are likely to have made their first appearance and were probably relatively imperfect. At this period, more than any other, paedomorphosis is likely to have been a relatively common occurrence.

The Olenellidae are amongst the earliest-known trilobites and four of the five species present in the early Cambrian rocks of north-west Scotland can be considered to have evolved by paedomorphosis. *O. (Olenelloides) armatus* will have undergone progenesis at the earliest stage, followed by *O. (Olenellus) intermedius*, *O. (Olenellus) hamoculus*, and *O. (Olenellus) reticulatus*. *O. (Olenellus) lapworthi* probably represents the non-paedomorphic form which has passed through all its moult stages before reaching sexual maturity and is thus the ancestral species to the four paedomorphic species. That the four species evolved by paedomorphosis and are not simply progenetic phenotypic variants of *O. (Olenellus) lapworthi* is illustrated by later developmental changes in shape of the cephalon and glabella during growth in the holaspid period.

To discover how the Scottish olenellids may have arisen by paedomorphosis, their ontogenetic growth has first to be considered. Unfortunately, early growth stages of *Olenellus* are lacking from the 'Fucoid' Beds. A few late meraspids are known (Walcott 1910, pl. 39, figs. 6, 8) but it is the earlier growth stages which show the most important morphological changes; thus one must turn to ontogenies of other olenellids. The most well-documented olenellid ontogenies are given by Palmer (1957) for *O. (Olenellus) gilberti* and *O. (Olenellus) clarki*, by Whittington (1957a) for *Elliptocephala asaphoides*, and by Hu (1971) for *O. (Olenellus) truemani* and *O. (Olenellus) canadiensis*.

The ontogenetic changes in *Olenellus* and *Elliptocephala* (text-fig. 2) can be summarized as a broadening of the cephalon, largely due to widening of the extraocular

area, whilst the interocular area becomes narrower and deflates; the frontal lobe migrates posteriorly causing the glabellar furrows to increase in sinuosity; the eye lobe and genal angle migrate posteriorly causing the anterior margin to become more rounded, whilst the intergenal angle migrates toward the genal angle, its spine degenerating at the expense of the genal spine. The thoracic pleural width increases at a faster rate than the axial width as new segments are added. *Bristolia* shows (Palmer in press, pl. 1, figs. 1–9, 11) the opposite developmental trends to *Olenellus*, the eye lobe shortening and, consequently, the genal angle and spine migrating anteriorly. There is no posterior movement of the frontal lobe, but a slight anterior expansion occurs in late meraspids and holaspids.
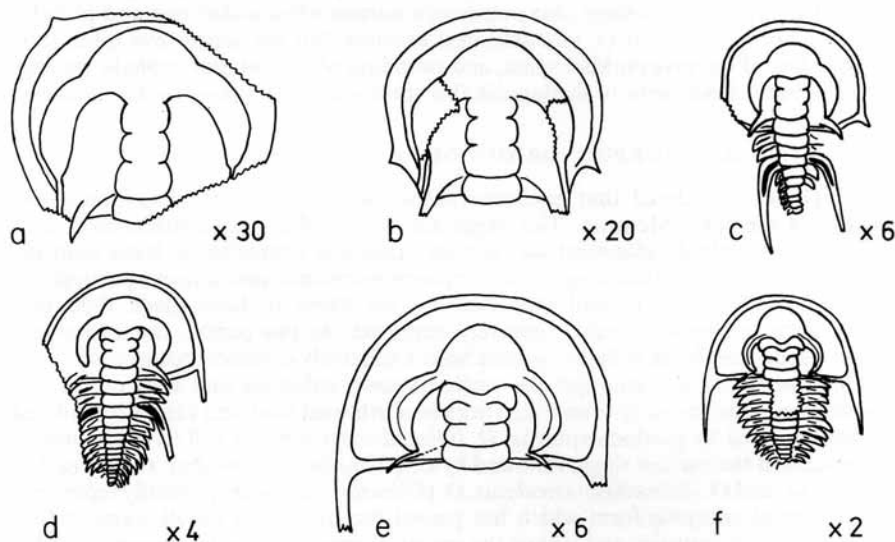

TEXT-FIG. 2. Ontogeny of *Elliptocephala asaphoides* (after Whittington 1957a); *a–c*, meraspids, *d–f*, holaspids.

These described olenellid ontogenies are for species which possess a long eye lobe even in early meraspids, whereas most of the species of *Olenellus* from north-west Scotland possess a short eye lobe. There is often an intimate relationship between the position of the posterior tip of the eye lobe and the genal angle, short-eyed forms, such as *Bristolia bristolensis* (Resser, 1928), *B. insolens* (Resser, 1928), *O. fremonti* Walcott, 1910, *Laudonia bispinosa* Harrington, 1956, and *O.* (*Olenellus*) *eagerensis* Best, 1952, generally possessing an advanced genal angle, although *Peachella*, which also has a short eye lobe, possesses a very broad-based, short genal spine which cannot be regarded as being in an advanced position (Walcott 1910, pl. 40, fig. 17; Palmer in press, pl. 5, figs. 1–9).

The anterior eye ridge, which bears the eye surface, may be regarded as being part of the same primary somite as the extraocular area and anterior and lateral cephalic

border (the genal segment); the extent of the pleural segment of this somite is reflected not only by the position of the genal angle and spine, but also by the eye lobe which will remain in a constant relative position. Thus the posterior migration of the genal angle which occurs during ontogeny is accompanied by a similar posterior migration of the eye lobe. The posterior eye ridge is regarded as being part of the palpebral segment continuous with the posterior of the frontal lobe (text-fig. 3). The pleural extension of the intergenal segment, however, migrates anteriorly during ontogeny. The distribution of these three cephalic segments is illustrated in two of the Scottish olenellid species to indicate the closer similarity of *O. (Olenelloides) armatus* to olenellid meraspid cephala (Palmer, 1957, text-fig. 8), particularly with respect to the intergenal segment. These segments correspond to the macropleural segments of Palmer (1957, pp. 122–123) with some modification to the anterior part of the cephalon.
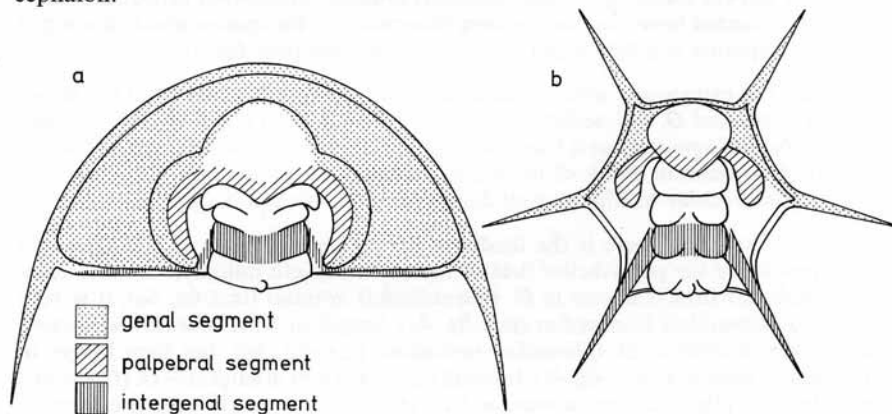
TEXT-FIG. 3. Cephala of *a*, *O. (Olenellus) lapworthi* and *b*, *O. (Olenelloides) armatus*, showing suggested distribution of macropleural segments.

By placing the five species of *Olenellus* from north-west Scotland in the sequence: *O. (Olenelloides) armatus*, *O. (Olenellus) intermedius*, *O. (Olenellus) hamoculus*, *O. (Olenellus) reticulatus*, *O. (Olenellus) lapworthi* (text-fig. 4), the following morphological trends can be seen:

(*a*) Cephalon. The cephalic shape varies both interspecifically, and intraspecifically. The anterior margin of the cephalon of the three earliest paedomorphs is almost transverse, but is more rounded in the other two species. The cephalon of the first three species has a hexagonal or subcircular outline, whereas in *O. (Olenellus) reticulatus* and *O. (Olenellus) lapworthi* it is parabolic in the former and semicircular in the latter. This tendency for a change from hexagonal or subcircular to parabolic or semicircular also occurs during growth within each species (text-fig. 4). This change in cephalic shape through the five species occurs within all olenellid ontogenies described, particularly in those described by Whittington (1957*a*, *b*) and Palmer (1957).

The maximum length of the cephalon of *O.* (*Olenelloides*) *armatus* is less than that of *O.* (*Olenellus*) *hamoculus* (*O.* (*Olenellus*) *intermedius* is not known from sufficient specimens) which is less than that of *O.* (*Olenellus*) *reticulatus*, which in turn is less than that of *O.* (*Olenellus*) *lapworthi* (text-figs. 4, 6) though Cowie and McNamara (1978) have assigned the two large specimens of '*O. gigas*' to *O.* (*Olenellus*) *reticulatus* (see below). Thus after progenesis occurred, growth of the cephalon continued at a much reduced rate, but probably by a consistent growth factor within each species. Rate of growth slackens in many aquatic invertebrates at the onset of sexual maturity (Newell 1949, p. 117). Gurney (1942, pp. 20, 82) has shown that in the Copepoda and Decapoda morphological development ceases with the ripening of the gonads, there being a marked decline in the rate of growth, as the initially rapid rate of growth is prematurely terminated. Thus as the species which evolved by paedomorphosis from the earliest growth stage, i.e. *O.* (*Olenelloides*) *armatus*, underwent progenesis when very small, it cannot have reached the same dimensions as the species which developed by paedomorphosis at a later stage in their development (text-fig. 5).

(*b*) Genae. The extraocular area increases in width appreciably between *O.* (*Olenelloides*) *armatus* and *O.* (*Olenellus*) *intermedius* (text-fig. 4*a*, *c*), but slightly through to *O.* (*Olenellus*) *lapworthi* as a function both of increase in over-all cephalic width and also of decrease in width of interocular area. Both increasing extraocular and decreasing interocular widths are well documented in ontogenies of *Olenellus*.

(*c*) Preglabellar field. There is the tendency during the ontogeny of *Olenellus* and *Elliptocephala* for the preglabellar field to increase in length initially, then decrease. The preglabellar field is absent in *O.* (*Olenelloides*) *armatus* (text-fig. 4*a*), it is very short in *O.* (*Olenellus*) *intermedius* (text-fig. 4*c*), longer in *O.* (*Olenellus*) *hamoculus* (text-fig. 4*e*), shorter in *O.* (*Olenellus*) *reticulatus* (text-fig. 4*g*), but then longer in *O.* (*Olenellus*) *lapworthi* (text-fig. 4*i*). In small cephala (3 mm in length) of *O.* (*Olenellus*) *hamoculus*, *O.* (*Olenellus*) *reticulatus*, and *O.* (*Olenellus*) *lapworthi*, the preglabellar field is shortest in *O.* (*Olenellus*) *hamoculus* (text-fig. 4*f*), whilst in *O.* (*Olenellus*) *reticulatus* (text-fig. 4*h*) and *O.* (*Olenellus*) *lapworthi* (text-fig. 4*j*) they are of similar length. It is in the adult of *O.* (*Olenellus*) *reticulatus* that the preglabellar field shortens, the reason for which is discussed below in section *g*.

(*d*) Genal angle. The genal angle is very advanced in *O.* (*Olenelloides*) *armatus* (text-fig. 4*a*) (opposite the 2p lobe), moderately advanced in *O.* (*Olenellus*) *intermedius* (text-fig. 4*c*) and *O.* (*Olenellus*) *hamoculus* (text-fig. 4*e*) (opposite the 1p lobe), slightly advanced in *O.* (*Olenellus*) *reticulatus* (text-fig. 4*g*), particularly in larger specimens (opposite the occipital furrow), almost normal (opposite the occipital ring) in *O.* (*Olenellus*) *lapworthi* (text-fig. 4*i*). This sequence corresponds to the posterior migration of the genal angle in the ontogeny of *E. asaphoides* (Whittington 1957*a*). An anterior migration in senile specimens has been noticed by Fritz (1972, p. 16) in *O.* (*Olenellus*) *truemani* Walcott. In forms where the genal angle is in an advanced position due to the species having evolved by paedomorphosis from an early larval stage, the margin between the genal and intergenal angles is straight or concave outwards; in late paedomorphs and non-paedomorphs the slight anterior migration of the genal angle in senile forms results in the same margin being convex outwards.
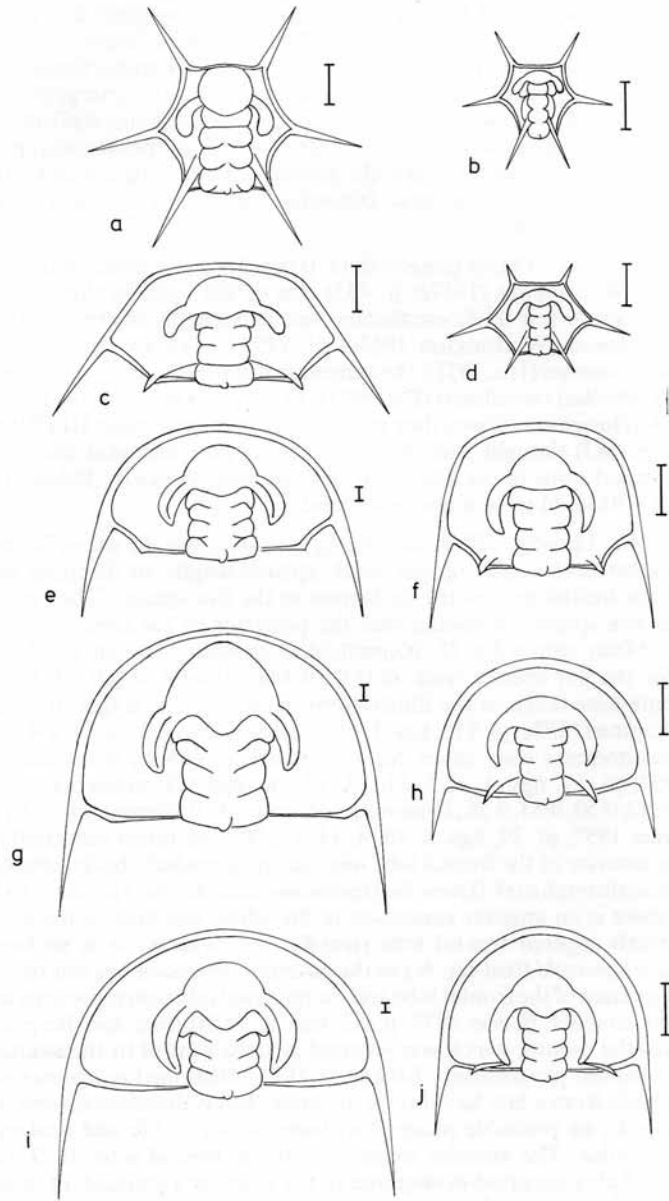
TEXT-FIG. 4. Reconstruction of adult and juvenile cephala of: *a, b, O. armatus*; *c, d, O. intermedius*; *e, f, O. hamoculus*; *g, h, O. reticulatus*; *i, j, O. lapworthi*. Reconstruction *d* is hypothetical. Scale represents 1 mm.

(e) Intergenal angle and spine. During the ontogeny of *E. asaphoides* and *O*. (*Olenellus*) *gilberti* the intergenal spine degenerates, whilst the intergenal angle migrates laterally (text-fig. 2). The extent of lateral migration in mature specimens varies between the Scottish species (text-fig. 4). In *O*. (*Olenelloides*) *armatus* the intergenal angle is set close against the glabella; it is only one-third the posterior margin width from the axial furrow. In late paedomorphs the intergenal angle of specimens approximately 10 mm in length is set less than half the posterior margin length in *O*. (*Olenellus*) *hamoculus*, a little over half-way in *O*. (*Olenellus*) *reticulatus*, and well over half-way in *O*. (*Olenellus*) *lapworthi*.

(f) Procranidial spine. This is present in *O*. (*Olenelloides*) *armatus* but absent in the other species. Whittington (1957b, p. 433) was of the opinion that this spine was absent or not preserved in *E. asaphoides*, but it is clearly visible on the smallest meraspis he figured (Whittington 1957a, pl. 115, fig. 1). In some olenellids, e.g. *O*. (*Olenellus*) *truemani* (Hu, 1971), the spines are not present at all, whereas in others, such as *O*. (*Olenellus*) *canadiensis* (Hu, 1971), they persist well into the later meraspid stages. In *O*. (*Olenellus*) *gilberti* they persist until meraspid stage III (Palmer 1957). Raw (1937, p. 583) thought that the procranidial spine migrated during ontogeny to form the genal spine in the adult, but this has been shown by Palmer (1957) and Whittington (1957a, b) to be a misunderstanding.

(g) Frontal lobe. Text-fig. 5 illustrates histograms showing the ratios of frontal lobe and preglabellar field length against total cephalic length, to illustrate the relative position of the medial part of the 3p furrow in the five species. The ratio increases through the five species indicating that the posterior of the frontal lobe migrated posteriorly. Mean values for *O*. (*Olenelloides*) *armatus* through to *O*. (*Olenellus*) *lapworthi* for the five species read: 0·3533, 0·4400, 0·4664, 0·5003, 0·5590. Similar measurements were taken of the illustrations of ontogenetic stages of *E. asaphoides* from Whittington (1957a, pl. 115, figs. 1-6); the values are: 0·35, 0·44, 0·47, 0·51, 0·56. Similar measurements were taken for *O*. (*Olenellus*) *gilberti* from illustrations of Palmer (1957, pl. 19, figs. 1, 6, 2, 11, 15, 12, 16, and 19); ratios were: 0·30, 0·41, 0·43, 0·44, 0·47, 0·50, 0·53, 0·56; these represent stages I-V. Similarly for *O*. (*Olenellus*) *clarki* (Palmer 1957, pl. 19, figs. 5, 10, 4, 14, 17, 20), the ratios increased from 0·35 to 0·56. The anterior of the frontal lobe migrates progressively back from *O*. (*Olenelloides*) *armatus* through to *O*. (*Olenellus*) *hamoculus* (text-fig. 4a–f), but in *O*. (*Olenellus*) *reticulatus* there is an anterior expansion in the adult, resulting in the development of an anteriorly tapered frontal lobe (text-fig. 4g), whereas it is well-rounded in *O*. (*Olenellus*) *lapworthi* (text-fig. 4i) as the anterior expansion has not occurred. The posterior migration of the frontal lobe and its increased inflation represents an increase in size of the stomach (Cisne 1975, p. 52, figs. 8, 9; Stürmer and Bergström 1973, p. 122). Thus the mouth, which was situated postero-ventral to the stomach (Cisne 1975, p. 52), moved progressively backward. If *O*. (*Olenellus*) *reticulatus* evolved by paedomorphosis from a late larval stage ancestor, and is therefore closest to *O*. (*Olenellus*) *lapworthi*, its probable progenitor, their modes of life and feeding were no doubt very similar. The anterior expansion of the frontal lobe of *O*. (*Olenellus*) *reticulatus* probably occurred in response to the need for a stomach of optimum size which was not fully attained during growth, as progenesis prematurely stopped the
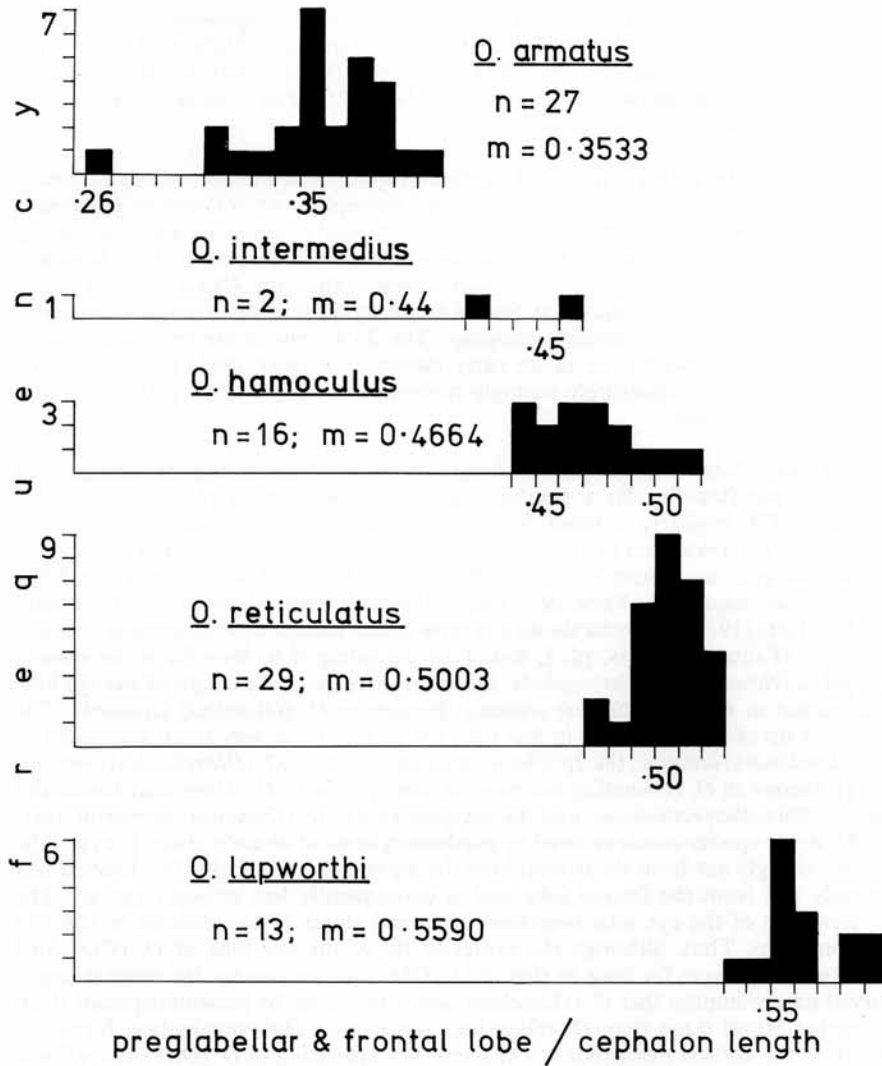
TEXT-FIG. 5. Histograms showing frequency of ratio of preglabellar and frontal lobe sagittal length to sagittal cephalic length, to illustrate the backward migration of the posterior of the frontal lobe through the five species.

growth of the stomach. The frontal lobe of *O.* (*Olenellus*) *lapworthi* extends more posteriorly than that of *O.* (*Olenellus*) *reticulatus*, but the frontal lobe of *O.* (*Olenellus*) *reticulatus* reaches further forward. The ratio of frontal lobe length to cephalic length remains constant in the two species, however, being 2:5; this ratio is 1:3 in *O.* (*Olenellus*) *hamoculus*.

(*h*) Glabella. The glabella of *O.* (*Olenelloides*) *armatus* is almost cylindrical (text-fig. 4*a, b*), whereas *O.* (*Olenellus*) *intermedius* through to *O.* (*Olenellus*) *hamoculus* (text-fig. 4*c–f*) it broadens, preferentially anteriorly and posteriorly, a distinct 'hour-glass' shape being developed. The glabella is more 'club-shaped' in *O.* (*Olenellus*) *reticulatus* (text-fig. 4*g*) and *O.* (*Olenellus*) *lapworthi* (text-fig. 4*i*) on account of the greater inflation of the frontal lobe. Such a trend, cylindrical to 'hour-glass' to 'club-shaped', is inherent in olenellid ontogeny. The 2p furrow is almost transverse in *O.* (*Olenelloides*) *armatus*, as in an early meraspis (Palmer 1957, pl. 19, fig. 11), becoming directed increasingly strongly posteriorly through to *O.* (*Olenellus*) *lapworthi*, as in ontogeny.

(*i*) Eye lobe. There is an increase in length of the eye lobe during the ontogeny of *Elliptocephala* (text-fig. 2); a similar increase is also seen in *Holmia hyperborea* Poulsen, 1974; similarly, a small degree of posterior migration occurs in the long-eyed forms *O.* (*Olenellus*) *clarki, O.* (*Olenellus*) *gilberti*, as illustrated in the d'Arcy Thompson grids by Palmer (1957, text-fig. 2), *O.* (*Olenellus*) *paraoculus* Fritz, 1972, *O.* (*Olenellus*) *sequomalus* Fritz, 1972, and *O.* (*Olenellus*) *puertoblancoensis* (Lochman, 1952) *in* Fritz (1972). *Bristolia* shows a reverse trend, the eye lobe shortening through ontogeny (Palmer, in press, pl. 1, figs. 1–9) indicating that *Bristolia* is not closely related to *Olenellus* or *Elliptocephala*. A similar increase in the length of the eye lobe is apparent in *O.* (*Olenelloides*) *armatus* through to *O.* (*Olenellus*) *lapworthi*. The posterior tip of the eye lobe is in line with the 2p furrow in very small specimens of *O.* (*Olenelloides*) *armatus*, the 2p lobe in large specimens of *O.* (*Olenelloides*) *armatus*, the 1p furrow in *O.* (*Olenellus*) *intermedius*, the 1p lobe in *O.* (*Olenellus*) *hamoculus* and *O.* (*Olenellus*) *reticulatus*, and the occipital ring in *O.* (*Olenellus*) *lapworthi* (text-fig. 4). In the species which evolved by paedomorphosis at an early stage, the eye lobe curves strongly out from the frontal lobe. In the late paedomorphs it is directed less strongly out from the frontal lobe and is consequently less strongly curved. The posterior tip of the eye lobe becomes positioned closer to the glabella in the late paedomorphs. Thus, although the posterior tip of the eye lobe of *O.* (*Olenellus*) *hamoculus* reaches as far back as that of *O.* (*Olenellus*) *reticulatus*, the more strongly curved nature implies that *O.* (*Olenellus*) *hamoculus* arose by paedomorphosis from an earlier larval stage than *O.* (*Olenellus*) *reticulatus*. The epipalpebral furrow is absent in the earliest meraspids of *Olenellus*, not appearing in *O.* (*Olenellus*) *gilberti* until stage V (Palmer 1957). Similarly, it is absent in the early meraspids of *E. asaphoides* (Whittington 1957*a*, pl. 115). It is absent in both *O.* (*Olenelloides*) *armatus* and *O.* (*Olenellus*) *intermedius*, but present in the other species. Consequently it would seem that both *O.* (*Olenelloides*) *armatus* and *O.* (*Olenellus*) *intermedius* may have evolved paedomorphically from earlier growth stages than stage V of the meraspid period.

(*j*) Hypostome. This is only known for *O. (Olenelloides) armatus* and *O. (Olenellus) reticulatus*. The hypostome of *O. (Olenelloides) armatus* is very similar to one of the stage III olenellid meraspids (Palmer 1957, pl. 19, fig. 8). The hypostome of *O. (Olenellus) reticulatus* (Cowie and McNamara 1978, pl. 69, fig. 8) compares more closely with that of the holaspis of *O. (Olenellus) gilberti*, the anterior lobe being more swollen than in *O. (Olenellus) armatus*, the posterior lobe having degenerated at its expense, and the border denticles having been reduced in number and relative size.

(*k*) Thorax. During the ontogeny of *E. asaphoides* eighteen thoracic segments were generated whereas in *O. (Olenellus) gilberti* only fourteen were developed. Concomitantly the pleurae broadened with respect to the axis, their lateral extent being demarkated by the position of the intergenal angle. Although the thorax is not known for either *O. (Olenellus) intermedius* or *O. (Olenellus) hamoculus*, it would be expected that the thoracic widths increase through the five species as the intergenal angle becomes positioned more laterally. The pleurae of *O. (Olenelloides) armatus* are very narrow (Pl. 71, fig. 4), occupying only one-third the axial width, whilst in *O. (Olenellus) reticulatus* the pleurae are almost equal in width to the axis (Cowie and McNamara 1978, pl. 70, fig. 12).

Four of the five species of *Olenellus* from north-west Scotland can thus be regarded as having evolved by paedomorphosis due to sexual maturity having been reached at different times owing to progenesis having occurred in the ancestral species (text-fig. 6). *O. (Olenelloides) armatus* is thought to have evolved by paedomorphosis from
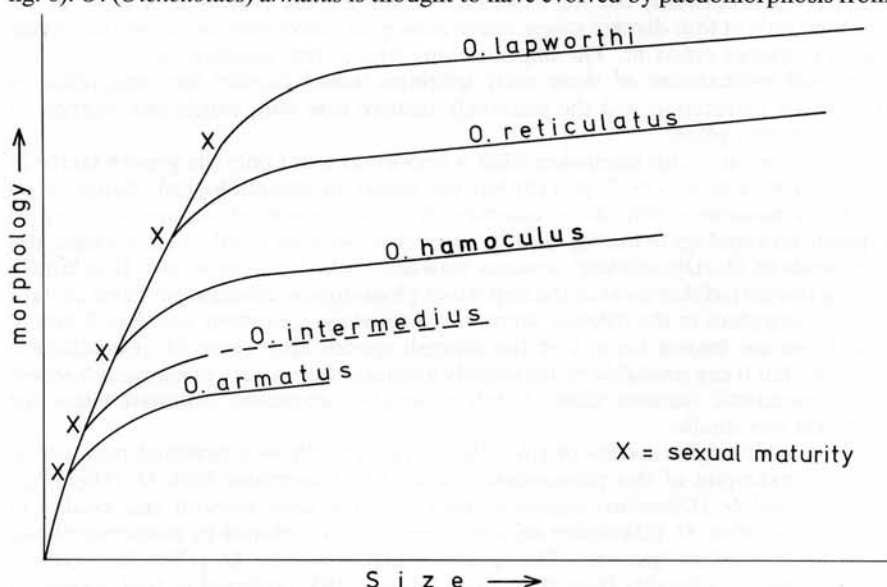
TEXT-FIG. 6. Diagrammatic graph to illustrate changes in morphology and size with growth of the five Scottish species of *Olenellus*.

an early meraspid larval stage when only nine thoracic segments had been generated. The similarity of the thorax of *O.* (*Olenelloides*) *armatus* to the meraspid thorax of *E. asaphoides* has been commented on above. The presence of only nine thoracic segments, whereas all other species of *Olenellus* possess fourteen, indicates that progenesis occurred when only nine thoracic segments had been generated.

The meraspis of *E. asaphoides* which possesses nine thoracic segments has, like *O.* (*Olenelloides*) *armatus*, prominent intergenal spines which are similar in size to the genal spines (Whittington 1957a, pl. 115, fig. 2; text-fig. 2c herein). Whittington (1957a, fig. 2b) illustrated a meraspis of *O.* (*Olenellus*) *yorkensis* Resser and Howell at the stage where it possessed nine thoracic segments. Like *O.* (*Olenelloides*) *armatus* it too possesses three pairs of cephalic spines whilst, as in *O.* (*Olenelloides*) *armatus*, the thoracic axis is broad in relation to the pleurae at this stage. *O.* (*Olenellus*) *intermedius* evolved from a slightly later meraspid larval stage, but probably prior to stage V of Palmer (1957). *O.* (*Olenellus*) *hamoculus* probably represents a paedomorphic species which evolved from a late meraspis, post stage V. *O.* (*Olenellus*) *reticulatus* evolved by paedomorphosis from a very early holaspis as it possesses the full complement of thoracic segments. *O.* (*Olenellus*) *lapworthi* probably represents a non-paedomorphic species of *Olenellus* and is probably the ancestral species from which the other contemporaneous species evolved by paedomorphosis. Palmer (1957, p. 114) calculated that *O.* (*Olenellus*) *gilberti* underwent ecdysis at least twenty-nine times. At each ecdysis *O.* (*Olenellus*) *lapworthi* would have had the possibility of undergoing progenesis, but the successful paedomorphic evolution of new species occurred only at four distinct stages where ecological niches were available into which the new species could fit. The imperfections which were probably inherent in the hormonal mechanisms of these early trilobites would explain the occurrence of precocious maturation and the seemingly relative ease with which this method of evolution took place.

In the context of this discussion what is important is not only the growth factor as discussed by Palmer (1957, p. 110) but the degree of morphological change (text-fig. 6), a parameter difficult to quantify. A great amount of change occurred in cephalic morphology in meraspids of *E. asaphoides* between 1 and 3 mm in length and meraspids of *O.* (*Olenelloides*) *armatus* between 1 and 2 mm in length. It is largely during this period that most of the important physiological changes are liable to have been taking place in the trilobite larva. Unfortunately, specimens less than 3 mm in length are not known for any of the Scottish species apart from *O.* (*Olenelloides*) *armatus*; but it can probably be reasonably assumed that as each paedomorph shows its characteristic features when 3 mm in length, progenesis occurred when the cephalon was smaller.

The paedomorphic species of *Olenellus* found in north-west Scotland may not be the only examples of this phenomenon. Best (1952) described both *O.* (*Olenellus*) '*gilberti*' and *O.* (*Olenellus*) *eagerensis* Best from the same horizon and locality in British Columbia. *O.* (*Olenellus*) *eagerensis* may have developed by paedomorphosis from *O.* (*Olenellus*) '*gilberti*'. The species which Best calls *O.* (*Olenellus*) *gilberti* differs quite considerably from that which Palmer (1957) referred to that species. It has a short eye lobe, slightly advanced genal angle, very short preglabellar field, and is thus best referred to *O.* (*Olenellus*) *truemani*. The paedomorphic condition of

O. (*Olenellus*) *eagerensis* is illustrated by the more advanced genal angle, intergenal angle set close to the glabella, frontal lobe close against the anterior border, less sinuous 2p furrow, more anteriorly positioned 3p furrow, shorter eye lobe, narrower extraocular area, and narrower thoracic pleurae.

Although *Bristolia* shows many reverse developmental trends in comparison with *Olenellus*, species described by Resser (1928) can still perhaps be regarded as having evolved by paedomorphosis, *B. bristolensis* having evolved from *B. insolens* by paedomorphosis.

PALAEOECOLOGICAL CONSIDERATIONS

It is now necessary to try and consider why paedomorphosis should have been such an important evolutionary mechanism operating on the early Cambrian olenellid fauna of north-west Scotland, and what adaptational advantage it conferred. Jell (in press) elegantly shows how genal caeca in many groups of trilobites can be regarded as having served a respiratory function. The caeca are only present on the extraocular area of the Olenellidae (Fritz 1972, pl. 11, fig. 13), so those species with the broadest extraocular area bear the greatest number of caeca. The very small extraocular areas and absence of caeca in *O.* (*Olenelloides*) *armatus* and olenellid meraspids may perhaps be attributed to their adaptation to highly oxygenated upper waters. The increase in extraocular area during ontogenetic sequences in *Olenellus* can perhaps be best explained by the adaptation to living in less oxygenated conditions as the pelagic larva becomes benthonic. Growth of the extraocular area is greater than would be expected from normal allometric growth of the cephalon. Palmer's (1957, text-fig. 2) illustration of the rate of growth of the cephalon of *O. gilberti* shows how the extraocular area developed at a much greater rate than the rate at which the glabella and eye lobes grew.

Lochman (1956, p. 1377) considered that *Elliptocephala asaphoides* inhabited deep water (400–600 ft) where the oxygen content and food content were low. *O.* (*Olenellus*) *thompsoni*, however, she regarded as having occupied shallow coastal waters a few inches to a few hundred feet in depth where the oxygen and food contents were higher. The middle meraspis of *E. asaphoides* (Whittington 1957a, pl. 115, figs. 2, 5; Lochman 1956, pl. 6, fig. 10) bears a striking resemblance to species of *O.* (*Olenellus*) not only with regard to cephalic characters, but also with respect to the presence of a third macropleural thoracic segment which is lost during the early holaspid period. Whereas *O.* (*Olenellus*) has fourteen thoracic segments, *Elliptocephala* possesses eighteen; thus *O.* (*Olenellus*) may have evolved from *Elliptocephala*, which it postdates, by paedomorphosis, arrestation of development having occurred in *Elliptocephala* after the generation of only fourteen thoracic segments. *Elliptocephala* probably occupied an outer shelf situation and is found associated with a cosmopolitan, open-ocean fauna like that of an Acado-Baltic assemblage. *O.* (*Olenellus*), however, was restricted to continental shelves (Fletcher pers. comm.). The development of broad genal areas in some later species of *O.* (*Olenellus*), and their occurrence in deeper-water areas on the continental shelf (such as the occurrence of *O.* (*Olenellus*) *thompsoni* in the Parker Shale of Vermont) suggests a reversion within some species of *O.* (*Olenellus*) to living in a deeper water, less well-oxygenated environment.
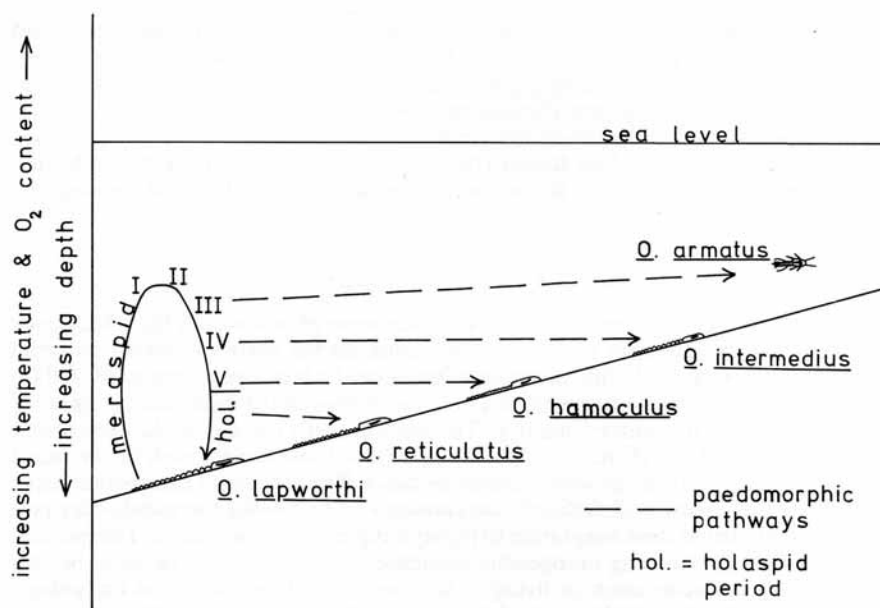
TEXT-FIG. 7. Diagrammatic representation of the effect of depth in controlling paedomorphism.

Text-fig. 7 illustrates the mechanism whereby the active, free-swimming olenellid larvae may have been adapted to higher-oxygenated conditions in shallower water. Progenesis would have resulted in the individual being able to remain at this level of oxygenation and depth of water, though it may well have become benthonic, inhabiting shallower water, when adult, than its progenitor. The enlargement of the frontal lobe in late stage meraspids and early holaspids may be regarded as an adaptation to a benthonic environment. Likewise, the tumid frontal lobe of the non-paedomorph and late paedomorphs suggests a benthonic mode of life. The frontal lobe of *O. (Olenelloides) armatus* is relatively less tumid which, in addition to the development of a spinose cephalon, broad axis, and narrow pleurae, suggests that it may have been planktonic throughout its life. The earliest paedomorphs originally developed by progenesis from the youngest larvae of the non-paedomorph which inhabited the upper waters. The later paedomorphs developed from later-stage larvae in progressively deeper water (text-fig. 7). The paedomorph is regarded as having inhabited the same depth of water as the larvae of the non-paedomorph from which it developed, but having occupied a benthonic environment.

If the supposition is made that *O. (Olenellus) lapworthi* lived in deeper water than *O. (Olenellus) reticulatus*, which in turn lived in deeper water than *O. (Olenellus) hamoculus*, and so on (text-fig. 7), this may imply a direct correlation between increasing size and increasing depth of water, and thus decreasing temperature. Newell

(1949, p. 120) and Bonner (1968, p. 5) have suggested that in some cold-blooded organisms, lower temperature has caused a delaying of sexual maturity, so that the gonads are not ripe until the organism is much larger than its counterpart living in a higher-temperature environment. The delaying of sexual maturity favours increased rate of growth. If one looks at this idea from another angle, then the occupation of an environment of higher temperature may, at times, cause premature ripening of the gonads, i.e. progenesis would occur. Thus water temperature may have been the initial controlling factor in triggering off progenesis and so causing the paedomorphic evolution of new species of *Olenellus* in north-west Scotland. As illustrated in text-fig. 7, the stratification of the olenellid larvae, with progressively more mature stages inhabiting progressively deeper zones and the paedomorphs settling in shallower water than the larvae, but water of similar temperature, is fundamental to the paedomorphic mechanism in these olenellids. Bogorov (1932) has shown that larvae of the decapod crustacean *Calanus finmarchicus* inhabit different strata at different stages of larval life. This has been shown (Gurney 1942, p. 92; Kikuchi 1927) to be controlled by phototaxis, the earliest larvae being attracted to light, but subsequent larvae being increasingly negatively phototactic.

The two very large specimens of *O. (Olenellus) reticulatus* ('gigas' of Peach 1894, p. 666) which are over twice the size of the next largest *O. (Olenellus) reticulatus*, probably represent individuals which never attained sexual maturity. Rothschild (1936) and Rothschild and Rothschild (1939) have shown that parasitic castration in pulmonates prolongs the early rapid rate of growth and results in larger individuals than the norm.

DISCUSSION

Whether paedomorphosis can be regarded as having played, and may still be playing an important role as an evolutionary mechanism, is still open to debate. Garstang (1928) laid great emphasis on the role of paedomorphosis in the phylogeny of the tunicates, whilst de Beer (1958), in an excellent discussion of the subject, tried to apply this evolutionary mechanism to many phyla. Gould (1968) has shown how paedomorphosis has been operative in the land snail *Peocilozonites* and how this rapid, saltating method of evolving may help explain some aspects of allopatric speciation. Gurney (1942, p. 22) has suggested that the Copepoda may have arisen from the Decapoda by paedomorphosis. He has further shown that decapod larvae often show paedomorphic characteristics, giant larvae, which have undergone neoteny, occurring quite frequently; these show the normal development of the sexual organs, but the retention of larval mouth parts and legs. Very few concrete examples of paedomorphosis in trilobites have been documented, although Stubblefield (1936) considered that proparian trilobites evolved from opisthoparian trilobites by 'neoteny'. He was also of the opinion that the 'dwarfed forms' the Burlingiidae, Norwoodiidae, and Eodiscidae represent 'neotenous' forms as they retain larval features, and never exceed 12 mm in length. The small size indicates that the paedomorphic mechanism which gave rise to these families, and possibly to proparian trilobites, was progenesis, not neoteny. Whittington (1957b, p. 460) considered the evidence for the importance of 'neoteny' as a process in evolution of trilobites as tenuous; however, Størmer

(1942) and Hupé (1953b) have regarded 'neoteny' (i.e. paedomorphosis) as an important evolutionary process in trilobites. Recently Clarkson (1971, 1975) has suggested that the schizocroal eye of trilobites may have been paedomorphic.

The olenellids from north-west Scotland, in response to the availability of unoccupied ecological niches, assisted by imperfections in their hormonal mechanisms, seem to have evolved with great rapidity and fluidity by means of paedomorphosis. Large-scale morphological changes were able to occur with only very small genetic changes taking place. It is plausible that the explosive radiations which characterize the onset of many phyletic lineages, may, in part, have been facilitated by paedomorphosis.

REFERENCES

BAER, K. E. VON. 1866. Über Prof. Nic. Wagner's Entdeckung von Larven, die sich fortpflazen, Herrn Ganin's verwandte und ergänzende Beobachtungen und über die Paedogenesis überhaupt. *Izv. imp. Akad. Nauk.* **9**, 64–137.

BEECHER, C. E. 1897. Outline of a natural classification of the trilobites. *Am. J. Sci.* Ser. 4, **3**, 181–207.

BERGSTRÖM, J. 1973. Classification of olenellid trilobites and some Balto-Scandian species. *Norsk geol. Tidsskr.* **53**, 283–314.

BEST, R. V. 1952. Two new species of *Olenellus* from British Columbia. *Trans. R. Soc. Canada*, **46**, 13–22.

BILLINGS, E. 1861. Palaeozoic fossils. Vol. I. *Geol. Surv. Canada.* 24 pp.

BOGOROV, B. G. 1932. Modifications in the biomass of *Calanus finmarchicus* in accordance with its age. *Byull. gosud. okeanogr. Inst.* **8**, 1–16. [In Russian with English résumé.]

BONNER, J. T. 1968. Size and change in development and evolution. *J. Paleont.* **42**, Memoir 2, 1–15.

CISNE, J. L. 1975. Anatomy of *Triarthrus* and the relationships of the Trilobita. *Fossils and Strata*, **4**, 45–63.

CLARK, R. B. 1964. *Dynamics of metazoan evolution.* Oxford. 313 pp.

CLARKSON, E. N. K. 1971. On the early schizocroal eyes of *Ormathops* (Trilobita, Zeliskellinae). *Mem. Bur. Rech. Geol. Min.* **73**, 51–63.

—— 1975. The evolution of the eye in trilobites. *Fossils and Strata*, **4**, 7–31.

COWIE, J. W. and MCNAMARA, K. J. 1978. *Olenellus* (Trilobita) from the Lower Cambrian, North-West Scotland. *Palaeontology*, **21**, 615–634.

DE BEER, G. 1958. *Embryos and ancestors.* Oxford. 190 pp.

FRITZ, W. H. 1972. Lower Cambrian trilobites from the Sekwi Formation type section, Mackenzie Mountains, northwest Canada. *Bull. geol. Surv. Can.* **212**, 1–89.

GARSTANG, W. 1928. The morphology of the Tunicata and its bearing on the phylogeny of the Chordata. *Q. Jl microsc. Sci.* **72**, 52–187.

GIARD, A. 1887. La castration parasitaire et son influence sur les caractères exterieurs du sexe male chez les crustacés décapodes. *Bull. scient. Dep. Nord.* 2nd ser. **10**, 1–28.

GOULD, S. J. 1968. Ontogeny and the explanation of form: an allometric analysis. *J. Paleont.* **42**, Memoir 2, 81–98.

—— 1977. *Ontogeny and phylogeny.* Harvard. xviii+501 pp.

GURNEY, R. 1942. *Larvae of Decapod Crustacea.* London. 306 pp.

HARRINGTON, H. J. 1956. Olenellidae with advanced cephalic spines. *J. Paleont.* **30**, 56–61.

HU, C. H. 1971. Ontogeny and sexual dimorphism of Lower Paleozoic Trilobita. *Palaeontogr. am.* **44**, 31–155.

HUPÉ, P. 1953a. Contribution a l'étude du Cambrien inferieur et du Précambrien III de l'Anti-Atlas marocain. *Notes Mém. Serv. Mines Carte géol. Maroc.* no. 103, 1–402.

—— 1953b. Classification des trilobites. *Ann. Paléontol.* **39**, 1–110.

JELL, P. A. (in press). Trilobite respiration and genal caeca. *Alcheringa* 2.

KIKUCHI, K. 1927. Notes on the diurnal migration of plankton in Kizaki Lake. *J. Coll. Agric. imp. Univ. Tokyo,* **9,** 177–197.

LAKE, P. 1937. A monograph of the British Cambrian trilobites. *Palaeontogr. Soc.* [*Monogr.*], (10), 225–248.

—— 1938. Ibid. (11), 249–272.

LOCHMAN, C. 1952. *In* COOPER, G. A. *et al.* Cambrian stratigraphy and paleontology near Caborca, north-western Sonara, Mexico. *Smithsonian Misc. Coll.* **119,** 60–161.

—— 1956. Stratigraphy, paleontology, and paleogeography of the *Elliptocephala asaphoides* strata in Cambridge and Hoosick quadrangles, New York. *Bull. geol. Soc. Am.* **67,** 1331–1396.

MOBERG, J. C. 1899. Sveriges älsta kända trilobiter. *Geol. För. Stöckh. Förh.* **21,** 309–348.

MOORE, R. C. (ed.) 1959. *Treatise on Invertebrate Palaeontology, Part O, Arthropoda,* **1,** xix. 560 pp. Geol. Soc. Amer. and University of Kansas Press.

NEWELL, N. D. 1949. Phyletic size increase, an important trend illustrated by fossil invertebrates. *Evolution,* **3,** 103–124.

PALMER, A. R. 1957. Ontogenetic development of two olenellid trilobites. *J. Paleont.* **31,** 105–128.

—— in press. The physical stratigraphy and biostratigraphy of the Lower and Middle Cambrian Carrara Formation in the southern Great Basin (western United States). *Prof. Pap. U.S. geol. Surv.*

PEACH, B. N. 1894. Additions to the fauna of the *Olenellus* zone of the northwest Highlands. *Q. Jl geol. Soc. Lond.* **50,** 661–675.

—— and HORNE, J. 1892. The *Olenellus* zone in the northwest Highlands of Scotland. Ibid. **48,** 227–242.

POULSEN, V. 1974. Olenellacean trilobites from eastern North Greenland. *Bull. geol. Soc. Denmark,* **23,** 79–101.

RAW, R. 1925. The development of *Leptoplastus salteri* (Callaway) and of other trilobites (Olenidae, Ptychoparidae [*sic*], Conocoryphidae, Paradoxidae, Phacopidae and Mesonacidae). *Q. Jl geol. Soc. Lond.* **81,** 223–324.

—— 1937. Systematic position of the Olenellidae (Mesonacidae). *J. Paleont.* **11,** 575–597.

—— 1957. Origin of chelicerates. Ibid. **31,** 139–192.

RAYMOND, P. E. 1920. The appendages, anatomy, and relationships of trilobites. *Mem. Conn. Acad. Arts Sci.* **7,** 169 pp.

RESSER, C. E. 1928. Cambrian fossils from the Mohave Desert. *Smithsonian Misc. Coll.* **81,** no. 2, 1–14.

ROTHSCHILD, A. and ROTHSCHILD, M. 1939. Some observations on the growth of *Peringla ulvae* (Pennant, 1777) in the laboratory. *Novit. zool.* **41,** 240–247.

ROTHSCHILD, M. 1936. Gigantism and variation, *J. mar. biol. Ass. U.K.* 20, 536–546.

STØRMER, L. 1942. The larval development, the segmentation and the sutures, and their bearing on trilobite classification. *Norsk geol. Tidsskr.* **21,** 49–164.

STUBBLEFIELD, C. J. 1936. Cephalic sutures and their bearing on current classifications of trilobites. *Biol. Rev.* **11,** 407–440.

STÜRMER, W. and BERGSTRÖM, J. 1973. New discoveries on trilobites by X-rays. *Paläont. Z.* **47,** 101–141.

VOGDES, A. W. 1893. A classed and annotated bibliography of the Paleozoic Crustacea, 1698–1892, to which is added a catalogue of North American species. *Calif. Acad. Sci. Occ. papers,* **4,** 412 pp.

WALCOTT, C. D. 1910. Cambrian geology and paleontology No. 6—*Olenellus* and other genera of the Mesonacidae. *Smithsonian Misc. Coll.* **53,** no. 6, 231–422.

WHITTINGTON, H. B. 1957a. Ontogeny of *Elliptocephala, Paradoxides, Sao, Blainia,* and *Triarthrus* (Trilobita). *J. Paleont.* **31,** 934–946.

—— 1957b. The ontogeny of trilobites. *Biol. Rev.* **32,** 421–469.

K. J. McNAMARA

Department of Geology and Geophysics,
University of Sydney,
N.S.W. 2006,
Australia