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Trilobite segmentation

ABSTRACT: Various lines of evidence indicate that the trilobite cephalon is composed of six somites in addition to the presegmental acron. Five of the somites are provided with typical appendages, four pairs of legs and one pair of antennae. The labrum (and its sclerite, the hypostome) appears to be formed, wholly or partly, by a sixth pair of modified preantennal appendages. The cephalic-thoracic boundary in trilobites as well as in most Palaeozoic xiphosurids is thought to be roughly intersegmental, and the thoracic sclerites probably largely correspond to somites. The concept of merocyclism is rejected.

INTRODUCTION

Our knowledge of the segmentation of the cephalon in trilobites is based primarily on the existence of serial similarity in the dorsal exoskeleton and on observations on the number of ventral appendages. Serial similarity is here defined as the result of a regular repetitive occurrence of distinctive features along the antero-posterior axis of the body (or along the length axis of an appendage). Certain conclusions must depend on the supposition that serial arrangement of sclerites, appendages, and particular morphological features such as glabellar lobation, reflect segmentation also in the soft parts of the animal. It seems that this supposition has never been questioned. There is also general agreement that segmentation was simple, with but one set of serial expressions in the exoskeleton pro segment. These suppositions seem to be well justified and need not be further discussed here. On the other hand there is considerable uncertainty as to the exact course of segmental boundaries in the exoskeleton but this does not affect the principles of segmentation or serial similarity.

CEPHALIC SEGMENTATION

In many cases speculations on cephalic segmentation have proceeded far beyond the limits given by appendage number and serial similarity. In this way not only the anterior lobe of the glabella has been identified as one or more segments, but also the frontal area and ventral structures (rostral plate, hypostome) have been pressed into a segmental pattern. In this way the total number of cephalic segments has been counted as up to 7 in the rhachial part (Hupé 1953), 3 in the frontal area (Palmer 1957), and 2 on the ventral side, regarded as the most anterior segments (rostral plate by Kiaer 1916, hypostome by Jaekel 1901 and others). Some important points may be given as a guide to ideas regarding the composition of the trilobite head tagma.

1. A presegmental complex or acron is present in all present-day arthropods and it is hardly probable that trilobites differed in this respect.
2. The acron includes the eyes in extant arthropods.
3. Somites never seem to be confined to pleural areas only.
4. The rhachial lobe ends anteriorly with the anterior glabellar lobe, and the area in front of this lobe is pleural.
5. The apodemes are intrasegmental and do not mark the exact boundaries between somites.

If these points are sound, the somital segments should be confined to the rhachial part of the cephalon and some lateral pleural areas, while at least anterior pleural areas and probably the anterior tip of the glabella should belong to the acral complex. In fact, this theory conforms well with the view on segmentation achieved from studies on appendages (e.g. Raymond 1920; Størmer 1930, 1951) and on serial similarity (this paper; combined studies or comments have been made by Størmer 1930, Öpik 1958, 1961, and others).

Here the discussion is concentrated to some early trilobites which show signs of unaltered segmentation particularly well. Particularly in many early trilobites serial similarity is strikingly obvious not only from the occipital ring (or lobes) backwards (occipital similarity of Öpik 1958, 1961), but also forwards. In many genera, such as *Olenellus*, *Nevadia*, *Wanneria*, *Kjerulfia*, *Holmia*, *Schmidtiellus*, *Redlichia*, and *Centropoleura*, there are at least three pairs of glabellar lobes (L1-3) with obvious serial similarity internally and backwards in adult specimens. It is particularly interesting to observe that the occipital furrow (S0) is commonly very similar to the anterior furrows (S1-3) both in course and depth, while the former is generally more pronounced than the latter in later trilobites.

In various trilobites there may be additional paired glabellar lobes. However, this is exception rather than rule, and it is necessary to be

cautious with judgments based on one or another exceptional case. One additional lobe (*L4*) is obviously present in some paradoxidids, such as *Hydrocephalus* and *Eccaparadoxides*. In this case there is considerable serial similarity between the glabellar lobes inclusive of *L4*. The discussed *L4* is present also in *Centropleura* and probably in species of *Olenellus*, *Fallotaspis*, *Wanneria?* and *Schmidtiellus*. Another two glabellar segments have been claimed to occur in *Daguinaspis*, *Choubertella*, *Fallotaspis*, and *Callavia* (Hupé 1953, pp. 261—263).

There is thus some morphological variation, and ideas about segmentation can not uncritically rely on the number of glabellar lobes in a single trilobite.

As segmentation probably greatly influences the early ontogenetic development in all arthropods, trilobite larvae may be supposed to reveal important features in cephalic metamerism. However, this does not mean that a simple counting of the number of rings of the rhachial lobe is sufficient. For instance, the number (including the anterior lobe) is 5 in olenellids like *Olenellus gilberti* Meek (see Palmer 1957, Text-fig. 6) but 6 in paradoxidids like *Eccaparadoxides pinus* (Westergård)? (see Westergård 1936, Pl. 4). In both species referred to the palpebral lobe terminates in or opposite to the anterior lobe of the larval glabella. Contrary to previous views, it must be recognized that the number of post-palpebral glabellar lobes is not constant in trilobites, this conditions first influenced the writer to believe that number of cephalic segments is one more in paradoxidids than in olenellids, but the explanation may be different, as seen in the discussion on the morphology of the cephalon.

In *Olenellus gilberti* the ontogenetic development is well known thanks to detailed work by Palmer (1957). In all stages the palpebral lobe is comparatively wide and terminates in the anterior lobe. Behind the anterior lobe there are four cephalic lobes (inclusive of occipital) which show a striking serial similarity in the first developmental stages (*I—IV* according to Palmer). In the fifth stage (Palmer 1957, Fig. 7; Pl. 19, Figs. 16, 19) lobes *L0-13* begin to differentiate, and the palpebral lobes divides into anterior and posterior palpebral or palpebro-ocular ridges. The proximal ends of these palpebral ridges lie opposite to the anterior and posterior parts of the anterior glabellar lobe, respectively. At the same time there is some diversification of the anterior glabellar lobe into a wide anterior and a narrow posterior part (Palmer Fig. 7:Ve).

The separation of anterior and posterior palpebro-ocular ridges is found in most olenellids, including species of *Olenellus*, *Fremontia*, *Nevadina*, *Wanneria*, *Kjerulfia*, *Holmia*, *Schmidtiellus*, *Bondonella*, *Fallotaspis*, *Daguinaspis*, and *Choubertella*. In several genera not listed here the conditions are probably similar.

It has been shown (Bergström, 1973) in *Wanneria? lundgreni* and *Schmidtiellus torelli* that the posterior palpebro-ocular ridge can be fol-

lowed into the glabella where it may possibly be distinguished as a glabellar lobe (*L4*) showing serial similarity backwards. In the same connection the anterior palpebro-ocular ridge was found to the side of the anterior glabellar lobe until it merges with this lobe anteriorly. An undifferentiated triangular glabellar field fills the space between the two ridges inside the glabella. The situation appears to be identical to that reported by Hupé (1953, pp. 261—263) in *Fallotaspis tazemmourtsensis* Hupé and *Callavia crosbyi* Walcott. Here *L4* is termed segment antennulaire (*A1*), the triangular field segment préantennulaire (*pnt*), and the anterior part of the anterior palpebro-ocular ridge segment *x* (*x*). However, as in *W.?* *lundgreni* and *S. torelli*, there is no particular sign of serial similarity in front of *L4* (except within the palpebro-ocular ridge), nor is there any other evidence for eventual somites corresponding to *pnt* and *x*. The situation may be more complicated in species of *Daguinaspis* and *Choubertella*; but it seems that the serial similarity seen in drawings of *Daguinaspis* (Hupé 1953, Figs 60—61) is much more convincing than that can be seen from the photographs (Hupé 1953, Pl. 5).

It is interesting to notice that in some olenellids the posterior palpebral ridge is adjoined posteriorly by an elongated (*transv.*) glabellar lobe *L3*, which is quite similar in general aspect to the posterior palpebral ridge though shorter. This is well seen in larval forms figured by Rasetti as *Paedumias?* sp. (Rasetti 1966, Pl. 12, Figs 19—20) and *Olenellus* sp. undet. (Rasetti 1966, Pl. 12, Figs 21—22). In holaspides an extension from glabellar lobe *L3* paralleling the posterior palpebral ridge is found in many species, including for instance forms described as *Olenellus* cf. *gilberti* Meek (cf. Walcott 1910, Pl. 41, Fig. 1), *O. logani* Walcott (cf. Walcott 1910, Pl. 41, Fig. 6), *O. alius* Resser & Howell (cf. Resser & Howell 1938, Pl. 6, Fig. 10), *O. simplex* Poulsen (cf. Poulsen 1932, Pl. 9, Figs 1—5), *O.?* *curvicornis* Poulsen (cf. Poulsen 1932, Pl. 10, Figs 2—3), "*Paedumias*" *yorkense* Howell & Resser (cf. Walcott 1910, Pl. 32, Fig. 13; Pl. 34, Fig. 3), "*P. transitans*" Walcott [= *Olenellus thompsoni* (Hall); cf. Walcott 1910, Pl. 34, Fig. 1], "*P.*" *tricarinatus* Poulsen (cf. Poulsen 1932, Pl. 11, Fig. 13), *Judomia dzevanovskii* Lermontova (cf. Moore 1959, Fig. 133 : 2), *Laudonia bispinosa* Harrington (cf. Harrington 1956, Pl. 15, Figs 4—5), and *Wanneria ruginosa* Poulsen (cf. Poulsen 1958, Pl. 6, Figs 1, 4). The posterior palpebral ridge is particularly clearly distinguished morphologically in *O.?* *curvicornis* (which may belong to Wanneriinae) and "*P.*" *tricarinatus*, and in those species and *Judomia dzevanovskii* the similarity between the ridges and *L3* is also particularly striking. In "*P.*" *tricarinatus* there is even an indication of a glabellar furrow (*S4*) in front of the termination of the ridge.

Still more evidence regarding cephalic segmentation may be gained from the morphology of the palpebral area in larval olenellids. Particularly the studies by Kiaer (1916) and Størmer (1942) on *Holmia kjerulfi*

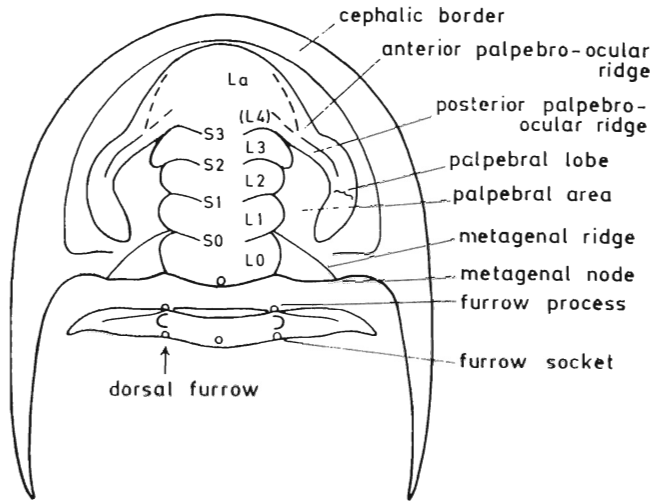


Fig. 1

Drawing based on the Lower Cambrian olenellacean *Wanneria? lundgreni* (Moberg) to show the terminology used in the text

Drawing made by Mrs Siri Bergström

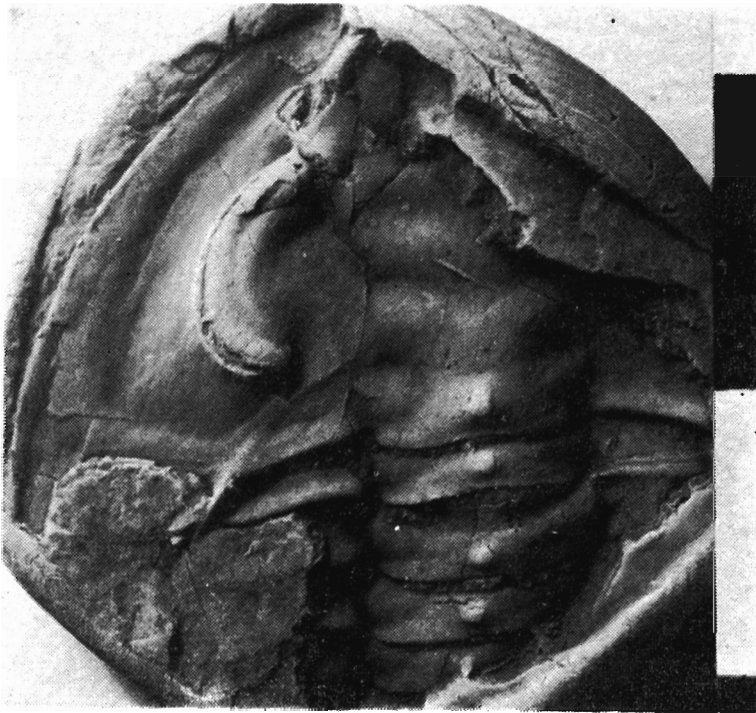


Fig. 2

Holmia kjerulfi (Linnarsson) from the Lower Cambrian *H. kjerulfi* Zone at Tømten, Norway; the specimen deposited at the Institute of Palaeontology in Lund, no. LO 4532t. It is plainly evident that the occipital ring (LO) shows serial similarity with the thoracic rhachial rings and corresponds to only one segment

Scale in cm; photograph taken by Mr Sven Stridsberg

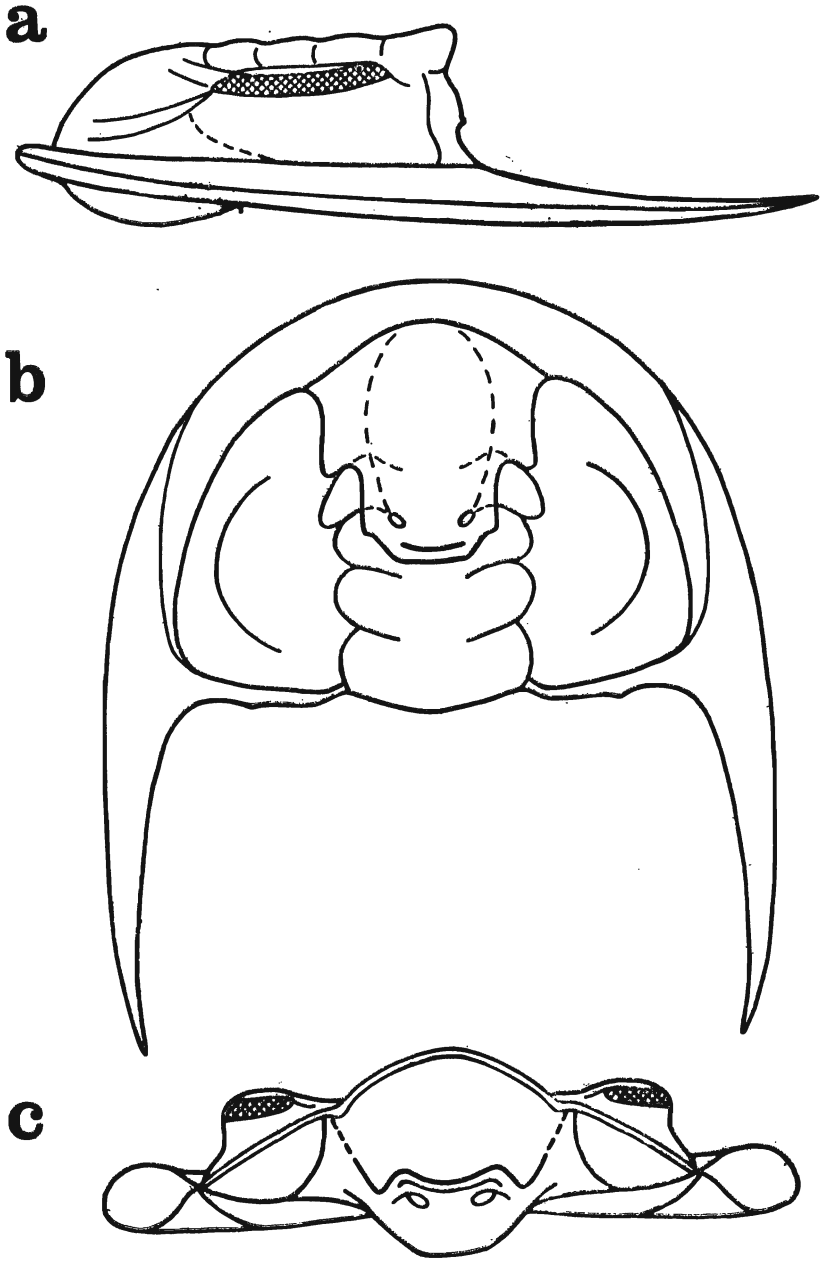


Fig. 3

Lateral (a), ventral (b), and posterior (c) views of *Wanneria? lundgreni* (Moberg). As seen in a and c, the anterior part of the glabella and the hypostome form a spacious case for the stomach and the probably surrounding hepato-pancreas. The anterior wings of the hypostome, seen in b, extend to the dorsum, as seen in c. The spot where each wing attaches is developed as a fossular apodeme in many trilobites.

Drawing made by Mrs Siri Bergström

(Linnarsson) and by Palmer (1957) on *Olenellus gilberti* Meek and "*Paedumias*" *clarki* Resser show that palpebral area is divided into compartments divided by furrows and corresponding in number and position to the glabellar lobes. If the glabellar lobes reflect somites, it is very unlikely that this is not also the case with the confluent larval lobes of the palpebral area, as also advocated by Størmer, Palmer, and other authors. Perfect serial similarity is commonly present in early stages in different olenellids including the three species mentioned above. This serial similarity unites the lobes of the palpebral area opposite to *L0-L3*. However, the palpebral lobe (or part of it) may possibly be included in this series, as indicated by the morphology in *Olenellus gilberti* (cf. Palmer 1957, Fig. 6: I, II), *Holmia kjerulfi* (cf. Kiaer 1916, Pl. 6, Fig. 1; Størmer 1942, Figs 4—5e), and *Elliptocephala asaphoides* Emmons (cf. Walcott 1910, Pl. 25, Fig. 9).

Regarding cephalic segmentation it should also be mentioned that Öpik (1937, p. 127, note) regards the occipital ring in *Holmia kjerulfi* (and in "*H.*" *mickwitzii* as erroneously figured by Schindewolf in 1927) to be formed by fusion of tergites of two segments, the posterior of which ontogenetically belongs to the thorax. This suggestion was criticized by Størmer in 1942 (p. 119), but was repeated without comments by Öpik in 1958 (p. 25). The idea of a double occipital ring was probably induced by Kiaer's (1916) Fig. 11e, in which there is a transverse line across the occipital ring. According to Kiaer this figure corresponds to the photographs given as Pl. 6: 10—11. A comparison with these photographs indicates that: (1) the occipital ring in Fig. 11e is drawn much too long (*sag.*); (2) the transverse line, which is apparently represented by a smooth furrow on the photographs, is overemphasized in the drawing; (3) the same transverse line has a distinctly incorrect curvature and is displaced forwards in the drawing. A comparison with other photographs (Kiaer 1916, Pl. 8; Figs 5, 7, 9, 11) and additional material at hand clearly indicates that the transverse furrow on the occipital ring is closely comparable with the similarly situated furrow on each of the thoracic rhachial rings. In fact, the similarity is so great that this is a perfect example of what Öpik (1958, p. 23) calls occipital similarity. Thus it can be considered as certain that the occipital ring in *Holmia kjerulfi* has a length (*sag.*) corresponding to only one segment.

Concluding this discussion based on olenellids, a few things should be pointed out. First, the palpebral lobe is a bifid structure, composed of anterior and posterior palpebral ridges (conditions are uncertain in some species). Second, the posterior palpebro-ocular ridge extends into or ends against the posterior part of what may be called the anterior glabellar lobe or *L4*, if that lobe is developed. Third, in some cases the posterior palpebro-ocular ridge and the connected part of the glabella (*L4*) reveals serial similarity with elements behind, indicating that this part of the

cephalon corresponds to one somite, provided that this is the case with the posterior glabellar lobes. Fourth, serial similarity is not found anterior to the posterior palpebro-ocular ridge or *L4*, and the number of developed cephalic somites is thus not likely to exceed five.

APPENDAGES AND MUSCLES

Although poorly known, the cephalic appendages certainly tell something about the segmentation. It is well known that there are one pair of antennae and four pairs of "normal" appendages in *Olenoides serratus*, *Triarthrus eatoni*, and *Ceraurus pleurexanthemus*. Some phacopids have a reduced number of cephalic appendages, but a total of five pairs seems to be normal. Hence, there is a minimum of five cephalic segments in addition to the acral complex in at least some trilobites.

In the dorsal exoskeleton furrows and apodemes mark the positions where the appendage muscles are attached. Apodemal pits tend to be situated fairly close to the dorsal furrow or between that furrow and the midline. In *Oryctocephalites gelasinus* (cf. Shergold 1969, Fig. 13; Pl. 5, Figs 7—10) there is a series of five pairs of furrows, including the occipital and four glabellar furrows. The most anterior furrow (*S4*) is closer to the dorsal furrow as a whole than are the posterior glabellar furrows. Slightly anterolaterally the fossula is developed in the dorsal furrow. A very similar situation is present in *Cybele grewingki* (cf. Öpik 1937, Fig. 36), although *L3* and *L4* are confluent in that species. Although the fossulae are wider apart than the glabellar furrows it is tempting to suggest that they are serially homologous. The serial similarity is even more impressive in larvae, for instance in *Peltura scarabaeoides* (cf. Whittington 1958, Pl. 38), *Ptarmigania aurita*, and *Glyphaspis* cf. *parkensis* (cf. Hu 1971, Pl. 10 and Pl. 11 respectively). If there is serial homology between the fossula and the glabellar furrows the fossula represents a sixth cephalic segment. In this respect the connection between the fossular apodeme (anterior boss) and the anterior wing of the hypostome (see Whittington & Evitt 1954, pp. 19—20 for discussion and references) is highly interesting. In a number of species the tip of the wing process appears to fit into a pit in the anterior surface of the fossular apodeme or at least to be connected by ligaments. Similar dorso-ventral connections in trilobites are indicated only between the rhachial apodemes or attachment surface and the ventral appendages. The connection therefore adds strongly to the probability that there is a serial similarity and homology between the fossula and the glabellar furrows. Consequently there would also be some kind of serial homology between at least the anterior wings of the hypostome and the appendages. It should be remembered that the hypostome is roughly the exoskeletal cover of the labrum, although

sutural rearrangements are responsible for somewhat different coverage in different trilobites.

In a review of head development in the arthropods, Manton (1960, pp. 274—278) states that the labrum may be formed in different ways. In the myriapod *Scolopendra* it forms ontogenetically out of a median labral rudiment. In insects preantennal limb rudiments fuse with a median labral rudiment to form the ultimate labrum. The condition in arachnids is uncertain, but it is possible that the labrum forms from a pair of limb rudiments without any addition of a median labral rudiment. According to Pross (1966, pp. 102—103) the arachnid labrum, if actually formed by limb rudiments, must have its origin in the preantennal (pre-precheliceral) limb rudiments.

The conditions in extant arthropods together with the above mentioned indications in trilobites make it plausible that the fossular apodeme and at least part of the hypostome including the anterior wing represent the altered remnants of a preantennal limb and its muscular attachment.

It is interesting that the hypostomal wing process does not appear to join with the tip of the fossular apodeme but with its anterior side. It is possible that antennal muscles attached to this apodeme or that (preantennal) muscles extending from the labrum or its covering hypostome reached this point.

SEGMENTATION OF PLEURAL AREAS

In the thorax the successive articulating sclerites undoubtedly express a segmentation of at least the exoskeletal cover. In the cephalon, the palpebral areas show segmentation in many trilobite larvae, e.g. in *Olenellus gilberti* as demonstrated by Palmer (1957).

Two different views are met with regarding the relation between the somites and the exoskeletal sclerites. Størmer (1942, Figs 14—15 and 17) advocated the view that the somites cut the boundaries between the sclerites. For instance, the occipital somite would have its central part under the occipital ring but distal extremities in the pleural spine of the first thoracic sclerite. This view, which was shared by Palmer (1957) and Hessler (1962), is mainly based on the disputed connection between the preoccipital glabellar segment (*L1*) and the intergenal spine in forms like *Holmia kjerulfi*, *Olenellus gilberti*, and *Eccaparadoxides pinus*(?). The next successive spine is the pleural spine of the first thoracic tergite, and this spine was therefore assigned to the occipital segment. The concept of secondary segmentation gained support from the condition in extant limulids, where the joint between prosoma and opisthosoma actually

cuts through the sixth metamere (cheliceral metamere counted as first; cf. Størmer 1942, Fig. 16).

Ross (1951, pp. 148—150) and Whittington & Evitt (1954, p. 28) believed that the intergenal spine in cheirurids is connected with the occipital ring, and did not accept Størmer's idea of segment-cutting sclerites in trilobites. The idea gains support from *Redlichia*, where arteries (?) extend along the cephalic-thoracic boundary on both sides. The one on the anterior side appears to extend from the occipital ring to the intergenal spine (cf. Öpik 1961, Fig. 8).

Provided that the furrows of the palpebral area in larval trilobites show the position of metamere boundaries, Palmer's (1957) material of *Olenellus gilberti* distinctly shows that the intergenal spine is connected with the preoccipital segment. Similar evidence is known from several other olenellid trilobites. The writer has also been able to follow a faint but distinctly visible furrow from *S1* to the outer side of the intergenal spine in a specimen of *Eccaparadoxides pinus* (?) (figured in Westergård 1936, Pl. 4, Fig. 13c; the furrow is not well visible in the published figure). The same specimen has a deep border furrow reminding of the pleural furrow of the thoracic tergites. This border furrow extends to the occipital ring and may give the impression that these features together with the intergenal spine mark an occipital segment. However, the border furrow is obviously a strengthening device present also in most other trilobites, while the faint furrow extending from *S1* apparently lacks functional significance and closely resembles the supposed segmental boundaries of olenellid larvae. In *Eccaparadoxides*, as well as in olenellids, there is therefore evidence that the intergenal spine belongs to the preoccipital segment. The cheiruraceans treated by Ross (1951) and Whittington & Evitt (1954) lack the non-functional larval intersegmental furrows and therefore tell nothing about the segmental position of the intergenal spine.

The comparison with limulids is fundamental to the idea of sclerites crossing the segmental boundaries. In the axial region of *Limulus*, segment 7 is the last in the prosoma, and segment 8 the most anterior in the opisthosoma. Segment 7 is rudimentary and confined to the axial region. Laterally the prosomal-opisthosomal hinge cuts through segment 6, a spine-like part of which is coalesced with segment 8 on the opisthosoma. However, this condition is obviously highly aberrant. In late Palaeozoic xiphosurids like *Euproops* and *Belinurus* the opisthosoma lacks the coalesced but distinctly set off spine (segment 6) characteristic of modern limulids. Instead there is an "intergenal" spine of the prosoma in many species. It is tempting to suggest that it is this "intergenal" spine that in later xiphosurids is fused to the opisthosoma. Apparently some Palaeozoic xiphosurids therefore had a reduced segment 7 without pleural extensions. In position with regard to the hinge behind the "head" this

segment corresponds to the occipital segment of trilobites. Segment 6 was in "preoccipital" position and yielded an "intergenal" spine. Segment 7 may have been fully developed in the Devonian xiphosurid *Weinbergina*, whereas it obviously was more or less reduced at least ventrally in eurypterids, just as it is in scorpions. In arachnids the pregenital segment 7 has always suffered some reduction and in most cases lost its intimate connection with the prosoma; it is counted with the opisthosoma.

If conditions in trilobites are at all similar to those of chelicerates, and particularly merostomes, it is probable that the following interpretation is correct. According to various observations the intergenal spine probably belongs to the preoccipital segment. What is left in front of the cephalic-thoracic joint is a reduced occipital segment without a corresponding pleural spine. In the thorax, the articulating units approximately correspond to somites, and the quite variably positioned pleural furrows are simple strengthening devices. This seems to be the simplest possible solution, and the solution best in accord with both observations on trilobites and comparisons with chelicerates.

In the cephalon the non-segmental eyes probably mark the boundary between a central segmented body and non-segmental extra-ocular cheeks. The genal spine apparently belongs to the non-segmental part of the cephalon. It should be remembered that also the pygidium includes a non-segmental portion, the post-segmental telson, from which the somites formed during the ontogeny.

THE CONCEPT OF MEROCYCLISM

Raw (1953, 1957) introduced the concept of merocyclism in the discussion of trilobite morphology. It was concluded that there is a cyclic development of the segments in trilobites and chelicerates, expressed by the excessive development of every third segment, which may be characterized by macrospines or rhachial spines. In developing the hypothesis, Raw based his countings on the remarkable supposition that the number of segments in the head tagma is the same in all trilobites and chelicerates.

The concept of triadic merocyclism has also been used by Palmer (1957) as a means of determining the number of segments in the trilobite cephalon. Assuming that the anterior lobe of the glabella and the palpebral lobes constitute one macropleural segment, and the anterior and lateral border another macropleural segment, there must be two normal segments in between those two according to the hypothesis. The minimum number of cephalic segments in this way is determined to eight.

However, as far as the position of the thoracic macropleural segments (or strictly speaking, tergites, as it is not objectively known if the

separate tergites correspond exactly to segments) there is much less constancy even among early trilobites than Raw seems to be aware of. In many olenellids *T3* (the third thoracic tergite) is macropleural, at least in some ontogenetic stages. This is the case in *Olenellus* and other members of Olenellinae and in *Fallotaspis*. On the other hand *Schmidtiellus panowi* (Samsonowicz) appears to show (cf. Samsonowicz 1959, Pl. 2, Fig. 12a, b) macropleural development of *T2*. In paradoxidids macropleural development is typical for *T1* and *T2* in ontogenetic stages; in this case macrospines are thus developed simultaneously on two consecutive tergites. Exactly the same condition with *T1* and *T2* macropleural is reported in meraspis stages of *Redlichia intermediata* Lu.

These facts definitely do not fit into Raw's hypothesis of the cyclic development and the great regularity of this feature. It would be better to base the ideas on observed facts than to try to fit the animals into hypothetical constructions.

CONCLUSIONS

Two main problems of trilobite segmentation are treated above. First, though the number of segments or somites involved in the formation of the cephalon has been discussed over and over again in the literature it is here treated anew, partly on the basis of new evidence. Second, it is debated whether the somites correspond roughly to the pattern of the thoracic sclerites or not. In addition, a meaningless and misleading mathematical game, the concept of merocyclism is treated briefly.

The maximum number of "typical" cephalic appendages suggests the presence of five corresponding somites. One kind of serial similarity between the distinct segments is found in the paired muscular apodemes of which there may be one set in each segment. In front of the five pairs there is a sixth pair, the fossular apodemes, slightly further apart than the others. While the posterior five pairs obviously are connected with the typical appendages through dorso-ventral muscles, the sixth pair is connected with the labrum and its covering sternite, the hypostome, either directly or through a tendon. The serial similarity between the apodemes and between the dorso-ventral connections piercing the cephalon indicates that the labrum or part of it consists of a pair of remodelled preantennal appendages. This conclusion gains support from the fact that modified preantennal appendages take part in the formation of the labrum in some extant arthropods. It seems justified to speak of six cephalic somites in the trilobite cephalon. In addition, a presegmental acron, no doubt, is involved in the formation of frontal and lateral parts of the cephalon.

The idea that the shape of the somites may differ considerably from the shape of the thoracic sclerites was based on a comparison with modern

xiphosurids, in which part of somite 6 is prosomal, part opisthosomal. However, unpublished research indicates that this condition is secondary and absent from most Palaeozoic xiphosurids. The prosomal-opisthosomal boundary of the latter is more suggestive of that of trilobites than of that of *Limulus*. The similarity includes the presence of a spine in "intergenal" position in many species. The spine apparently corresponds to the opisthosomal part of segment 6 in *Limulus*, which means that the entire segment is prosomal in the Palaeozoic xiphosurids. Supposed arteries parallel the tergal borders in some trilobites and support the idea that the intersegmental boundaries parallel the intertergal ones. This does not mean that linear features on the trilobite exoskeleton show the exact boundaries of somites.

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PROBLEM SEGMENTACJI U TRYLOBITÓW

(Streszczenie)

Przedmiotem pracy jest dyskusja nad poglądami dotyczącymi zagadnień segmentacji u trylobitów, ze szczególnym uwzględnieniem problemu ilości segmentów, ze zrośnięcia których powstał cefalon, oraz rozpatrzeniem charakteru granicy pomiędzy cefalonem i toraksem. W oparciu o różnorodny materiał analityczny wykazano (por. fig. 1—3), że cefalon składa się w zasadzie z sześciu segmentów, z których pięć zaopatrzonych jest w typowe odnóża, zaś u szóstego odnóża uległy modyfikacji i weszły w skład labrum oraz hypostomy.

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